Forest Health **Technology Enterprise Team**

TECHNOLOGY TRANSFER

Biological Control

Biological Control of Invasive Plants in the Eastern United States



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Forest Health Technology Enterprise Team—Morgantown, West Virginia



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BIOLOGICAL CONTROL OF INVASIVE PLANTS IN THE EASTERN UNITED STATES

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On the cover:

- Upper photo set: infestation of *Pistia stratiotes* L. (waterlettuce) on Torry Island in Lake Okeechoee, Florida, before and after introduction of the weevil *Neohydronomus affinis* Hustache, pictured at right. (Photographs courtesy of USDA, ARS Invasive Plant Research Laboratory.)
- Lower photo set: infestation of *Euphorbia esula* L. (leafy spurge) at Forget-Me-Not Lake, Becker Co., Minnesota, before and after introduction of *Aphthona nigriscutis* Foudras (flea beetle), pictured at left. (Photographs by Robert Richard, USDA-APHIS-PPQ.)

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INTRODUCTION

Invasive plants are species that, after they have been moved from their native habitat to a new location, spread on their own. Some invasive plants reach high densities and cause economic or environmental harm or harm to humans (National Invasive Species Council, 2001).

Problems caused by invasive species have increased dramatically in recent decades due, in part, to an increasing human population (e.g., increased international travel, globalization of world trade). In response, the President issued Executive Order 13112 on Invasive Species in February 1999. The Order established the National Invasive Species Council to provide national leadership to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause.

The Weed Science Society of America recognizes about 2,100 invasive plant species (i.e., noxious or weedy plants) in the United States and Canada. Currently, 94 kinds of invasive plant species are officially recognized as Federal Noxious Weeds and many more species are designated on State noxious weed lists. In the United States, invasive plant species comprise from 8 to 47 percent of the total flora of most States. In 1994, the economic impact of weeds on the United States economy was estimated to be \$20 billion annually (Westbrooks, 1998).

Once an invasive plant species becomes established it is not easily suppressed nor eliminated as these species often possess characteristics that favor their population increase, such as early maturation, profuse reproduction by seeds and/or vegetative structures, long life of seeds in the soil, adaptation for spread, and production of biological toxins that suppress the growth of other plants. In addition, many invasive plants are free of attack in their invaded range by specialized insects or plant pathogens, allowing plant resources to be shifted from defense to growth and reproduction.

Integrated invasive plant management relies on a combination of control technologies. These include biological, mechanical, chemical, and cultural applications. Before the mid-1950s, chemical and mechanical applications were the main tactics used to suppress invasive plants in the continental United States. In the 1940s, classical biological plant control efforts were initiated and significantly increased in the United States and since then, biological control has become the most widely used tactic for weed suppression.

Biological control is the science of reconnecting invasive plants with the specialized natural enemies that often limit their density in their native ranges. This process consists of surveys in the plant's area of origin to discover candidate natural enemies, studies on their biology and host specificity and release and evaluation of their impacts on the target plant. The U.S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) is responsible for controlling introductions of species brought into the United States for biological control of plants, in accordance with the requirements of several plant quarantine laws, the National Environmental Policy Act, and the Endangered Species Act. Petitions for release of plant biological control agents are judged by a Technical Advisory Committee (TAG), which represents the interests of a diverse set of federal and other agencies.

Biological weed control has been most successful outside of crop lands, primarily in rangeland, pastures, and water bodies. Many projects have been conducted on grazing lands in the semiarid western United States. In the eastern United States, projects have been targeted against aquatic, pasture, and forest weeds. Projects in the western United States have been summarized previously by the W-84 project (Nechols et al., 1995). No such compilation has yet been done for the eastern United States.

The purpose of this book is to provide a reference guide for field workers and land mangers concerning the historical and current status of the biological control of invasive plant species in the eastern United States. Weeds associated with lakes, ponds and rivers (Section I); wetlands (Section II); prairies and grasslands (Section III); old fields and pastures (Section IV); and forests (Section V) are discussed. Authors are leaders in research on biological control of the plant species they discuss. Each chapter compiles published articles, unpublished reports and personal experiences of the authors, and provides the most up-to-date and accurate information concerning biological control of each invasive plant species.

The choice of plant species included in this book was based on information found in Julien and Griffiths' World Catalog of Agents and Their Target Weeds (1998) and 5 years (1995-1999) of programs from National Meetings of the Entomological Society of America. This initial list was reviewed by leading weed biological control scientists (Bernd Blossey, Gary Buckingham, Alex McClay, Loke Kok and Jack DeLoach) before settling on the 31 invasive plant species included here.

We provide this information to assist in the planning and execution of weed biological control projects in the region. We believe that weed biological control projects will increasingly be seen as an essential approach to protecting natural areas, waterbodies, forests, and pastures in the region.

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SECTION I: WEEDS OF LAKES, PONDS, AND RIVERS

Alligatorweed Floating Fern Water Chestnut Waterhyacinth Waterlettuce Eurasian Watermilfoil Hydrilla

1 Alligatorweed

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PEST STATUS OF WEED

Alligatorweed (*Alternanthera philoxeroides* [Mart.] Griseb.) is a South American immigrant that has invaded waterways in the United States, primarily in the southeastern states. It also is a weed in tropical and mild temperate regions around the world. Alligatorweed roots readily along waterways and then grows over the water surface as an anchored floating plant. It also grows terrestrially during dry periods. Alligatorweed is a federal noxious weed and a prohibited or noxious plant in Arizona, California, Florida, and South Carolina (USDA, NRCS, 1999).

Nature of Damage

Economic damage. Alligatorweed disrupts many economic uses of water (Anonymous, 1987; Holm et al., 1997). Thick mats prevent drainage canals, ditches, streams, and other small waterways from emptying rapidly during periods of heavy water load, thus causing flooding (Fig. 1). If mats break loose, they create obstructions by piling up against bridges, dams, and sharp bends in waterways. Thick mats also increase mosquito habitat. Navigation of small waterways is obstructed, as is shoreline navigation in large waterways. Efficiency of irrigation systems is decreased. Fishing and swimming can be affected, although a small fringe of alligatorweed probably benefits fishing. A perusal of various commercial Internet sites in April, 2001 indicated that costs would be approximately \$170 to \$370/ha for control of alligatorweed with the herbicides glyphosate and fluoridone.

Ecological damage. Alligatorweed, like many other invasive aquatic plants, displaces native plants in ditches, along banks, and in shallow water (Holm *et al.*, 1997). Vogt *et al.*, (1992) discussed competition with native plants before and after insect



Figure 1. Alligatorweed mats grow from shore and often cover entire waterways, thereby disrupting water flow and causing flooding. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

biological control agents were released. Alligatorweed disrupts water flow causing increased sedimentation, and it shades submersed plants and animals causing reduced oxygen levels beneath the mat (Quimby and Kay, 1976).

Extent of losses. Current data on the extent of infestation and control costs are lacking. At the beginning of the biological control program in 1963, there were an estimated 65,723 ha of water infested in eight southern states and 26,933 ha of plants in 1970 (Coulson, 1977). The largest infestation, 22,700 ha, was in Louisiana and the smallest, 21 ha, in Mississippi. In 1981, the infestation in the southern states was estimated to have increased, but only because of increases in Texas and Louisiana (Cofrancesco, 1988). All other states reported a decrease. Even though the infestation estimate had tripled in Louisiana, state officials considered biological control to be satisfactory. Much of the increase was due to terrestrial invasion by alligatorweed.

Geographical Distribution

Alligatorweed, a South American native, grows in the coastal plain from Virginia, ca. 37° N, to southern Florida, ca. 25° N, and westward along coastal areas to Texas. It is also found in southern California (Reed, 1970). A distribution map provided by Reed (1970) indicates that the northern limit inland is at about the middle of Alabama, Georgia, and South Carolina, ca. 33.5° N, with an extension slightly further north in the warmer Mississippi Valley, ca. 35° N, and Tennessee are included within its range on the USDA PLANTS Database on the Internet (USDA, NRCS, 1999).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Alligatorweed is in the tribe Gomphreneae, subfamily Gomphrenoideae, family Amaranthaceae (Mabberley, 1997), order Caryophyllales, subclass Carvophyllidae (Cronquist, 1988). There are an estimated 170 species of Alternanthera in the Western Hemisphere with 120 species in South America alone (Vogt et al., 1979). Less than 5% of the species in South America are amphibious with most being mesophytic or xerophytic. Kartesz (1994) listed 15 species of Alternanthera, including ornamentals and immigrants, in the United States and Canada. There are a few species in Asia, mostly introduced from South America. Engler (1934) included A. philoxeroides in the subgenus Telanthera, section 1. Alternanthera can be differentiated from related aquatic species by the opposite, non-succulent leaves; white flowers in short, headlike spikes; and by the presence of a style (Figs. 2, 3). Wain et al. (1984) reported two diverse forms of alligatorweed - one with slender stems and short, rounded leaves, and the other with broad stems and long, slender leaves. Their isozyme study indicated that the genetic difference between the forms was similar to the distances reported between subspecies in other plant studies. The importance of these forms in plant invasion and in control efforts has not been investigated. Julien and Broadbent (1980) listed the synonymy for A. philoxeroides.



Figure 2. Alligatorweed has opposite, nonsucculent leaves. (Photograph courtesy USDA, ARS.)



Figure 3. The white alligatorweed flowers are arranged in stalked, short, headlike spikes, and have a style. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

Biology

Alligatorweed initially roots in wet soil on banks or in shallow water along shorelines and then grows out into waterways. Penfound (1940) reported that beginning in March in Alabama, shoots grew to 38 cm in 1.5 months, to 145 cm in 2.5 months., and to 508 cm in 5.5 months. By September, the mat extended up to 4.6 m away from shore. Alligatorweed is a perennial with hollow stems that buoy the shoots. Floating mats expand over surfaces of all types of waterways and are practically impenetrable. If a waterway dries, alligatorweed changes to a terrestrial form with smaller, tougher leaves and stems. Only vegetative growth has been reported in the United States, although viable seeds have been found in the United States (Holm *et al.*, 1997). Roots develop at closely spaced nodes along stems. When the stems break, floating sections are able to establish readily on moist soil. Alligatorweed has been reported to reproduce by seeds in South America (Holm *et al.*, 1997).

Analysis of Related Native Plants in the Eastern United States

There are no native Alternanthera in the aquatic habitats of the United States. A second introduced species, Alternanthera sessilis (L.) R. Br. ex DC., which is pantropical, is reported to be naturalized in the Florida panhandle (Godfrey and Wooten, 1981). As the name implies, the flowers of A. sessilis are sessile compared with flowers of alligatorweed, which are stalked. According to Vogt et al. (1979), the South American Alternanthera pungens Kunth also is established in the United States. Three additional genera in the Amaranthaceae are associated with aquatic habitats. Amaranthus has six species in the range of alligatorweed in the southeastern United States, Iresine has one species, and Blutaparon has one species, Blutaparon (=Philoxerus) vermiculare (L.) Mears or silverhead, which occurs in maritime habitats. Corell and Corell (1972) placed some of the wetland species of Amaranthus in the genus Acnida. One Amaranthus in the eastern United States, Amaranthus pumilus Raf. (dwarf or seabeach amaranth) is federally listed as threatened. Its range might overlap with the distribution of alligatorweed biological control agents along the coast of South Carolina, but it is found mostly north of their ranges (Godfrey and Wooten, 1981).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

In 1959, the U.S. Army Corps of Engineers requested that the U.S. Department of Agriculture, Agricultural Research Service evaluate the potential for biological control of alligatorweed (Zeiger, 1967; Buckingham, 1994). Consequently, field surveys and studies of biologies and host ranges of potential biological control agents were conducted in South America (Buckingham, 1996; Coulson *et al.*, 2000). Ultimately, three insect species, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae), *Amynothrips* *andersoni* O'Neill (Thysanaptera: Phlaeothripidae), and *Arcola* (as *Vogtia*) *malloi* (Pastrana) (Lepidoptera: Pyralidae, Phycitinae), were introduced into the United States (Coulson, 1977).

Area of Origin of Weed

Alligatorweed is native along the coast of South America from Venezuela to Buenos Aires Province in Argentina (Vogt *et al.*, 1979). It also was reported from the upper and middle Amazon River basin and the Paraná River basin (Vogt *et al.*, 1979). Sites with alligatorweed were most common in Paraguay, Uruguay, and northern Argentina, but this might reflect more intensive surveys for biological control agents in those areas.

Areas Surveyed for Natural Enemies

Annual surveys from 1960 to 1962 covered eastern and northern South America from Argentina to Venezuela, including Trinidad (Coulson, 1977). Additional surveys were conducted in Argentina and Uruguay (Coulson *et al.*, 2000). Surveys also were conducted in the southeastern United States (Coulson, 1977).

Natural Enemies Found

As many as 40 insect species (not all could be identified to species level) were recorded on alligatorweed (Vogt, 1973). Five of the 40 species were considered to suppress alligatorweed (Vogt, 1973). These five were: A. hygrophila, A. andersoni, A. malloi, Herpetogramma bipunctalis (F.) (Lepidoptera: Pyralidae), and Prodenia sp. (Lepidoptera: Noctuidae) (Maddox et al., 1971; Vogt, 1973). The flea beetle Disonycha argentinensis Jacoby (Coleoptera: Chrysomelidae) was later considered a potential agent for control of terrestrial alligatorweed (Cordo et al., 1984). No species able to suppress the weed were discovered in the United States, but native species of Disonycha and the moth H. bipunctalis were commonly found on alligatorweed in the United States (Vogt et al., 1992).

A fungus native to the United States, *Nimbya* (=*Alternaria*) *alternantherae* (Holcomb and Antonopoulus) Simmons and Alcorn (Hyphomycetes), causes purplish leaf spots and can defoliate plants. However, damage is rarely severe (Holcomb, 1978). In Brazil where it also is native, *N. alternantherae* was not particularly damaging, but preliminary studies indicated possible potential as a mycoherbicide (Barreto *et al.*, 2000). Damage by a second Brazilian fungus, *Cercospora alternantherae* Ellis and Langlois, was occasionally severe and this species might have potential as a biocontrol agent. (Barreto *et al.*, 2000). A virus-like disease that stunts alligatorweed in Florida has not been studied (Hill and Zettler, 1973).

Host Range Tests and Results

Four insect species were tested in host range experiments in Argentina and Uruguay and in quarantine in Albany, California. Maddox et al. (1971) reported that 14 plant species were tested with the alligatorweed flea beetle, but they did not list the species. Buckingham (1996) reported that the 14 species were apparently in 12 genera of eight families. These families were Amaranthaceae, Brassicaceae, Chenopodiaceae, Cucurbitaceae, Malvaceae, Nymphaeaceae, Poaceae, and Polygonaceae. For the flea beetle, A. hygrophila, slight adult feeding was found on apical leaves of Chenopodium ambrosioides L. and larval feeding and development on Atriplex patula var. hastata (L.) Gray, but only one malformed adult emerged (Maddox and Resnik, 1969; Maddox et al., 1971). Field observations in South America also played a role in obtaining approval of the flea beetle for introduction into the United States (Anderson, 1963). At least 14 species of aquatic or related plant species in proximity to damaged alligatorweed in Argentina were examined for flea beetles, as were crop plants in the vicinity. No beetles or damage were found.

The alligatorweed thrips, *A. andersoni*, was tested on 21 species in 13 genera of six families (Maddox, 1973). Families were the same as those tested with the flea beetle except Cucurbitaceae and Malvaceae were not tested with the thrips. No development took place in the no-choice and choice experiments except on alligatorweed. Vogt found thrips on the native *Alternanthera hassleriana* Chod. in Argentina (Maddox *et al.*, 1971), but that species has not been reported as naturalized in the United States. Field examinations in Argentina of 46 other plant species in 26 genera of 11 families yielded no *A. andersoni* or its damage (Maddox, 1973).

The alligatorweed stem borer, *A. malloi*, was tested in choice and no-choice tests on 30 plant species in 17 genera of the six families tested with the

thrips (Maddox and Hennessey, 1970). Although there was some feeding on test plants in no-choice tests, development of third or younger instars was restricted to alligatorweed. A few older larvae finished their development on five species in the same amaranth tribe as alligatorweed, Gomphrenae. Field examinations of 51 plant species in Argentina from 1962 through 1967 discovered this moth only on alligatorweed (Maddox and Hennessey, 1970). In South American surveys, moths were reared from *A*. hassleriana and from the closely related Philoxerus portulacoides St. Hil. (Vogt et al., 1992). After the moth was released in the United States, it was reared from the native species Blutaparon vermiculare, collected in Louisiana and Texas and from subsequent cage tests (Vogt et al., 1992). However, the numbers reared from *Philoxerus* and *Blutaparon*, which are closely related, were small. Pemberton (2000) reported rearing this species from Alternanthera flavescens Kunth., a native of coastal hammocks in Florida.

The flea beetle, D. argentinensis, was tested on 54 species in 38 genera of 19 families in no-choice larval tests (Cordo et al., 1984). All of the eight families used in tests with A. hygrophila were included along with additional families containing crop and ornamental species. Flea beetle larvae fed moderately on four species of Amaranthaceae and two species of Chenopodiaceae, but development to adults was restricted to Alternanthera paronychioides St. Hilaire (6.4%) and Beta vulgaris L. (3.0%), while 44% completed development on alligatorweed. The development on beets, B. vulgaris, prevented release of this species in the United States. Interestingly, Australia tested this species with 36 species in 31 genera of 18 families (Sands et al., 1982). In those tests, no development was observed on beets, but the smaller number of larvae used in the tests (52 versus 234 in the American tests) could have accounted for the slight difference between the two studies. Based upon the American test results (3% development), only one adult would have been expected in the Australian tests and, indeed, one of the 52 larvae did develop to the last instar. Both Australia and New Zealand released this species, but it did not establish (Julien and Griffiths, 1998).

No host range tests were conducted with the other two major biotic suppressants listed by Vogt (1973), *H. bipunctalis* and *Prodenia* sp. The former, the southern beet webworm, also is native to North

America. The latter pupates in the soil, which prevented its use for control of aquatic alligatorweed that was the target of the biological control program (Maddox *et al.*, 1971). If there is future interest in controlling terrestrial alligatorweed, which is commonly eaten by cattle, the *Prodenia* sp. could be studied further although it also attacked *Amaranthus* sp.

Releases Made

Field-collected alligatorweed flea beetles from Argentina were processed through quarantine and released in 1964 in California and South Carolina and in 1965 in Florida (Coulson, 1977). Beetles from Uruguay also were released in South Carolina and a mixed quarantine colony started with beetles from both Argentina and Uruguay was released in Mississippi (1965). Later, beetles collected at release sites, mostly in Florida, were redistributed in Alabama (1967), Arkansas (1969), Georgia (1966), Louisiana (1970), North Carolina (1967), Tennessee (1968), and Texas (1967). Beetles from a quarantine colony held in Gainesville, Florida (of insects originating from Necochea, Argentina) were released in 1979 in Alabama, Florida, North Carolina, and South Carolina (Buckingham et al., 1983).

A quarantine colony of alligatorweed thrips from Argentina was released in Alabama (1968), California (1967), Florida (1967), Georgia (1967), Mississippi (1968), South Carolina (1967), and Texas (1968) (Coulson, 1977).

Eggs from alligatorweed stem borer females collected as larvae in Argentina and held in quarantine were first released in Florida and Georgia in 1971 (Coulson, 1977). Eggs from females collected at Necochea, Argentina, and held in quarantine were released in Georgia and South Carolina in 1972 in an attempt to establish more cold-tolerant populations. Most of the other releases in 1971 and 1972 were from quarantine (Albany) or greenhouse (Gainesville) colonies started with part of the eggs collected in Necochea. Releases were made in the preceding states and in Alabama (1972) and North Carolina (1971).

A handbook that provides instructions for release of the alligatorweed agents was prepared by the U.S. Army Engineer Waterways Experiment Station, based upon the successes of these releases (Anonymous, 1981).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae)

Adults are small (4 to 6 mm long), black and yellow striped beetles that jump when disturbed (Selman and Vogt, 1971). Feeding causes "shot holes" in the leaves, but with heavy adult and larval feeding the leaves are completely eaten, as are upper portions of the stems (Fig. 4). Females deposited clusters of 12 to 54 eggs in two contiguous rows on the underside of apical leaves (Maddox, 1968). The yellowish eggs hatched in four days at 20 to 30 °C. Dark colored larvae ate leaf tissue but often left one epidermis intact, creating a window in the leaf. The three instars developed in eight days at 20 to 30 °C. Mature larvae pupated one to two days after entering stems. The pupal period lasted five days and a premating and preoviposition period lasted about six days. The total life cycle from egg to egg was completed in 25 days at 20 to 30 °C. Females lived about 48 days and usually deposited only one egg cluster per day for an average of 1,127 total eggs (Maddox, 1968). Beetles were multivoltine near Buenos Aires, Argentina, producing five generations per year (Maddox, 1968) and probably four to six generations in Florida and the lower Mississippi River Valley (Coulson, 1977; Vogt et al.,1992).



Figure 4. Adults and larvae of the alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt, devour leaves and upper portions of stems. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

Most feeding and oviposition by A. hygrophila is on aquatic alligatorweed. Flea beetles, especially larvae, rarely attack plants rooted on shore or in moist ditches. What appears to be typical feeding damage is occasionally observed on terrestrial plants, but it is usually nocturnal feeding by native Disonycha flea beetles. In laboratory experiments in Argentina, females oviposited equally on aquatic and terrestrial alligatorweed (Maddox, 1968), but in my experience, females stopped ovipositing almost immediately when fed terrestrial plants. Beetles are specific to alligatorweed and have not been reported on other host plants in the United States even after almost 40 years. A flavone feeding stimulant, 7-a-L-rhamnosyl-6-methoxyluteolin (I), has been isolated from alligatorweed (Zielske et al., 1972) and may be the basis for this specificity.

Alligatorweed thrips, *Amynothrips andersoni* O'Neill (Thysanaptera: Phlaeothripidae)

Adults are small (ca. 2 mm long), black elongate insects with fringed wings (O'Neill, 1968). Larvae, in contrast, are bright orange (Fig. 5). Both feed in the tips of stems where they cause leaf deformation and stunting of the plant (Fig. 6). Often, the edges of leaves curl inwards which provides excellent shelter. Females had a four-day preoviposition period after which they deposited a mean of 201 eggs on hairs in the nodes of the apical leaves (Maddox and Mayfield, 1979). The elongated oval eggs were amber colored. Larval development took eight to 13 days at 24 °C and the whole life cycle from egg to egg required 28 days on average. There were two larval stages, followed by a resting pupal stage on the plant. Unmated females produced only males, but fertilized females produced equal numbers of males and females. Maddox and Mayfield (1972) reported a method for rearing and studying the thrips in the laboratory.

In Argentina, larvae were most abundant in the spring and declined through late summer (Maddox and Mayfield, 1979). Adults were the predominant overwintering stage, although small numbers of larvae and eggs also were present. There were four or five generations, with no reproductive diapause. Predation by spiders and hemipterous insects appeared to be an important regulating factor in Argentina, especially for pupae (Maddox *et al.*, 1971). Dispersal is limited by wing length. Short-winged adults were present in Argentina at most times, but long-winged,



Figure 5. Larvae of the alligatorweed thrips, *Amynothrips andersoni* O'Neill, are bright orange. (Photograph courtesy USDA, ARS.)



Figure 6. Leaf distortion and stunting of the plants is characteristic of feeding by adults and larvae of the alligatorweed thrips, *Amynothrips andersoni* O'Neill. (Photograph courtesy USDA, ARS by G. R. Buckingham.)

dispersing adults were present in the spring (Maddox and Mayfield, 1979). Long-winged forms were believed to be absent in the United States (Coulson, 1977) but were later reported (Buckingham, 1989; Vogt *et al.*, 1992). Unlike the flea beetle, the thrips attacks both aquatic and terrestrial plants, although Maddox *et al.* (1971) reported that it preferred terrestrial plants in Argentina.

Alligatorweed stem borer, *Arcola malloi* (Pastrana) (Lepidoptera: Pyralidae, Phycitinae)

This inconspicuous, light tan moth has a 20 mm wingspan and rests with its folded wings curled partly around its body (Fig. 7). Wing tips lie against the plant, but the head is held aloft with the body at an angle to the plant. Pastrana (1961) provides a more complete description. Females deposited single white eggs on the undersides of apical leaves (Maddox, 1970). After a preoviposition period of less than 24 hours, moths laid an average of 267 eggs over six to eight days. The eggs hatched in three to four days. Newly hatched larvae tunneled into tips of stems and bored downwards. As they matured, they exited the stems and dropped down on silken threads to bore into other stems. Damaged tips quickly wilted and heavily damaged stems turned yellow and died (Fig. 8). Whitish larvae have wavy, tan, longitudinal stripes. There are five instars that developed in about 24 days (Maddox, 1970). Mature larvae bored through nodes and sealed the holes with masticated tissue apparently to protect against water intrusion. Larvae then



Figure 7. Adults of the alligatorweed stem borer, *Arcola malloi* (Pastrana), are inconspicuous light tan moths that rest with wings held closely to the body. (Photograph courtesy USDA, ARS by Willey C. Durden.)



Figure 8. Stems damaged internally by larvae of the alligatorweed stem borer, *Arcola malloi* (Pastrana), wilt, turn yellow, and die. (Photograph courtesy USDA, ARS.)

chewed exit holes to the outside epidermis, which was left intact as escape hatches for the emerging moths. Amber colored pupae darkened as they developed inside silken cocoons. The life cycle from egg to egg required about 39 days at 23 °C. There were three to four generations per year near Buenos Aires (Maddox, 1970). The moth was multivoltine in the lower Mississippi River Valley, but the number of generations was not determined (Vogt et al., 1992). Brown and Spencer (1973)reported parasitism by Trichogramma sp. (Hymenoptera: Trichogrammatidae) on eggs and by Gambrus spp. (Hymenoptera: Ichneumonidae) on larvae in newly established populations in Florida.

Both aquatic and terrestrial alligatorweed plants are attacked by *A. malloi*. Stems collapse, turn yellow and die, and heavily damaged mats eventually rot and sink (Brown and Spencer, 1973). Leaves remain on damaged stems, distinguishing stem borer damage from that caused by flea beetles. Vogt *et al.* (1992) discussed the migratory behavior of *A. malloi* in the Mississippi River Valley, where it flew in spring and summer from winter refuges near the Louisiana coast north to Arkansas and northern Mississippi, up to 900 to 1000 km.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Alligatorweed flea beetles did not establish in Arkansas, California, North Carolina, or Tennessee. It was hoped that the population from Necochea, Argentina, might be more cold tolerant than the first beetles released, but there have been no reports of an increase in the flea beetle's range after those 1979 releases. Langeland (1986) reported that releases of the Necochea population were unsuccessful at two study sites in North Carolina. Flea beetles survive mostly in coastal areas or where the mean January temperature is 11.1 °C or higher (Coulson, 1977; Vogt *et al.*, 1992).

Coulson (1977) reported the establishment of alligatorweed thrips in Florida, Georgia, and South Carolina. In 1981, thrips were still present in South Carolina (Buckingham, unpublished data) and in 1982 they were reported in Alabama, Florida, Louisiana, Mississippi, and Texas (Cofrancesco, 1988). The alligatorweed stem borer successfully established at release sites in all states except Alabama and North Carolina (Coulson, 1977). Later, Cofrancesco (1988) reported it in Alabama and North Carolina as well as in Louisiana, Mississippi, and Texas. Vogt *et al.* (1992) discussed this moth's long distance dispersal ability and noted that in summer it is present in Arkansas.

Suppression of Target Weed

Alligatorweed flea beetle damage was spectacular in the early phases of the program. Vast areas were defoliated (Fig. 9). Mats attacked by the stem borer turned yellow and died (Fig. 10). These two agents have suppressed alligatorweed in much of the warmer parts of its range, so that control efforts are needed only sporadically. In the Carolinas, Tennessee, and the northern regions of the Gulf Coast states, the plant is usually not controlled biologically unless flea beetles are released early in the season from field collections made in Florida or other southern sites. In the Mississippi River Valley, moths and/or flea beetles often migrate north early enough to provide local control (Vogt et al., 1992). Fortunately, alligatorweed is not as invasive at the margin of its range as it is further south.

Cofrancesco (1988) surveyed aquatic plant managers in 1981 about the importance of alligatorweed in ten southern states. None reported that it was a major problem, although some reported locally serious problems, and none reported chemical control efforts directed specifically at it. Chemical controls were usually incidental to waterhyacinth control efforts.

Recovery of Native Plant Communities

There was relatively little evaluation of the biological control of alligatorweed program, mostly because of the speed of the control and the desire to quickly begin programs for biological control of waterhyacinth (*Eichhornia crassipes* [Martius] Solms-Laub.) and hydrilla (*Hydrilla verticillata* [L. f.] Royle). However, Vogt *et al.* (1992) did conduct long term studies in the lower Mississippi River Valley. They reported observations of native plant populations increasing after alligatorweed was suppressed and included tables of the species involved; however, they did not collect quantitative data.



Figure 9. Alligatorweed mats often are completely defoliated by the alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt. Willey Durden collected flea beetles by "walking on water" during the initial establishment phase of the program. (Photograph courtesy USDA, ARS.)



Figure 10. Alligatorweed mats killed by the alligatorweed stem borer, *Arcola malloi* (Pastrana), turn yellow but still retain leaves, in contrast to the yellow stems defoliated by the alligatorweed flea beetle, *Agasicles hygrophila* Selman and Vogt. (Photograph courtesy USDA, ARS.)

Economic Benefits

Long-term economic benefits of alligatorweed control have not been estimated. The fact that most control efforts are now incidental to waterhyacinth control instead of directed at alligatorweed (Cofrancesco, 1988) suggests substantial benefit from reduced chemical control costs. Undoubtedly, there also are indirect cost savings from reduced ditch and canal clearing and from reduced local flooding. Andres (1977) discussed the costs and benefits of the alligatorweed program, including a 76% reduction in the hectares treated by the U.S. Army Corps of Engineers and a 92% reduction in weed control costs at one lake in Georgia. However, I am unaware of any newer studies on the costs or benefits of alligatorweed control.

RECOMMENDATIONS FOR FUTURE WORK

Alligatorweed has invaded regions in the United States with climates colder than the native regions in South America. Therefore, there might not be natural enemies suitable for use in the northern parts of alligatorweed's range in the United States. However, more complete control in the warmer areas of the range might be possible by using some of the originally discovered agents that were not pursued or new, as yet, undiscovered agents. Recent surveys in the Amazon River drainage for waterhyacinth insects have located several species that had not been found during earlier surveys (DeQuattro, 2000). A similar situation might be true for alligatorweed. Also, pathogens, both in South America and in the United States, should be more carefully evaluated, especially for their potential to complement insect damage.

Vogt *et al.* (1992) suggested that *Alternanthera* species in Asia should be examined as sources of biological control agents for alligatorweed. Herbivorous insects and pathogens on Asian plants in this genus, if specific both to *Alternanthera* and to aquatic habitats, should be safe for use in the United States and might be more damaging than co-adapted agents from the target plant.

The terrestrial South American flea beetle *D. argentinensis*, which has been released in Australia, should be re-evaluated for its safety and potential use in the United States, if there are no conflicts over control of terrestrial alligatorweed, as there have been in the past (Coulson, 1977). The flea beetle might reduce the invasion of ditches, canals, and shallow ponds when water returns after a drought.

Additional attempts could be made to establish the alligatorweed flea beetle and the stem borer in California, where they did not establish. In the eastern United States, these two species have probably established in all areas where the long-term climate allows. Annual importation from overwintering sites in Florida or coastal areas will be necessary in northern areas of the range, as has been done with alligatorweed flea beetles by the U.S. Army Corps of Engineers (Zattau, 1989). A supply of these insects should be created for use by agencies and individuals other than the Corps of Engineers.

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2 FLOATING FERN (SALVINIA)

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PEST STATUS OF WEED

Salvinia molesta D. S. Mitchell is a floating fern native to South America that in the last half of the twentieth century spread widely throughout the tropics and subtropics, moved in part by the trade in ornamental plants for fish tanks and ponds. It forms dense mats over lakes and slow moving rivers and causes large economic losses and a wide range of ecological problems to native species and communities. It is of interest in the United States because of its recent establishment in east Texas.

Nature of Damage

Economic damage. Mats of *S. molesta* (referred to hereafter as salvinia) impede access to and use of waterways for commercial and recreational purposes and degrade waterside aesthetics (Fig. 1). Mats reduce habitats for game birds, limit access to fishing areas, and probably alter fisheries, all with negative economic consequences. Salvinia can clog water intakes and interfere with agricultural irrigation, water supply, and electrical generation. It provides habi-



Figure 1. *Salvinia molesta* D. S. Mitchell covering a farm pond in Texas restricts commercial and recreational use and degrades aesthetics. (Photograph by T. Center.)

tats for vectors of human disease with serious socioeconomic impacts.

In developing countries, the impact of salvinia can be devastating because weed mats block the use of waterways for transportation, cutting off access to important services, farm lands, and hunting grounds. The harm from salvinia mats to fisheries also can be very significant to communities dependent on fish for local consumption (sometimes as the main source of protein) or in areas where fish sales are the main source of cash income (Bennett, 1966; Thomas and Room, 1986). Salvinia also is a weed of paddy rice that reduces production by competing for water, nutrients and space (Anon., 1987).

Ecological damage. The ability to grow very quickly (Cary and Weerts, 1983; Mitchell and Tur, 1975; Mitchell, 1978/9; Room, 1986) and blanket water bodies makes salvinia an aggressive and competitive weed (Fig. 2). Initially, salvinia forms a single layer over water, but with continued growth the mats become multi-layered and can reach up to 1 m in thickness (Thomas and Room, 1986). Thick mats support other colonizing plants, and the high biomass



Figure 2. Salvinia molesta D. S. Mitchell covering a waterbody and supporting the growth of other plant species in Kakadu National Park, Australia. (Photograph by M. Julien.)

and stability of such mats make them difficult to dislodge and destroy (Storrs and Julien, 1996).

Plants and animals dependent on open water to gain sunlight, oxygen, and space for sustenance and growth, or for landing, fishing, nest building, or mating, are displaced by dense salvinia infestations. Water under mats of salvinia has a lower oxygen concentration (due to reduced surface area of water available for oxygenation, inhibition of photosynthesis by submerged plants, and consumption of dissolved oxygen by decaying salvinia), higher carbon dioxide and hydrogen sulphide concentrations, lower pH, and higher temperatures than nearby open water (Mitchell, 1978; Thomas and Room, 1986).

Through high growth rates and slow decomposition rates, salvinia reduces the concentration of nutrients that would otherwise be available to primary producers and organisms that depend on them (Sharma and Goel, 1986; Storrs and Julien, 1996).

Mats of salvinia provide ideal habitat for *Mansonia* mosquitoes, a principal vector of rural elephantiasis in Sri Lanka (Pancho and Soerjani, 1978), and for other mosquito species involved in the transmission of encephalitis, dengue fever, and malaria (Creagh, 1991/92). Two species of *Mansonia* that occur in the United States, *Mansonia dyari* Belkin and *Mansonia titillans* (Walker), have been implicated in the transmission of St. Louis encephalitis and Venezuelan equine encephalitis, respectively (Lounibos *et al.*, 1990).

Extent of losses. The most detailed assessment of costs caused by salvinia was conducted in Sri Lanka using 1987 as the base year (Doeleman, 1989). Paddy rice losses, fishing losses, other losses (power generation, transport, washing and bathing, etc.), health costs, abatement costs, and economic benefits were considered. No environmental costs were included. but they were recognized as important. There were no identified benefits from salvinia. Total costs associated with salvinia were estimated to be between 24.7 million and 56.7 million rupees (in Australian dollars, between 0.9 and 2.1 million) for 1987. This information was used to determine the benefits from biological control over the following 25 years. The benefits were 53 rupees or dollars per rupee or dollar invested, or 1,673 man-hours per man-hour invested.

Using this information as a guide, Room and Julien (1995) estimated that the annual benefits gained from successful biological control of salvinia worldwide were approximately \$150 million U.S.

Geographical Distribution

The native range of salvinia is an area in southeastern Brazil (Forno and Harley, 1979). Its first recorded exotic establishment was in Sri Lanka in 1939 (Williams, 1956). It has since become established in India (Cook and Gut, 1971), Australia (Room and Julien, 1995), Papua New Guinea (Mitchell, 1979), Cuba, Trinidad, Guyana, Columbia (Holm et al., 1979), South Africa (Cilliers, 1991), Botswana (Edwards and Thomas, 1977), Kenya, Zambia (Mitchell and Tur, 1975), Namibia (Forno and Smith, 1999), Madagascar (Room and Julien, 1995), Ghana and Cote D'Ivoire (M. Julien, pers. obs.), Indonesia (Java, Borneo, Sulawesi), Malaysia (mainland Sabah, Sarawak) (R. Chan, pers. comm.), the Philippines (Pablico et al., 1989), Fiji (Kamath, 1979), and New Zealand (Randall, 1996).

Salvinia was first reported outside of cultivation in the United States in 1995 at a pond in southeastern South Carolina (Johnson, 1995). It was eradicated before spread occurred. It was next found in Houston, Texas, in May 1998, and then at other sites in Texas and in Louisiana during 1998. During 1999 it was found in ponds and rivers in Alabama, Arizona, California, Florida, Georgia, Hawaii, Mississippi, and Oklahoma (Jacono *et al.*, 2000; see also Jacono's web site). Salvinia is readily available for purchase in the United States, particularly through the Internet.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The aquatic fern family Salviniaceae is placed within the order Hydropteridales and consists of a single genus, *Salvinia*. Ten species of *Salvinia* occur worldwide (Herzog, 1935; de la Sota, 1962, 1963, 1964, 1982; Mitchell, 1972). None are native to the United States (Jacono *et al.*, 2000) although seven species originate in the Americas (de la Sota, 1976). *Salvinia molesta* was given recognition as a species in 1972 (Mitchell, 1972) and is grouped within the *Salvinia auriculata* complex, together with *Salvinia auriculata* Aublet, *Salvinia biloba* Raddi, and *Salvinia herzogii* de la Sota (Mitchell and Thomas, 1972). Species within this complex are characterized by the presence of divided but apically joined "basket" hairs on the abaxial surface, which produce an "egg-beater-like" appearance (Fig. 3a) (de la Sota, 1962; Mitchell and Thomas, 1972; Forno, 1983). *Salvinia molesta* can be distinguished from species within the *S. auriculata* complex by the arrangement of sporangia, the shape of sporocarps (Mitchell and Thomas, 1972; Mitchell, 1972), and by the pattern of leaf venation (Forno, 1983).

The accepted common name is salvinia, but it also is called Kariba weed, water fern, or African pyle (in Africa); giant azolla or Australian azolla (in the Philippines); and giant salvinia, water spangles, or floating fern (in the United States).

Salvinia minima Baker, the only other *Salvinia* species present in the United States also is exotic and can be distinguished by the presence of divided hairs on the abaxial leaf surface that are spreading and free at the tips (Fig. 3b).



Figure 3a.





Figure 3. *Salvinia* species in the United States can be distinguished by their leaf hairs. (a) In *Salvinia molesta* the hairs form an 'eggbeater' shape at the tips, while in *Salvinia minima* (b) the hairs are separated at the tips. (Photographs by M. Julien [a] and T. Center [b].)

Biology

Plant form. Salvinia is a free-floating aquatic fern with a horizontal rhizome just beneath the water surface (Bonnet, 1955; Room, 1983). Each plant is a colony of ramets. Each ramet comprises an internode, a node, a pair of floating leaves, the submerged 'root,' and associated buds. The 'root' is a modified leaf that looks and functions like a root (Croxdale 1978, 1979, 1981).

Salvinia is morphologically variable, primarily in response to the level of crowding and availability of nutrients. These two factors are largely independent of one another. There are three growth forms, with a continuum among them, that are associated with the degree of crowding experienced by the plant (Mitchell and Tur, 1975).

The *primary form* (Fig. 4a) occurs as isolated plants in the initial 'invading' stage of an infestation. This form has small, oval leaves less than 15 mm wide that lie flat on the water surface.

The secondary form (Fig. 4b) occurs when plants have been growing over open water for some time, either freely or on the edge of stable mats. Internodes are longer, with larger, boat-shaped (slightly keeled) leaves that have rounded apices and are variable in size, but are normally between 20 mm and 50 mm wide. The entire lower leaf surface is in contact with the water.

The *tertiary form* (Fig. 4c) occurs when plants are growing in crowded mat conditions associated with mature infestations. Internodes are short with large heart-shaped, or oblong and deeply keeled leaves up to 60 mm in width when fully opened. The undersides of adjacent leaves are in contact with each other.

Growth and reproduction. Salvinia is pentaploid, has a chromosome number of 45, and is incapable of sexual reproduction (Loyal and Grewal, 1966). Each node bears a series of up to three axillary buds that develop successively under normal growing conditions (Room, 1988), and up to six in response to damage (Julien and Bourne, 1986). The number of axillary buds that grow, the rate of growth, and plant size are largely dependent on available nutrients. Growth is apically dominant and progresses by expansion of apical and axillary buds, the latter forming branches. New plants form when older plants break apart due to senescence or damage (Room, 1983).



Figure 4a.



Figure 4b.



Figure 4c.

Figure 4. The three growth forms of *Salvinia molesta* D. S. Mitchell: (a) the primary form, (b) the secondary form, and (c) the tertiary form. (Photographs by M. Julien.)

Factors affecting growth. Salvinia is a perennial plant with no seasonal periodicity, although changes in growth may be related to seasonal variations such as changes in temperature. Salvinia is well adapted to growth in low nutrient waters and can take up nutrients quickly when they become available (Room and Thomas, 1986).

The proportion of axillary buds that develop is correlated with the nitrogen content of the plant (Room, 1983; Julien and Bourne, 1986), and the nitrogen content increases following removal of buds by insects or other agents (Room and Thomas, 1985; Julien and Bourne, 1986; Forno and Semple, 1987). At low levels of nitrogen leaves are larger, 'roots' longer, sporocarps occur more frequently, and rhizome branching is reduced (Room, 1983; Julien and Bourne, 1986; Room, 1988; Room and Julien, 1995). The nitrogen content of salvinia ranges from 0.6 to 4.0% dry weight (Room and Thomas, 1986). The maximum rate of nitrogen uptake, calculated from rates of growth, is near 8 mg nitrogen/g dry weight of salvinia/day or about 6,000 kg nitrogen/ha/year (Room, 1986). Actual measurements at a sewage treatment lagoon indicated an uptake of 1,580 kg nitrogen/ha/year (Finlayson et al., 1982).

The optimum temperature for growth is 30°C. Room (1986) described the effect of temperature, above and below 30°C, on relative growth rates and predicted no growth below 10°C and above 40°C. Temperature does not affect the proportion of axillary buds that expand to initiate new branches (Room, 1988). Exposure to temperatures below -3° C or above 43°C for more than two hours kills salvinia (Whiteman and Room, 1991). Leaf temperatures that exceeded 40°C and sometime approached 50°C for the hottest parts of days did not obviously affect growth, but water temperatures remained below 40°C and probably acted as a heat sink for the plants (Storrs and Julien, 1996). Plants may be killed by frost but protected parts and unfrozen buds survive. Water bodies are normally cooler than the air in summer and warmer in winter due to thermal inertia. This helps protect salvinia from temperature extremes.

Mats of salvinia can grow in water bodies with conductivities ranging from 100 μ S/cm to 1,400 μ S/ cm (Mitchell *et al.*, 1980; Room and Gill, 1985). In water with 10% of the salinity of seawater (4,800 μ S/ cm), growth was reduced by 25% (Divakaran *et al*, 1980); at 20% salinity, growth was very slow; while at 30%, plants died after 30 minutes exposure (Room and Julien, 1995). Optimum pH for growth is 6.0 (Cary and Weerts, 1984). In the field the plant grows at pH values from 5.2 to 9.5 (Holm *et al.*, 1977; Mitchell *et al.*, 1980). Salvinia compensates for the destruction of buds by initiating growth of dormant buds. Complete compensation occurs only when high levels of nitrogen are available (Julien and Bourne, 1986; Julien *et al.*, 1987). Destruction of leaves (Julien and Bourne, 1988) and rhizomes (Julien and Bourne, 1986) does not induce compensatory growth.

Growth rates and density. On Lake Kariba, Zimbabwe, numbers of leaves (ramets) doubled in eight to 17 days (Gaudet, 1973; Mitchell and Tur, 1975). In the Kakadu National Park, Australia, dry weight doubled in five to 30 days (Storrs and Julien, 1996). Under ideal growth conditions, biomass and numbers of ramets typically double in two to three days (Mitchell and Tur, 1975; Cary and Weerts, 1983). Densities from as high as 2,500 large tertiary form ramets per m² (in nutrient-poor water) to 30,000 small tertiary form ramets (in nutrient-rich waters) have been noted. At these densities, natality is equaled by mortality (Room and Julien, 1995). Salvinia is 95% water by weight and biomass of living shoots can exceed 600 g/m² of dry weight, while biomass of living and dead shoots and 'roots' may exceed 1,600 g/ m² of dry weight or 400 t/ha of fresh weight (Room and Julien, 1995). Fresh weight biomass in Texas varied through the year, reaching a high in October 1999 of 248 t/ha and a low of 84 t/ha in January 2000 (P. Tipping, unpub. data).

Spread. Salvinia is spread within and between aquatic systems mainly by people. It is spread accidentally when equipment or boats are moved and deliberately when it is used as a pond, aquarium, or water-garden plant or as a biological weapon (Gewertz, 1983). It is carried on animals as they move from infested water bodies (Forno and Smith, 1999). Dispersal within a water body or catchment is by wind and water currents (Room and Julien, 1995). Currents and floods wash mats away and growth is best in still or slow moving water.

In its native range in southeastern Brazil, salvinia is a component of floating and emergent plant communities. Salvinia supports a variety of natural enemies (Forno and Bourne, 1984), and it normally does not form the extensive mats prevalent in its exotic range.

Analysis of Related Native Plants in the Eastern United States

The Salviniaceae are included within a monophyletic clade of heterosporous genera that also encompasses the Azollaceae and Marsileaceae (Pryer and Smith, 1998; Pryer *et al.*, 1995; Hasebe *et al.*, 1995), all aquatic leptosporangiate ferns. This clade includes ten species in the North American flora. The Azollaceae once were included within the Salviniaceae, but the relationship is not close and they have since been separated (Lumpkin, 1993).

Azollaceae consists of the single genus Azolla. There are three species of Azolla – Azolla caroliniana Willdenow, Azolla mexicana C. Presl, and Azolla filiculoides Lamarck - that are native to North America (Lumpkin, 1993). The Marsileaceae includes two genera, Marsilea and Pilularia, both of which occur in North America. Seven species within these two genera are part of the North American flora (Johnson, 1993): Marsilea quadrifolia Linnaeus, Marsilea ancylopoda A. Braun, Marsilea oligospora Gooding, Marsilea mollis B. L. Robinson and Fernald, Marsilea macropoda Engelmann, Marsilea vestita Hooker and Greville, and Pilularia americana A. Braun. Marsilea quadrifolia, a native of Europe and Asia, is introduced and *M. ancylopoda* is extinct, so only eight native species remain.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Weed

The native range of *Salvinia molesta* includes a relatively small area (20,000 km²) in southeastern Brazil, including the states of Sao Paulo, Paraná, Santa Catarina and Rio Grande do Sul. It occurs between the latitudes 24°05' S and 32°05' S; at altitudes 0 to 500 meters; and up to 200 km inland (Map 1). Salvinia occurs in natural lagoons, artificial dams, swamps, drainage canals, and along margins of rivers (Forno and Harley, 1979).



Map 1. Countries where *Salvinia molesta* has been or is still a serious problem and countries where biological control by the weevil *Cytrobagous salviniae* has been successful.

Areas Surveyed for Natural Enemies

The first surveys for potential biological control agents for *S. molesta* were conducted in Trinidad, Guyana and northeastern Brazil from 1961 to 1963 (Bennett, 1966), and in Argentina prior to 1975 (Bennett, 1975), where species in the *S. auriculata* complex other than *S. molesta* occur. At this time the true identity and the native range of *S. molesta* were not known.

Surveys for natural enemies were conducted in Trinidad, Venezuela, Guyana, Uruguay, Paraguay, Brazil, and Argentina during 1978 to 1981. In 1978, the previously unknown range of *S. molesta* was identified (Forno and Harley, 1979), permitting surveys to focus on the relatively small native range of the target weed rather than the larger range of the *S. auriculata* complex (Forno and Bourne, 1984).

Natural Enemies Found

The natural enemies of S. molesta and the related species in the S. auriculata complex are listed in Forno and Bourne (1984), including species collected by Bennett (1975). Twenty-five phytophagous or possibly phytophagous species have been recorded from S. molesta, compared to 49 species from the four species of the S. auriculata complex. Four of these species have been used as biological control agents against S. molesta. The first three, Cyrtobagous singularis Hustache, Paulinia acuminata (De Geer), and Samea multiplicalis (Guenée) (identified during the early exploration [Bennett, 1966]) have not been successful control agents. The fourth, Cyrtobagous salviniae Calder and Sands, was found during later work (Sands, 1983) and has been extremely successful.

Host Range Tests and Results

Host range studies on the three unsuccessful species are summarized in Bennett (1966), Sankaran and Ramaseshiah (1973), Sands and Kassulke (1984, 1986), and Knopf and Habeck (1976).

Host range tests to assess feeding by C. salviniae were carried out in Australia on 46 species from six families of Pteridophyta (ferns), eleven families of Monocotyledons, and sixteen families of Dicotyledons (Forno et al., 1983). (This weevil was later found to be a new species and subsequently described as C. salviniae Calder and Sands). Test plants were exposed to mature weevils in three replicates in choice tests. Adult feeding occurred on Pistia stratiotes L., but the insect was unable to reproduce on that species. Minor leaf feeding was observed in choice tests on Ipomea batatas (L.) Lam. (sweet potato) when the leaves were held in contact with water, an abnormal condition. Adults failed to feed on I. batatas in no-choice tests in a non-aquatic situation and died within seven days. Host specificity tests indicated that this weevil was restricted to S. molesta. It has never been observed attacking plants other than Salvinia species in the field in South America, including those that grew in association with S. molesta such as water fern (Azolla sp.), waterhyacinth (Eichhornia crassipes [Mart.] Solms-Laubach), and waterlettuce (P. stratiotes) (Forno et al., 1983). Importantly, this weevil has not been found to attack any other plants even when huge populations were starving following population crashes of salvinia.

Releases Made

The grasshopper *P. acuminata*, collected from *S. auriculata* in Trinidad, was released in Zimbabwe (in 1969 and again in 1971), Kenya and Zambia (1970), Botswana (1971 and 1975), Sri Lanka (1973 and 1978), India (1994), and Fiji (1975). It failed to establish in Botswana, Kenya, and Sri Lanka and does not provide control in the countries where it established. The weevil *C. singularis*, collected from *S. auriculata* in Trinidad, was released in Botswana (in 1971 and 1976), Zambia (1971), and Fiji (1976). It is established in each country but is not providing control. The moth *S. multiplicalis*, also collected from *S. auriculata* in Trinidad, was released in Zambia (1970), Botswana (1972), and Fiji (1976). It failed to establish in Fiji and Zambia and does not control the weed in

Botswana (Julien and Griffiths, 1998). It was later collected from *S. molesta* in Brazil and released in Australia during 1981, where it established widely but failed to provide control (Room *et al.*, 1984; Forno, 1987).

Releases of *C. salviniae* from *S. molesta* in southeastern Brazil were made first in Australia in 1980. This weevil now controls the weed in most tropical and subtropical areas (Fig. 5) and in some temperate climates (Fig. 6). It has been released in 15 countries and controls the weed in at least 12 of these (Table 1). In Cote D'Ivoire, insufficient time has elapsed to measure success. Information on project results is not available for the Philippines or Indonesia. Map 1 shows the countries that have or have had serious salvinia problems and those where biological control has been successful.







Figure 5b.

Figure 5. (a) Lake Moondarra, Australia covered with *Salvinia molesta* D. S. Mitchell before the use of biological control; (b) More than 90% of salvinia on Lake Moondarra was destroyed within 14 months by the salvinia weevil, *Cyrtobagous salviniae* Calder and Sands. (Photographs by P. Room.)



Figure 6a.



Figure 6b.

Figure 6. (a) A creek in temperate Australia, near Sydney, infested with *Salvinia molesta* D. S. Mitchell, and (b) three years later after the salvinia weevil *Cyrtobagous salviniae* was released. (Photographs by M. Julien.)

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

A weevil found attacking *S. minima* in Florida was identified as *C. singularis* (Kissinger, 1966), but Calder and Sands (1985) listed *Cyrtobagous* specimens from Florida as *C. salviniae* and did not consider the range of *C. singularis* to include North America. When *S. molesta* was found in the United States and biological control was considered, further morphological examination of weevils from Florida suggested that they were *C. salviniae* (C. O'Brien, pers. comm.). This weevil was collected from *S. minima* in Florida by scientists from the USDA, ARS Invasive Plant Research Laboratory and released at sites in Liberty, Bridge City, and Toledo Bend Reservoir in Texas, and at Salter Creek in Louisiana during 1999.

Country	Initial Release Date	Status
Australia	1980	Control in tropical and subtropical areas; some control in temperate areas
Botswana	Spread from Namibia	Control in 1 to 5 years
Cote D'Ivoire	1998	Established and spreading
Fiji	1991	Successful control
Ghana	1996	Control
India	1983	Control at Bangalore and Kerala
Indonesia	1997	Status is unknown
Kenya	1990	Control except where affected by herbicide
Malaysia	1989	Control where released. Needs redistribution
Namibia	1984	Good control
Papua New Guinea	1982	Good control
Philippines	1989	Established on Panay. Impact unknown
Republic of South Africa	1985	Successful control within 2 years
Sri Lanka	1986	Successful control
Zambia	1990	Excellent control
Zimbabwe	1992	Good control within 2 years

When another USDA laboratory planned to release an Australian population of *C. salviniae*, a molecular comparison of the D2 gene was made between Florida and Australian material to provide a means of distinguishing between weevils from the two sources. Several base pair differences were found but the taxonomic significance of this is not yet clear. Further studies utilizing molecular, morphological and bioassay methods are planned. Until these differences are explained, further release of the Florida population will be suspended. No release of Australian material has been done yet.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Salvinia weevils, *Cyrtobagous salviniae* and *C. singularis* (Coleoptera: Curculionidae)

The genus Cyrtobagous Hustache was originally thought to be monotypic, containing only the species C. singularis. This weevil was known to feed on various South American Salvinia species and had been used unsuccessfully as a biological control agent for salvinia during the 1970s (Julien and Griffiths, 1998). Discovery of the native range of S. molesta in the late 1970s allowed surveys for natural enemies to concentrate on the target weed. A weevil thought to be C. singularis was collected from S. molesta and subsequently released in Australia, where it controlled the weed. Comparative studies determined that this was a new species, subsequently named C. salviniae (Fig. 7). Differences in the biology between the two species explained why one species failed to cause significant damage to the weed while the other proved to be an excellent control agent. Larvae of C. salviniae tunnel within the rhizomes causing them to disintegrate. Larvae also tunnel in the buds and adults eat buds, thus suppressing growth and vegetative propagation of this sterile weed. Larvae and adults of C. singularis feed on leaves and other tissues but don't affect the rhizomes or meristems. This research provided a classic example of the importance of careful taxonomic study of both the weed and the insects for successful biological control (Thomas and Room, 1986). Other important differences between the two species are that C. salviniae has a higher intrinsic rate of increase, lays seven times more eggs, and oviposits with greater frequency. Furthermore, this species' oviposition is less affected by changes in the nutrient status of the host plant, and larval and pupal survival rates are higher (Sands et al., 1986).

C. salviniae. The adult male of *C. salviniae* (1.8 x 0.9 mm) is slightly smaller than the female (2.2 x 1.2 mm). Newly emerged adults are brown, darkening to black in about five days. Detailed descriptions are given in Calder and Sands (1985) of the features that distinguish this species from *C. singularis.* Adults are found on or beneath young leaves, on or inside the developing leaves or among 'roots'. When under



Figure 7. The salvinia weevil *Cyrtobagous salviniae* Calder and Sands. (Photograph by R. Chan.)

water, adults respire by means of an air bubble (called a plastron) that adheres to their ventral surface (Forno et al., 1983). Multiple matings occur five to 26 days after emergence. At 25.5°C, oviposition begins after six to 14 days. Eggs (0.5 x 0.24 mm) are laid singly in cavities excavated by adults in lower leaves, developing leaves, rhizomes, and 'roots.' At 25.5°C, females lay one egg every two to five days for at least 60 days (Forno et al., 1983). Eggs hatch in 10 days at this temperature. Newly emerged larvae (1 mm) are white. They feed initially on 'roots' in or on the small buds, and later inside rhizomes, completing three instars in approximately 23 days (Forno et al., 1983). Development rate is dependent on temperature and the nutrient status of the host plant, larval development taking 13.4 days at 31°C on 'high' nitrogen plants. Larvae prefer to tunnel in young rhizomes and more tunneling occurs if plants are low in nitrogen. Larvae do not survive below 16.3°C (Sands et al., 1983). Pupation occurs in a cocoon (2 x 2.6 mm), which is woven from 'root hairs' and attached underwater to the 'roots,' rhizomes or leaf bases. At 25.5°C, pupae require 12.6 days for full development. Pupal duration is not affected by plant quality (Forno et al., 1983; Sands et al., 1983). Oviposition does not occur below 21°C, and eggs fail to hatch below 20°C or above 36°C. Adults feed between 13°C and 33°C (Forno et al., 1983). The lower lethal temperature at which 50% of the adult population would be expected to die is -5.2°C (Reaney 1999).

Population densities of *C. salviniae* are capable of reaching 300 adults and 900 larvae per m², levels estimated as necessary for control (Room, 1988, 1990; Room and Thomas, 1985).

Weevils in the genus *Cyrtobagous* were first recorded from the United States in Florida at the Archbold Biological Station (Highlands County) in 1962 (Kissinger, 1966). It is assumed that these weevils were accidentally introduced from South America, because of the lack of any earlier U.S. records and the adventive status of its host plant, S. minima. Kissinger (1966) considered the Florida weevils to be C. singularis, but this was before C. salviniae was recognized as a separate species. Calder and Sands (1985) later classified the Florida specimens as C. salviniae, but noted that the C. salviniae from S. minima in Florida were significantly smaller than those from S. molesta in Brazil. Based solely on morphological features, the weevils from Florida (later released in Texas) seem to be C. salviniae (C. O'Brien, pers. comm.). However, recent DNA assessments suggest that the Florida material differs from C. salviniae from Australia in some respects (Goolsby et al., 2000). Whether these differences imply separate species status is under investigation.

C. singularis. The biology of C. singularis is less well known and it is presumably similar to C. salviniae. For morphological differences between adults of this species and those of C. salviniae see Calder and Sands (1985), and for larvae, May and Sands (1986). Feeding differences between the species are outlined in Sands and Schotz (1985), and other differences in life history and intrinsic rates of increase are discussed in Sands et al. (1986). Adults are small (2 to 3 mm), black, sub-aquatic weevils that reside on or beneath leaves. While under water they respire using a plastron. Adults preferentially feed on apical leaves but also on the second to fifth pair of leaves, buds, and petioles (Sands and Schotz, 1985). Eggs are laid singly in cavities made by females in leaves. Unlike C. salviniae, whose larvae feed internally, those of C. singularis feed on the outer surfaces of submerged buds, rhizomes, and petioles. Feeding results in bud destruction, but not rhizome disintegration, and plants retain their capacity for regrowth (Sands and Schotz, 1985). Field population densities of C. singularis do not exceed 50 adults per m^2 (Schlettwein, 1985), a level that is insufficient to significantly damage salvinia (Room, 1990). This insect has not been a useful biological control agent (Julien and Griffiths, 1998).

Waterlettuce moth, *Samea multiplicalis* (Lepidoptera: Pyralidae)

Larvae and adults of *S. multiplicalis* are very similar to the closely related species, *Niphograpta (Sameodes)*

albiguttalis (Warren) (waterhyacinth moth, Pyralidae). Center et al. (1982) give characters to separate larvae of these species. Samea multiplicalis was originally described from Brazil where it was observed feeding on waterhyacinth. It is widely distributed throughout warmer regions of North and South America. In Florida, it is most commonly found on waterlettuce but also is present on A. caroliniana and S. minima. It is occasionally abundant on small waterhyacinth plants, feeding within inflated leaf petioles (Knopf and Habeck, 1976). This species was introduced into Australia for biological control of both S. molesta and P. stratiotes (Sands and Kassulke, 1984).

Adults (Fig. 8) are 6.5 to 10.5 mm long (Sands and Kassulke, 1984), tan, with brown and cream markings on both fore and hind wings. Females lay approximately 300 eggs during their four-to-sevenday life span (Knopf and Habeck, 1976; Sands and Kassulke, 1984; Taylor, 1984). Moths prefer to lay eggs on undamaged salvinia plants with high nitrogen content (Taylor and Forno, 1987). Most eggs are laid singly among the epidermal plant hairs on the lower surfaces of waterlettuce leaves, on the upper surfaces of Salvinia leaves, or lodged between the leaves of Azolla species. Eggs hatch in about four days at 26°C. Larvae (Fig. 9) may feed from within a refugium (made of silk and plant hair) attached to the external leaf surface or, for waterlettuce, within galleries in the leaves. Larvae periodically extend the refugium to reach fresh leaf material (Knopf and Habeck, 1976). Larger larvae feed on the buds of plants, often killing the growing apex. Larvae also will eat mature waterlettuce fruits and consequently destroy enclosed seeds.

On salvinia, temperature and plant quality interact to determine rates of insect growth, number of larval instars, fecundity, and survival (Taylor and Sands, 1986; Taylor, 1984, 1988, 1989). Optimum temperature for development for all stages is 28 to 30°C. Fecundity is greatest at 20 to 22°C and egg survival highest at 25 to 26°C (Taylor, 1988). Larvae complete development in 17 to 35 days on salvinia (Sands and Kassulke, 1984; Taylor, 1984). Development on waterlettuce and other salvinia species is described in Bennett (1966) and Knopf and Habeck (1976).

Pupation occurs within a silken cocoon. On waterlettuce, this cocoon is usually formed within the spongy portion of a leaf but on *S. molesta* it is



Figure 8. Adult *Samea multiplicalis* (Guenée). (Photograph by R. Chan.)



Figure 9. Larva of *Samea multiplicalis* (Guenée). (Photograph by P. Room.)

constructed among old leaves. Pupal development requires four to seven days at 28°C on waterlettuce and *S. minima* (Knopf and Habeck, 1976) and eight to nine days at 26°C on *S. molesta* (Sands and Kassulke, 1984). Total development (egg to adult) requires 24.6 (Knopf and Habeck, 1976) to 42 days (Sands and Kassulke, 1984).

Intrinsic rates of increase are highest in autumn and decline in summer and winter (Room *et al.*, 1984; Taylor, 1988). Levels of parasitism (24%) and disease in Australian populations on salvinia do not explain the seasonal variation in population growth rates (Semple and Forno, 1987); rather, field population densities are strongly determined by temperature and the nutritional quality of the plant (Taylor, 1988).

Salvinia grasshopper, *Paulinia acuminata* (Orthoptera: Pauliniidae)

This semi-aquatic grasshopper (Fig. 10) is adapted to living on floating mats of host plants where humidity is constantly high. *Paulinia acuminata* can complete its development on *Salvinia* spp., *P. stratiotes*, Azolla sp., and Hydromystria sp. and will feed on a range of other plant species (Bennett, 1966; Sands and Kassulke, 1986). It feeds on all species in the S. auriculata complex from Trinidad to northern Argentina and Uruguay (Bennett, 1966). Eggs of P. acuminata, in an ootheca, are attached underwater to the undersides of leaves and hatch in 19 to 21 days. Out of water, eggs fail to hatch (Bennett, 1966). There are five or six nymphal stages, six being common when temperatures are lower (Thomas, 1980). Eggs take 17 to 20 days to hatch; six nymphal instars complete development after 47 days; the pre-ovipositional period takes eight to 10 days; and duration from egg to adult is 67 days on average (Sands and Kassulke, 1986).



Figure 10. The salvinia grasshopper *Paulinia acuminata* (De Geer). (Photograph by P. Room.)

Females live 50 days or more and lay 200 or more eggs. Adults usually are brachypterous but macropterous forms occasionally occur in the field and are frequent in laboratory cultures (Bennett, 1966). Adults and nymphs feed on all plant parts above the water level when food is scarce. Grasshoppers prefer to feed on new growth and oviposition is reduced when the weed is matted (Mitchell and Rose, 1979). Under extremely hot conditions adults shelter in the water with their heads exposed (Thomas, 1980). In the field at Lake Kariba, where the mean annual temperature was 24 to 28°C, it was estimated that *P. acuminata* could complete three generations per year (Thomas, 1980).

A significant reduction in salvinia on Lake Kariba occurred in 1972/3, following the release of *P. acuminata* in 1970. However, the decline of the weed at this location has been attributed to other factors such as nutrient stress on the weed (Mitchell and Rose, 1979; Marshall and Junor, 1981). Chisholm (1979) demonstrated that densities of more than 85 *P. acuminata* per m² feeding for 24 days were required to reduce production of new leaves. On Lake Kariba during the period when salvinia was a problem the maximum grasshopper density recorded was 27 per square meter (Marshall and Junor, 1981), suggesting that the insect might not have been a primary cause of decline in the weed. Sands and Kassulke (1986) noted that field populations in Africa of 45 to 54 *P. acuminata* per m² grazed up to 87% of leaves without affecting apical or lateral growth or killing plants.

EVALUATION OF PROJECT OUTCOMES

In the United States, *S. molesta* is a new problem so evaluations are premature. As mentioned previously, *C.* salviniae, a naturalized species on *S. minima* in Florida, was released in Texas in 1999. It will take another year to determine if establishment has occurred.

RECOMMENDATIONS FOR FUTURE WORK

Currently, three release sites and three insect-free control sites are being monitored monthly in water bodies in eastern Texas and western Louisiana infested with *S. molesta* using standard protocols. In addition, molecular techniques are being utilized to identify and compare at least six salvinia species, including those outside of the *S. auriculata* complex. This will provide a means of identifying *Salvinia* species should any new invasions occur in the United States or elsewhere. Similar molecular testing of *Cyrtobagous* sp. collected from different salvinia species may provide insights to the taxonomy of this group and their associated host ranges.

We anticipate that the same favorable results as obtained in at least 12 countries on three continents can be repeated in the United States, namely, reductions in the density and abundance of *S. molesta* to acceptable levels. Reductions may range from local extinctions to maintenance of small populations of the weed along the fringes of ponds, lakes, and rivers.

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3 WATER CHESTNUT

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PEST STATUS OF WEED

Water chestnut (*Trapa natans* L.) (Fig. 1), also known as horned water chestnut or water caltrop, is an aquatic weed of the northeastern United States that can dominate ponds, shallow lakes, and river margins (Fig. 2). It displaces native vegetation and limits navigation and recreation. It occurs from the northeast, west to the Great Lakes, and south to Washington, D. C. The plant has the potential to spread into the warm temperate and subtropical regions of the United States, such as Florida, which prohibits importation of the plant (State of Florida, 1996).

Nature of Damage

Economic damage. This weed is difficult and expensive to control, and if unmanaged can increase dramatically (Bogucki et al., 1980). When the plant occupies a site, most recreational activities such as swimming, fishing from the shoreline, and the use of small boats are eliminated or severely impeded. The primary economic costs related to T. natans are associated with the costs of chemical and mechanical control efforts. Vigorous management efforts by the U.S. Army Corps of Engineers during the 1950s and 1960s brought T. natans populations in the United States. largely under control, but these control programs were suspended because the programs' success and because of budgetary constraints (Madsen, 1994). During the 1970s, T. natans populations began to increase, and by 1994 the weed infested more areas than before the control programs (Madsen, 1994). The cost of these control programs was not well documented (J. Madsen, pers. comm.). Currently, the largest control program is in Vermont, where \$500,000 will be spent for the year 2000 to remove the plants, primarily by use of mechanical harvesters and hand removal. (H. Crosson, pers. comm.).



Figure 1. Single rosette of water chestnut (*Trapa natans*) showing the horned fruits and the inflated leaf petioles that enable the rosette to float. (Photograph by Al Colfancesco, U.S. Army Corps of Engineers.)



Figure 2. Infestation of *Trapa natans* on Lake Champlain, New York. (Photograph by Al Cofrancesco, U.S. Army Corps of Engineers.)

Ecological damage. Trapa natans grows best in waters that are nutrient rich and moderately alkaline (Papastergiadou and Babalonas, 1993; Kiviat, 1993). It can grow in water up to 5 m deep, but prefers shallow waters (0.3 to 2.0 m deep) (Papastergiadou and Babalonas, 1993). Where *T. natans* is abundant, up to 50 rosettes can grow in 1 m², which enables it to cover the water with up to three layers of leaves

(Tsuchiya and Iwaki, 1984). Heavy shade from *T. natans* suppresses both submersed and other floating plants. The weed's extensive clonal propagation ability enables it to successfully colonize and monopolize aquatic habitats (Groth *et al.*, 1996). The Nature Conservancy's (TNC) concern about water chestnut's impact on local flora in the Vermont areas of Lake Champlain has stimulated the TNC to create large teams of volunteers to hand pull the rosettes (S. Crawford, pers. comm.)

Geographical Distribution

Trapa natans was first observed in North America, growing "luxuriantly" in Sanders Lake, Schenectady, New York, in 1884 (Wibbe, 1886). The plant subsequently spread to many other areas in the northeastern United States including Connecticut, Delaware, Maryland, Massachusetts, New Hampshire, Pennsylvania, Vermont, Virginia, and Washington D.C. (Crow and Hellquist, 2000). The plant is now present in the Great Lakes Basin (Mills *et al.*, 1993; Groth *et al.*, 1996) and recently has been found in Quebec, Canada (C. B. Hellquist, pers. comm.).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Trapa natans often is considered to belong to the Trapaceae, a monogeneric family that is widely distributed in the Eastern Hemisphere (Cook et al., 1974). Historically, the genus Trapa has been placed in both the Onagraceae (Cronquist, 1981) and the Lythraceae (Fassett, 1957). After being considered part of an independent family for some years, modern molecular research places Trapa species once more in the Lythraceae in the order Myrtales (The Angiosperm Phylogeny Group, 1998). Because of the morphological variation in Trapa species, there has been little agreement about the number of species in the genus. Various classification schemes have designated from one to 30 Trapa species (Cook, 1978). Trapa species are determined by fruit morphology and plants with four stout horns on the fruit most often are called Trapa natans. The two commonly cultivated species in Asia, Trapa bicornis Osbeck and Trapa bispinosa Roxburgh, have two horns and are considered by some workers to be agricultural selections of *T. natans* (Kadono, pers. comm.). Unfortunately, an unrelated edible aquatic plant, *Eleocharis dulcis* (Burm.f.) Trin. ex Henschel, a sedge in the Cyperaceae, also is called water chestnut. The corm of *E. dulcis* is the familiar water chestnut, or Chinese water chestnut, sold in cans and commonly served in Chinese restaurants.

Biology

Trapa natans is an annual herb with a floating rosette of leaves around a central stem that is rooted in the hydrosoil. The spongy inflated leaf petioles enable the rosette to float. The plant produces new leaves from a central terminal meristem in the rosette near the surface of the water. The inconspicuous flowers are born in the leaf axils of younger leaves above the water. As the meristem elongates and produces new leaves, the older leaves and developing fruit move, in effect, down the stem and underwater. The singleseeded mature fruit are woody and bear four sharply pointed horns. When mature, the fruits fall from the plant and sink to the bottom of the water body. A seed dormancy period of four months has been found (Cozza et al., 1994). The horns may act as anchors to limit the movement of the seed, keeping them in suitable depths of water. The seeds overwinter at the bottom of the water body and germinate during and throughout much of the warm season to produce shoots that grow to the water surface, where the typical rosette is formed. Seed can remain viable for up to five years (Kunii, 1988).

Analysis of Related Native Plants in the Eastern United States

If *T. natans* is considered to be a member of the mongeneric Trapaceae, a family native to the Eastern hemisphere, then there are no native family members in the New World. If, however, *Trapa* is considered to belong to the Lythraceae, it has confamilial native relatives in North America. The Lythraceae is a small family in North America containing 18 to 20 species in eight genera (*Ammannia, Cuphea, Decodon, Didiplis, Heimia, Lythrum, Nesaea,* and *Rotala*) (Soil Conservation Service, 1982). Six of these genera (all but *Heimia* and *Nesaea*) have species that are broadly sympatric with *T. natans* in North America (Soil Conservation Service, 1982).

HISTORY OF BIOLOGICAL CONTROL EFFORTSIN THE EASTERN UNITED STATES

Area of Origin of Weed

The native area of *T. natans* is from western Europe and Africa to northeast Asia including eastern Russia, China, and southeast Asia, through to Indonesia (Sculthorpe, 1967; Oliver, 1871; Voroshilov, 1982). The starchy nut-like fruit of *T. natans* and its cultivars have been used as food by people in much of the native range and are widely cultivated in Asia (Tanaka, 1976).

Areas Surveyed for Natural Enemies

The specific geographic origins of the T. natans genotype(s) that has become a problem in the United States are unknown. The weed usually is thought to be from Eurasia but recent work considers it of Asian origin (Crow and Hellquist, 2000). The two regions surveyed for insect and pathogen natural enemies of T. natans are northeast Asia and western Europe, which represent the eastern and western areas of the plant's temperate zone distribution (Pemberton, 1999). China, Japan, eastern Russia, and South Korea were surveyed in 1992 and 1993. These areas were selected because of previous records of damaging insects on wild populations of Trapa and published accounts of pest insects of cultivated Trapa in the region (Lu et al., 1984; Hayashi et al., 1984). Some of these natural enemies on Trapa occurred in areas with climates similar to those of the infested areas of North America. In Asia, surveys were carried out on populations of the wild forms of Trapa japonica Flerov and T. natans, and on the cultivated forms of T. bicornis and T. bispinosa, which are thought to be agricultural selections of T. natans. Trapa species and cultivars were locally common in China, South Korea, and Japan, but much scarcer in eastern Russian. Trapa natans, the only European Trapa (Tutin et al, 1968), was surveyed in France, Germany, Italy, Poland, and Switzerland in 1995. Trapa natans is a rare plant in Europe and the subject of conservation efforts to preserve and restore populations.

Natural Enemies Found

Tables 1 and 2 list the insects found associated with *Trapa* species in northeast Asia and in western Europe (Pemberton, 1999). Among the insects found,

the leaf beetle Galerucella birmanica Jacoby was the most common and damaging species found in Asia, causing complete defoliation of whole populations of plants. Nymphuline pyralid moths also were common and at times damaging. Both the beetle and the moths feed and develop on unrelated plants, so have no potential as T. natans biological control agents in North America. Because of the possibility of sibling Galerucella species with different host plants, G. birmanica may warrant additional study. Two Nanophyes weevils, which feed in the floating leaf petioles, were found in Asia. They are thought to be specific to Trapa but were not observed to be damaging. Low density populations of polyphagous Homoptera were common. Chironomid midges also were frequently associated with the plants, but for the most part were filter feeders, not herbivores. In Europe, a similar insect fauna was found, but no species were very damaging to the plant. One Italian weevil, Bagous rufimanus Hoffmann, feeds within the fruit stalk (Mantovani et al., 1992) and might be more damaging at higher than observed population levels.

Host Range Tests and Results

To date, this biological control project has been limited to surveys and monitoring of South Korean populations of *T. japonica* for natural enemy activity and damage. No host specificity testing has yet been done.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Galerucella birmanica Jacoby and Galerucella nymphaeae L. (Coleoptera: Chrysomelidae)

Galerucella birmanica (= G. nipponesis Laboissiere) was abundant in most regions surveyed in northeast Asia, except for Hokkaido in Japan and the Russian Far East. All life stages of the beetle are found on the upper leaf surfaces. The adults and larvae feed on the leaf blades of the plants. Young larvae scrape the upper surface of the leaves, while older larvae and adults consume the blade tissue, often leaving a skeletal leaf comprised of main veins. This beetle can be very damaging, causing whole mats of rosettes to be defoliated. There are several overlapping generations in most areas which enables the populations to rapidly increase. It is the most important pest of cultivated *Trapa* in China and India (Khatib, 1934;

Table 1. Natural Enemies of Trapa Species in Northeast Asia (Pemberton, 1999)

Natural Enemy Species	Country	Feeding Site	Host Range
INSECTS			
Aphididae (Homoptera)			
1. Rhopalosiphum nymphaeae (L.)	China, Japan, S. Korea	Leaves	Polyphagous
Cicadellidae (Homoptera)			
2. Macrosteles purpurata Kuoh et Lu	China, Russia	Leaves	Polyphagous
Chrysomelidae (Coleoptera)			
3. Galerucella birmanica Jacoby (=G. nipponensis Laboissiera)	China, Japan, S. Korea, Russia	Leaves	Oligophagous
Curculionidae (Coleoptera)			
4. Nanophyes japonica Roelofs	China, Japan	Petiole floats	Stenophagous
5. Nanophyes sp.	China, Russia	Leaf blades, petiole floats	Stenogphagous
Pyralidae (Lepidoptera)			
6. Nymphula interruptalis (Pryer)	China, Japan, S. Korea,	Leaves and buds	Polyphagous
7. Nymphula responsalis (Walker) (=N. turbata Butler)	China, Japan, S. Korea	Leaves	Polyphagous
8. Paraponyx vittalis (Bremer)	China	Leaves	Polyphagous
Noctuidae (Lepidoptera)			
9. Spodoptera litura Fabricius	China	Leaves	Polyphagous
Lepidoptera			
10. Unknown leafminer	China, Japan	Leaves	?
Chironomidae (Diptera)			
11. Chironomus spp.	China, Japan, S. Korea, Russia	Petiole floats	Filter feeder
12. Unknown spp.	China, Japan, S. Korea, Russia	Leaves and buds	?
MOLLUSKS			
13. Radix auricularia L.	China	Leaves	Broad
FUNGI			
14. <i>Cercospora</i> sp.	China	Leaves	Broad
15. Sclerotium rolfsii Scaccardo	China	Whole plant	Broad
16. Botrytis cinerea Persoon et Fries	China	Whole plant	Broad
OTHER PATHOGENS			
17. Unknown, possible virus	China	Whole plant	?

Natural Enemy Species	Country	Feeding Site	Host Range
Aphididae (Homoptera)			
1. Rhopalosiphum nymphaeae (L.)	France, Poland	Leaves	Polyphagous
Cicadellidae (Homoptera)			
2. Unknown leafhopper species	France, Italy	Leaves	Probably polyphagous
Curculionidae (Coleoptera)			
3. Bagous rufimanus Hoffman	Italy	Fruit epidermis and peduncle, stem	Stenophagous
Chrysomelidae			
4. Galerucella nymphaeae (L.)	France, Italy, Poland	Leaves	Oligophagous
Pyralidae (Lepidoptera)			
5. <i>Nymphula</i> sp.	France, Poland	Leaves	Probably polyphagous
Chironomidae (Diptera)			
6. Unknown sp. 1	France, Germany, Italy, Poland	Leaf petiole	Filter feeders
7. Unknown sp. 2	Poland	Apical bud, leaves	?

Table 2. Natural Enemies of Trapa natans in Western Europe (Pemberton, 1999)

Lu et al., 1984). The beetle also was noted on cultivated Trapa along the Mekong River in Vietnam, where farmers use insecticides against it. The beetle eats and develops on unrelated plants, including Brasenia schreberi J. Gmelin (Cabombaceae) (Hayashi et al., 1984; Lu et al., 1984), which gives it its common Japanese name "junsai mushi," which translates as Brasenia schreberi insect. It also appeared to be using a floating Polygonum sp. (Polygonaceae) as a host plant in northern China. It is possible that G. birmanica could represent more than one species with different host plants even though it is a well known pest insect in Asia. Sibling Galerucella species with different host plants are known (Blossey, pers. comm.).

Galerucella nymphaeae L. was the most apparent natural enemy of *T. natans* in Europe, occurring in all areas except Germany. This species is very similar to the Asian *G. birmanica*, with regard to appearance, life cycle, and manner of feeding. It was not observed to be very abundant or damaging anywhere in Europe. The beetle feeds on many different unrelated plants, including water lilies. This beetle is a holartic species (Horn, 1893), so already occurs in the United States, where it also feeds on *T. natans*, and unrelated plants (Schmidt, 1985).

Nanophyes japonica Roelofs and Nanophyes sp. (Coleoptera: Curculionidae)

Two *Nanophyes* weevils were observed to attack the leaves of *Trapa* spp. in Asia. A brief description of leaf and rosette characteristics is provided here to aid the understanding of the weevils' life cycles. The rosettes of plants float because each leaf stalk (petiole) is enlarged and filled with spongy tissue that forms a float. The leaf position within the rosette changes with age; young leaves expand from the meristem in the center of the rosette, and move outward as the petiole lengthens. As the meristem produces new leaves, it elongates upward, which places older leaves further down on the stem below the surface of the water.

Nanophyes japonica Roelofs is abundant in central Japan and the Nanjing area of China. The adults feed on the upper leaf blades and females lay eggs in the floating leaf petioles. The larvae feed and pupate within these spongy petioles. Attacked petioles are

Natural Enemy Species	Country	Feeding Site	Reference
INSECTS			
Curculionidae (Coleoptera)			
Bagous tersus Egorov et Gratshev	Russia	Petiole	Egorov and Gratshev, 1990
Bagous trapae Prashad	India	?, on stem	Prashad, 1960
Bagous vicinus Hustache	India	?	Bharadwaj and Chandra, 1980
Bagous sp.	India	?, reduces crop	Batra, 1962
Nanophyes rufipes Motschulsky	India	?	Bharadwaj and Chandra, 1980
Chrysomelidae (Coleoptera)			
Galerucella singhara Lefroy	India	Leaves	Bharadwaj and Chandra, 1980
Galerupipla sp. near brunnea Walker	Thailand	Leaves	Cantelo, 1965
Haltica cyanea Weber	India	Leaves	Batra, 1962
Pyralidae (Lepidoptera)			
Nymphula gangeticalis Lederer	India	Leaves	Bharadwaj and Chandra, 1980
Nymphula crisonalis Walker	Thailand	Leaves	Cantelo, 1965
DISEASE			
Fungus			
<i>Bipolaris tetramera</i> (Mckinney) Shoemaker	India	Leaves	Singh and Lal, 1965

Table 3. Reported Natural Enemies of Trapa of Potential Interest (Pemberton, 1999)

often reddish in color and frequently have indented areas where the eggs have been laid. At times, particularly in smaller plants, the petiole becomes galllike, with thickened outer walls. Several larvae may occupy an attacked petiole. Blades of leaves with infested petioles are normal in color and appearance, and infested plants produce many fruit, suggesting that the weevil does little damage.

Another unidentified *Nanophyes* species was found in the Harbin area of China and at Hinkanski in Russia. This weevil lays a single egg in the central vein of the upper side of the leaf blade. The newly hatched larva mines the central vein of the leaf blade downward into the petiole float where it finishes feeding and pupates. There is only one larva per leaf, and even though almost all leaves of some plants may be attacked, the leaves and plants remain normal and healthy. Adult feeding on the leaves is minor. The developmental periods (from egg to adult) for both of these weevils appear to be the same as the life span of a single leaf in which the development takes place, which is usually one to two weeks depending on the temperature. The eggs of both weevils are laid in young recently expanded leaves near the center of the rosette and the pupae of both species are found in old submerged leaves on the stem below the water's surface. This synchrony of weevil development with leaf age suggests extreme host specialization. Nanophyes japonica has not been recorded from plants other than Trapa, and it seems that both of these weevils are limited to Trapa species. They are the most specialized natural enemies of Trapa species found in northeast Asia.

RECOMMENDATIONS FOR FUTURE WORK

Although *T. natans* continues to be a problem that requires expensive control efforts, no biological control research is being conducted at this time, but future research could help develop biological controls for the weed.

Because the very damaging, Asian leaf beetle *G. birmanica* might be composed of sibling species with different host plants, it would be worthwhile to determine the identities of populations of the beetle associated with different host plants with molecular tools. D2 gene comparisons, which are a useful and inexpensive method for determining species identities of many insect groups (J. Goolsby, pers. comm.), could be used to examine *G. birmanica*.

Surveys for natural enemies have examined widely separated populations of T. natans and other Trapa spp., but large regions remain unexamined. It is probable, however, that these surveys provide a good indication of what exists in the temperate part of the plant's range, given the similarities in the natural enemies in the far eastern and western parts of the plant's native range. Some temperate areas remain that might contain promising natural enemies. One of the most interesting areas is Kashmir, which has large populations of Trapa in an area that is isolated from the rest of temperate Asia by the Himalayan Mountains. There is a diverse fauna of Trapa in the warmer areas of India (Table 3), and some of these species might be adapted to the colder climate of Kashmir. The Volga River Delta at the north end of the Caspian Sea also has large Trapa populations, and people living there call themselves the Trapa eaters (M. Volkovitsh, pers. comm.). Trapa populations in this area may lack the isolation needed for them to acquire a natural enemy fauna that is different from that which occurs in temperate Eurasia.

Trapa natans is native also to areas with tropical and subtropical climates including Africa, southern Asia, and southeast Asia. If this weed becomes a problem in the warmer parts of North America, insect natural enemies of the plant from warm areas could become important and might have promise as biological control agents. A number of insects have been reported to attack *T. natans* in warm areas (Table 3), such as India and Thailand. Some of the weevil species are known to reduce fruit yield (Batra, 1962).

Insecticides are used against some of these insects, another indication of their impact on the plants (Bharadwaj and Chandra, 1980). Most of these insects are related to species found in surveys in Europe and northeast Asia. They include *Bagous* and *Nanophyes* weevils, Nymphuline moths, a third *Galerucella* sp., and two additional genera of leaf beetles. Some of these may have more specificity and/ or ability to damage the plants than the natural enemies encountered to date.

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4 WATERHYACINTH

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PEST STATUS OF WEED

Waterhyacinth, *Eichhornia crassipes* (Mart.) Solms.-Laubach (Fig. 1), is considered one of the world's worst weeds (Holm *et al.*, 1977), invading lakes, ponds, canals, and rivers. It was introduced into many countries during the late 19th and early 20th centuries, where it spread and degraded aquatic ecosystems. It is still rapidly spreading throughout Africa, where new infestations are creating life-threatening situations as well as environmental and cultural upheaval (Cock *et al.*, 2000). Control with herbicides, particularly 2,4-D, is feasible, but is costly and temporary.

Nature of Damage

Economic damage. Waterhyacinth grows rapidly (Penfound and Earle, 1948) forming expansive colonies of tall, interwoven floating plants. It blankets large waterbodies (Fig. 2), creating impenetrable barriers and obstructing navigation (Gowanloch and Bajkov, 1948; Zeiger, 1962). Floating mats block drainage, causing flooding or preventing subsidence of floodwaters. Large rafts accumulate where water channels narrow, sometimes causing bridges to collapse. Waterhyacinth hinders irrigation by impeding



Figure 1. Waterhyacinth growing in the Marañon River, Peru. (Photo by T. D. Center, USDA, ARS.)

water flow, by clogging irrigation pumps, and by interfering with weirs (Penfound and Earle, 1948). Multimillion-dollar flood control and water supply projects can be rendered useless by waterhyacinth infestations (Gowanloch and Bajkov, 1948).

Infestations block access to recreational areas and decrease waterfront property values, oftentimes harming the economies of communities that depend upon fishing and water sports for revenue. Shifting waterhyacinth mats sometimes prevent boats from reaching shore, trapping the occupants and exposing them to environmental hazards (Gowanloch and Bajkov, 1948; Harley, 1990). Waterhyacinth infestations intensify mosquito problems by hindering insecticide application, interfering with predators, increasing habitat for species that attach to plants, and impeding runoff and water circulation (Seabrook, 1962).

Ecological damage. Dense mats reduce light to submerged plants, thus depleting oxygen in aquatic communities (Ultsch, 1973). The resultant lack of phytoplankton (McVea and Boyd, 1975) alters the composition of invertebrate communities (O'Hara, 1967; Hansen *et al.*, 1971), ultimately affecting fisheries. Drifting mats scour vegetation, destroying



Figure 2. A waterhyacinth infestation in southern Florida. (Photo by T. D. Center, USDA, ARS.)

native plants and wildlife habitat. Waterhyacinth also competes with other plants, often displacing wildlife forage and habitat (Gowanloch, 1944). Higher sediment loading occurs under waterhyacinth mats due to increased detrital production and siltation. Herbicidal treatment or mechanical harvesting of waterhyacinth often damages nearby desirable vegetation.

Extent of losses. Waterhyacinth caused annual losses (all causes) of \$65 to 75 million in Louisiana during the 1940s (Gowanloch and Bajkov, 1948). Fish and wildlife losses alone in the six southeastern states exceeded \$4 million per year in 1947 and waterhyacinth control provided a benefit to cost ratio of 15.3:1 (Tabita and Woods, 1962). Holm et al. (1969) ascribed losses of \$43 million in 1956 to waterhyacinth infestations in Florida, Mississippi, Alabama, and Louisiana. The U.S. Army Corps of Engineers estimated benefits from waterhyacinth control programs at nearly \$14 million in 1965 (Gordon and Coulson, 1974). Florida spent more than \$43 million during 1980 to 1991 to suppress waterhyacinth and waterlettuce (Schmitz et al., 1993). Currently, annual costs for waterhyacinth management range from \$500,000 in California to \$3 million in Florida (Mullin et al., 2000). The largest infestations occur in Louisiana, where the Department of Fisheries herbicidally treats about 25,000 acres of waterhyacinth per year, mostly at boat ramps, at an annual cost of \$2 million (R. Brassette, pers. comm.).

Geographical Distribution

Waterhyacinth was introduced into the United States around 1884 and has since become pan-tropical. Worldwide, the limits of distribution are at 40° N and S latititude (Gowanloch and Bajkov, 1948; Bock, 1968; Holm *et al.*, 1969; Ueki, 1978; Kolbek and Dostálek, 1996; Gopal, 1987). In the United States, waterhyacinth is most abundant in the Southeast (Fig. 3). It also occurs in California and Hawaii, with scattered records in other states (USDA, NRCS, 1999).

BACKGROUND INFORMATION ON THE PEST PLANT

Taxonomy

The English common names of the plant are waterhyacinth, water hyacinth, and water-hyacinth.

Waterbyacinth is the standardized spelling adopted by the Weed Science Society of America (WSSA, 1984) to denote that it is not an aquatic relative of true "hyacinth" (Hyacinthus spp.), as the two-word spelling suggests.

The taxonomic placement of waterhyacinth, based on Cronquist (1988), Thorne (1992), and Takhtajan (1997), is as follows: division Magnoliophyta; class Liliopsida; subclass Commelinidae (Liliidae [Cronquist, 1988; Thorne, 1992]); superorder Commelinanae (Thorne, 1992); order Pontederiales (Liliales [Cronquist, 1988]; Philydrales [Thorne, 1992]); family Pontederiaceae, genus *Eichhornia*; specific epithet *crassipes* (Martius) Solms-Laubach.

Biology

Waterhyacinth is an erect, free-floating, stoloniferous, perennial herb (Fig. 4). The bouyant leaves vary in size and morphology. The short, bulbous leaf petioles produced in uncrowded conditions provide a stable platform for vertical growth. Plants in crowded conditions form elongate (up to 1.5 m) petioles (Center and Spencer, 1981). Leaves are arranged in whorls of six to 10, and individual plants develop into clones of attached rosettes (Center and Spencer, 1981).

The lavender flowers display a central yellow fleck and are borne in clusters of up to 23 on a single spike (Barrett, 1980). The flowers may have short, medium, or long styles, but only the short- and longstyle forms occur in the United States (Barrett, 1977). The 14-day flowering cycle concludes when the flower stalk bends, positioning the spike below the water surface where seeds are released (Kohji et al., 1995). Seed capsules normally contain fewer than 50 seeds each (Barrett, 1980). Each inflorescence can produce more than 3,000 seeds and a single rosette can produce several inflorescences each year (Barrett, 1980). The small, long-lived seeds sink and remain viable in sediments for 15 to 20 years (Matthews, 1967; Gopal, 1987). Seeds germinate on moist sediments or in warm shallow water (Haigh, 1936; Hitchcock et al., 1950) and flowering can occur 10 to 15 weeks thereafter (Barrett, 1980). Lack of germination sites limits seedling recruitment except during drought, on decaying mats after herbicide applications (Matthews, 1967), or at the margins of waterbodies. Populations increase mainly by vegetative means.

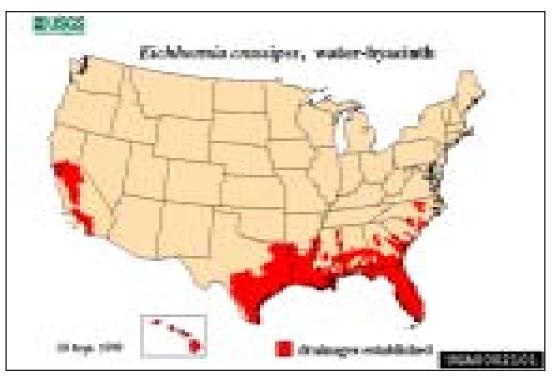


Figure 3. Drainages infested by waterhyacinth in the United States. (Map courtesy of the U.S. Biological Survey, Colette Jacono).

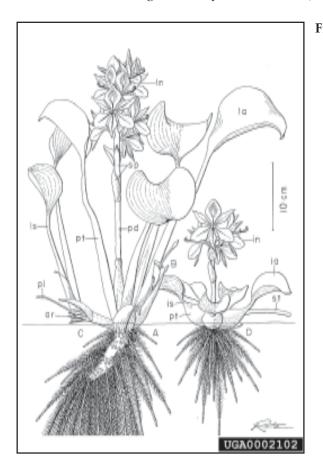


Figure 4. Morphology of waterhyacinth plants (A. the "attenuated-petiole" rosette form produced in crowded conditions; B. an expanding axillary bud; C. a developing ramet; and D. the "bulbous-petiole" rosette form produced in open conditions. Abbreviations: ar – adventitious root; bb – bud bract; in – inflorescence; is – leaf isthmus; la – leaf blade; pl – primary leaf; pd – peduncle of flower spike; pt – leaf petiole; rh – rhizome; sp – spathe; st – stolon.

Weber (1950), Richards (1982), Watson (1984), and Watson and Cook (1982, 1987) describe waterhyacinth growth and population expansion as the result of differentiation of apical or axillary meristems. The single apical meristem on each stem tip can be vegetative, producing leaves with axillary buds, or reproductive, producing flowers. If an inflorescence develops, termination of the apical meristem halts leaf production. In this event, the axillary bud immediately below the inflorescence differentiates into a continuation shoot. This produces a new apical meristem that allows leaf production to proceed. If the axillary bud doesn't form a continuation shoot, then it produces a stolon. Elongation of the stolon internode moves the axillary bud apex away from the parent rosette. It then produces short internodes that grow vertically into a new rosette.

Waterhyacinth grows best in neutral pH, water high in macronutrients, warm temperatures (28° to 30°C), and high light intensities. It tolerates pH levels from 4.0 to 10.0 (Haller and Sutton, 1973), but not more than 20 to 25% sea water (Muramoto *et al.*, 1991). The plants survive frost if the rhizomes don't freeze, even though emergent portions may succumb (Webber, 1897). Prolonged cold kills the plants (Penfound and Earle, 1948), but reinfestation from seed follows during later warmer periods. Ueki (1978) matched the northern limit of waterhyacinth to the 1°C average January isotherm in Japan. Growth is inhibited at water temperatures above 33°C (Knipling *et al.*, 1970). Plants stranded on moist sediments can survive several months (Parija, 1934).

Analysis of Related Native Plants in the Eastern United States

Waterhyacinth is a member of the pickerelweed family (Pontederiaceae). Families most closely allied with the Pontederiaceae are Commelinaceae, Haemodoraceae (including Conostylidaceae [Takhtajan, 1997]), Philydraceae, and Hanguanaceae (Hahn, 1997; APG, 1998). The subclass Commelinidae includes the Arecales, Poales, Commelinales, and Zingiberales (APG, 1998).

The Pontederiaceae is a small family of herbaceous monocotyledons that includes six genera and 30 to 35 species (Eckenwalder and Barrett, 1986). All are palustrine or aquatic and most are confined to the Americas. All seven members of the genus *Eichhornia* originated in tropical America, except for *Eichhornia natans* (P. Beauv.), which is from tropical Africa. Fourteen species of Pontederiaceae occur in the U.S./Canadian flora (Table 1), six of which are adventive; none are considered threatened or endangered (USDA, NRCS, 1999).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The diversity of other species of *Eichhornia*, particularly the more primitive *Eichhornia paniculata* (Spreng.) Solms. and *Eichhornia paradoxa* (Mart.) Solms., and the overlapping range of the closely

Table 1. Species of Pontederiaceae in the United
States.

Native Species	Introduced Species
Heteranthera dubia (Jacq.) MacM.	Eichhornia azurea (Sw.) Kunth
Heteranthera limosa (Sw.) Willd.	Eichhornia crassipes (Mart.) Solms.
Heteranthera mexicana Wats.	Eichhornia diversifolia (Vahl) Urban
<i>Heteranthera multiflora</i> (Griseb.) Horn	Eichhornia paniculata (Spreng.l) <i>Solms</i>
<i>Heteranthera penduncularis</i> Benth.	Monochoria hastata (L.) Solms
<i>Heteranthera reniformis</i> Ruiz López & Pavón	<i>Monochoria vaginalis</i> (Burm. f.) K. Presl
<i>Heteranthera rotundifolia</i> (Kunth) Griseb.	
Pontederia cordata L.	

related *Eichhornia azurea* (Sw.) Kunth suggest that *E. crassipes* arose in tropical South America.

Areas Surveyed for Natural Enemies

Although several expeditions have been made to South America to survey for natural enemies of waterhyacinth (Center, 1994), most were limited in scope and failed to encompass the upper Amazon basin where waterhyacinth may have originated. Bennett and Zwölfer (1968) explored the northernmost range of the plant. Other authors have explored the eastern parts of the range but the western portion has seldom been visited. The discovery of new organisms associated with waterhyacinth was thought to be unlikely because of the long history of exploration in South America. Recent findings of new, potentially useful natural enemies suggest otherwise (Cordo, 1999).

Natural Enemies Found

Beginning in the early 1970s, the USDA and CIBC (now CABI-Bioscience) released the weevils *Neochetina eichhorniae* Warner, *Neochetina bruchi* Hustache, and, later, the pyralid moth *Niphograpta* (=*Sameodes*) *albiguttalis* (Warren). These three agents, plus the mite *Orthogalumna terebrantis* Wallwork, are now widely used (Table 2). Many countries that have initiated biological control programs against waterhyacinth have reported successes (Julien and Griffiths, 1998). All four agents are important, although the two *Neochetina* weevils seem most successful. Nonetheless, the control achieved has not always been sufficient. The relatively slow action of the biological control agents is sometimes incompatible with other management practices (Center *et al.*, 1999a). In other cases, the explosive growth of waterhyacinth stimulated by high nutrient levels precludes effective control (Heard and Winteron, 2000). Clearly, needs exist to develop and use compatible management practices and to seek new agents that are capable of rapid population growth.

About 19 of 43 species (Table 2) have been indentified as potential control agents because of the damage they cause or because of their narrow host range (Perkins, 1974). This list suggests that there are additional safe and effective agents among those already known, while others remain to be discovered.

Host Range Tests and Results

The two weevil species (*N. eichhorniae* and *N. bruchi*) have been released on waterhyacinth in 30 and 27 countries, respectively. Both have been subjected to extensive screening. They have been tested against 274 plant species in 77 families worldwide (Julien *et al.*, 1999). Some use of a few non-target species, mainly other Pontederiaceae, was observed that was insignificant when compared to waterhyacinth.

The other agents released on waterhyacinth, the fungus Cercospora piaropi Tharp, the mirid Eccritotarsus catarinensis (Carvalho), the moths N. albiguttalis and Xubida infusellus (Walker), and the mite O. terebrantis, have been introduced to fewer countries and have therefore been subjected to fewer host specificity trials. However, no host range extensions by these species have been recorded except for the predicted feeding by the weevils on pickerelweed Pontederia cordata L. (Center, 1982; Hill et al., 2000; Stanley and Julien, unpub).

Post-release evaluations of natural enemies in countries of introduction can provide additional biosafety data and render further quarantine-based trials unnecessary. For example, field cage studies in Australia showed that the moth *X. infusellus* would harm pickerelweed (Julien, pers. comm.). It is therefore no longer being considered for release in the United States. On the other hand, the mirid *E. catarinensis* fed and developed on pickerelweed during quarantine trials in South Africa, but subsequent field trials in that country showed that it inflicted little damage to pickerelweed and didn't readily colonize isolated pickerelweed stands (Hill *et al.*, 2000).

Many of the plant-feeding insects associated with waterhyacinth in South America utilize other species of Pontederiaceae (Table 2). Therefore, decisions for their release must rely on a risk-benefit analysis between the importance of native Pontederiaceae and the potential benefits offered by the natural enemy.

Releases Made

Three insects, all originally from Argentina, have been released in the United States. The weevils *N. eichhorniae* and *N. bruchi* were released in Florida in 1972 and 1974, respectively, followed by the pyralid moth *N. albiguttalis* in 1977.

Other Agents That Have Been, or Now Are, Under Consideration

Three native North American species sometimes severely affect waterhyacinth populations, as well. These are the noctuid moth *B. densa*, the oribatid mite *O. terebrantis*, and the spider mite *Tetranychus tumidus* Banks.

The moth X. infusellus has been rejected for release in the United States because it is clearly a threat to pickerelweed (DeLoach et al., 1980; Julien and Stanley, 1999). Cordo's (unpublished report) conclusion that the arctiid Paracles tenuis Berg was polyphagous led to its rejection as well. Silveira Guido and Perkins (1975) and, later, Hill (unpub.) tested the grasshopper Cornops aquaticum (Bruner). Although Silveira Guido and Perkins (1975) considered it to be specific, concerns for pickerelweed precluded further consideration for release in the United States. The mirid E. catarinensis is still under consideration as the risk to pickerelweed seems minimal under field conditions (Hill et al., 2000), but information on its efficacy is needed for a proper risk-benefit analysis. Dolichopodid flies in the genus Thrypticus and planthoppers in the genera Megamelus and Taosa are now under consideration.

Species	Field and Laboratory Host Plants	Attributes, Limitations and Current Status of Research		
First Priority – Agents In Use Worldwide				
1. Neochetina eichhorniae Warner (Col.: Curculionidae)	E. crassipes	In use in North America, Australia, Africa and Asia (Julien and Griffiths, 1998)		
2. <i>Neochetina bruch</i> i Hustache (Col.: Curculionidae)	E. crassipes	lbid.		
 Niphograpta albiguttalis (Warren) (Lep.: Pyralidae) 	E. crassipes	lbid.		
 Orthogalumna terebrantis Wallwork (Acarina: Galumnidae) 	E. crassipes, E. azurea, Pontederia cordata, Reussia subovata	lbid.		
Second F	Priority – Candidates Recently Released Or U	nder Testing		
5. Eccritotarsus catarinensis (Carvalho) (Heter.: Miridae)	Field: <i>E. crassipes</i> , Lab.: <i>E. crassipes, E. natans, P. cordata,</i> Heteranthera, Monochoria	Heavy attack at Belem, Brazil (Bennett and Zwölfer, 1968);Tested in South Africa, liberated in 1996 and established (Hill et al., 1999, 2000)		
6. <i>Xubida</i> (<i>=Acigona</i>) <i>infusellus</i> (Walker) (Lep.: Pyralidae)	Field: <i>E. crassipes, E. azurea, P. cordata,</i> <i>P. rotundifolia</i>	Liberated in Australia September 1981; not established. Reimported in 1995 and liberated in 1996 (Julien and Griffiths, 1998)		
 Cornops aquaticum (Bruner) (Orth.: Acrididae, Leptysminae) 	Field: E. crassipes, E. azurea, P. cordata	Testing underway in quarantine in South Africa (Hill, unpubl. reports)		
8. <i>Bellura densa</i> (Walker) (Lep.: Noctuidae)	Field: P. cordata, E. crassipes, Colocasia esculenta	Testing underway in quarantine in South Africa. Release rejected as hazard to <i>Colocasia esculenta</i> (Hill, unpubl. reports)		
9. Paracles (=Palustra) tenuis (Berg) (Lep.: Arctiidae)	Field: <i>E.azurea, P. cordata, E. crassipes</i> Lab.: Various plants in different families	Polyphagous in laboratory testing. It developed readily on <i>P. rotundifolia</i> , <i>Alternanthera, Canna, Limnobium</i> , and <i>Sagittaria</i> . Rejected from consideration (Cordo, unpub. rpt.)		
10. <i>Thrypticus</i> spp Seven species- (Dip.: Dolichopodidae)	Field: <i>E. crassipes, E. azurea, P. cordata,</i> and <i>Pontederia subovata</i>	Under study at SABCL. Two species apparently monophagous on water hyacinth. Very promising (Cordo, unp. rep.)		
Third Priorit	y - Candidates Poorly Known Or Of Questiona	ble Specificity		
11. <i>Brachinus</i> sp. (Col.: Carabidae)	Field: <i>E. crassipes, E. azurea, P. cordata,</i> and perhaps others	Feeding on flowers (Silveira Guido, 1965). May be the same as the <i>Callida</i> sp. found in Argentina (Cordo, Hill, and Center, unpubl.)		
 Argyractis subornata Hampson (Lep.: Pyralidae) 	Field: <i>E. crassipes</i> and perhaps others. Lab: <i>E. crassipes</i> and <i>Pistia stratiotes</i> L.	Root feeder; life history and biology studied by Forno (1983)		
 Macocephala acuminata Dallas (Heter.: Pentatomidae) 	Field: E. crassipes and perhaps others	Root feeder; a pest of rice (Silveira Guido, 1965)		
14. <i>Taosa inexacta</i> Walker (Homoptera: Dictyopharidae)	Field: <i>E. crassipes, P. rotundifolia</i> and perhaps others.	Feeding weakens plants and hastens deterioration; moderate degree of specificity (Cruttwell, 1973)		
 Megamelus electrae Muir and Megamelus scutellaris Berg (Hom.: Delphacidae) 	Field: <i>E. crassipes, E. azurea, P. cordata</i> and perhaps others	Trinidad to Argentina. No visible damage caused to plants (Cruttwell, 1973). High levels of damage seen in Rio Janeiro, Brazil, in 1967 (Bennett, 1967). <i>M.</i> <i>scutellaris</i> under study in Argentina		

Table 2. Characterization of Major Arthropods Associated with Waterhyacinth.

Species	Field and Laboratory Host Plants	Attributes, Limitations and Current Status of Research	
Third Priority - Candidates Poorly Known Or Of Questionable Specificity			
16. <i>Eugaurax setigena</i> Sabrosky (Diptera: Chloropidae)	Field: <i>E. crassipes, E. paniculata</i> and perhaps others	Little known on food habits; <i>Eugaurax</i> <i>floridensis</i> Malloch reared from <i>Sagittaria</i> <i>falcata</i> Pursh. <i>Eugaurax quadrilineata</i> reared from eggplant (Sabrosky, 1974)	
17. <i>Chironomus falvipilus</i> Rempel (Diptera: Chironomidae)	Field: <i>E. crassipes</i> and perhaps others	In petioles of waterhyacinth in Surinam and Brazil. Undetermined chironomid from Uruguay (Silveira Guido, 1965)	
18. <i>Hydrellia</i> sp. (Dip.: Ephydridae)	Field: <i>E. crassipes, P. lanceolat</i> a and perhaps others	Common in Uruguay (Silveira Guido, 1965)	
19. <i>Flechtmannia eichhorniae</i> Keifer (Acarina: Eriophyidae)	Field: <i>E. crassipes</i> and perhaps others	Described for Brazil (Kiefer, 1979). Mentioned from Uruguay (Silveira Guido, 1965) as being a new species and genus; host specificity is promising	

Table 2. Characterization of Major Arthropods Associated with Waterhyacinth (continued).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Neochetina eichhorniae and *N. bruchi* (Coleoptera: Curculionidae)

Members of the genus *Neochetina* are semiaquatic weevils that feed only on species of Pontederiaceae. Center (1994) reviewed the biologies of *N. eichhorniae* and *N. bruchi*. Adults of the two species (Fig. 5) are distinguished by the color and pattern of the scales on the elytra (Warner, 1970; DeLoach, 1975; O'Brien, 1976). *Neochetina bruchi* is typically brown with a tan band across the elytra. *Neochetina eichhorniae* is usually mottled gray and brown. Both species have two parallel tubercles on the elytra on either side of the mid-line, which are short and situated near mid-length on *N. bruchi*, but are longer and further forward on *N. eichhorniae*.



Figure 5. *Neochetina bruchi* (right) and *N. eichhorniae* (left) adults. (Photograph courtesy of W. C. Durden, USDA, ARS.)

The whitish, ovoid eggs (0.75 mm in length) are embedded in plant tissue. Larvae are whitish with a yellow-orange head (Fig. 6). They have no legs or prolegs, only enlarged pedal lobes bearing apical setae. Larvae can be distinguished by the presence (*N. bruchi*) or absence (*N. eichhorniae*) of setal-bearing protuberences on these pedal lobes (Habeck and Lott, unpub. report). Neonate larvae are about 2 mm and fully-grown third instar larvae are 8 to 9 mm in length. Pupae are white and enclosed in a cocoon that is attached to a root below the water surface.



Figure 6. Late-stage *Neochetina* sp. larvae feed at the base of leaf petioles, often damaging subtending axillary buds. (Photograph courtesy of W. C. Durden, USDA, ARS.)

Neochetina eichhorniae deposits eggs singly, whereas N. bruchi often deposits several in the same site. Neochetina bruchi prefers leaves with inflated petioles, especially those at the periphery of the plant (DeLoach and Cordo, 1976a), whereas eggs of N. eichhorniae are found in intermediate-aged leaves (Center, 1987a). Eggs hatch in seven to 10 days at 24°C.

The first instar larva excavates a sub-epidermal burrow and tunnels downwards. There are three instars and late-instar larvae are generally found near the crown where they often damage axillary buds. The entire larval period requires 30 to 45 days with *N. bruchi* developing somewhat faster than *N. eichhorniae* (Center, 1994). The fully developed larva exits the plant and crawls to the upper root zone to pupate. The pupal stage requires about seven days, but teneral adults may remain in cocoons for extended periods.

Emerging adults climb onto emergent plant parts to feed and mate, often aggregating within a furled expanding leaf or beneath membranous ligules. Females lay their first eggs soon after emergence (DeLoach and Cordo, 1976a, b). As many as 300 to 400 eggs are produced cyclically over a life span of up to 300 days (Center, 1994).

Both species of *Neochetina* undergo flight muscle generation and degeneration (Buckingham and Passoa, 1985), possibly reflecting alternating dispersive and reproductive phases. Center and Dray (1992) theorized that plant quality and phenostage influenced the weevil's propensity to switch between phases, with *N. bruchi* being more sensitive to plant quality (see also Heard and Winterton, 2000) and more likely to disperse.

Adult feeding creates characteristic rectangular scars on the leaves, about 2 to 3 mm in width and of variable length, sometimes girdling the leaf petioles at the distal end and causing the blade to dessicate (see DeLoach and Cordo, 1983; Wright and Center, 1984; Center *et al.*, 1999a). Moderate to severe weevil infestations cause plants to be shorter with smaller leaves, fewer offsets and flowers, lower tissue nutrient content, and reduced overall vigor (Fig. 7) than uninfested or lightly infested plants (Center and Van, 1989).



Figure 7. Waterhyacinth plants stressed by weevils tend lose buoyancy and to be of small stature. (Photo courtesy of W. C. Durden, USDA, ARS.)

Eccritotarsus catarinensis (Heteroptera: Miridae)

Eccritotarsus catarinensis (Fig. 8) is a leaf-sucking bug (2 to 3 mm long). Eggs are inserted into the leaf tissue parallel to the surface and the four nymphal instars feed gregariously with the adults on the underside of the leaves, causing severe chlorosis. Development of the eggs and nymphs requires 23 days and adults live 50 days (Hill *et al.*, 1999).



Figure 8. An adult *Eccritotarsus catarinensis*. (Photo courtesy of John Stanley, CSIRO.)

Bennett and Zwölfer (1968) observed a mirid on waterhyacinth in Belém, Brazil, but the insect was never collected or named. A mirid later collected in Rio de Janeiro during 1989 was identified as *E. catarinensis*. It was imported to quarantine in South Africa in 1992 from Canavieras, Brazil (Hill *et al.*, 1999). More recently, it was found on the Kumaceba River in the upper reaches of the Amazon River, near Iquitos, Peru in 1999 (Cordo *et al.*, unpub.).

Host specificity of this mirid was determined in South Africa from tests using 67 species in 36 families. Some feeding and development occurred on three native African Pontederiaceae, (i.e., Eichhornia natans [P. Beauv.], Monochoria africana [Solms-Laubach], and Heteranthera callifolia Kunth.), but the risk to these plants was deemed minimal and the insect was released in 1997 (Hill et al., 1999, 2000). This insect was later imported to Australia, where additional host specificity testing was done. However, the potential for damage to native Australian Monochoria species precluded its use (Stanley and Julien, 1999). Some Monochoria species are serious weeds of rice paddies and not considered to have conservation value in Asia. As a result, E. catarinensis has been released in China (Ding et al., 2001) and imported into Thailand for pre-release evaluation (A. Winotai, pers. comm.).

This mirid is being considered for release in the United States. However, host specificity trials in both South Africa and Australia demonstrated feeding and development on pickerelweed (Hill *et al.*, 1999; Stanley and Julien, 1999). Pickerelweed, being an introduced plant in both of these countries, played no role in the decision to release this insect. But pickerelweed is native to North America, so any threat to it would be unacceptable in the United States. Several studies are therefore being undertaken in South Africa to quantify the impact of *E. catarinensis* on pickerelweed under field conditions.

Eccritotarsus catarinensis is now established in South Africa (Hill and Cilliers, 1999) and its effects are being monitored. Although the impact of this insect on waterhyacinth performance has not yet been quantified, it does reach very high densities in tropical areas of the country where it is capable of causing severe die back of the plants (Fig. 9). It also has been released in Benin, Zambia, and Malawi, and cultures have been sent to Zimbabwe, Thailand, and China.



Figure 9. A waterhyacinth mat in South Africa in decline due to infestation by *E. catarinensis.* (Photo courtesy of C. Cilliers, PPRI.)

Niphograpta albiguttalis (Lepidoptera: Pyralidae)

The small (ca. 0.3 mm), spherical, and creamy-white eggs of *N. albiguttalis* take three to four days to hatch at 25°C. The newly emerged larva (1.5 mm in length) is brown with darker spots and has a dark brown head (Fig. 10). There are five larval instars, the last of which grows to about 2 cm long, with a dark orange head and a cream-colored body covered with conspicuous dark brown spots. Larval development requires about two weeks. The fully-grown larva excavates a cavity in a healthy leaf petiole, in which it forms its cocoon. Pupation occurs in the cocoon and the pupal stage lasts seven to 10 days. The emerging adult moth exits the petiole through a silken tunnel prepared by the larvae before pupation.



Figure 10. *Niphograpta albiguttalis* larva. (Photo courtesy of W. C. Durden, USDA, ARS.)

Adults (Fig. 11) live about seven to 10 days. Mating occurs shortly after emergence from the pupa and the female lays the majority of her eggs the following night. An average female will deposit 450 to 600 eggs. The entire life cycle requires three to four weeks. Center *et al.* (1982a) provide further information on the biology and identification of this species.



Figure 11. An adult male *Niphograpta albiguttalis*. (Photo courtesy of W. C. Durden, USDA, ARS.)

Orthogalumna terebrantis (Acarina: Galumnidae)

The waterhyacinth mite, *O. terebrantis* (Fig. 12), like other mites, has piercing mouthparts with which it sucks plant juices. Its host plants include pickerelweed and waterhyacinth (Gordon and Coulson, 1969).



Figure 12. The waterhyacinth mite *Orthogalumna terebrantis*. (Photo courtesy of W. C. Durden, USDA, ARS.)

Cordo and DeLoach (1975, 1976) described the biology and life history of *O. terebrantis*. Adults are shiny black, about 0.5 mm long and narrowed anteriorly. Females lay their eggs in small round holes chewed in the leaves. Eggs hatch in seven to eight days (at 25°C) and produce small (less than 0.24 mm), whitish, slow-moving larvae. Complete development requires about 15 days (at 25°C).

Feeding damage is restricted to the leaf blades. Larval feeding causes small reddish spots on the leaf surface and the nymphs produce galleries that extend about 6 mm towards the apex. The adults emerge through round exit holes at the end of the gallery.

Large mite populations produce up to 2,500 galleries on a single leaf, which desiccate the blade (Gordon and Coulson, 1969). Severe damage is usually localized or confined to a few plants but, when combined with other stresses, it can contribute to declines (Delfosse, 1978).

Xubida infusellus (Lepidoptera: Pyralidae)

Silveira Guido (1965, 1971) considered the pyralid *X. infusellus* (Fig. 13) to be one of the most important phytophagous species on waterhyacinth in South America. Larvae (Fig. 14) severely damage leaf petioles and can destroy shoots by feeding on apical meristems and burrowing into rhizomes. Although damage is similar to that of *N. albiguttalis* or *B. densa*, it was thought that the introduction of *X. infusellus* might complement the effects of *N. albiguttalis* (Bennett and Zwölfer, 1968; DeLoach *et al.*, 1980). *Xubia infusellus* prefers advanced phenostage plants with elongate leaf petioles (see Center *et al.*, 1999a), whereas *N. albiguttalis* prefers younger plants with inflated leaf petioles. Sands and Kassulke (1983) describe the adults in detail.

Silveira Guido (1965, 1971), DeLoach *et al.* (1980), and Sands and Kassulke (1983) provide notes on the life history of *X. infusellus*. The nocturnal females lay egg masses in crevices such as the folds of leaves or the overlapping edges of furled leaves. Females lay indiscriminantly, sometimes on plants not used as larval hosts or, in the laboratory, on cage materials. Numbers of eggs per egg mass vary from a few to several hundred. Eggs hatch in six to seven days at 26° C.



Figure 13. An adult of *Xubida infusella*. (Photo courtesy of John Stanley, CSIRO)



Figure 14. *Xubida infusella* larva. (Photo courtesy of M. P. Hill, PPRI)

First instar larvae briefly feed externally, sometimes girdling a petiole before entering it, but then feed internally. They burrow downward, sometimes transferring to adjacent leaves, until they eventually encounter the rhizome. The number of larval instars varies from seven to ten, and development requires about 48 days (Sands and Kassulke, 1983). Larvae become about 25 mm long when fully grown (DeLoach et al., 1980). Late instar larvae form large burrows, causing extensive damage. Larvae cut emergence holes in the petiole prior to pupation that they close with silk, and then pupate just below the covered opening. The pupal stage lasts about nine days and total developmental requires 64 days at 26°C (Sands and Kassulke, 1983). The adult lives four to eight days (Silveira Guido, 1965, 1971; Sands and Kassulke, 1983).

This insect has established in Australia (Julien and Griffiths, 1998). It also was released in Papua New Guinea (Julien and Stanley, 1999). A decision was made not to release it in the United States due to the threat to pickerelweed.

Thrypticus spp. (Diptera: Dolichopodidae)

Thrypticus species (Fig. 15) are all phytophagous stem miners of monocots in the Cyperaceae, Graminiaceae, and Juncacaeae. Females possess a characteristic sclerotized, blade-like structure used to pierce stems in preparation for oviposition. These tiny flies are generally found in wet grassland or marsh habitats (Bickel, 1986). The genus is nearly cosmopolitan, with 71 known species and a broad radiation in the neotropics (Bickel, 1986). Bennett and Zwölfer (1968) found Thrypticus species associated with waterhyacinth in Trinidad, Guyana, Surinam, and Brazil, but Bennett (1972) failed to note its presence in Belize, Jamaica, Barbados, or St. Vincent. Mitchell and Thomas (1972) found members of the genus in Argentina, Uruguay, Brazil, Guyana, and Trinidad. The species found by Bennett and Zwölfer (1968) in northern South America was later identified as Thrypticus insularis Van Duzee (Bennett, 1976) and still later synonomized with Thrypticus minutus Parent (Dyte, 1993). However, this specific epithet was rarely referred to in later literature and the insect continued to be known as Thrypticus sp. Dr. Christian Thompson of the U.S. National Museum concluded that several Thrypticus species collected in Argentina probably represented undescribed species.



Figure 15. *Thrypticus* sp. adult reared from waterhyacinth. (Photo courtesy of C. A. Bennett, University of Florida.)

Cruttwell (1973) described the life history of a *Thrypticus* sp. from waterhyacinth in Trinidad. The adults are 1.5 to 2 mm long and light brown in color. Females lay eggs singly in young petioles of *E. crassipes*, inserting eggs into the tissues, usually just above the water line. Eggs are yellow, 0.5 mm long

and 0.17 mm in diameter, curved, with one end narrower than the other. Petioles are suitable for oviposition only when recently separated from the sheath; thus all galleries in an individual petiole are of similar age. Eggs hatch in a few days and the larvae tunnel horizontally, making a second exit hole at the other end of the gallery. Larvae continue to feed in galleries, which they enlarge and lengthen. There are three instars and the larval stage lasts 35 to 42 days. Mature larvae are about 4 mm long. They prepare an emergence window in the petiole before pupating in an enlarged chamber below the exit hole. Adults emerge in seven to 12 days and lay up to 50 eggs.

When petioles have large numbers of larval galleries, damage can be extensive (Fig. 16). Mitchell and Thomas (1972) noted that nearly all plants attacked at Santos, Brazil, showed extensive rotting of petioles bases and, in many cases, had completely collapsed.



Figure 16. Damage to a waterhyacinth leaf petiole caused by larvae of *Thrypticus* sp. (Photo courtesy of H. A. Cordo, USDA, ARS.)

Larvae do not leave their galleries; so ovipositing females select the larval host plant. Cruttwell (1973) exposed rice, yam, and sweet potato plants to *Thrypticus* sp. in tanks that also contained waterhyacinth. She noticed that adults regularly rested on waterhyacinth but never on the test plants. Also, galleries never appeared on the test plants even though the waterhyacinth exhibited galleries after eight to 11 days.

Thrypticus were found attacking *E. crassipes*, *E. azurea*, *P. cordata*, and *Pontederia rotundifolia* L. in northern Argentina (H. Cordo, unpub.). Comparisons of genitalia and larval mining patterns of insects from various Pontederiaceae suggested that several distinct species were represented, some of which seemed restricted to waterhyacinth.

The effects of the mining damage caused by *Thrypticus* species on waterhyacinth performance have not been measured. However, the strict monophagy, ubiquity, and abundance of these species make them promising as biological control agents. The tiny, but often abundant, tunnels produced by the larvae of these species have been judged trivial by some authors, but the damage may enhance the stress produced by other agents. The apparent high degree of specialization of *Thrypticus* species among species of Pontederiaceae suggests that they are host specific and augurs well for their potential use in biological control.

Cornops aquaticum (Orthoptera: Acrididae)

Perkins (1974) considered the grasshopper *C. aquaticum* to be among the most damaging of the South American insects associated with waterhyacinth (Fig. 17). Despite heavy egg predation by the weevil *Ludovix fasciatus* (Gyllenhal), *C. aquaticum* is abundant and very damaging. Its broad distribution from Argentina through Mexico indicates that it can tolerate a wide range of climatic conditions. However, concern over its host specificity has precluded consideration for release in the United States.



Figure 17. The waterhyacinth grasshopper *Cornops aquaticum* feeds on leaves producing a characteristic "tattered" appearance. (Photo courtesy of H. Oberholzer, PPRI.)

Females lay groups of 30 to 70 eggs enclosed in egg cases that are inserted into the youngest leaf petiole on a plant (Silveira Guido and Perkins, 1975). Eggs hatch in 25 to 30 days, producing green-and-redstriped nymphs (Fig. 18). There are six or seven nymphal instars and development requires about 50 days. Nymphs are highly mobile and very damaging. The dark green adults copulate soon after emergence, and produce up to eight egg cases 25 to 30 days later. Adults live up to 110 days, are mobile, strong fliers, and are extremely damaging to the plant (Fig. 19).



Figure 18. *Cornops aquaticum* nymph. (Photo courtesy of S. Neser, PPRI.)



Figure 19. *Cornops aquaticum* adult. (Photo courtesy of S. Neser, PPRI.)

Cornops aquaticum feeds and develops on waterhyacinth, E. azurea, P. cordata, and Commelina sp. under laboratory conditions (Silveira Guido and Perkins, 1975). We observed C. aquaticum on E. azurea, P. cordata, P. rotundifolia and Pontederia subovata (Seub. in Markt.) Lowden, in addition to waterhyacinth (H. Cordo et al., unpub.) during field surveys in northern Argentina (1997) and the upper Amazon River in Peru (1999). This oligophagous species is clearly not suitable for release in the United States. Despite these results, *C. aquaticum* is under study in South Africa where its oligophagy, including development on *P. cordata* and *Canna indica* L. (Cannaceae), has been confirmed. Further large-scale, multi-choice trails will quantify the threat of *C. aquaticum* to African Pontederiaceae.

Cercospora spp. (Hyphomycetes)

Cercospora piaropi and *Cercospora rodmanii* Conway cause dark brown leaf spots on waterhyacinth that can lead to necrosis of older leaves and petioles. Characters used to separate these two species are variable, so these fungi may represent a single species (Morris, 1990). *Cercospora piaropi*, described in 1917 from Texas, was apparently introduced into the United States with the plant (Tharp, 1917). Extensive research has been conducted on the use of this species as a natural enemy of waterhyacinth (Freeman and Charudattan, 1984). Charudattan *et al.* (1985) investigated application techniques for *C. rodmanii* and concluded that this pathogen was unlikely to control the plant with a single application.

In 1986, Cercospora piaropi was found in South Africa associated with the decline of a waterhyacinth mat at a reservoir in the eastern province of Mpumulanga (Morris, 1990; Morris et al., 1999). It is now established throughout South Africa as the result of transplanting infected plants. Cercospora rodmanii was introduced to South Africa from Florida in 1988. Although these pathogens now occur widely in the western Cape province, there has been no resultant decline in weed populations.

Other Species

There are a number of other species about which little is known but which may have potential as control agents. They include the following:

(1) Bellura densa (Walker) (Lepidoptera: Noctuidae) is a native North American moth (Fig. 20). The natural host is pickerelweed, but it commonly feeds and develops on waterhyacinth and taro (Colocasia esculenta Schott) (Center and Hill, 1999). Parasitoids, predators, and diseases limit its abundance in the United States (Center, 1976; Baer and Quimby, 1982).

Females lay about 300 eggs, in masses of up to 40 eggs each, on host leaves. Egg masses are covered with cream-colored scales. A scelionid parasitoid (*Telenomus arzamae* Riley) kills most of the outer eggs in the masses, but the innermost eggs survive.



Figure 20. *Bellura densa* adult. (Photo courtesy of W. C. Durden, USDA, ARS.)

Eggs hatch in six days and larval development requires five weeks. Larvae pupate in petioles and produce naked, reddish brown pupae. The pupal stage lasts 10 days, with complete development requiring about 50 days.

The damage caused by *B. densa* is similar to that by *N. albiguttalis*, but more severe. Older caterpillars extensively excavate petioles and burrow deep within the rhizomes, fragmenting the stems and killing the shoots. This species is the most damaging of the insects that feed on waterhyacinth (Fig. 21). Vogel and Oliver (1969a, b) and Center (1976) provide further information on the biology of *B. densa* and its effects on waterhyacinth.



Figure 21. Larva of the moth *Bellura densa*. (Photo courtesy of S. Neser, PPRI.)

(2) Brachinus larvae and adults (Coleoptera: Carabidae) feed on the flowers of *E. crassipes*, *E. azurea*, and *P. cordata*. Larvae feed in the ovaries and pupate inside the peduncle. Two other carabids commonly found in collections from waterhyacinth are *Pionicha tristis* Gory and *Alachnothorax bruchi* Libke. The taxonomy, feeding habits, and plant associations of these insects are in need of clarification. They could have value as flower feeders, a part of waterhyacinth otherwise free from attack. (3) *Chalepides* species (Coleoptera: Scarabaeidae) are sometimes found tunneling in the crowns of *E. crassipes*, *E. azurea* and *Pistia stratiotes* (Fig. 22). However, larvae, which are believed to feed on the roots of grasses, have never been associated with the Pontederiaceae.



Figure 22. The scarab *Chalepides* sp. (Photo courtesy of S. Neser, PPRI.)

(4) *Hydrellia* sp. (Diptera: Ephydridae) mines the leaf blades of young waterhyacinth before descending into the bulbous petioles. It can be quite damaging, but is usually not abundant.

(5) *Taosa inexacta* Walker (Homoptera: Dictyopharidae) weakens plants and hastens their deterioration under laboratory conditions. Preliminary feeding tests suggest that it is specific to the Pontederiaceae (Cruttwell, 1973). The injury caused by this planthopper (Fig. 23) is similar to that from *Megamelus* species and can be devastating to waterhyacinth populations (De Quattro, 2000). The *Taosa* species found on different species of Pontederiaceae probably include three or more undescribed species, some of which may be waterhyacinth specialists.

(6) Megamelus electrae Muir (Heteroptera: Delphacidae) was once considered for waterhyacinth biological control (Cruttwell, 1973), but investigations were never completed. There are no host records for the other four neotropical species. We found several delphacids associated with waterhyacinth and its relatives, in both Argentina and the upper Amazon Basin, including several



Figure 23. Waterhyacinth extensively damaged by the planthopper Taosa inexacta. (Photo courtesy of H. A. Cordo, USDA, ARS.) Megamelus species. One species, Megamelus scutellaris Berg (Fig. 24), seems restricted to E. crassipes. Host plant associations were observed in the field and host specificity has been tested in Argentina (H. Cordo, unpub.). Specimens of *M. scutellaris* were field-collected only on *E. crassipes*. When the insects were allowed to move freely among several pools containing cultures of different Pontederiaceae, one Megamelus sp. developed on several species of Pontederiaceae. In contrast, M. scutellaris developed only on waterhyacinth and did not attack pickerelweed varieties from Argentina, the United States, or South Africa. High densities of *M. scutellaris* are uncommon in the field, where parasitoids and predators are abundant. When protected from natural enemies, M. scutellaris produces large populations and thus seems a promising biological control candidate.

(7) Paracles (=Palustra, in part) species, including *P. tenuis* (Lep.: Arctiidae) (Fig. 25) are associated with waterhyacinth and related aquatic plants. Silveira-Guido (1965) first suggested that some of these species might be useful for waterhyacinth control. Mitchell and Thomas (1972) found adults, but not larvae and little evidence of larval damage, associated with waterhyacinth in Uruguay. Perkins (1974) noted their importance as defoliators of waterhyacinth in South America, but that they also fed on other aquatic plants. Its polyphagy was confirmed in the mid-1990s (H. Cordo, unpub.).



Figure 24. The planthopper *Megamelus* sp. (Photo courtesy of C. A. Bennett, University of Florida.)



Figure 25. Larva of the arctiid moth *Paracles tenuis.* (Photo courtesy of H. A. Cordo, USDA, ARS.)

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Neochetina eichhorniae was released in southern Florida in 1972, using eggs from 2,479 adults sent from Argentina during August 1972 to March 1973. Adults removed from founder colonies were then redistributed by numerous agencies. As a result, *N. eichhorniae* was released at 199 sites in Florida, 492 sites in Louisiana, one site in Texas, and four sites in California (Manning, 1979; Cofrancesco, 1984, 1985). This intensive effort seemed necessary because of the belief that this species didn't fly. However, *N. eichhorniae* was already present when initial releases were made in Texas, having apparently dispersed from southern Louisiana, and by 1984 it was at several waterhyacinth infestations between Port Arthur and Corpus Christi (Cofrancesco, 1984; Stewart, 1987). Large numbers of weevils, many actively flying, were observed at lights in southern Louisiana during 1980 (Center, 1982), clearly indicating a capacity to disperse.

When *N. bruchi* became available, there was no similar dissemination campaign. As a result, it was released at only 40 sites: 21 in Florida, 10 in Louisiana, five in Texas, and four in California (Manning, 1979; Stewart, 1985, 1987). Despite this disparity in release efforts, both species are now ubiquitous in Florida (Center and Dray, 1992; Center *et al.*, 1999a), but the status of *N. bruchi* elsewhere is unclear.

Niphograpta albiguttalis was initially released only in southern Florida, but populations dispersed more than 500 km within 18 months (Center, 1984). This moth was released at two sites in Louisiana during May 1979 and collected 27 km from the nearest release site a year later (Brou, undated). Niphograpta albiguttalis appeared to be absent from Texas in 1985, and so was released at a few sites during May 1986. It was widely dispersed by July 1986 (Stewart, 1987), probably originating from Louisiana, rather than the more recent Texas releases. DeLoach and Center (unpub.) found N. albiguttalis in Mexico near Veracruz and near Tapachula, the latter being on the Pacific coast near the border with Guatamala. This insect was never released in Mexico (Julien and Griffiths, 1998). So it is likely that these populations derived from ones in the United States, with the nearest release site being about 1,600 km away. Likewise, although there are no recorded releases of N. albiguttalis in Puerto Rico (Julien and Griffiths, 1998), larvae were collected near San Juan in 1995 (specimen records, Malaria Canal, 18 April, 1995, collector T. D. Center; Lago Loiza, 19 April, 1995, collector T. D. Center). Labrada (1996) reported its presence in Cuba, too, so perhaps N. albiguttalis "island hopped" from Florida to the West Indies.

Suppression of Target Weed

Numerous field studies document the decline of waterhyacinth in diverse geographical areas of the United States after introductions of biological control agents (i.e., Goyer and Stark, 1981, 1984;

Cofrancesco, 1985; Cofrancesco et al., 1985; Center and Durden, 1986; Center, 1987b). Waterhyacinth now occupies one-third of its former acreage in the Gulf Coast states (Cofrancesco et al., 1985; Center et al., 1990) (Fig. 26). This reduction resulted from both direct plant mortality and reduced regrowth after winter diebacks, perhaps along with reduced flowering and seed production (Center et al., 1999a, b). Feeding by insects destroys meristematic tissue causing the plants to lose their ability to replace senescent tissue. They then lose bouyancy and sink. Often, they merely stop growing as the destruction of axillary buds and reduced carbohydrate reserves prevents clonal expansion. In recent experiments, for example, plots with weevils doubled or tripled in coverage, whereas uninoculated controls expanded nearly six-fold during the growing season (Center et al., 1999b). Hence, control stems from growth suppression, reduction of the seed bank, and destruction of existing plants.

The most recent and most spectacular effects of the waterhyacinth weevils have occurred at Lake Victoria in East Africa (Fig. 27). Waterhyacinth was first recorded on the lake in 1980 and by the mid-1990s some 12,000 ha of the weed were clogging bays and inlets. Uganda made the first introductions of N. eichhorniae and N. bruchi in 1995, followed by Kenya and Tanzania in 1997 (Anon., 2000). A significant reduction in the extent of the weed on the Ugandan shore was evident by November 1998, with many of the mats having sunk. These results were later repeated on the Kenyan and Tanzanian shores. An estimated 75% of the mats on the Kenyan side had sunk by December 1999 (Anon., 2000). The spectacular results of the biological control program on Lake Victoria using the two weevil species are the same as those achieved on Lake Kyoga (Uganda) (Ogwang and Molo, 1999) and on the lagoons of the Sepik River (Papua New Guinea) (Julien and Orapa, 1999). Similar results have been obtained in Sinaloa, Mexico where the release of N. eichhorniae and N. bruchi during 1995 to 1996 reduced 3,041 ha of waterhyacinth distributed over seven impoundments by 62% (to 1,180 ha) by 1998 (Aguilar, pers. comm.). These successes reaffirm earlier reports from Australia (Wright, 1979, 1981), Argentina (DeLoach and Cordo, 1983), India (Jayanth, 1987, 1988), and the Sudan (Girling, 1983; Beshir and Bennett, 1985).

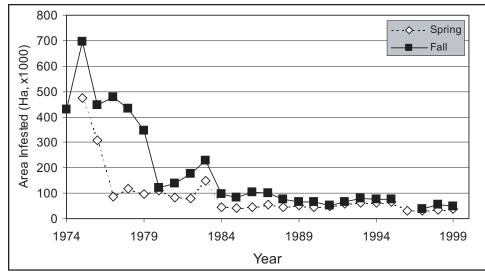


Figure 26. Data from Louisiana showing reduced waterhyacinth acreage and limited annual growth after introduction of *Neochetina eichhorniae* in 1974, *N. bruchi* in 1975, and *Niphograpta albiguttalis* in 1979.



Figure 27A.



Figure 27C.



Figure 27B.





Figure 27. *Neochetina* spp. were released at Lake Victoria in Uganda during 1996 and Kenya during 1997. These "before" and "after" photographs of waterhyacinth infestations show the effects of biological control. A. Kisumu Yacht Club, Kenya, 6 June 1999 (Photo courtesy of M. H. Julien); B. Kisumu Yacht Club, Kenya, 16 December 1999 (Photo courtesy of M. H. Julien) ; C. Port Bell, Uganda, 1 June 1997 (Photo courtesy of K.L.S. Harley); D. Port Bell, Uganda, 11 December 1999 (Photo courtesy of M. H. Julien).

Factors that Accelerate Success and Factors that Limit Control

Factors associated with successful control include presence of the infestation in tropical and subtropical areas; infestations manifested as monocultures in free-floating mats that are able to sink when damaged; and mats that are stable (i.e., undisturbed) over long periods of time. Factors that might accelerate control include wave action, reduced growth (due to the action of biological control agents), and high nutrient levels (since high quality plants enhance insect population growth). Factors that limit control include removal of mats by herbicidal or mechanical means (thus disrupting agent populations), shallow water (damaged plants being unable to sink), ephemeral water bodies, toxicity effects in polluted waters, low temperatures at high-altitude or temperate sites, high nutrients at temperate sites, and limited releases (small, inoculative releases as opposed to mass releases or serial releases) (Julien, 2001; Hill and Olckers, 2001).

RECOMMENDATIONS FOR FUTURE WORK

Future Needs for Importation or Evaluation

Surveys done by Center et al. (1999a) confirmed that waterhyacinth populations not subjected to repeated control operations become stressed by biological control agents, particularly the two Neochetina species. On the other hand, water bodies subjected to continual herbicidal control actions generally have small weevil populations, due to instability of the weevil's food supply. Such sites produce healthier plants due to the reduced level of herbivore damage. The stressed plants typical of many unmanaged sites tend to be of lower nutritional quality than those at managed sites. The breeding condition of the female weevils correlates with host nutritional quality, so routine maintenance probably enhances the potential development of weevil populations by keeping host quality high, even though the actual populations are small. This suggests numerous possibilities for integrated approaches designed to overcome interference between the two control methods. However, the present maintenance program is considered to be effective, efficient, and affordable. In contrast, an integrated program involving management of populations of biological control agents in concert with herbicide application would probably be more expensive, difficult to implement, and possibly less reliable. Hence, the present system is unlikely to change. Therefore, new agents are needed to improve upon the level of biological control now realized. In particular, more mobile agents, with short life cycles and high reproductive capacities, are needed that can survive non-cyclical disruptions of waterhyacinth communities induced by herbicide applications. Currently, the candidates that best meet these criteria include the doliochopodid fly *Thrypticus* sp., planthoppers in the genera *Taosa* and *Megamelus*, and possibly the mirid *E. catarinensis*.

Plans for Future Work

Further work on the biological control of waterhyacinth is needed in five areas. First, available species should be fully evaluated. Second, additional natural enemies should be sought for use where existing control is less than desired. Third, more active approaches to biological control (e.g., mass or supplemental releases, serial releases) should be examined. Fourth, better methods to integrate biological control with other control options must be evaluated. Finally, the factors that accelerate success or limit control need further delineation.

Despite a fairly long history of biological control of waterhyacinth in the world, and the number of successful programs now reported, much additional research is needed. As new agents are released there will be a need to quantify their impacts. In addition, some available agents have not been fully evaluated. Lack of a quantitative evaluation of *O. terebrantis*, for example, has resulted in it possibly being underrated as a control agent despite its significant effect on waterhyacinth on the Shire River in Malawi (Hill, unpublished data).

A recent survey of the upper Amazon basin near Iquitos, Peru, identified several new candidate agents. The synergy observed between the insect damage and plant pathogens mandates further study. This brief trip was restricted to a small portion of the upper Amazon between Iquitos and Nauta. We do not consider this fruitful area to be fully explored and encourage further exploration. Surveys in other areas, such as the Pantanal region of Brazil and the Orinoco River system in Venezuela, also should be considered. Other insects that have been mentioned by explorers, for which basic information is not available, should be investigated to determine their field host plant ranges as a first step to assessing their potential for use in biological control efforts. These include the petiole-mining flies *Eugaurax setigena* Sabrosky (Diptera: Chloropidae), *Hydrellia* sp. (Diptera: Ephydridae), and *Chironomus falvipilus* Rempel (Diptera: Chironomidae); the flower-feeding carabid *Calleida* (= Brachinus); and the eriophyd mite *Flechtmannia eichhorniae* Keifer.

The variable results given by biological control efforts against waterhyacinth in different areas have been ascribed to a lack of climate matching between the region of origin and the region of introduction (Hill and Cilliers, 1999). Investigations into the cold tolerances of the agents are required to determine their suitability for use in temperate areas.

The biological control of waterhyacinth is perceived by water authorities to happen too slowly. Therefore, there have been a number of attempts to integrate biological control with other, quicker control options (herbicide application and mechanical control) (Delfosse *et al.*, 1976; Center *et al.*, 1982b, 1999a; Jones and Cilliers, 1999). The integration of two or more control options requires them to be compatible or, at least, not antagonistic. Further studies are needed to identify herbicides and adjuvants that are not toxic to the agents (e.g., Ueckermann and Hill, in press) and to determine more compatible methods of herbicide application.

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5 WATERLETTUCE

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PEST STATUS OF WEED

Waterlettuce, Pistia stratiotes L., (Fig. 1) is a floating, herbaceous hydrophyte first recorded from Florida during the 18th century (Stuckey and Les, 1984). It forms extensive mats (Fig. 2) capable of blocking navigational channels, impeding water flow in irrigation and flood control canals, and disrupting submersed animal and plant communities (Sculthorpe, 1967; Attionu, 1976; Bruner, 1982; Sharma, 1984). Waterlettuce is among the world's worst weeds (Holm et al., 1977). It has been placed on prohibited plant lists in Florida (FDEP, 2000), Louisiana (LDWF, 2000), Mississippi (MDAC, 1997), and Texas (TPWD, 2000), and is considered a noxious species (an invasive species of concern, but not regulated) in South Carolina (SCDNR, 2000) and Delaware (DDFW, 2000).



Figure 1. The waterlettuce, *Pistia stratiotes* L. (Photograph courtesy of USDA, ARS Invasive Plant Research Laboratory.)



Figure 2. A severe waterlettuce (*Pistia stratiotes* L.) infestation on Lake Okeechobee in southern Florida. (Photograph courtesy of USDA, ARS Invasive Plant Research Laboratory.)

Nature of Damage

Economic damage. Waterlettuce is a serious weed of rice crops in other countries (Suasa-Ard, 1976), but has not been reported as interfering with production in the United States. It also can interfere with hydroelectric operations (Napompeth, 1990), but has not done so in the United States. Consequently, direct losses attributable to waterlettuce result primarily from restricted water flow in irrigation and flood control canals in Florida. Unfortunately, the economic costs associated with such damage have not been quantified, but federal and state waterlettuce control operations in Florida cost nearly \$650,000 annually (Center, 1994). Other states treat intermittently as nuisance populations arise, but seldom more than a few hundred acres each year. Estimates of expenditures by local agencies and private agricultural interests are unavailable.

Indirect losses accrue when large floating mats interfere with recreational activities such as boating and fishing, but these have not been quantified. Also, several species of mosquitoes that breed on waterlettuce are important vectors of malaria, encephalitis, and filariae (Dunn, 1934; Bennett, 1975; Lounibos and Dewald, 1989; Lounibos *et al.*, 1990). Outbreaks of St. Louis encephalitis are generally rare; there were 223 reported cases with 13 deaths in Florida in 1990 and nine cases (one death) in 1997 (FDOH, 2000a). Equine encephalitis, also vectored by mosquitoes associated with waterlettuce, affects about 50 horses in Florida each year as well (FDOH, 2000b). Costs associated with these diseases are unknown, and the portion of mosquito control operations directed toward waterlettuce-borne mosquitoes has not been reported.

Ecological damage. There are few reports of deleterious ecological impacts associated with P. stratiotes infestations and these studies have generally been limited in scope. Sculthorpe (1967), for instance, noted that the intertwined root systems (composed of long adventitious roots arrayed with copious lateral rootlets) of extensive infestations accelerate siltation rates as they slow water velocities in rivers and streams (see also Anonymous, 1971). The resultant degradation of benthic substrates under these infestations has never been studied directly, but accelerated siltation often renders the affected benthos unsuitable as nesting sites for various fish species (Beumer, 1980) and as macroinvertebrate habitat (Roback, 1974). The accumulation of waterlettuce-generated detritus under large infestations only adds to this problem, and likely increases sediment and nutrient loadings much as it does under waterhyacinth mats (Schmitz et al., 1993). Furthermore, Sridhar (1986) reports that waterlettuce can bioaccumulate considerable amounts of heavy metals, so the detritus under some mats could be toxic.

The waters under dense waterlettuce populations in lakes can become thermally stratified (Sculthorpe, 1967; Attionu, 1976), with reduced dissolved oxygen levels and increased alkalinity (Yount, 1963; Attionu, 1976; Sridhar and Sharma, 1985). Prolonged oxygen deficits reduce plankton abundance (Hutchinson, 1975), and cause increased mortality of fish (Ayles and Barica, 1977; Clady, 1977) and macroinvertebrates (Roback, 1974; Cole, 1979). Although these effects likely occur in waterlettucedominated systems, they have not been investigated. Finally, Sharma (1984) reported that the evapotranspiration rate over a waterlettuce mat in one African lake was ten-fold greater than the evaporation rate over open water (but see the discussion on this topic and common misconceptions in Allen et al., 1997). However, the implications of this finding for hydrologic cycles in U.S. waterways has not been determined.

Extent of losses. In Florida, waterlettuce infests about 2,500 acres of public waterways (after control operations), and a large, but uncounted number of acres of irrigation and flood control canals (Schardt, 1992). Based on the annual costs associated with controlling waterlettuce on at least 10,000 acres of public waterways (Schardt, 1992; Center, 1994), it is reasonable to estimate that total expenditures exceed \$1 million annually in Florida. Other states in the eastern United States spend a combined total of less than \$100,000/yr on waterlettuce control.

Geographical Distribution

Paleobotanical evidence suggests that prior to the Pleistocene the genus Pistia extended well beyond its present range into what is now temperate Asia, Europe, and North America (Dorofeev, 1955, 1958, 1963; Friis, 1985; Mai and Walther, 1983; Stuckey and Les, 1984; Stoddard, 1989). Today, waterlettuce is primarily pan-tropical (Sculthorpe, 1967; Holm et al., 1977), although it also occurs in the Netherlands where it dies back in winter and then reinfests from seeds each spring (Pieterse et al., 1981). This habit could permit populations to persist in states with cold temperate climates. Populations have been recorded from as far north as the Erie Canal in upstate New York and Lake Erie in northern Ohio (Mike Weimer, US Fish and Wildlife Service, Buffalo, New York, and Doug Wilcox, US Geological Survey, Great Lakes Science Center, Ann Arbor, Michigan, pers. comm.).

Subtropical Florida harbors the most abundant waterlettuce populations in the eastern United States (Fig. 3). Other principal infestations occur in the warm temperate regions of the Gulf Coast states (Godfrey and Wooten, 1979), with the exception of Alabama (Kartesz, 1999). Scattered ephemeral populations - those that occur outside the naturalized range of waterlettuce and are of relatively recent origin, but which have been present for several years have been recorded from Virginia, North Carolina, South Carolina, Mississippi, and northern Louisiana (USGS 2001). Some of these populations may persist over winter in the form of seeds, but others are likely being re-introduced each year. A few occasionally achieve nuisance proportions. Waterlettuce also occurs in California, Arizona, Puerto Rico, the Virgin Islands, and Hawaii (Degener, 1938; Kartesz, 1999;



Figure 3. The distribution of waterlettuce, *Pistia stratiotes* L., in drainage basins (USGS Hydrologic Unit 8) in the United States (data from USGS, 2001).

USGS, 2001), but we have been unable to confirm reports (Kartesz, 1999) of isolated occurrences in Georgia, Maryland, and New Jersey.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Waterlettuce is a perennial herb in the aroid family (Araceae). The plant consists of free-floating rosettes of many leaves. The rosettes occur singly or connected by short stolons. Leaves are gray-green, densely pubescent, and wedge shaped (obovate-cuneate). They have conspicuous parallel veins, frequently have thick spongy parenchymous tissue at the base, and vary from being slightly broader (at apex) than long to much longer than broad. Leaves range from 2 to 35 cm long. Roots are numerous and feathery. The inflorescences are inconspicuous pale-green spathes near the center of the rosette. Each spathe is constricted near the middle, with a whorl of

male flowers above and a single female flower below the constriction. Fruits are many-seeded green berries, and the mature seed coat is thick, golden-brown, and wrinkled.

Pistia is a monotypic genus in the subfamily Aroideae (Grayum, 1990). There are at least two extinct species: *Pistia siberica* Dorofeev (Dorofeev, 1955, 1958, 1963) and *Pistia corrugata* Lesquereux (Stockey *et al.*, 1997). The genus also is closely associated with the fossil genus *Limnobiophyllum* Krassilov, through which it is related to the Lemnaceae (Kvacek, 1995; Stockey *et al.*, 1997).

Biology

Waterlettuce inhabits lakes, ponds, canals, and slowflowing streams. The rosettes are perennial along the Gulf Coast, but act as annuals in more temperate zones. Waterlettuce exhibits seasonal growth in Florida with high rosette densities during winter and spring, and low densities during late summer and early autumn (Dewald and Lounibos, 1990; Dray and Center, 1992). Conversely, leaf size, leaf density per rosette, and total biomass increase during spring and summer then begin to decline during late autumn (Dewald and Lounibos, 1990; Dray and Center, 1992). Population expansion is primarily by vegetative propagation. Up to 15 secondary rosettes may be attached to a single primary plant, and up to four generations of rosettes may be interconnected by stolons (Dray and Center, 1992). Standing crops may reach 2,000 g/m² by the end of the growing season (Dray and Center, 1992). Flowering occurs yearround in southern Florida, but peaks during summer and early autumn (Dray and Center, 1992). Dray and Center (1989) reported a crop of 726 seeds/m² on the rosettes at one site. The hydrosoil under that waterlettuce infestation held 4,196 seeds/m². Mature seeds in fruits had an 84% germination rate, as did seeds in the upper 15 cm of the hydrosoil (Dray and Center, 1989). Historically, waterlettuce has been known to form large floating islands, nearly blocking upper reaches of the St. Johns River (Stuckey and Les, 1984), but these are uncommon today. Sculthorpe (1967) attributes this to suppression of waterlettuce by waterhyacinth after the latter was introduced into Florida during the late 19th century (see also Stoddard, 1989). Competition experiments between the two species support this conclusion (Tag el Seed, 1978; Agami and Reddy, 1990).

Analysis of Related Native Plants in the Eastern United States

Recent molecular phylogenetic analyses have unified the Lemnaceae within the Araceae, and shifted the aroids into the order Alismatales (Bremer et al., 1999; Chase et al., 2000). The resulting family contains more than 2500 species in about 150 genera (Zomlefer, 1994) and is distributed primarily throughout the tropics. Kartesz (1999) lists 40 native aroid species in 16 genera for the United States, many (12 species in six genera) of which are limited to Puerto Rico and the Virgin Islands. Nine of the remaining genera, containing a total of 26 species, occur in the eastern continental United States (USDA, 1999). Among these, Pistia forms a monophyletic group with the duckweed (Lemnaceae) genera (Stockey et al., 1997), all of which have species native to the eastern United States (Spirodela, two species; Lemna, nine species; Wolffia, four species; Wolffiella, three species) (USDA, 1999). Pistia's next closest affinities are with Arisaema (three species), which, like waterlettuce, belongs to the subfamily Aroideae

(Grayum, 1990). Lasioideae is the subfamily most closely allied with the Aroideae, and it contains two genera with native representatives in the east: Orontium and Symplocarpus (one species each) (Grayum, 1990; USDA, 1999). The other aroid subfamily with native genera is the Calloideae, which is represented by Calla (one species) and Peltandra (two species). An examination of the conservation status of the Araceae shows that half of the 26 species in the eastern United States are considered imperiled in at least one state where Pistia occurs: Spirodela polyrrhiza (L.) Schleiden, Wolffia brasiliensis Weddell, Wolffia columbiana Karst., Lemna gibba L., Lemna perpusilla Torr., Lemna trisulca L., Lemna valdiviana Phil., Wolffiella oblongata (Phil.) Hegelm., Symplocarpus foetidus (L.) Nutt., Orontium aquaticum L., Arisaema dracontium (L.) Schott., Calla palustris L., and Peltandra sagittifolia (Michx.) Morong. (ABI, 2000). The latter five species do not occur in the same habitat as *Pistia*, however.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Grayum (1990) suggested that Pistia is an ancient genus with subtropical Laurasian origins, which then migrated into tropical West Gondwanaland. This view is supported by recoveries of fossil Pistia species in strata from the Upper Cretaceous Period (103 to 65 million years ago [MYA]) in the United States (Wyoming and North Carolina) and southern France, and in strata from the Tertiary Period (65 to 2.5 MYA) in the southern United States and western Siberia (Stoddard, 1989). The colder climates associated with the Pleistocene Epoch (2.5 to 0.01 MYA) undoubtedly forced a sharp contraction of the genus' distribution worldwide. Stoddard (1989) argues that Florida served as a refugium for Pistia during this period, and that the genus is therefore native to the United States. However, July temperatures in the southeastern United States averaged 12°C lower during the Pleistocene than today (Watts, 1980) and winters were almost certainly punctuated by severe freezes, so it is likely that the genus became extinct in the United States (Stuckey and Les, 1984). Support for this hypothesis is found in the paucity of specialist herbivores found on waterlettuce in Florida

as compared to other regions of the world (Dray *et al.*, 1993). For example, South America hosts at least thirteen specialist phytophagous insects (Dray *et al.*, 1993) and at least two mosquitoes that are ovipositional specialists (Lounibos *et al.*, 1992), which suggests a lengthy tenure on that continent (Bennett, 1975). Also, ancient folk medicines using *Pistia* are known from Africa and Asia (Stoddard, 1989), arguing for their antiquity in these regions. The extent of *P. stratiotes*' distribution in Florida by the mid-18th century suggests that re-introduction into the United States occurred soon after European settlements were established (Stuckey and Les, 1984).

Areas Surveyed for Natural Enemies

Few surveys for natural enemies have specifically targeted P. stratiotes, aside from searches in Florida (Dray et al., 1988, 1993). However, several general aquatic plant surveys in India (Rao, 1964, 1970; Sankaran and Rao, 1974), Indonesia (Mangoendihardio and Nasroh, 1976; Mangoendihardjo and Soerjani, 1978; Mangoendihardjo et al., 1979), and Thailand (Napompeth, 1990) noted the occurrence of herbivores on waterlettuce. Similarly, biological control scientists conducting surveys on Salvinia spp. and waterhyacinth in South and Central America recorded natural enemies of waterlettuce (Bennett, 1975; DeLoach et al., 1976, 1979; Cordo et al., 1978, 1981; Cordo and DeLoach, 1982). Further, ecological studies of the Argentine waterlettuce fauna produced a few observations on herbivorous species (Poi de Neiff and Neiff, 1977; Poi de Neiff, 1983). Natural enemies have seldom been reported from Africa despite the presence of waterlettuce there for several millennia (Stoddard, 1989).

Natural Enemies Found

Dray *et al.* (1993) and Center (1994) discuss the herbivorous entomofauna reported from *P. stratiotes* worldwide. Among the species known or suspected to be plant-feeders, 44 include waterlettuce in their diets at least occasionally. The Neotropics harbor 21 waterlettuce-feeding insects, including at least 14 species of weevils – many of which are known only from this plant. Five waterlettuce herbivores have been reported from Africa, including a weevil (*Bagous pistiae* Marshall) known exclusively from *P. stratiotes*. The African fauna also contains a collembolan known exclusively from waterlettuce, but it is unclear whether this insect is a herbivore. Eleven phytophagous insects, including eight moth species (one of which is a specialist – *Spodoptera pectinicornis* [Hampson]), have been observed feeding on waterlettuce in Asia. Nine insects feed on waterlettuce in Florida, including a moth (*Argyractis* [=*Petrophila*] *drumalis* [Dyar]) whose larvae only have been found on waterlettuce roots (Dray *et al.*, 1989; Dray *et al.*, 1993; Habeck and Solis, 1994).

Host Range Tests and Results

Host range trials have been conducted on several of the Neotropical weevil species, a Neotropical grasshopper, and two moth species (one Asian and one Neotropical). DeLoach et al. (1976), Harley et al. (1984), and Thompson and Habeck (1989) studied the host range of the weevil Neohydronomus affinis Hustache (as N. pulchellus Hustache), testing a total of 89 species in 66 genera and 37 families. Aside from waterlettuce, only duckweed (Spirodela and Lemna) and frogbit (Limnobium) species sustained any oviposition or meaningful feeding. As noted above, the duckweeds and *Pistia* group together in a single clade within the Araceae, and Limnobium has spongy tissues similar to *Pistia* (Thompson and Habeck, 1989) as well as being in a family (Limnocharitaceae) closely related to the aroids (Chase et al., 1995). Cordo et al. (1978) reported that adults of the weevil Argentinorhynchus bruchi (Hustache) fed and oviposited, and larvae completed development, only on waterlettuce (with very slight feeding on Spirodela intermedia W. D. J. Koch) among the 31 plant species (21 genera, 12 families) they tested. Host range trials conducted by Cordo et al. (1981) demonstrated that the weevil Pistiacola (as Onychylis) cretatus (Champion) has a diet similar to N. affinis. These authors also reported that the weevil Ochetina bruchi Hustache has a broad food-host range, but failed to identify its developmental host.

Larvae of the pyralid moth Samea multiplicalis (Guenée) fed on eight of 17 species (15 genera, 11 families) included in two separate host range studies, but adults oviposited almost exclusively on waterlettuce (Knopf and Habeck, 1976; DeLoach et al., 1979). Food hosts are summarized by Center (1994). The noctuid moth S. pectinicornis (= Proxenus hennia, variously placed in the genera Xanthopter, Athetis, Namangana, and Episammia) was tested against a total of 125 plant species (in 103 genera and 49 families), but completed development only on waterlettuce (Mangoendihardjo and Nasroh, 1976; Suasa-Ard, 1976; Habeck and Thompson, 1994). Feeding and oviposition also were largely confined to this plant. The acridid grasshopper *Paulinia acuminata* (De Geer) feeds and develops on the waterferns (*Salvinia* spp. and *Azolla* sp.) as well as waterlettuce (Bennett, 1966; Vieira, 1989).

Releases Made

Only two insects have been released into the United States as biological control agents against this weed, the South American weevil *N. affinis* and the Asian moth *S. pectinicornis* (Dray *et al.*, 1990, 2001).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Neohydronomus affinis Hustache (Coleoptera: Curculionidae)

Adult *N. affinis* (Fig. 4a) weevils are small (3 mm long) and have a nearly straight rostrum that is strongly constricted ventrally at the base. *Neohydronomus affinis* ranges in color from uniform bluish gray to reddish brown with a tan, chevron-like band across the elytra. Further information on the identification of this species may be found in DeLoach *et al.* (1976) or O'Brien and Wibmer (1989). The following summary of this weevil's biology is based on DeLoach *et al.* (1976) and Thompson and Habeck (1989).

Eggs are cream colored and subspherical (0.33 x 0.4 mm). Females chew a hole about 0.5 mm diameter in the leaf (usually on the upper surface near the leaf edge), deposit a single egg inside this puncture, and close the hole with a black substance. Eggs hatch within four days (at temperatures above 24° C). Young larvae (Fig. 4b), which are very small (head diameter of 0.2 mm), burrow under the epidermis and work their way toward the spongy portions of the leaf at a rate of about 1.5 to 2.0 cm/day.

Larval mines (Fig. 4c) often are visible in the outer third of the leaf where tissues are thin, but are less apparent in the central and basal portions of the leaf. The first molt occurs when larvae are about three days old, the second molt occurs 3 to 4 days later. The three larval stages last 11 to 14 days in total.



Figure 4a.



Figure 4b.





Figure 4. Adult (a) and pupa (left) and larva (right) (b) of the waterlettuce weevil *Neohydronomus affinis* Hustache. Mining by larvae produces characteristic tunnels (c). (Photograph courtesy of USDA, ARS Invasive Plant Research Laboratory.) Third instars are generally found excavating the spongy portions of the leaf where they pupate. Under optimal temperatures, 4 to 6 weeks are required for *N. affinis* to develop from egg to adult. Adults chew holes (about 1.4 mm in diameter) in the leaf surface and burrow in the spongy tissues of the leaf. The characteristic round feeding holes are easily observed when weevil populations are large (several hundred insects per m²), but may be concentrated near leaf edges and more difficult to observe when populations are small.

Samea multiplicalis (Guenée) (Lepidoptera: Pyralidae)

The following section summarizes the biology of the pyralid moth S. multiplicalis based on observations of several authors (Knopf and Habeck, 1976; Deloach et al., 1979; Center et al., 1982; Sands and Kassulke, 1984). Adults are small (wingspread about 17 mm), tan moths with dark markings on fore and hind wings (Fig. 5a). Females each lay about 150 eggs during their brief life span (four to seven days). Eggs most often are laid singly among the epidermal host plant hairs on the lower surfaces of waterlettuce leaves or the upper surface of Salvinia leaves, or lodged between the scale-like leaves of Azolla. Eggs hatch in about four days (at 28° C). Larvae (Fig. 5b) may feed from within a refugium made of silk and hairs of the host plant attached to the external leaf surface, or within galleries in the leaves (waterlettuce). The refugium, when present, consists of a silk canopy stretched across the surface of the leaf. Larvae periodically extend the area covered to reach fresh leaf material. Larger larvae feed on the buds of plants, often killing the growing apex. Larvae also will eat mature waterlettuce fruits and consequently destroy the enclosed seeds. The larval stage is composed of five to seven instars, which require 15 to 16 days for development at 28°C when fed waterlettuce or S. minima and 21 to 35 days at 26°C when fed S. molesta.

Pupation occurs within a silken cocoon. On waterlettuce, this cocoon usually is formed within the spongy portion of a leaf, but on *S. molesta* it is constructed among old leaves. Pupal development requires four to seven days at 28°C on waterlettuce and eight to nine days at 26°C on *S. molesta*. The total developmental times (egg to adult) are 25 and 42 days under the two respective temperature/host plant regimens.



Figure 5a.



Figure 5b.

Figure 5. Adult (a) and larvae (b) of the waterlettuce moth *Samea multiplicalis* (Guenée). (Photograph courtesy of USDA, ARS Invasive Plant Research Laboratory.)

Populations of *S. multiplicalis* tend to be sporadic, possibly due to high parasitism rates. Nonetheless, densities can become exceedingly high during intervals of peak abundance. If this coincides with cooler periods and correspondingly slow waterlettuce growth, massive destruction of the mat results. Nonetheless, because of lack of persistence by this species, the waterlettuce mats normally recover later during the growing season.

Spodoptera pectinicornis (Hampson) (Lepidoptera: Noctuidae)

Several authors have reported on the noctuid moth *S. pectinicornis* (Fig. 6a) (George, 1963; Suasa-Ard, 1976; Mangoendihardjo and Soerjani, 1978; Suasa-Ard and Napompeth, 1982; Habeck and Thompson 1994). The following section summarizes their observations. Female *S. pectinicornis* oviposit on both surfaces of waterlettuce leaves. Eggs are laid in masses

(Fig. 6b) of up to 150 eggs each (average 94 eggs per mass) and covered by a substance produced by the female, perhaps scales from her abdomen. Oviposition lasts two to six days and each female lays up to 990 eggs (average 666 eggs per female). The incubation period ranges from three to six days (average 4.4 days). Eggs are subspherical, about 0.03 mm in diameter, greenish when newly deposited, and turn yellow as they develop.

First instars are creamy white and feed within the leaf on the spongy tissues. Larval development progresses through seven instars and requires 17 to 20 days (average 18 days). Fully-grown larvae attain lengths of up to 25 mm. They pupate in a leaf base or between the leaves, or between the thick ribs on the underside of the leaf. The pre-pupal period lasts one to two days and the pupal stage lasts 3.5 to 5.5 days. Total generation time is about 30 days.

Caterpillar feeding causes plant destruction. Although considerable damage accrues on leaves (Fig. 6c), this alone probably would not kill plants. However, larvae also destroy meristematic tissue, which prevents leaf replacement and impedes asexual reproduction. George (1963) estimated that one hundred caterpillars from one average-sized egg mass could destroy the waterlettuce within a 1 m² area. He also calculated that a single caterpillar, during its larval development, eats two sizable waterlettuce rosettes at a rate of one leaf per day.

In India, periods of peak *S. pectinicornis* occurrence coincide with monsoons and with periods of rapid waterlettuce growth. During these periods, moth infestations occur at most sites and the destruction to waterlettuce mats frequently exceeds 75%. During dry periods, fewer sites are infested and smaller proportions of the waterlettuce populations are affected. However, moth populations are reportedly present all year and produce continuous, overlapping generations.

Synclita obliteralis (Walker) (Lepidoptera: Pyralidae)

The following information is derived from Lange (1956), Kinser and Neunzig (1981), and Habeck (1991). Adults (Fig. 7a) are small moths; males are distinctly smaller (wingspread 11 to 13 mm) than the females (wingspread 15 to 19 mm). The wings of males are dark in coloration, but interspersed with brown and white markings. The wings of females



Figure 6a.



Figure 6b.





Figure 6. Adult (a) and egg mass (b) of the waterlettuce moth *Spodoptera pectinicornis* (Hampson). Damage from larval feeding (c) can destroy leaves. (Photograph courtesy of USDA, ARS Invasive Plant Research Laboratory.)

are paler grayish brown with orange and dark markings.

The whitish eggs are oval and flattened, appearing domelike. They are laid near edges of submersed leaf-surfaces of aquatic plants and are placed singly or slightly overlapping, often in ribbon like masses. Larvae (Fig. 7b) reside between two roundish pieces of leaves that form a sandwich-like portable case. When feeding on small plants, these cases can consist of whole leaves or even whole plants. Cases are usually, though not exclusively, constructed from the plant species on which the larva is feeding. The cases made by young larvae are waterfilled, and these lar-



Figure 7a.





Figure 7. Adult (a) and larvae (b) of the waterlily leafcutter *Synclita obliteralis* (Walker) which feeds on waterlettuce. (Photograph courtesy of USDA, ARS Invasive Plant Research Laboratory.)

vae obtain oxygen through their skin. Cases of older larvae are airfilled. Larvae extend the anterior portion of their bodies out of the case to feed on surrounding plants. They abandon smaller cases as they grow larger, and then cut pieces from new leaves to construct larger cases.

Unlike most nymphulines, larvae of *S. obliteralis* lack tracheal gills. The general body color is creamy white grading into brownish anteriorly (towards the segments that protrude from the case). The epidermal surface is textured with minute papillae that create a distinctive satiny appearance. The head is yellowish or brownish with patches of slightly darker coloration. Before pupation, larvae attach their cases to leaves of aquatic plants either above or below the water surface. They then spin cocoons within the cases in which to pupate.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Dray et al. (1990) describe the release and establishment of the weevil N. affinis, which was initially released at seven sites in southern Florida in 1987 and 1988. Populations established at four of these sites within a year. By fall of 1990, the weevils had dispersed to waterlettuce-infested canals and ponds up to 25 km from initial release sites on Lake Okeechobee (Dray and Center, 1992). Collaborators with the South Florida Water Management District and the Florida Department of Environmental Protection collected infested waterlettuce plants and transplanted them into about 30 additional waterways throughout the state in the spring of 1989 (Dray and Center, 1992). The weevil also was recovered from several sites in southern Louisiana during surveys in spring and summer 1990, although how it arrived there remains unclear (Grodowitz et al., 1992). Surveys during the fall of 1991 showed N. affinis populations had become established at 45 sites in Florida and six sites in Louisiana (Dray and Center, 1993). The weevil also was released at one site in Texas in the fall of 1991 (Grodowitz et al., 1992).

The moth *S. pecitnicornis* was released at 22 sites in southern Florida from 1990 to 1997 (Dray *et al.*, 2001). Several provisionally established populations developed, but ultimately failed to persist (Dray *et al.*, 2001).

Suppression of Target Weed

Neohydronomus affinis has produced dramatic declines (up to 90%) in waterlettuce abundance at five sites in Florida (Fig. 8) and two in Louisiana (Dray and Center, 1992, 1993). Long-term suppression of this weed has not occurred, however, although in at least one site in Florida there were annual cycles from 1990 to 1994 in which spring increases in waterlettuce abundance were followed by sharp declines attributable to the weevil (Dray, unpub.). Plants under stress from weevil feeding are typically smaller, have fewer leaves, and grow less rapidly than un-infested plants (Dray and Center, 1992).



Figure 8a.



Figure 8b.

Figure 8. A 10-acre pond on Torry Island in Lake Okeechoee, Florida, before (a) and after (b) suppression of waterlettuce (*Pistia stratiotes* L.) by *Neohydronomus affinis* Hustache. (Photographs courtesy of USDA, ARS Invasive Plant Research Laboratory.)

Recovery of Native Plant Communities

There have been no studies investigating the re-emergence of native plant communities at sites where waterlettuce control has occurred.

Economic Benefits

There are no known economic benefits accruing from this project.

RECOMMENDATIONS FOR FUTURE WORK

Future Needs for Importation or Evaluation

Although the weevil *N. affinis* has been used successfully in other countries, it has had only limited effect in Florida (Dray and Center 1992). Furthermore, the moth *S. pectinicornis* has failed to establish (Dray *et al.* 2001). Hence, new biocontrol agents are needed. Many additional natural enemies are known from South America that should be studied further to assess their value. Waterlettuce has never been thoroughly surveyed for natural enemies, having generally been a side project of research focused on waterhyacinth or *Salvinia molesta*. Hence, it is anticipated that intensive faunal surveys would reveal many more potential biological control agents.

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6 EURASIAN WATERMILFOIL

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PEST STATUS OF WEED

Eurasian watermilfoil, Myriophyllum spicatum L., (Fig. 1) is a submersed aquatic plant that has become a major aquatic nuisance throughout much of North America. Plants are rooted at the lake bottom and grow rapidly creating dense canopies (Aiken et al., 1979). Eurasian watermilfoil is able to form dense beds (Fig. 2) with stem densities exceeding $300/m^2$ in shallow water (Aiken et al., 1979). Plants typically grow in water depths of 1 to 4 m, but have been found growing in water as deep as 10 m (Aiken et al., 1979). Conventional control efforts have been unsuccessful in providing more than short-term relief. Herbicide applications may suppress regrowth from as little as six weeks or up to one year (Aiken et al., 1979), but have considerable non-target effects (e.g., fish kills, increased algal growth, water supply contamination, native macrophyte die-off). Mechanical harvesters, rototillers, cultivators, barriers, dredges and other physical control techniques have resulted in short term, often localized reductions of M. spicatum populations, but these methods are disruptive, costly, and labor intensive. For continued effect, they need to be maintained long term (Boylen et al., 1996).

Nature of Damage

Economic damage. High densities of Eurasian watermilfoil negatively affect wildlife and fish populations and make recreational use difficult or impossible. Direct financial damages to recreation (boating, swimming, fishing) have not been assessed. Eurasian watermilfoil continues to be the most important waterweed in the continental United States with millions of dollars spent nationwide for control efforts (U.S. Congress, Office of Technology Assessment, 1993). In New York state alone, annual costs are estimated at \$500,000.



Figure 1. Eurasian watermilfoil plant. Cornell University Research Ponds, Ithaca, New York, July 1997. (Photo courtesy of Robert L. Johnson, Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York)



Fig. 2. Dense *Myriophyllum spicatum* canopy at lake surface. Cayuga Lake, Ithaca, New York, August 1989. (Photo courtesy of Robert L. Johnson)

Ecological damage. With the expansion of Eurasian watermilfoil, species diversity and abundance of native macrophytes declines (Smith and Barko, 1990; Madsen et al., 1991). Although in small tank experiments the native northern watermilfoil (Myriophyllum sibiricum Kom.) appears competitively superior, in the field, however, M. spicatum has replaced M. sibiricum over much of the temperate range of this species in North America (Valley and Newman, 1998). Suppression of native macrophytes is enhanced through the formation of a Eurasian watermilfoil canopy at the water surface, reducing light penetration. This canopy often forms early in the season before native macrophytes reach their maximum growth potential. Eurasian watermilfoil beds contain significantly fewer macroinvertebrates than native macrophyte communities (including benthic invertebrates) and have a reduced abundance of native fish species (Keast, 1984). Fish spawning areas and fish growth are reduced in lakes with large infestations of Eurasian watermilfoil. During certain times in winter, waterfowl forage extensively in milfoil beds in Alabama (McKnight and Hepp, 1998; Benedict and Hepp, 2000), although the same species largely avoid Eurasian watermilfoil in the Great Lakes (Knapton and Pauls, 1994).

Extent of losses. Direct losses are difficult to quantify due to lack of data from long-term monitoring programs.

Geographical Distribution

From the initial points of introduction in the Northeast, M. spicatum has spread to 44 states and at least three Canadian provinces (Creed, 1998) and is now considered a major nuisance species throughout the Northeast, northern Midwest and Pacific Northwest of the United States (Couch and Nelson, 1985, White et al., 1993). The mode of dispersal is not completely understood, but M. spicatum can be spread short distances as fragments tangled on boats and trailers (Nichols and Shaw, 1986). Also, human activities, such as motor boating and mechanical weed harvesting, produce and distribute stem fragments allowing increased propagation (Nichols and Shaw, 1986). Long distance dispersal has been linked to the aquarium and aquatic nursery trade (Reed, 1977), and the species continues to expand its range in North America.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Eurasian watermilfoil belongs to the watermilfoil family, Haloragaceae, which has two genera in the eastern United States, Myriophyllum L. (10 species, the watermilfoils) and Proserpinaca L. (two species, the mermaid-weeds) (Gleason and Cronquist, 1991). All species are hydrophytes with many finely divided leaves. All Haloragaceae species are herbs submersed in quiet waters or rooted on muddy shores. The similarity of the species has led to much confusion about species identity, and most species in the family cannot be separated using only individual specimens or ones without flowers. The date of introduction of *M*. spicatum to North America is debated and some authorities consider reports before 1940 as taxonomic misidentifications of *M. sibiricum* (= *M. exalbescens* Fern.) (Johnson et al., 1998). Myriophyllum spicatum is variable in appearance with long stems, and usually 12 to 21 leaflet pairs, which are limp when out of the water. In contrast, the very similar M. sibiricum usually has five to 10 leaflet pairs with leaflets that stay rigid when out of the water. Leaf morphology may be used to separate these two very similar species successfully (Gerber and Les, 1994). Plants often branch at the water surface (or in response to herbivore damage to apical meristems) and flowers are arranged on emersed spikes (associated with a dramatic shift in plant morphology). The flower spike bears whorls of female flowers basally and whorls of male flowers apically. Each female flower produces four small nutlike fruits (2 to 3 mm).

Biology

Eurasian watermilfoil occurs in ponds, lakes, and pools that vary from rather deep to very shallow (from more than 100 m to a few cm), and may be stagnant or slowly moving fresh to slightly brackish water (Spencer and Lekic, 1974). Plants overwinter rooted in the sediment and grow rapidly once favorable temperatures are reached. Flowering can occur in early summer and can continue for several months (Spencer and Lekic, 1974). Eurasian watermilfoil reproduces by seed, but fragmentation is the most likely mode of spread in the northern parts of the range in North America. Sexual reproduction appears unimportant in shaping population structure of Eurasian watermilfoil in Minnesota (Furnier and Mustaphi, 1992); however, significant germination is observed in Lake George in New York State (Hartleb *et al.*, 1993). Seeds require high temperatures (above 14°C) for germination. Light is not considered a limiting factor, but increased sedimentation can greatly suppress germination (Hartleb *et al.*, 1993). Under unfavorable conditions or when plants are attacked by herbivores, plants may not reach the water surface and do not flower. Fragmentation still allows populations to expand and colonize adjacent areas or reach more distant areas through the aquarium trade, transport in currents, or through recreational activities.

Analysis of Related Native Plants in the Eastern United States

The genus *Myriophyllum* belongs to the taxonomically isolated watermilfoil family, Haloragaceae, in the order Haloragales. The genus Myriophyllum is representative of this order; more distantly related species occur in the southern hemisphere. There has been much confusion about taxonomic status and identity of *Myriophyllum* species. Muenscher (1944) lists approximately 20 species of Myriophyllum in North America; Gleason and Cronquist (1991) list 10 species in the eastern United States. Three of the 10 Myriophyllum species mentioned by Gleason and Cronquist (1991) are species introduced to North America, including parrotfeather, Myriophyllum aquaticum (Velloso) Verdc, another invasive species. According to Gleason and Cronquist (1991), only one other genus within the Haloragaceae occurs in eastern North America represented by the two species of mermaid weeds: Proserpinaca palustris L. and Proserpinaca pectinata Lam. These species occur in the range of *M. spicatum* in North America and are widely distributed. Another North American genus, Hippuris (mare's tail), has sometimes been included in the Haloragaceae but now is considered an independent family and outside the order Haloragales (Gleason and Cronquist, 1991). Another closely related order with many wetland plant species is the Myrtales, of which four families (Lythraceae, Thymelaceae, Onagraceae, and Melastomataceae) are native to much of North America. These groups also include invasive introduced species such as purple loosestrife (Lythrum salicaria L.) and water chestnut (Trapa natans L.) (see also the discussions of native species in these chapters). The closest relative to *M. spicatum* is northern milfoil *M. sibiricum* and the ranges of these species overlap widely in the temperate regions of North America.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

For almost 30 years, overseas and domestic research has evaluated potential agents (insects and pathogens) for the biological control of Eurasian watermilfoil (Buckingham et al., 1981; Creed et al., 1992; Creed and Sheldon, 1993, 1995; Shearer, 1994; Sheldon and Creed 1995; Cofrancesco, 1998; Creed, 1998; Johnson, et al., 1998; Mazzei et al., 1999; Gross et al., 2001). Several species of insects have been identified feeding on and damaging Eurasian watermilfoil in North America (Batra, 1977; Buckingham and Bennett, 1981; MacRae et al., 1990; Creed and Sheldon, 1993). Some of these species appear to be native to North America and to have switched from their original hosts; others may have been accidentally introduced from Europe along with M. spicatum (Buckingham et al., 1981). Since 1963, the grass carp, Ctenopharyngodon idella (Cuvier and Valenciennes), has been released to suppress Eurasian watermilfoil and other nuisance aquatic plants in numerous sites within North America (Julien and Griffiths, 1998).

Reports of recent declines in Eurasian milfoil abundance in some lakes in North America have been attributed to feeding damage of three herbivores, the midge *Cricoptopus myriophylli* Oliver, the weevil *Euhrychiopsis lecontei* Dietz, and the pyralid moth *Acentria ephemerella* Denis and Schiffermüller (syn.: *Acentria nivea* Olivier) (Painter and McCabe, 1988; MacRae *et al.*, 1990; Creed and Sheldon, 1993; Sheldon and Creed, 1995; Newman *et al.*, 1996, 1998; Johnson *et al.*, 1998).

Area of Origin of Weed

Myriophyllum spicatum is native to Europe, Asia, and North Africa, where the species is widely distributed. Eurasian watermilfoil appears to have been accidentally introduced into North America sometime between the late 1800s and 1940 (Nichols and Mori, 1971; Couch and Nelson, 1985). The taxonomic difficulty in separating the native *M. sibiricum* and *M. spicatum* has made the exact date of introduction difficult to determine. A record of the accidentally introduced moth *A. ephemerella* from 1927 (Sheppard, 1945) suggests that *M. spicatum* arrived early in the 20th century or the moth was introduced with another plant species.

Areas Surveyed for Natural Enemies

Surveys for insects and pathogens with potential for biological control have been conducted throughout North America and in Europe (England, Denmark, former Yugoslavia) and Asia (Pakistan, Bangladesh, Korea, China) (Buckingham *et al.*, 1981; Cofrancesco, 1998).

Natural Enemies Found

More than 20 insect species have been identified as feeding on *M. spicatum* overseas (Spencer and Lekic, 1974; Buckingham et al., 1981; Cofrancesco, 1998), but few were ever seriously investigated to determine their potential as biological control agents (Buckingham and Bennett, 1981; Buckingham and Ross, 1981), in part because many appear to lack necessary host specificity. Native or accidentally introduced insect herbivores with potential for control of Eurasian watermilfoil have received increasing attention over the past 30 years (Buckingham and Bennett, 1981; MacRae et al., 1990; Creed and Sheldon, 1995; Sheldon and Creed, 1995; Newman et al., 1996; Johnson et al., 1998; Creed, 2000; Gross et al., 2001). More recently, several pathogens have been evaluated as potential biological control agents (Smith et al., 1989; Shearer, 1994). Even though these pathogens, have occasionally shown promise in laboratory tests and been hypothesized to contribute to recent field declines of Eurasian watermilfoil (Shearer, 1994), none has been approved for field use.

Among the insect species studied is the weevil *Litodactylus leucogaster* (Marsham), which appears to be a native North American species with a holarctic distribution (Buckingham and Bennett, 1981). Adults and larvae live on emersed flower spikes of various milfoil species. Since unfavorable growing conditions and herbivore attack often prevent *M. spicatum* from flowering, *L. leucogaster* appears to have little use in biological control programs.

A second species, the aquatic midge *Cricotopus myriophylli*, has been reported as causing recent declines of Eurasian watermilfoil in British Columbia (MacRae *et al.*, 1990). Laboratory experiments have demonstrated a negative impact of *C. myriophylli* on *M. spicatum* growth and biomass production (MacRae *et al.*, 1990). This midge appears to be widely distributed in North America, from British Columbia to New York. However, taxonomic problems in the entire group make species identification difficult. Despite its wide distribution, and the potential it shows in the laboratory, little research has focused on quantifying the impact this herbivore may have on *M. spicatum* populations in the field. The midge does not appear to contribute significantly to declines in Eurasian watermilfoil performance, although field evidence is lacking.

The most promising natural enemies meriting further investigation are the naturalized pyralid moth *A. ephemerella* and the native weevil *E. lecontei*. These species are discussed in detail in the Host Range Tests and Results section that follows.

Host Range Tests and Results

Formal host specificity screening has been conducted with *A. ephemerella* (Buckingham and Ross, 1981; Johnson *et al.*, 1998; Gross *et al.*, 2001) and to some extent with *C. myriophylli* (MacRae *et al.*, 1990). Some initial screening tests have resulted in the immediate rejection of some candidate biological control agents (Buckingham *et al.*, 1981).

Acentria ephemerella. Tests with A. ephemerella specimens collected and tested in North America confirm reports from Europe (Berg, 1942) that the species has a preference for Eurasian watermilfoil, but is not monophagous. In the late 1970s, tests were conducted in quarantine using 20 test plant species with A. ephemerella specimens collected from New York state (Buckingham and Ross, 1981). In nochoice tests, larvae fed on almost all test plants offered but primarily on two species of mermaid weeds (P. pectinata and P. palustris), Hydrilla verticillata (L. fil) Royle, and several species of Potamogeton (pondweeds) (Buckingham and Ross, 1981). These results reduced the interest in using this generalist feeder as a potential biological control agent.

Subsequent reports that *A. ephemerella* may be causing significant declines of Eurasian watermilfoil rekindled interest in the specificity of the species and Johnson *et al.* (1998) and Gross *et al.* (2001) conducted additional tests. In laboratory feeding assays, *A. ephemerella* larvae showed a clear preference for *M. spicatum* over *Elodea canadensis* Michx. (Gross *et al.*, 2001). The lack of effect on the native *E. canadensis* was, in part, explained by differences in plant architecture. These results confirmed field observations that A. ephemerella has a feeding preference for *M. spicatum*, even though larvae can sometimes be observed feeding and overwintering on other submersed aquatic macrophytes. Larval feeding and cocoon/retreat construction on and near the apical meristem of Eurasian watermilfoil substantially reduces plant growth and often inhibits canopy formation. Similar feeding and cocoon/retreat construction on other co-occurring plant species attacked occasionally by A. ephemerella does not affect these species in this way due to differences in plant morphology and growth patterns (Johnson et al., 1998). No-choice feeding rate tests (Johnson et al., 1998) using seven species not previously tested by Buckingham and Ross (1981) showed that A. ephemerella feeds on other macrophytes but feeding rates are highest on Eurasian watermilfoil and pondweeds. On less preferred plant species, A. ephemerella larvae often consume plant tissue but fail to build cocoons and retreats resulting in reduced survival.

Cricotopus myriophylli. In no-choice feeding and starvation trials using 12 different native macrophyte species (MacRae *et al.*, 1990), larvae of the midge *C. myriophylli* fed to some extent on a native pondweed Potamogeton natans L., but regular feeding and construction of a case was only observed on *M. exalbescens* (= *M. sibiricum*). The strong feeding preference of *C. myriophylli* for *M. spicatum* and the absence of the species in areas outside the distribution of the introduced Eurasian watermilfoil suggests the species may be an accidental introduction (MacRae *et al.*, 1990).

Euhrychiopsis lecontei. The host specificity of the native weevil *E. lecontei* has not been investigated beyond comparing its preference for *M. sibiricum* versus the introduced *M. spicatum* (Solarz and Newman, 1996; Newman *et al.*, 1997; Solarz and Newman, 2001). These tests showed that the host plant of the larvae influences performance and host plant choice of the progeny and that *M. spicatum* is usually the preferred host over *M. sibiricum* (Newman *et al.*, 1997).

Releases Made

Releases of grass carp have been made throughout North America for control of aquatic nuisance species, including *M. spicatum*. The flower-feeding weevil *L. leucogaster* was released at a single location in Florida (Buckingham *et al.*, 1981), but the species did not establish. Experimental releases of *A. ephemerella* were made in three New York state lakes (Hairston and Johnson, 2001), and in enclosure experiments. Several releases of *E. lecontei* were made throughout the region covered in this book including those conducted by lake associations and management agencies as well as researchers. The weevil is now commercially available. No other intended releases of insect herbivores have been made.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Acentria ephemerella Denis and Schiffermüller (Lepidoptera: Pyralidae)

The aquatic moth *A. ephemerella* is native to and widespread in Europe. The species is considered a generalist herbivore feeding on a variety of aquatic plants including Eurasian watermilfoil (Berg, 1942). The species was first reported in North America near Montreal in 1927 (Sheppard, 1945). Today, this moth has been found from Massachusetts to Iowa. Declining Eurasian watermilfoil populations in Ontario, Canada, and New York state have been associated with population explosions of *A. ephemerella* (Painter and McCabe 1988; Johnson *et al.*, 1998; Gross *et al.*, 2001).

Moths are white and 5 to 9 mm long. Males (Fig. 3) are short-lived (one or two days) and engage in courtship flights after emergence from the water. Females are normally wingless (Figs. 4), but under some circumstances winged females occur (Fig. 5). Wingless females, after emergence, float on the water surface until they have mated. After mating, wingless females seek out their host plants and lay clutches of 100 to 300 eggs (Figs. 4 and 5). Winged females are less fecund and usually lay fewer than 100 eggs (Johnson, pers. obs.).

Larvae (0.25 mm in length) mine inside the small leaflets of Eurasian watermilfoil after hatching, until they are large enough to build resting shelters of leaflets and small branches that are attached to plant stems. The small size and cryptic behavior of the larvae make them difficult to detect and even trained observers often overlook them. Larvae disperse by crawling upward to feed on the apical meristem as they grow. Larvae are almost transparent, greenish caterpillars, usually with a visible dark green gut (ingested plant material). There are four or five larval



Figure 3. Acentria ephemerella male. Cornell University Research Ponds, Ithaca, New York, June 1997. (Photo courtesy of Robert L. Johnson.)



Figure 4. Acentria ephemerella "wingless" female laying eggs. Cornell University Research Ponds, Ithaca, New York, June 1997. (Photo courtesy of Robert L. Johnson.)



Figure 5. Acentria ephemerella winged female underwater in egg laying position. Cornell University Research Ponds, Ithaca, New York, July 1997. (Photo courtesy of Robert L. Johnson.)

instars and mature larvae are 10 or 12 mm long. When ready to pupate, they build a cocoon, often by removing the plant tip, adding it to a lower portion of the stem, and spinning a cocoon between them. Two generations of *A. ephemerella* per year have been observed in the field. Adults of the first generation emerge and lay eggs in June. Second generation larvae grow rapidly during the summer months and second generation adults emerge and lay eggs in late summer. Eggs laid late in summer hatch and larvae overwinter as various instars.

Euhrychiopsis lecontei Dietz (Coleoptera: Curculionidae)

The weevil *E. lecontei*, a native North American species and watermilfoil specialist, traditionally feeds on the native northern watermilfoil (*Myriophyllum sibiricum*). Although this weevil is widely distributed throughout the continent, little is known about its regional or local distribution (Jester *et al.*, 1997). This weevil also feeds on Eurasian watermilfoil and may contribute to population declines. Weevils have reached extremely high densities at some locations (Newman *et al.*, 1996; Johnson *et al.*, 1998; Creed, 2000) occasionally as high as two or three adults or larvae per stem (Hairston and Johnson, 2001).

Adult weevils overwinter in soil, leaf litter, and other cover close to shore and return to their summer habitat in lakes and ponds from overwintering sites in late April or early May depending on local weather conditions. Extensive shoreline development reduces suitable overwintering habitat and may limit winter survival of *E. lecontei* (Johnson *et al.*, 1998). Weevils climb through existing vegetation or swim from shore to reach Eurasian watermilfoil beds. Fish predation may be an important weevil mortality factor (Sutter and Newman, 1997) and appears to greatly limit weevil populations in ponds (Hairston and Johnson, 2001).

Adult weevils are small (3 mm in length) and dark-colored, with brownish black and yellowish stripes on the upper half of the body. These stripes fade to a lighter yellow-beige underneath (Fig. 6). Adults feed primarily on leaves and stems, causing a decrease in the amount of photosynthetic tissue. After mating, females may lay hundreds of eggs with an average of 1.9 eggs per day (Sheldon and O'Bryan 1996), usually one egg per watermilfoil apical meristem. However, water temperatures need to have reached at least 10°C for eggs to be laid (Mazzei *et* *al.*, 1999). Eggs (0.5 mm in diameter) are round and opaque yellow; larvae are creamy greenish or whitish tan with a dark purple-black head capsule. Larvae feed on the apical meristem and then mine the stem of the plant, consuming the cortex (Newman *et al.*, 1996) (Fig. 7). As larvae near pupation, they turn purplish gray. Mature larvae prepare a pupation chamber further down the stem where they complete development. Each larva needs about 15 cm of Eurasian watermilfoil stem to complete development (Mazzei *et al.*, 1999). Adults leave the pupal chamber to mate and lay eggs or swim ashore to overwinter (late summer generation).

Developmental rate is linearly related to temperature up to a threshold of 29°C with fastest development occurring above 25°C (Mazzei *et al.*,



Figure 6. *Euhrychiopsis lecontei* adult near adult feeding scars on *M. spicatum*. Cornell University Research Ponds, Ithaca, New York, June 1997. (Photo courtesy of Robert L. Johnson.)



Figure 7. *Euhrychiopsis lecontei* larva in stem nearing pupation. Cornell University Research Ponds, Ithaca, New York, June 1997. (Photo courtesy of Robert L. Johnson.)

1999). Eggs hatch within 12 days at 15°C and within 4.2 days at 31°C. Complete development from egg to adult ranged from 16.6 days at 29°C to 61.7 days at 15°C with a lower developmental threshold of about 10°C (Mazzei *et al.*, 1999). Complete development in the field typically requires 20 to 30 days. These data suggest that up to five generations per year are possible in the temperate parts of North America. However, in the field female weevils often appear to stop oviposition in mid August and prepare to overwinter, thus rarely allowing completion of even a fourth generation.

The recent transfer of *E. lecontei* from the native northern watermilfoil, M. sibiricum, to the introduced M. spicatum did not result in performance declines on the new host (Newman et al., 1997). Data collected by Creed and Sheldon (1993) indicated that E. lecontei will feed on M. sibiricum when M. spicatum is not available but prefers *M. spicatum* when given a choice. In performance experiments, weevil survival on the two host plants did not differ significantly, but progeny of adults reared on Eurasian watermilfoil performed more poorly on northern watermilfoil than did progeny of adults reared on northern watermilfoil and development times were significantly longer on the native M. sibiricum (Solarz and Newman, 1996; Newman et al., 1997; Solarz and Newman, 2001).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Grass carp have been widely used to suppress many different aquatic nuisance plants. Regulations as to whether individual states allow grass carp releases vary widely. By 1991, grass carp had been introduced into 35 states, following initial releases in Arkansas and Alabama in 1963. In 14 states, releases of both fertile diploid and sterile triploid fish have been allowed; 15 states have allowed only sterile triploids, and 19 states have prohibited all importations (Julien and Griffiths, 1998). Problems associated with the use of grass carp include difficulties in guaranteeing sterility, escape of individuals into areas with native fish species and, in particular, lack of specificity. In fact, in choice-tests with different plant species, *M. spicatum* was the least preferred food for grass carp (Pine and Anderson, 1991) The voracious appetite of this fish has potential to eliminate much of the aquatic plant biomass, greatly reducing the native plants that serve as important food and shelter for invertebrates, fish, and waterfowl (McKnight and Hepp, 1995).

The aquatic moth *A. ephemerella* now appears widespread from the east coast to Minnesota and Wisconsin (Johnson *et al.*, 1998); however, the species is cryptic and probably often overlooked, particularly as early instars. Regional surveys in New York show that *A. ephemerella* is widespread and occasionally abundant in most lakes in New York State (Johnson *et al.*, 1998).

The midge *C. myriophylli* has been collected at the Cornell Experimental Ponds (Ithaca, New York) and at many other places throughout North America. Indeed, it may be present in many lakes, but taxonomic difficulties in identifying larvae have prevented an easy assessment of the species distribution (Johnson *et al.*, 1998).

The weevil *E. lecontei* occurred in 24 of 26 lakes surveyed in New York (Johnson *et al.*, 1998) and appears widely distributed in North America. The species is now commercially available, but releases into lakes and ponds often only supplement existing (often much larger) populations (Hairston and Johnson, 2001) and therefore may not expand the range of the species. Several states require that the mass-reared individuals used for releases be offspring of locally collected weevils.

Suppression of Target Weed

In laboratory and in lake-enclosure experiments, *A. ephemerella* successfully controls Eurasian watermilfoil growth by destroying the apical meristem, reducing biomass and plant height, and preventing canopy formation. Long-term monitoring in Cayuga Lake, New York, showed a dramatic decline of Eurasian watermilfoil associated with large populations of *A. ephemerella* (Johnson *et al.*, 1998; Gross *et al.*, 2001). Ten years after the initial decline in Cayuga Lake, Eurasian watermilfoil biomass remained at very low levels with no canopy formation. The reduction in Eurasian watermilfoil constituted a 90% decline of the species in Cayuga Lake. As the Eurasian watermilfoil population declined, native plant species returned and they now dominate the plant

community (Johnson *et al.*, 1998; Gross *et al.*, 2001). Prevention of canopy formation in Eurasian watermilfoil due to *A. ephemerella* herbivory was the most likely mechanism explaining the shift in dominance from *M. spicatum* to *E. canadensis* in Cayuga Lake (Gross *et al.*, 2001).

In the laboratory, in lake-enclosure experiments, and in the field, E. lecontei is capable of causing high levels of damage to the host plant (Creed and Sheldon, 1995; Sheldon and Creed, 1995; Newman et al., 1996; Hairston and Johnson, 2001; Newman and Biesboer, 2001). Certain declines of Eurasian watermilfoil have been associated with large populations of *E. lecontei* (Creed and Sheldon, 1995; Sheldon and Creed, 1995; Newman and Biesboer, 2001), and E. lecontei seems to be contributing to declines in Eurasian watermilfoil in some lakes in Vermont, Minnesota, and New York, (Creed and Sheldon, 1995; Sheldon and Creed, 1995; Newman et al., 1996; Newman and Biesboer, 2001) but not in others (Hairston and Johnson, 2001). High levels of seasonal weevil damage does not always translate into long-term declines in Eurasian watermilfoil populations (biomass or plant height) in lakes due to recovery of *M. spicatum* after adult weevils move to shore for overwintering (Hairston and Johnson, 2001).

Recovery of Native Plant Communities

One of the best documented long-term shifts in plant populations associated with feeding by aquatic herbivores occurred in Cayuga Lake in New York state, where standardized surveys for aquatic plant growth and associated herbivores have been conducted for more than a decade (Johnson et al., 1998). In years of greatest abundance of *M. spicatum* in Cayuga Lake, few other macrophytes were present and usually in low abundance. Since the discovery of A. ephemerella in 1991, Eurasian watermilfoil biomass has dramatically declined at both the north and south end of the lake to less than 10% of the original abundance. Although A. ephemerella is a generalist species found feeding on other macrophytes, the net result of the population explosion of this aquatic caterpillar has been a selective suppression of *M. spicatum* (Johnson et al., 1998). Although E. canadensis is a suitable (but not preferred) food plant in the field and in no-choice tests with A. ephemerella, E. canadensis is now the most abundant plant species in Cayuga Lake. Both the north and the south end exhibit a very different macrophyte community structure dominated by native plants such as *Chara vulgaris* L., *Heteranthera dubia* (Jacquin) MacMillan, and *Vallisneria americana* Michx. (Johnson *et al.*, 1998). For most other locations, similar long-term data sets using standardized collection techniques and monitoring of aquatic herbivores are not available.

Economic Benefits

The successful control and further implementation of the biological control program in Cayuga Lake in New York has reduced herbicide use. In addition, lakeside communities that previously suffered economically due to reductions in boating, swimming, and fishing have rebounded.

RECOMMENDATIONS FOR FUTURE WORK

Areas of Needed Work

At present, the focus in the biological control program against *M. spicatum* is on evaluation of impact and additional releases of E. lecontei (Creed, 2000). In addition, in some areas in New York state, the mass production of A. ephemerella, and development of procedures for its release and evaluation are underway (Hairston and Johnson, 2001). Evaluations of releases should be based on use of standardized monitoring protocols that provide baseline data on the macrophyte communities and their associated herbivores (such as described by Johnson et al., 1998). Monitoring should be of long duration and done by trained personnel to avoid overlooking the effects or presence of cryptic species such as A. ephemerella. More information is needed on the efficacy of making additional releases of *E. lecontei*, particularly releases where well established weevil populations already are present. An additional focus should be the continued evaluation, under field conditions, of the effects of A. ephemerella on native macrophyte communities. Results from Cayuga Lake show that the net result of feeding by this species can be an increase in native species diversity and abundance (Johnson et al., 1998; Gross et al., 2001). If this species is found to be beneficial despite its host-range, further releases and redistribution, as well as release and mass production procedures should be developed.

Future Needs for Evaluation Studies

The presence of several species of milfoil herbivores could allow research and monitoring programs to test the assumption of cumulative effects of herbivores. Combinations of agents are likely to be more destructive to plants than a single species alone (Harris, 1981; Malecki et al., 1993). However, even spatially separated herbivores can compete via their common host plant (Masters et al., 1993; Denno et al., 1995). Moreover, all species considered destructive on M. spicatum attack the apical meristems and are not spatially separated. Whether these potential competitive interactions have any influence on control of *M. spicatum* where E. lecontei, A. ephemerella, and C. myriophylli co-occur requires further study. Results from experiments and monitoring at Dryden Lake in New York state seem to suggest that large populations of E. lecontei can suppress A. ephemerella populations to very low levels by almost completely destroying Eurasian watermilfoil apical meristems and toppling the plants early in the season just as A. ephemerella larvae require them for cocoon building and adult emergence (Hairston and Johnson, 2001). However, *M. spicatum* is able to recover after the collapse and the weevils leave the lake to overwinter; yet A. ephemerella populations remain suppressed. Despite the mid-summer population crash, Eurasian watermilfoil continues to be the dominant plant species in Dryden Lake and E. lecontei is unable to control its population. Weevil densities in Dryden Lake (3.58 individuals per stem) are beyond the density of 1.5 weevils per stem that have been reported to be able to control Eurasian watermilfoil elsewhere (Newman et al., 1996; Sheldon 1997). The end result of this competitive interaction (at least in shallow Dryden Lake) of the two herbivores is that a species unable to permanently control the host plant, E. *lecontei*, is in fact reducing the impact of a successful biological control agent, A. ephemerella (Hairston and Johnson, 2001). This would be the first case where an unsuccessful biological control agent is able to interfere with control through a second species (Crawley, 1989; Lawton, 1990); however, these results may be restricted to shallow lakes (Johnson et al., 2000) and need further evaluation. Evidence from five lakes in New York suggests that A. ephemerella densities are negatively correlated with M. spicatum biomass, while *E. lecontei* densities are positively correlated with *M. spicatum* biomass (Johnson et al., 2000). In addition, *A. ephemerella* appears more abundant in larger, deeper lakes while *E. lecontei* populations are negatively correlated with lake mean depths (Johnson *et al.*, 2000). Overall, moth densities are negatively correlated with weevil densities, further suggesting important interspecific competition (Johnson *et al.*, 2000). However, we need a larger sample size to substantiate these results from New York.

Mechanical harvesting or application of herbicides removes the host plants and any herbivores feeding on them. Such actions reduce populations of A. ephemerella, E. lecontei and C. myriophylli, and limit their potential to control Eurasian watermilfoil. In many areas where harvesting operations occur regularly, Eurasian watermilfoil beds are lush and show very little feeding damage, while Eurasian watermilfoil beds in the same lake that have remained unharvested collapse due to feeding by aquatic herbivores (Johnson, pers. obs.). The pressure by lake associations and recreational users for quick action and immediate reductions of aquatic macrophytes may prevent a longer lasting, ecologically sound, and less expensive biological control program from achieving its full potential. Additional demonstration projects and evaluation of the long-term effects of the available biological control agents are needed to withstand the constant pressure for a quick reduction in aquatic vegetation.

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7 Hydrilla

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PEST STATUS OF WEED

Hydrilla verticillata (L.f.) Royle (hereafter, referred to as "hydrilla") (Fig. 1) is a submersed, rooted aquatic plant that forms dense mats in a wide variety of freshwater habitats (canals, springs, streams, ponds, lakes, rivers, and reservoirs) (Langeland, 1990). Plants grow from the substrate to the water's surface in both shallow and deep water (0-15 m in depth) (Langeland, 1990; Buckingham, 1994). This plant is listed on the 1979 federal noxious weed list (USDA-NRCS, 1999) and also is identified in the noxious weed laws of Florida (FDEP, 2000), Louisiana (LDWF, 2000), Texas (TPWD, 2000), California (CDFA, 2000a), South Carolina (SCDNR, 2000), North Carolina (NCAWCA, 2000), Oregon (OSDA, 2000), Washington (WSDA, 2000), and Arizona (ERDC 2001b). In addition, the states of Alabama, Georgia, Maryland, Mississippi, Tennessee, and Virginia, have programs for the control of this invasive plant (Eubanks, 1987; Earhart, 1988; Zattau, 1988; Bates, 1989; Henderson, 1995; Center et al., 1997).

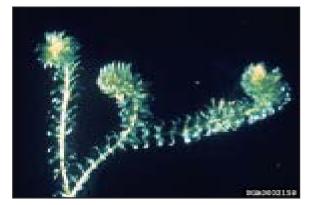


Figure 1. Growing tip of hydrilla. Note crowded internodes at tips.

Nature of Damage

Economic damage. In the United States, hydrilla often dominates aquatic habitats causing significant economic damage (Fig. 2). Hydrilla interferes with a wide variety of commercial operations. Thick mats hinder irrigation operations by reducing flow rates by as much as 90% (CDFA, 2000a) and impede the operation of irrigation structures (Godfrey et al., 1996). Hydroelectric power generation also is hindered by fragmented plant material that builds up on trash racks and clogs intakes. During 1991, hydrilla at Lake Moultrie, South Carolina shut down the St. Stephen powerhouse operations for seven weeks resulting in \$2,650,000 of expenses due to repairs, dredging, and fish loss. In addition, during this repair period, there was an estimated \$2,000,000 loss in power generation for the plant (letter from Charleston District Engineer to Commander, South Atlantic Division, dated March 8, 1993).



Figure 2. Heavy infestation of hydrilla at Rodman Reservoir (August 2, 1978). The rapid underwater growth "pushes" a portion of the mat above the water, giving the reservoir a field-like appearance.

Boat marinas have been reported closed for extended periods on the Potomac River, Virginia; Lake Okeechobee, Florida; Santee Cooper Reservoirs, South Carolina; and Clear Lake, California. Propeller driven boats are hampered by thick mats of hydrilla that form at the water's surface, requiring frequent cleaning to progress short distances. The fragmented plant material removed from the propellers can easily colonize new areas. In the late 1980s, hydrilla populations at Lake Guntersville, Alabama increased rapidly. Henderson (1995) examined the economic impact of aquatic plant control programs on recreational use of this lake between 1990 and 1994. He found that the greatest economic value for recreation (\$122 million annually) occurred when vegetation levels were 20% of the total lake area, and that revenue declined as hydrilla acreage increased.

Although California does not consider hydrilla established, the state has, for decades, aggressively pursued an eradication program that seeks to rapidly eliminate new infestations as they are discovered. California officials have stated that if infestations are not contained and treated promptly, hydrilla will spread throughout the state and cost millions of dollars annually to manage (CDFA, 2000b).

Ecological damage. Native plants act as the primary producers in most ecosystems (Drake et al., 1989; Pimm, 1991). In the United States, hydrilla frequently forms large monocultures that displace native vegetation (Haller, 1978), reducing biodiversity and altering native ecosystems. These alterations also affect the primary and secondary consumers in affected communities (Westman, 1990; Frankel et al., 1995; Schmitz and Simberloff, 1997). Massive amounts of hydrilla can alter dissolved oxygen, pH, and other water chemistry parameters (Smart and Barko, 1988). The portion of the water column occupied by aquatic plants also influences the presence and size distribution of fish (Killgore et al., 1993; Harrel et al., 2001). In dense hydrilla mats, feeding by certain predatory fish is hampered, and small insectivores predominate, reducing community diversity. (Dibble et al., 1996).

Extent of losses. Hydrilla is a major aquatic weed problem throughout the southeastern United States (Center *et al.*, 1997). It was introduced to North America in 1951 or 1952 by an aquarium plant dealer who discarded six bundles of hydrilla into a canal near his business in Tampa, Florida (Schmitz *et al.*, 1991). Since then, it has spread explosively because it

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can reproduce from very small fragments (Langeland and Sutton, 1980). Apparently, recreational boaters and fishermen quickly spread hydrilla to new locations when fragments of hydrilla are transported on boats, motors, and trailers. Once an aquatic site is infested, eradication of hydrilla is very difficult. It produces specialized asexual, reproductive 'buds' on stems (referred to as turions) and on the underground stolons (tubers). These tubers and turions assist hydrilla in reinfesting a site after a drought, or after application of herbicides. Langeland (1990) reported that the annual control cost to manage 7,600 ha of hydrilla in Florida exceeds \$5 million. The U.S. Army Corps of Engineers spends more than one million dollars per year to suppress hydrilla populations in the Jacksonville District and more than \$400,000 annually to treat infestations of this plant at Lake Seminole, a 30,000-acre lake located on the borders of Florida, Alabama, and Georgia. Since 1989, millions of dollars have been spent to introduce the triploid grass carp into the Santee Cooper Reservoirs (70,000 ha) for the management of more than 17,000 ha of hydrilla (Morrow et al., 1997; Kirk et al., 1996, Kirk et al., 2000). Grass carp populations have reduced the infestation levels of hydrilla; however, additional stocking may be needed to maintain the current level of control (Kirk et al., 2000), which will also add to the management costs of this program.

Hydrilla was first reported in California in 1976, and at that time the state established an eradication management plan. This program has eradicated hydrilla from various sites in ten counties. At some sites, treatment of hydrilla continued for six to eight years before eradication was achieved. Funding for this program has gradually increased over time, and during the last three years, California has spent more than \$5.39 million (nearly \$1.8 million annually) to eradicate hydrilla infestations in that state (CDFA, 2000a).

Geographical Distribution

Hydrilla is now almost cosmopolitan in its distribution. Antarctica and South America are the only continents from which it has not been recorded. It is very common on the Indian subcontinent, many of the Middle East countries, Southeast Asia, and northern and eastern Australia. Based on C. D. K. Cook's (pers. comm.) list of herbarium specimens, hydrilla is found in the Southern Hemisphere as far south as the North Island of New Zealand (approximately 40° S). In the Northern Hemisphere hydrilla is found as far north as Ireland, England, Poland, Lithuania and Siberia. The Lithuanian sites, at about 55° N latitude, are the furthest from the equator that hydrilla is known to occur. Since virtually the entire continental United States, except Alaska, lies below a latitude of 48°, hydrilla is climactically suited for growth in any of the contiguous states as well as Hawaii. Even Alaska cannot be considered entirely safe from invasion by hydrilla since places such as Juneau are at approximately the same latitude as the hydrilla infestations in Lithuania and Siberia (Balciunas and Chen, 1993).

The female form of dioecious hydrilla arrived in Florida in the early 1950s (Schmitz et al., 1991) and quickly spread throughout the southeastern United States. Although the monecious biotype of hydrilla was not detected in the United States until the late 1970s (Haller, 1982; Steward et al., 1984), it too is now spreading rapidly, especially into northern states. Monecious hydrilla has now been detected as far north as the Columbia River in Washington state in the western United States, and in Pennsylvania and Connecticut in the eastern United States (Madeira et al., 2000). An excellent color map showing the current U.S. distribution of both biotypes of hydrilla can be found in Madeira et al. (2000).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The following description is compiled primarily from Cook and Lüönd (1982), Sainty and Jacobs (1981), and Godfrey and Wooten (1979). Hydrilla is a perennial, submerged, rooted, vascular plant. Roots are long, slender, and simple and are whitish or light brown in appearance. They are usually buried in hydrosoil, but also form adventitiously at nodes. Stems are long, usually branching, growing from the hydrosoil and frequently forming dense, intertwined mats at the surface of the water. Detached portions of hydrilla plants remain viable and are a common mode for infestation of new areas. Below the hydrosoil, the stems are horizontal, creeping, and stoloniferous. Leaves are verticillate, and along most of the stem, usually number three to five per node. Apical portions of the stem usually have the nodes tightly clustered, with each verticil bearing up to eight leaves. The leaves are usually strongly serrated with the teeth visible to the naked eye, and each leaf terminates in a small spine. The midvein is sometimes reddish in color, and is usually armed with an irregular row of spines. The squamulae intravaginales (nodal scales) are small (ca. 0.5 mm long), paired structures at the base of the leaves and are lanceolate, hyaline, and densely fringed with orange-brown, finger-like structures called fimbrae. Flowers are imperfect (unisexual), solitary, and enclosed in spathes. The female flower is white, translucent, with three broadly ovate petals, about 1.2 to 3.0 mm long; the three petals alternate with the sepals that are much narrower and slightly shorter; the three stigmas are minute; the ovary is at the base of a long (1.5 to 10+ cm) hypanthium. The male flower is solitary in leaf axils. Mature flowers abscise and rise to the surface. Sepals and petals are similar in size and shape to those of female flowers. Each of three stamens bears a fourcelled anther that produces copious, minute, spherical pollen. Hydrilla plants occur as two biotypes. They can be either dioecious, with flowers of only one sex being produced on a particular plant, or monecious, with flowers of both sexes on the same plant. Fruits are cylindrical, about 5 to 10 mm long, usually with long, spine-like processes. Seeds are smooth, brown, usually five or less, 2 to 3 mm long and borne in a single linear sequence. Two types of hibernacula are produced—a brown, bulb like type is produced at the ends of the stolons (Fig. 3), while a green, conical form is found in axils of branches. In the United States, the first type is usually called tubers and the latter turions.



Figure 3. Subsoil turions (tubers) at the end of horizontal stolons. These asexual reproductive structures are resistant to herbicides, and allow for rapid recolonization of a treated site by hydrilla.

Biology

Although the female biotype of hydrilla quickly became widespread throughout the southeastern United States, it was not until 1976 that a male flower was observed in the United States (Vandiver et al., 1982). The female flowers can only be pollinated in the air. The female flower reaches the water surface by elongation of the hypanthium (flower "stalk"). The petals and sepals of the female flower form an inverted bell with an air bubble when growing to the surface, and if after reaching the surface the flower becomes submerged, the petal and sepals revert to this position, and enclose an air bubble thus preventing wetting of the stigmas and ensuring air pollination. The male flower lacks a hypanthium, and reaches the surface by detaching from the plant and floating up as a ripe, air-filled bud. The perianth segments recurve towards the water surface and eventually the anthers dehisce, explosively scattering pollen in a radius of about 10 cm around the flower. Where male hydrilla flowers are present, the water surface frequently becomes visibly greenish-white due to the floating pollen grains and discarded male flowers.

Hydrilla is usually a gregarious plant that frequently forms dense, intertwined mats at the water's surface. Approximately 20% of the plant's biomass is concentrated in the upper 10 cm of such a mat (Haller and Sutton, 1975). The plants grow and spread quickly. Small fragments of the plant, containing but a single node, can quickly develop adventitious roots and eventually produce an entire plant.

Hydrilla has very wide ecological amplitude, growing in a variety of aquatic habitats. It is usually found in shallow waters, 0.5 m or greater in depth. In very clear waters it can grow at depths exceeding 10 m. It tolerates moderate salinity – up to 33 percent of seawater (Mahler, 1979). While hydrilla flourishes best in calcareous ponds and streams, water quality rarely seems to be limiting, since it is found in both acidic and alkaline waters. It also grows well in both oligotrophic and eutrophic waters, and even tolerates high levels of raw sewage (Cook and Lüönd, 1982). Sediments with high organic content provide the best growth, although hydrilla also is found growing in sandy and rocky substrates.

While hydrilla does not grow well in deeply shaded areas, it is adapted to grow under very low light conditions (Bowes *et al.*, 1977), and this may account for its rapid growth and quick dominance over native vegetation.

Analysis of Related Native Plants in the Eastern United States

While hydrilla can assume widely different forms when growing in different environments, all are now considered to be a single species of Hydrilla verticillata (Cook and Lüönd, 1982). There are no other species in the genus Hydrilla, which is placed in the frog's bit family, Hydrocharitacae. There are eight other genera from this family in the eastern United States, two of which (Halophila and Thalassia) are native "marine grasses" that grow in shallow coastal waters (Godfrey and Wooten, 1979). The other native Hydrocharitacae, all of which grow in shallow freshwaters, include Blyxa aubertii Rich., Elodea (two species, Elodea canadensis Michaux and Elodea nutallii [Planch.] St. John), Limnobium spongia (Bosc.) Steud., and Vallisneria americana Michx. (Godfrey and Wooten, 1979). There also are three additional introduced Hydrocharitaceae in the United States: Egeria densa Planch., Hydrocharis morus-ranae L., and Ottelia alismoides (L.) Pers. The two native Elodea species, and the introduced Egeria densa, are difficult to distinguish readily from hydrilla. Hydrilla, however, is unique in having nodal scales (squamulae intravaginales) and specialized, asexual reproductive organs - tubers and turions.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The area of origin of *Hydrilla verticillata* is not clear, but appears to be a broad region encompassing a large part of the Eastern Hemisphere and adjacent areas. Cook and Lüönd (1982), along with many other botanists, indicate that "its centre of origin lies in the warmer regions of Asia." However, hydrilla has been in central Africa for a long time — it was collected by Speke during his 1860 to 1863 expedition to find the sources of the Nile (Speke, 1864) — and some botanists believe that it originated there (Tarver, 1978). Mahler (1979) is even more precise, stating "...with a center of distribution or origin in southeastern Uganda and northwestern Tanzania." Hydrilla is also considered by some to be native to Australia (Sainty and Jacobs, 1981). The first records from Australia are from the early nineteenth century, soon after the arrival of European settlers.

A recent DNA analysis of hydrilla collections from around the world (Madeira *et al.*, 1997) supports the hypothesis of multiple introductions into the United States. The authors found that dioecious samples from the southern United States are more closely aligned with those from the Indian subcontinent, while the monoecious samples most closely resembled those from South Korea.

Domestic Surveys and Natural Enemies Found

Prior to initiating a biological control project, it is recommended that the target weed be surveyed to determine what natural enemies are already associated with it in the invaded area. Native insects or pathogens might be suppressing a target weed at some sites, or non-native natural enemies may have been introduced accidentally. The Army Corps of Engineers Waterways Experiment Station funded thorough faunistic surveys of U.S. hydrilla populations by University of Florida entomologist, Joe Balciunas. Between 1978 and 1980, he made 289 collections of hydrilla at 75 sites, 58 of which were in Florida (Balciunas and Minno, 1984). More than 17,000 insect specimens, comprising nearly 200 species, were collected and identified (Balciunas and Minno, 1984), but of these only 15 were feeding on hydrilla (Balciunas and Minno, 1985). Among the most damaging of the insects found in Florida was the introduced Asian moth Parapoynx diminutalis Snellen. This moth was first detected in south Florida (Delfosse et al., 1976), but dispersed rapidly to additional areas, at some of which it caused heavy damage to hydrilla (Balciunas and Habeck, 1981).

Other researchers (Cuda *et al.*, 1999, 2002; Epler *et al.*, 2000) have commented on the feasibility of using the midge *Cricotopus lebetis* Sublette (Diptera: Chironomidae) as a biological control agent for hydrilla.

The feasibility of using native pathogens to control hydrilla also has been investigated. In the fall of 1987 and 1988, surveys were conducted in 15 lakes and 3 rivers in southeastern United States for pathogens of hydrilla (Joye and Cofrancesco, 1991). Nearly 200 fungal and 27 bacterial isolates were collected from hydrilla foliage. An endemic fungal pathogen originally identified as *Macrophomina phaseolina* (Tassi) Goid. and later determined to be *Mycoleptodiscus terrestris* (Gerd.) Ostazeski was collected from hydrilla growing in Lake Houston, Texas in 1987 (Joye, 1990; Shearer, 1996). Field and laboratory studies have shown that the fungus can significantly reduce hydrilla biomass after inoculation compared with untreated plants (Joye, 1990; Shearer, 1996). Disease symptoms appear in 5 to 7 days after inoculation as interveinal chlorosis followed by a complete loss of color. Within 10 to 14 days, plants treated with *M. terrestris* begin to disintegrate (Joye, 1990; Shearer, 1996). Transmission electron microscopy studies have shown that the fungus attaches to lower epidermal cells of hydrilla leaves within eight hours postinoculation and penetration through the cell wall is completed within 40 hours (Joye and Paul, 1992). The fungus then completely colonizes the host, resulting in collapse of the entire plant. While not currently available as a product, M. terrestris is undergoing evaluation for its potential as a bioherbicide for hydrilla management. As an initial step in the process, the U.S. Army Engineer Research and Development Center Environmental Laboratory (ERDC), Vicksburg, Mississippi and the USDA, ARS National Center for Agricultural Utilization Research in Peoria, Illinois are studying fermentation methods that will yield high concentrations of effective propagules at a low cost. SePro Inc. (Carmel, Indiana) also is involved as a cooperator in the project. The goal is to produce a bioherbicide that can be competitive with chemical herbicides.

Overseas Areas Surveyed and Natural Enemies Found

Determining the native range of a weed is extremely important in biological control programs since the center of origin is usually considered to be the best area to begin searches for natural enemies. In its native range, the weed should have a greater array of natural enemies that coevolved with it. Since evidence to pinpoint hydrilla's evolutionary origin was lacking, searches have been made in several regions, including Africa, Asia, and Australia.

Opportunistic surveys began in India in 1968, and since that time surveys have been conducted in at least 15 additional countries. A time-line and list of overseas research to develop biocontrol agents for hydrilla is presented in Table 1. Only the major overseas projects will be discussed here, as it is beyond the scope of this chapter to completely review the results of all the surveys noted in Table 1. For a more complete review of the history of foreign exploration

Table 1. Chronology of foreign	searches for insect enemies	s of hydrilla (<i>Hydrilla verticillata</i>)	

Year	Search
1971	CIBC initiates search for insect enemies of hydrilla in Pakistan.
1973	Varghese begins studies of insect enemies of hydrilla in Malaysia.
1973	Baloch et al. (1972) present preliminary report on natural enemies of hydrilla in Pakistan. Of the eight insects and two snails found, only the ephydrid fly <i>Hydrellia</i> sp., the moth <i>Parapoynx diminutalis</i> , and the weevil <i>Bagous</i> sp. nr. <i>limosus</i> Gyllenhal are considered to be promising biological control agents.
1975	Delfosse et al., (1976) discover <i>Parapoynx diminutalis</i> Snellen in Fort Lauderdale, Florida. This Asian species was probably introduced in a shipment of aquarium plants.
1975	George Allen (USDA, ARS, Gainesville, Florida) searches in Africa and Indonesia for insect enemies of hydrilla. Results not reported.
1976	Varghese and Singh (1976) present final report on studies in Malaysia. Only two insect enemies were recorded, an aphid and a moth, probably <i>Parapoynx diminutalis</i> .
1976	Baloch et al. (1980) submit final report on insect enemies of hydrilla in Pakistan. Species discussed included a <i>Bagous</i> sp. weevil that feeds on hydrilla tubers, <i>Parapoynx diminutalis</i> , and a leaf-mining <i>Hydrellia</i> sp.
1976	Pemberton (1980) and Lazor conduct surveys in Africa for insect enemies. Hydrilla not found until late in three- month survey and only one possible enemy, the larvae of a midge (Chironomidae), probably in the genus <i>Polypedilum</i> , is observed.
1978	Sanders and Theriot discover a moth, later identified as P <i>arapoynx</i> sp. nr. <i>rugosalis</i> (prev. <i>P. rugosalis</i>), damaging hydrilla and Najas (Balciunas and Center, 1981).
1979	Balciunas and Center (1981) study <i>Parapoynx</i> prob. <i>rugosalis</i> in Panama and find that it feeds primarily on hydrilla and Najas.
1980	Buckingham receives permission to bring Panamanian <i>Parapoynx</i> into quarantine facilities in Gainesville for further testing. However, the species tested by Balciunas and Center can no longer be located in Panama.
1981	CIBC begins search for insect enemies of hydrilla in East Africa.
1981	Balciunas (1982) spends four months searching for natural enemies of hydrilla in tropical Asia. Most of the species previously recorded on hydrilla in Asia are found.
1982	Habeck and Bennett made two unsuccessful trips to Panama searching for <i>Parapoynx</i> sp. nr. <i>rugosalis</i> (prev. P. <i>rugosalis</i>) and the <i>Parapoynx</i> sp. tested by Balciunas and Center (Habeck pers. comm.).
1982	Balciunas (1983) spends six months searching for natural enemies of hydrilla in Kenya, India, Southeast Asia, and northern Australia. Several new moth species are found damaging hydrilla, along with approximately 15 new species of <i>Bagous</i> weevils.
1982	Balciunas sends Bagous spp. weevils from India to Gainesville quarantine.
1983	Markham (CIBC) (1986) begins studies of insects attacking hydrilla in Burundi, Rwanda, and Tanzania.
1983	CIBC scientists in India send several shipments of Bagous affinis Hustache to Gainesville quarantine.
1983	Balciunas (1984) spends five months searching for natural enemies of hydrilla in the Philippines, Borneo, Malaysia, Bali, Papua New Guinea, northern Australia, Myanmar, and India. Weevils including <i>Bagous</i> spp. were again collected along with pyralid moths from the genus <i>Parapoynx</i> and ephydrid flies from the genus <i>Hydrellia</i> .
1985	Balciunas sets up a laboratory in Townsville and another in Brisbane (Queensland, Australia) to collect and evaluate biological control candidates.
1985	The leaf-mining fly Hydrellia pakistanae Deonier is first shipped to Gainesville quarantine.

Table 1. Chronology of foreign searches for insect enemies (continued)

Year	Search				
1987	First shipment of the hydrilla stem borer weevil <i>Bagous hydrillae</i> O'Brien from Australia to the Gainesville quarantine facility in Florida.				
1987	First field release of Hydrellia pakistanae in Florida.				
1987	First field release of Bagous affinis in Florida.				
1988	First shipment of the hydrilla leaf-mining fly Hydrellia balciunasi Bock from Australia to the Gainesville quarantine in Florida.				
1988	USDA establishes the Sino-American Biological Control Laboratory (SABCL) in Beijing, China, to search for and evaluate temperate biological control agents of hydrilla.				
1989	Balciunas (1990) and Buckingham, along with cooperating scientists from SABCL, begin annual surveys in China for insects on hydrilla and Eurasian watermilfoil. A new species of <i>Hydrellia</i> , later identified as <i>Hydrellia</i> sarahae var. sarahae Deonier, is found and shipped to the Gainesville quarantine for evaluation.				
1989	University of Florida biological control laboratory in Australia becomes a USDA facility, called the Australian Biological Control Laboratory (ABCL); Balciunas appointed director.				
1989	First field release of Hydrellia balciunasi in Florida.				
1991	First field release of Bagous hydrillae in Florida.				
1991	Buckingham and Pemberton (Buckingham 1993) survey hydrilla in Korea and Japan. A new, undescribed species of <i>Hydrellia</i> from Japan is sent to Florida, but a colony is not established.				
1992	Dale Habeck (1996) spends five months studying stream-dwelling moths in north Queensland, Australia. Two of these moths, <i>Theila siennata</i> Warren (prev. <i>Aulacodes sienatta</i>) and <i>Ambia ptolycusalia</i> Walker (prev. <i>Nymphula eromenalis</i>), are sent to quarantine facilities in the United States.				
1996	Balciunas et al. (1996a) present final report on Australian surveys. Four Australian insects exported, and two of these released in the United States.				
1997	Scientists from the USDA, ARS Invasive Weed Lab, along with cooperators from Australia (ABCL) and Thailand's National Biological Control Research Center (NBCRC) begin surveys for hydrilla biocontrol agents in Thailand and Vietnam; several new insects are found and some are sent to Florida (Table 2) for further evaluation (Buckingham pers. comm., Center pers. comm.).				

for hydrilla agents, readers should consult Balciunas (1985), Buckingham (1994), and Balciunas *et al.*, (1996a).

Many of the overseas surveys consisted of either brief trips to one or more countries, or efforts in which hydrilla was added as a target to a larger, ongoing project in a specific region. While these opportunistic surveys frequently noted potential agents, as of 2000, none of these had been approved or released in the United States. The most productive overseas studies have been intensive, multi-year projects concentrating on hydrilla natural enemies in a particular region. The first of these was the USDA-sponsored project in Pakistan from 1971 to 1976, conducted by scientists from CIBC (Commonwealth Institute of Biological Control). Ten insects were studied (Baloch and Sana-Ullah, 1974), but only three were recommended for importation into the United States (Baloch *et al.*, 1980). Unfortunately, these recommendations were not acted upon, possibly because there was no USDA scientist or facility available at that time to work on hydrilla insects.

In 1981, Joe Balciunas, a University of Florida entomologist, began systematic, intensive world-wide surveys to locate potential biocontrol agents for hydrilla. These surveys, funded by the Army Corps of Engineers (COE) Waterways Experiment Station (WES) and USDA, ARS, consisted of three, 5 to 6 month around-the-world trips. During these three trips, he visited 10 countries, made 180 collections, and found at least 45 different insects damaging hydrilla (Balciunas, 1985; Center *et al.*, 1990) (Figure 4). His surveys had two immediate consequences. First, they resulted in the importation and quarantine

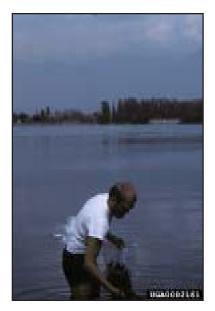


Figure 4. Joe Balciunas surveying for hydrilla agents at Lake Dal, Kashmir, India (August 1983). Of the four agents approved for release, two were shipped from India.

evaluation of four weevils and a leaf-mining fly (Table 2). Although all five of these insects had been previously studied in Pakistan, Balciunas's studies and shipments rekindled interest in these potential agents. The second outcome was that in 1985, Balciunas established a laboratory in Townsville, Australia, along with a substation in Brisbane, Australia, to further evaluate several promising insects that he had collected there during his worldwide surveys. Although hydrilla is widespread throughout tropical and eastern Australia, it seldom becomes abundant enough there, to be considered a problem.

Between 1985 and 1992, Balciunas and his Australian staff made more than 100 non-quantitative collections and 588 quantitative collections of hydrilla at 70 sites in Australia (Balciunas *et al.*, 1996a). In order to ascertain the field host range of the potential agents, he and his team also made 1,007 quantitative collections of 47 other aquatic plant species from 27 families (Balciunas *et al.*, 1996a). Balciunas and his team evaluated six insects for their potential as biological control agents for hydrilla. Four of these were exported to the Florida quarantine for further evaluation (Table 2), and two were eventually released.

In 1989, Balciunas joined USDA, ARS, and for three years headed a project, based at the Sino-American Biological Control Laboratory (SABCL), to find new agents for both hydrilla and Eurasian milfoil, *Myriophyllum spicatum L.*, in temperate parts of China. Since then, the USDA, ARS Invasive Plant Laboratory in Ft. Lauderdale, Florida has led the searches in China for hydrilla natural enemies, and has expanded the surveys to Thailand and Vietnam (Table 1). Staff of this laboratory have been assisted in these surveys not only by SABCL scientists, but by other scientists from the United States and the Australian Biological Control Laboratory (ABCL). The most promising insects identified during the past decade are listed in Table 2.

Overseas pathogens for controlling hydrilla also have been investigated, but far less extensively than the insects. During a three-month period in 1971 and 1972, surveys were conducted in India for pathogens of hydrilla (Charudattan, 1973). Of 40 fungi and 15 bacteria isolated and screened for pathogenicity, only two species, a Pythium sp. and a Sclerotium sp., were found to be damaging. Charudattan et al. (1980) reported that a pathogen, Fusarium roseum (Link ex Fr.) var. culmorum Snyd. and Hans. found on diseased Stratiotes aloides L. in The Netherlands, was efficacious on hydrilla. Staff of the Sino American Biological Control Laboratory also conducted surveys in the People's Republic of China in 1994 and 1995 for pathogens of hydrilla. All isolates were subsequently deposited at the USDA, ARS quarantine facility located at Fort Detrick, Frederick, Maryland. Following identification of the isolates, they were subjected to pathogenicity screening on the host. Six isolates (an unidentified Moniliaceous hyphomycete, an unidentified Coelomycete, Phoma sp., Colletotrichum gloeosporioides [Penz.] Penz. and Sacc. in Penz., and M. terrestris were found to induce disease symptoms on hydrilla. Additional pathogenicity testing on rooted plants has yet to be completed. If potential biological control candidates are found among the isolates they will have to undergo intense host specificity testing because some have been reported on other hosts (Farr et al., 1989).

Host Range Tests and Results

The host range tests on the more than two dozen non-U.S. species of insects or pathogens that have been considered as potential biological control agents for hydrilla have been recorded in more than a hundred (mostly unpublished) reports. In Table 2, we summarize the primary test results for these potential agents. Only a few agents were tested extensively

Potential Agent	Primary Damage to Hydrilla	Country and Year First Collected	Where Tested	Test Results	References
Coleoptera: Chrysome	lidae, subfamily Donaciina	e			
<i>Donacia australasiae</i> Blackburn	larvae feed externally on stems	Australia 1985	Australia	no adults emerged; testing incomplete	Balciunas et al., 1996a
prob. <i>Donacia</i> sp.	larvae feed externally on stems	Vietnam 1996	Florida		Buckingham, pers. comm.
prob. <i>Macroplea</i> sp. 1	larvae feed externally on stems	China 1992	Florida	unable to rear adults from quarantine; additional field information needed	Buckingham, 1998
Coleoptera: Curculioni	idae				
Bagous affaber Faust (prev. B. sp. nr. limosus Gyllenhal, and B. dilgiri Vazirani)	larvae bore stems; adults feed on submersed stems and leaves	India 1982	Pakistan Florida	reproduced on Potomogeton nodosus; lab colony destroyed	Baloch et al., 1980 Balciunas, 1985 Buckingham and Bennett, 1998
<i>Bagous affinis</i> Hustache	larvae bore and develop inside tubers	Pakistan 1971	Pakistan India Florida	sufficiently host specific; released in Florida in 1987	Baloch et al., 1980 Balciunas, 1985 Buckingham, 1988 Buckingham and Bennett, 1998
<i>Bagous hydrillae</i> O'Brien	larvae bore stems; adults feed on submersed stems and leaves	Australia 1982	Australia Florida	narrow laboratory host range, and Australia field data confirming lack of impact on other hosts allows approval and release in 1991	Balciunas, 1985 Balciunas and Purcell, 1991 Buckingham, 1994 Balciunas et al., 1996b
<i>Bagous laevigatus</i> O'Brien and Pajni	larvae bore and develop inside tubers	Pakistan 1971 misidentified and tested with <i>B.</i> <i>affinis</i>	Pakistan Florida	prefers sago pondweed (<i>Potomogeton</i> <i>pectinatus</i> L.) tubers; lab colony destroyed	Baloch et al., 1980 Buckingham, 1994 O'Brien and Pajni, 1989 Bennett and Buckingham, 1991
Bagous latepunctatus Pic	larvae tunnel in stems; adults feed on submersed stems and leaves	India 1982 (mixed with <i>B. affinis</i>) Thailand 1997	Florida	completed life cycle on hydrilla and Najas in laboratory; further testing needed	Bennett and Buckingham, 2000
Bagous subvittatus O'Brien and Morimoto	larvae tunnel in stems; adults feed on submersed stems and leaves	Thailand 1997	Florida	broad host range in laboratory; additional data on field host range needed	Bennett and Buckingham, 2000
<i>Bagous vicinus</i> Hustache(prev., <i>B</i> . sp. nr. <i>lutulosus</i> Gyllenhal)	larvae feed on dessicating hydrilla; adults feed on submersed stems and leaves	Pakistan 1971	Pakistan Florida	since larvae damages only dessicating hydrilla, dropped from future consideration as a potential agent	Baloch et al., 1972 Baloch and Sana- Ullah, 1974 Baloch et al., 1980 Bennett, 1986 Buckingham, 1994
<i>Bagous</i> n. sp. (Thailand)	larvae bore stems; adults feed on submersed stems and leaves	Thailand 1997	Florida	broad host range in laboratory; additional data on field host range needed	Bennett and Buckingham, 1999

Table 2. Candidate biological control agents evaluated for use against hydrilla.

Potential Agent	Primary Damage to Hydrilla	Country and Year First Collected	Where Tested	Test Results	References
Diptera: Chironomidae					
Polypedilum sp.	burrows into stem tips	Tanzania (Lake Tanganyika) 1977	Florida	unable to rear under laboratory conditions	Pemberton, 1980 Markham, 1986
Polypedilum dewulfi Goetghebuer and Polypedilum wittae Freeman	burrows into stem tips	Burundi 1990	Florida	unable to rear under laboratory conditions	Buckingham, 1994
Diptera: Ephydridae					
Hydrellia balciunasi Bock	larvae mine leaves	Australia 1982	Australia Florida	specific to hydrilla; released in Florida in 1989	Balciunas, 1985 Balciunas and Burrows, 1996 Buckingham et al.,1991
<i>Hydrellia pakistanae</i> Deonier	larvae mine leaves	Pakistan 1971	Pakistan Florida	hydrilla preferred host; released in Florida in 1987	Baloch et al., 1980 Balciunas, 1985 Buckingham et al., 1989
<i>Hydrellia sarahae sarahae</i> Deonier (prev., <i>Hydrellia</i> n. sp. CH-1, and "silver-faced Hydrellia")	larvae mine leaves	China 1989	China India Florida	host range appears broad; more field data needed	Balciunas, 1990 Krishnaswamy and Chacko, 1990 Bennett, 1993 Bennett and Buckingham, 1999
<i>Hydrellia</i> n. sp. (Japan)	larvae mine leaves	Japan 1991		laboratory colony not established	Buckingham, 1994
<i>Hydrellia</i> n. sp. (Korea)	larvae mine leaves	Korea 1991		laboratory colony not established	Buckingham, 1994
<i>Hydrellia</i> n. sp. (Thailand)	larvae mine leaves	Thailand 1997	Florida	testing incomplete	Bennett and Buckingham, 1999
Lepidoptera: Pyralidae					
Ambia ptolycusalia Walker (prev., Nymphula eromenalis Snellen)	larvae eat leaves, defoliating the stems	Australia 1982	Australia Florida	laboratory colony not established; research incomplete	Balciunas et al., 1989 Buckingham, 1994
Margarosticha repetitalis Warren (prev., Strepsinoma repititalis Walker)	larvae eat leaves, defoliating the stems	Australia 1982	Australia	present on other hosts in the field in Australia, not recommended for use as biological control agent	Balciunas et al., 1989 Balciunas et al., 1996a
Parapoynx diminutalis Snellen (prev., Nymphula dicentra Meyrick)	larvae eat leaves, defoliating the stems	India 1971 Pakistan 1971	India Malaysia Pakistan Phillipines Florida	host range determined too broad for release, but was later discovered to have immigrated to Florida	Rao, 1969 Baloch and Sana- Ullah, 1974 Varghese and Singh, 1976 Chantaraprapha and Litsinger, 1986 Buckingham and Bennett, 1996

Table 2. Candidate biological control agents evaluated for use against hydrilla (continued).

Potential Agent	Primary Damage to Hydrilla	Country and Year First Collected	Where Tested	Test Results	References
Lepidoptera: Pyralidae	(continued)				
Parapoynx sp. nr. rugosalis (prev., P. rugosalis)	larvae eat leaves, defoliating the stems	Panama 1977	Panama	larvae prefer hydrilla and Najas; tests attempted but <i>P</i> . sp. nr. <i>rugosalis</i> could not be recollected in Panama (completely replaced by <i>P</i> . <i>diminutalis</i>)	Balciunas and Center, 1981 Buckingham and Bennett, 1996 Habeck, pers. comm.
Theila siennata Warren (prev., Aulacodes siennata Warren)	larvae eat leaves, defoliating the stems	Australia 1982	Australia Florida	laboratory colony not established; research incomplete	Balciunas et al., 1989 Buckingham, 1994 Balciunas et al., 1996a
Pathogens					
<i>Fusarium roseum</i> (Link ex Fr.) var. <i>culmorum</i> Snyd. and Hans. (Hyphomycetes)		The Netherlands	Florida		Charudattan and McKinney, 1977 Charudattan et al., 1980 Charudattan et al., 1984

Table 2. Candidate biological control agents evaluated for use against hydrilla (continued).

overseas, and their host range tests subsequently published in refereed journals, e.g., Balciunas and Center (1981), Balciunas and Burrows (1996), and Balciunas et al. (1996b). Nearly 20 hydrilla insect species were shipped to the quarantine facility in Gainesville, Florida for evaluation (Table 2). The testing there was conducted by Gary Buckingham, USDA, ARS, and University of Florida cooperators. Heightened concern for safety has increased the number of plant species tested, and the hydrilla agents eventually approved for release were tested on more than 60 species of plants in 30 families (Buckingham, 1994). Although a few species were conclusively ruled out as having too broad a host range, testing of many remains incomplete. Eventually, however, sufficient laboratory and field data was gathered to gain approval for release of two weevils and two leaf-mining flies. Although none of these four insects were strictly monophagous, hydrilla was greatly preferred, and the risk to the few other alternate hosts was considered very minimal.

Releases Made

Many of the natural enemies identified during overseas surveys still have not been fully evaluated to judge their safety as potential biological control agents for hydrilla. Only four hydrilla insects have been released in the United States: The tuber attacking weevil *Bagous affinis* Hustache (Coleoptera: Curculionidae) and the leaf mining fly *Hydrellia pakistanae* Deonier (Diptera: Ephydridae) were both released in 1987; another leaf-mining fly *H. balciunasi* Bock (Diptera: Ephydridae) was released in 1989; and the stem-mining weevil *B. hydrillae* O'Brien (Coleoptera: Curculionidae) was released in 1991 (Buckingham, 1994).

The leaf-mining flies have been the most extensively released species. Hydrellia pakistanae has been released at more than 50 sites in Alabama, California, Florida, Georgia, Louisiana, and Texas (Center et al., 1997). About 1.2 million individuals were obtained, mainly from greenhouse colonies maintained at the U.S. Army Engineer Research and Development Center in Vicksburg, Mississippi and various USDA, ARS facilities, along with an additional two million insects from a Tennessee Valley Authority pond-based rearing facility (Grodowitz and Snoddy, 1995). These releases ended in 1995. Recently (September 2000), releases resumed using Hydrellia-containing hydrilla obtained from ponds at the Lewisville Aquatic Ecosystem Research Facility, Lewisville, Texas with more than 300,000 immatures being released in Lake Raven in Huntsville State Park, Texas. Although considerably less effort went into the release of *H. balciunasi*, still close to one million individuals were released at 11 sites in Florida and Texas only (Grodowitz *et al.*, 1997).

Bagous affinis was extremely difficult to maintain under mass-rearing conditions. This was due primarily to the high demand of tubers for larval feeding. However, over 10,000 individuals were released in three states (i.e., California, Florida, and Texas) at more than 10 locations (Godfrey *et al.*, 1994; Grodowitz *et al.*, 1995).

A larger effort went into the release of the stemfeeding weevil, *B. hydrillae*. For example, close to 300,000 individuals have been released in four states (Florida, Texas, Georgia, and California) at more than 15 locations (Grodowitz *et al.*, 1995).

No overseas pathogens have yet been approved for release to control hydrilla.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Hydrellia pakistanae - "Asian Hydrilla Leaf Mining Fly" and Hydrellia balciunasi -"Australian Hydrilla Leaf Mining Fly" (Diptera: Ephydridae)

Hydrellia pakistanae and *H. balciunasi* are small leafmining ephydrid flies. *Hydrellia pakistanae* (Fig. 5) is an Asiatic species, first released in the United States on Lake Patrick, Florida in 1987 (Buckingham *et al.*, 1989). It is very similar in habit and appearance to another introduced ephydrid, *H. balciunasi*, an Australian species first released in the United States in 1991 (Buckingham *et al.*, 1991). Both species are small, about 2 mm in length, and live almost exclusively on or near hydrilla infestations. The introduced *Hydrellia* spp. are apparently not strong flyers and appear to hop along the water surface from one resting place to another (Deonier, 1971).

Adult *H. pakistanae* and *H. balciunasi*, the two introduced *Hydrellia* spp. can be difficult to identify because of their small size, lack of obvious distinguishing characters, and similarity to other native species of *Hydrellia* (including *H. bilobifera* Cresson and *H. discursa* Deonier). Examinations of reproductive organs are frequently required for positive identification. Adult male *H. pakistanae* can be distinguished from other commonly collected native *Hydrellia* spp. and *H. balciunasi* by several charac-102



Figure 5. Adult female *Hydrellia pakistanae* on hydrilla leaf (photograph courtesy of USDA, ARS).

ters, including the length of the thorax in comparison to the abdomen length, the presence of crossed or cruciate macrochaetae, and the shape and size of the macrochaetae (ERDC 2001a, b).

To separate the introduced *Hydrellia* spp. from native individuals, the size of the abdomen and the shape and position of the macrochaetae are used. The abdomen in both species of introduced *Hydrellia* is relatively short and is roughly the same size as the thorax (Fig. 6). In contrast, for males of all the commonly encountered native *Hydrellia*, the abdomen is 1.5 to 2 times the length of the thorax. In addition, both *H. pakistanae* and *H. balciunasi* have crossed or cruciate macrochaetae (Fig. 6).

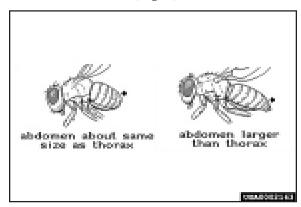


Figure 6. Diagram of relative sizes of the abdomen in both the native *Hydrellia spp.* (right) and the introduced species (left).

The only way to accurately separate *H. pakistanae* from *H. balciunasi* is by the shape and size of the macrochaetae, which are small hair-like structures associated with the male external reproductive structures and are thought to be responsible for holding the female in place during copulation (Deonier, 1971). In both introduced species of *Hydrellia*, the

macrochaetae are crossed or cruciate, but in *H. pakistanae* they are small and more distinctly needle-shaped, while those of *H. balciunasi* are larger and appear flattened at the tip (Fig. 7).

Female *Hydrellia* are distinguished from native and other introduced *Hydrellia* by the morphology of the genitalia, especially the shape of the cerci (ERDC 2001a, b). The cerci are hooked or L-shaped in *H. pakistanae* as compared to arrow- or diamondshaped in *H. balciunasi* (Fig. 8).

The larvae are cream colored and relatively nondescript. There are few morphological differences between the species; the most notable being in the feeding apparatus and spiracular peritreme (Deonier, 1971).

Eggs are laid on hydrilla or almost any emergent aquatic vegetation near hydrilla infestations (Buckingham *et al.*, 1989; Buckingham *et al.*, 1991). Females lay eggs singly, and each female can produce several hundred eggs during her reproductive period. Eggs hatch in three to four days, depending on temperature. Larvae tunnel or mine hydrilla leaves, feeding and destroying about nine to 12 leaves during the three larval stages. Late third instars pierce the stem tissues with portions of the spiracular peritremes, which are modified into two needle-like projections that subsequently provide oxygen to the pupae (Deonier, 1971). Pupae are formed within a puparium, and the pupal stage lasts six to 15 days attached to the stem typically in the leaf axils, after which the adult floats to the surface in an air bubble after emerging from the puparium. Total development time is from 20 to 35 days. The overwintering stage is unknown but larvae have been found on hydrilla throughout the entire winter. The total number of generations per growing season appears to be highly variable and related to geographic area but may be as high as seven.

From a distance, a hydrilla mat containing large numbers of *Hydrellia* spp. appears brown, and upon close examination, one can observe clusters of leaves along the stem where feeding has occurred. Damage

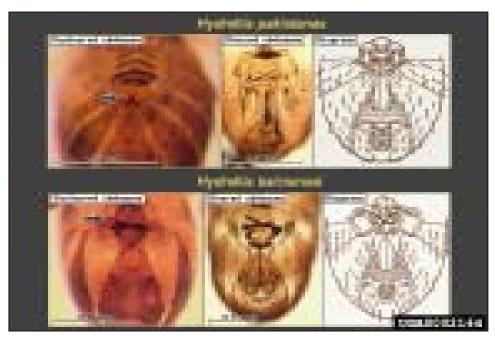


Figure 7. Ventral views of the abdomens' of both *H. pakistanae* and *H. balciunasi* showing the morphology of the external male genitalia. Note the cruciate or crossed macrochaetae in both species, a configuration that is not found in native *Hydrellia* species. The primary difference between the two introduced species is the size and shape of the macrochaetae. In *H. pakistanae*, the macrochaetae are smaller and needle-like in comparison to *H. balciunasi* where the macrochaetae are larger and spoon-shaped at the ends. (Photographs courtesy of ERDC 2001a, b.)

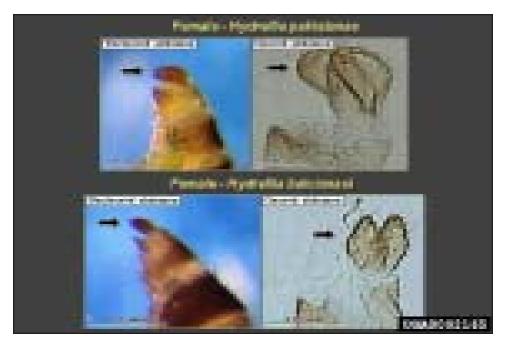


Figure 8. The cerci, located at the posterior end of the abdomen, are used to identify female *Hydrellia*. In *H. pakistanae*, the cerci are distinctly L-shaped in contrast to *H. balciunasi*, where the cerci are roughly triangular. (Photographs courtesy of ERDC 2001a, b.)

to hydrilla is probably due to a reduction in total photosynthetic area caused by the leaf damage (Doyle *et al.*, 2002), which reduces growth and vigor and leads to a decrease in the competitiveness of the affected plants. In addition, some evidence suggests that feeding may reduce the buoyancy of the plant and allow the stem to become more brittle in areas of heavy feeding, leading to stem fragmentation (Grodowitz *et al.*, 1999). Limited field observations suggest that *Hydrellia* feeding may predispose the plant to infection by fungi and other pathogens.

Bagous affinis - "hydrilla tuber weevil" (Coleoptera: Curculionidae)

Adult weevils are brown to dark brown, and frequently have a mottled appearance (Fig. 9) (ERDC 2001a, b; Bennett and Buckingham,1991). Unlike the hydrilla stem-feeding weevil, the tuber weevil cannot live if submerged for extended periods. Adults are relatively long-lived, surviving under laboratory conditions from 55 to 225 days. Females are known to produce upwards of 650 eggs throughout their reproductive period. Eggs are roughly spherical and creamy white. Eggs are laid on hydrilla stems, tubers, or moist wood and apparently not on any submersed material. Eggs hatch after three to four days, and the emerging larvae crawl through the drying sediment in search of tubers. There are three larval instars and 104 they are non-descript and typically creamy-white. The larvae can be found on or within the hydrilla tubers, where they burrow and feed. The larvae pupate within the tubers but also can pupate in nearby moist wood. The duration of the larval stage is anywhere from 14 to 17 days. The pupal stage lasts four to six days.

While the adults feed on the tubers, their damage is minimal compared to the destructiveness of the larvae. The larvae can attack and destroy tubers deep within the sediment. High weevil populations have been reported from hydrilla-infested ponds in the insect's native range.

Bagous hydrillae - "hydrilla stem weevil" (Coleoptera: Curculionidae)

Adult *B. hydrillae* are dark brown with a distinctly mottled body appearance (Fig. 10) (ERDC 2001a, b; Balciunas and Purcell, 1991). In many individuals, two to four light spots can be seen on the posterior portion of the elytra. There are three larval instars, each lasting from three to four days. The pupa is naked, with no cocoon or other protective structure. Total development time ranges from 2.5 to 3 weeks (Buckingham and Balciunas, 1994).

Adults can be found on submersed hydrilla as well as on hydrilla that washes up on the shoreline. Adults feed externally on leaf and stem tissues of

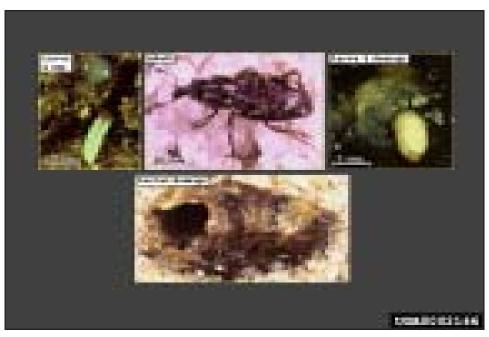


Figure 9. The life stages and feeding damage of *Bagous affinis*. (Photographs courtesy of ERDC 2001a and b and USDA, ARS.)



Figure 10. *Bagous hydrillae* adult and larvae, and associated larval damage. (Photographs courtesy of ERDC 2001a and b and USDA, ARS.)

drying or submersed hydrilla, apparently preferring the stem tissue at the internodes. Eggs are laid within stem tissues usually at the leaf nodes. Eggs hatch in three to four days and larvae feed throughout internal stem tissues. Larval feeding subsequently fragments the stem, which floats to the shoreline where the third instars exit and subsequently pupate within soil or drying hydrilla. Pupation must take place under relatively dry conditions. The pupal period lasts from three to four days depending on the ambient temperature.

Since no permanent populations of *B. hydrillae* exist in the United States, large-scale damage has not been observed; however, researchers in Australia have indicated that larval feeding by *B. hydrillae* causes the plants to have a mowed appearance due to the

removal of the hydrilla from the surface to a depth of 100 cm (Balciunas and Purcell, 1991).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Although four insects have been released, neither of the weevils appears to have established, and H. balciunasi has only been recovered from a few sites in east Texas (Bennett and Buckingham, 1999; Grodowitz et al., 2000a). However, H. pakistanae established and dispersed readily and is now found throughout Florida; north to Muscle Shoals, Alabama; west to Austin, Texas; and south to the lower Rio Grande Valley (Center et al., 1997; Grodowitz et al., 1997; Grodowitz et al., 2000a). Populations of both species, but especially H. pakistanae, have expanded in distribution considerably since they were first released. For example, H. pakistanae was released in the early 1990s at only one location, Lake Boeuf in extreme southern Louisiana, but surveys conducted in 2000 revealed its presence at several locations up to 300 km west and north of the original introductions (Freedman and Grodowitz, unpub.). In Florida, H. pakistanae is found associated with a majority of sites containing hydrilla infestations, indicating considerable range expansion (Center, 1992; Center, pers. comm.). In Texas, populations of H. pakistanae and H. balciunasi also have increased considerably from the four original release sites. One of the most interesting findings has been the discovery of H. pakistanae in the extreme south central portion of Texas on the Rio Grande, more than 250 km from the nearest release site (Grodowitz et al., 1999). Such range extensions are surprising since the introduced Hydrellia spp. are relatively weak fliers with short adult life spans. In addition, the non-contiguous lake systems in both Texas and Louisiana should have hampered range extension for these species. At many sites throughout the country, especially non-release sites, Hydrellia spp. population levels appear minimal with less than 200 immature insects/kg wet weight of hydrilla and leaf damage not exceeding 2%.

Bagous affinis was originally described from India and Pakistan and was first released in the United States in Florida in 1987 (Bennett and Buckingham, 1991). As of the spring of 2001, no permanent populations were known to exist in the United States. Because of its strict environmental requirement for distinct wet/dry periods to allow access to buried tubers, this species has not been released at many sites. Releases in California, at locations where water levels can be controlled, have indicated that this weevil can successfully establish and, with appropriate water level management, overwinter (Godfrey *et al.*, 1996). Unfortunately, because of the hydrilla eradication program in California, the hydrilla at the California site was destroyed soon after verifying overwintering. The use of biological control in conjunction with an aggressive eradication program is counterproductive.

Bagous hydrillae was first released in the United States in Florida in 1991 (Grodowitz *et al.*, 1995), but no established populations have been confirmed. Extensive surveys were initiated, however, no weevils have been recovered at actual release sites even after extended periods. *Bagous hydrillae* adults have only been collected after suspension of releases at one site, Choke Canyon Reservoir, Texas during 1993 and 1994 (Grodowitz et al., 1995). However, soon after the termination of releases *B. hydrillae* adults were no longer observed at Choke Canyon Reservoir.

Suppression of Target Weed and Recovery of Native Plant Communities

Impact of the introduced Hydrellia spp. has apparently been observed at several release sites in Georgia, Florida, and Texas. For example, significant changes have been observed in the hydrilla status at Lake Seminole, Georgia, over the last few years, following the release of more than 1.5 million H. pakistanae in 1992 (Grodowitz et al., 1995; Grodowitz, Cofrancesco, Stewart, and Madsen, unpub.). For the first several years following this large release, numbers of H. pakistanae in Lake Seminole remained at low but detectable levels based on the presence of immatures on randomly selected stem pieces and Berlese funnel extraction of plant material. Beginning in 1997, hydrilla populations began to decline in various areas of the lake and increases in plant diversity were observed that appeared related to increasing H. pakistanae populations. In 1999, large numbers of H. pakistanae adults were observed throughout large areas of the lake and these correlated with significant decreases in hydrilla populations and increases in other native plants, including several species of Potamogeton and Najas. Quantitative sampling of *Hydrellia* immatures based on stem counts and quantification of number of leaves damaged in September 1999 revealed the presence of more than 2,000 immatures per kg wet weight of hydrilla and close to 20% of the total number of leaves damaged. Quantitative plant sampling conducted during November showed significant reductions (ca. four-fold) in tuber numbers and three-fold increases in species richness in areas significantly affected by *H. pakistanae* feeding as observed in September.

While reductions in tuber numbers were surprising, such reductions have been substantiated during large-scale, long-term replicated tank studies conducted recently (Grodowitz et al., 2000b; Doyle, Grodowitz, Smart, Owens, unpub.) and in short-term small container studies (Doyle et al., 2002). In these studies, lower number of tubers and biomass occurred in biological control treatments where damage exceeded 40% of the leaves only for short durations. Similar reductions in hydrilla were observed at Coleto Creek Reservoir, Texas in 1999 and 2000. Reductions in hydrilla were first observed in the two original release sites in 1998 continuing through 1999. Currently, only small quantities of hydrilla persist at the original release sites and reductions in hydrilla have been observed in a nearby cove where fly densities and hydrilla status were quantified for many years to be used as a control. In 1999, higher fly levels were observed in the control cove followed by substantial hydrilla declines in 2000. Observations of the lake in 2000 have shown increasing fly numbers and associated damage throughout the entire reservoir. Sampling of stems during November 2000 demonstrated leaf damages in the 12 to 15 % range for hydrilla located in the extreme northern portion of the lake (Grodowitz et al., 1999; Grodowitz, unpub.). Similar effects also have been observed in Sheldon Reservoir near Houston, Texas (Grodowitz et al., 1999). In these situations, as the hydrilla declined, it was apparently replaced with a mixture of submersed plants, including Eurasian watermilfoil (Myriophyllum spicatum L.), star grass (Heteranthera dubia [Jacquin] MacM.), coontail (Ceratophyllum demersum L.), and various species of Potamogeton and *Najas*, as well as an emergent species, American lotus (Nelumbo lutea [Willd.] Pers.). Unfortunately, the causal relationship between fly establishment and decline in hydrilla is frequently difficult to document. Declines may only be partial and localized. Detailed data are not available to document high levels of larvae in leaves of hydrilla before declines, and natural fluctuations in densities of submersed aquatic plants, such as hydrilla, are common.

Economic Benefits

Economic benefits of the introduced leaf-mining flies in the genus *Hydrellia* cannot yet be evaluated. The effects of these species are just now becoming visible and ongoing evaluation programs will be needed to measure any economic benefits procured.

RECOMMENDATIONS FOR FUTURE WORK

There are four major areas that should to be considered for future work: 1) domestic surveys to evaluate the current expansion and effect of the *Hydrellia* spp. flies that are already established; 2) assessing the influence abiotic and biotic factors have on establishment success and population build-up of these species; 3) developing improved methods for their mass rearing; and 4) conducting overseas surveys to locate previously identified and new biological control agents, especially in regions not studied previously.

Continued field monitoring is needed to gain a clearer understanding of the potential impact of species of Hydrellia flies. This effort should include the development of lower cost, labor-efficient methods to measure hydrilla declines. Measuring changes in submersed plant populations has proven to be more difficult and costly than for terrestrial or floating plants. While range expansion of biological control agents is relatively easy to quantify, it is difficult to measure their impact since weed population changes occur over several growing seasons, with gradual replacement of hydrilla monocultures by mixtures of various native and non-native submersed plants (Grodowitz et al., 1999). Such evaluations are made even more difficult by the patchy distributions of these flies, which also can vary greatly between years at single locations. Reasons for such variation is unknown but could possibly be related to a complex of abiotic and biotic factors including overwintering conditions, plant nutritional variation, parasite loads, etc. For example, Grodowitz et al. (1995) cited that unusually cold weather and the lack of large releases was apparently the cause of declines in *H. pakistanae* populations in 1994 in Muscle Shoals, Alabama ponds.

While many widespread releases of hydrilla biological control agents were made in the early 1990s, introductions into new areas have virtually ceased. Recent research indicates that population size of leafmining flies in a given water body is related to release status. For example, more than seven-fold higher numbers of immatures and percentage leaf damage was associated with actual release sites in Texas, Florida, and Georgia surveyed during 1998 and 1999 (Fig. 11). This strongly indicates the need for further releases of large numbers of individuals at sites that have never had releases previously.

However, rearing large numbers of flies is expensive, with costs per fly exceeding \$0.50 per immature in greenhouse mass-rearing colonies (Freedman and Grodowitz, unpub.). Hence, a typical release of 50,000 individuals per site would cost more than \$25,000 and be prohibitively expensive. Research to develop more cost effective rearing procedures is underway. For example, a mass-rearing facility based on the use of small ponds at an abandoned fish hatchery of the Tennessee Valley Authority Reservation in Muscle Shoals, Alabama, was highly successful (Grodowitz and Snoddy, 1995). A single harvest from a pond at this facility yielded more than 1.5 million flies and resulted in fly establishment throughout Lake Seminole, a large reservoir that borders both Florida and Georgia (Grodowitz, Cofrancesco,

Stewart and Madsen, unpub.). While exact production costs are unknown it was significantly lower than the \$0.50 per fly costs associated with greenhouse rearing techniques. Recently, a mass rearing system using a series of small ponds was implemented at the Lewisville Aquatic Ecosystem Research Facility in Lewisville, Texas. During 2000 and 2001 these ponds produced more than 600,000 individuals. Rearing costs were significantly lower, being less than \$0.03 per immature (M. J. Grodowitz and R. Bare, unpub.). A similar, but smaller facility is currently under construction at the U.S. Army Engineer Research and Development Center in Vicksburg, Mississippi. Such facilities and procedures can significantly increase the number of sites at which releases can be made; however, local cooperation by state wildlife personnel and local water authorities is needed to facilitate the release of mass-reared flies.

Another area where more work is needed is in the understanding of the influence that abiotic and biotic factors have on fly establishment and population increase. Both laboratory and tank studies have quantified the influence of the plant's nutritional composition on growth of *Hydrellia* spp. flies (Wheeler and Center, 1996; Doyle, Grodowitz, and Smart, unpub.). Tissue nutritional components can significantly affect fly survival, development times, fecundity, and female weight (an indicator of overall

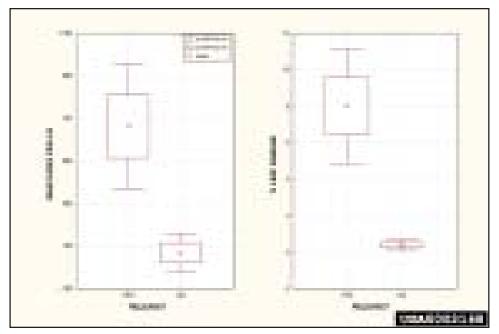


Figure 11. Mean number of immatures per kg and % leaf damage at release and non-release sites during 1999 and 2000 for sites in Texas, Georgia, and Florida.

Hydrilla

health). Nutritional components that appear to be important include nitrogen content and possibly phosphorus content, with higher levels increasing the overall health and vigor of the flies. Preliminary field data has indicated higher fly damage at sites with higher nitrogen levels (Wheeler and Center 2001; Grodowitz and Freedman, unpub.) but further information is needed to verify relationships between establishment success and population increase with plant nutritional composition.

Among biotic factors of importance, more research is needed evaluating the impact of the pupal parasite *Trichopria columbiana* Ashmead, a diapriid wasp that attacks native *Hydrellia* species. Parasitism of the introduced *Hydrellia* species by *T. columbiana* can reach 30% by the end of the growing season in small ponds (Snell and Grodowitz, unpub.). However, the actual effect on fly population growth of removing 30% of the pupae from a given habitat is unknown. Also, *T. columbiana* may induce even higher mortality by probing pupae and hence causing mortality while searching for suitable oviposition sites (Bare and Grodowitz, unpub.).

Highest priority for additional research needs to be given to the collection and study of new agents from overseas locations that attack permanently submersed hydrilla. Complexes of organisms that feed on and damage a variety of plant tissues are frequently needed to effectively suppress a target plant. In the case of hydrilla only one part of the plant, the leaves, are affected by established biological control agents. For efficient suppression, other agents are needed that, for example, could damage stems, roots, apical tips, turions, and/or tubers. Foreign exploration should target areas of the world that have received only limited previous attention, such as Southeast Asia. For example, several weevil species with potential as hydrilla herbivores have previously been identified (Table 2) but were never examined in any great detail.

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SECTION II: WEEDS OF WETLANDS

Australian Paperbark Tree Common Reed Old World Climbing Fern Purple Loosestrife Japanese Knotweed

8 AUSTRALIAN PAPERBARK TREE (MELALEUCA)

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PEST STATUS OF WEED

The exotic tree *Melaleuca quinquenervia* (Cav.) Blake (commonly referred to as melaleuca or paperbark tree) aggressively invades many south Florida ecosystems (Fig. 1), including the Everglades (Hofstetter, 1991; Bodle *et al.*, 1994). It was introduced during the early 1900s or late 1800s (Gifford, 1937; Meskimen, 1962; Dray, pers. comm.). *Melaleuca quinquenervia* displaces native vegetation, degrades wildlife habitat, creates fire hazards, and causes human health problems (Morton, 1962; Diamond *et al.*, 1991). Florida state laws enacted in 1990 and 1993 prohibit the sale, cultivation, and transportation of *M. quinquenervia*. It was placed on the United States Department of Agriculture's Federal Noxious Weed List in 1992 (Bodle *et al.*, 1994; Laroche, 1994).

Although *M. quinquenervia* is a major pest in south Florida, it is considered threatened in its native Australia. Therefore, conservation groups in Australia advocate its protection. *Melaleuca quinquenervia* habitat in Australia comprises lowlying, high-rainfall areas, primarily in coastal regions (Resource Assessment Commission, 1992). Most of the remaining and remnant *M. quinquenervia* woodlands in Australia are located on private land, where clearing for commercial development continues.

Nature of Damage

Economic damage. Melaleuca quinquenervia flowers several times a year producing large amounts of pollen, allegedly a mild respiratory allergen (Morton, 1962; Lockey *et al.*, 1981; Stanaland *et al.*, 1986), from which as much as 20% of the population may suffer allergic reactions (Diamond *et al.*, 1991). In addition, *M. quinquenervia* trees burn with extremely hot crown fires due to high foliar concentrations of essential oils. These fires are difficult to extinguish, often threatening buildings near *M. quinquenervia*-infested areas and causing local municipalities to incur additional fire fighting costs (Diamond *et al.*, 1991).

Melaleuca quinquenervia infested areas become less attractive and monocultures become impenetrable to tourists, hikers, boaters, and other recreational users. Such impacts result in decreased revenues for parks and harm the economies of surrounding communities that rely on tourism associated with wilderness areas (Diamond *et al.*, 1991).

Ecological damage. Prolific seed production, tolerance of brackish water, flooding, and fire enable M. quinquenervia to aggressively invade various wetland habitats and diminish the value of these habitats for native plant communities and associated wildlife (Meskimen, 1962; Crowder, 1974; Myers, 1975; Hofstetter, 1991). Melaleuca quinquenervia may accelerate loss of groundwater due to increased evapotranspiration (Alexander et al., 1977), although this view has been challenged (Allen et al., 1997). Trees produce allelopathic chemicals (Di Stefano and Fisher, 1983), which may enhance their ability to displace native flora. Melaleuca quinquenervia invasion has resulted in significant (60 to 80%) losses of biodiversity in freshwater herbaceous marsh communities in south Florida (Austin, 1978).

Extent of losses. The extent of the *M. quinquenervia* infestation in southern Florida (the area south of Lake Okeechobee) has been estimated at 0.20 to 0.61 million ha of the total 3.04 million ha (7 to 20% of the total) in the region (Bodle *et al.*, 1994). It has been suggested that many of the remaining natural areas within this region will be overtaken by uncontrolled growth of *M. quinquenervia* within 30 years (Bodle *et al.*, 1994).

The National Park Service, the U.S. Fish and Wildlife Service, the U.S. Army Corps of Engineers, and the South Florida Water Management District repeatedly conduct costly and labor-intensive operations to control *M. quinquenervia*. Mechanical removal of a moderately thick stand (about 988 trees/



Figure 1a.



Figure 1b.



Figure 1c.

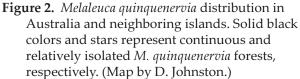
Figure 1. *Melaleuca quinquenervia* in Florida: (a) Flowering sapling representing early invasion stage in seasonally flooded habitat; (b) A wellestablished mature stand in a permanently flooded sawgrass habitat in the Everglades, note the tree stand is surrounded by sawgrass; (c) Vertical section of a stand in seasonally flooded site in the Everglades. (Photographs by M. Rayamajhi and W. Durden.) ha) cost \$2,080/ha (McGehee, 1984), whereas ground herbicide treatment using tree injection techniques cost \$1,330/ha (Laroche et al., 1992). Aerial treatments are less expensive but less effective and cause more damage to non-target plant species. Additionally, seed release is accelerated among trees stressed by herbicides and new infestations are created by dispersal of these seeds (Laroche and Ferriter, 1992). This regeneration of treated stands necessitates repeated herbicidal applications, which compromises environmental preservation. According to a recent estimate, the South Florida Water Management district alone spent more than \$13 million from 1991 to 1998 for M. quinquenervia control in water conservation areas, Lake Okeechobee, and Loxahatchee Wildlife Refuge (Laroche, 1999). Millions of dollars also have been spent by other agencies such as Loxahatchee National Wildlife Refuge, Big Cypress National Preserve, Everglades National Park, Lee County, Miami-Dade County, and Palm Beach County.

Melaleuca quinquenervia trees benefit Florida's beekeeping, chip, mulch, lumber, and pulp industries. However, M. quinquenervia honey is less valuable than that from fruit tree sources. Furthermore, access to M. quinquenervia infestations limits commercial utilization. Failure to control expanding M. quinquenervia infestations would result in an estimated loss of \$168.6 million/year in revenue from reduced ecotourism of the Florida Everglades (Schmitz and Hofstetter, 1999).

Geographical Distribution

Native range. Melaleuca quinquenervia is the southern-most member of the *M. leucadendra* complex. It is distributed within a 40-km-wide zone along Australia's northeastern coast from Sydney in New South Wales to the tip of Cape York peninsula in northern Queensland; in New Guinea; and in New Caledonia (Fig. 2) within the range of 11 to 34° S latitude (Boland *et al.*, 1987). Its altitudinal range is from sea level to about 100 m, sometimes up to 165 m (Boland *et al.*, 1987). It occurs in coastal wetlands that are at least seasonally inundated, such as freshwater swamps, stream banks, and in brackish water behind mangrove swamps. The center of diversity for the *M. leucadendra* complex is on the Cape York Peninsula in northern Queensland (Turner *et al.*, 1998). Barlow





(1988) noted the genus *Melaleuca* to be of northern Australian (tropical) origin, with the high diversity in temperate areas representing a secondary area of species radiation.

Florida. The main infestations of M. *quinquenervia* exist along both coasts of southern Florida with scattered infestations in between (Fig. 3). The northernmost records (ca. 30° N latitude) are in Gainesville (Turner *et al.*, 1998).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The taxonomic position of *M. quinquenervia* according to Cronquist (1988) is as follows: class Magnoliopsida (Dicot), subclass Rosidae, order Myrtales, family Myrtaceae, subfamily Myrtoidea, tribe Leptospermae, genus *Melaleuca*, species *quinquenervia* (Cav.) Blake. Synonyms include *M. leucadendra* L., *M. viridiflora* var. *angustifolia* (L.f.) Byrnes, *M. viridiflora* var. *rubiflora* Brong. and Gris., and *Metrosideros quinquenervia* Cav.

Linnaeus coined the genus name *Melaleuca* (Greek *melas* = black and *leucos* = white), probably in reference to the fire-charred white bark (Holliday, 1989). The genus contains at least 219 and perhaps more than 250 species (Craven and Lepschi, 1999) and is the third largest angiosperm genus in Australia (Barlow, 1986). *Melaleuca quinquenervia* is a member of the *M. leucadendra* (L.) L. group, 15 species that are mostly large shrubs or trees and occur primarily in northern and northeastern Australia (Boland *et al.*, 1987; Craven, 1999).

Biology

Holliday (1989) and Bodle *et al.* (1994) describe *M. quinquenervia* as being erect trees up to 25 m tall with multi-layered, thick white or grayish papery bark that insulates the trunk and branches. Leaves are lanceolate-elliptical to oblanceolate with five prominent longitudinal veins; up to 3 cm broad and 10 cm long; and flat, stiff, and leathery when mature. In general, woody biomass constitutes a major portion (83 to 96%) of dry weight across habitats (non-flooded, seasonally flooded, and permanently flooded), with the remaining portion (4 to 17%) being comprised of foliage and seed capsules (Rayachhetry *et al.*, 2001).

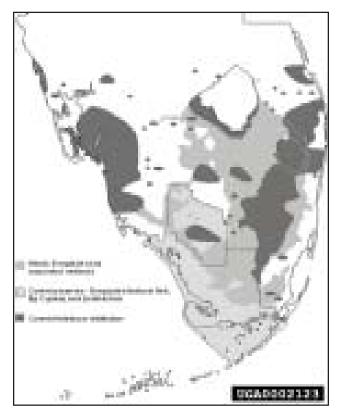


Figure 3. *Melaleuca quinquenervia* distribution in Florida. Note stand concentrations along east and west cost of central and south Florida and scattered stands in between. (Map by D. Johnston.)

In Florida, some M. quinquenervia trees become reproductive within a year of germination, and flowering events occur several times a year (Meskimen, 1962). Inflorescences are indeterminate, 2 to 5 cm long, and arranged in bottlebrush-like spikes (Holliday, 1989). Flowers are white or cream colored, with tripartite ovaries surrounded by five sepals. Five petals surround 30 to 50 stamens, and a pistil. Capsular fruits are persistent, arranged in the series of clusters, and may remain attached to the trunks, branches, or twigs for several years (Meskimen, 1962). In Florida, a flower spike can produce 30 to 70 sessile capsules (Meskimen, 1962). In excess of seven linearly occurring capsule clusters (each separated by series of leaves) have been recorded from M. quinquenervia branches (Rayachhetry et al., 1998). Seed capsule biomass (dry weight) on trees in permanently flooded habitats is two-fold greater compared to seasonally flooded habitats (3 to 4% vs. 2% of total biomass). These serotinous capsules release seeds when their vascular connections are disrupted by increased bark thickness or stresses such as fire, frost, mechanical damage, herbicide treatments, or self-pruning of branches (Woodall, 1982; Hofstetter, 1991). The canopy of a mature tree (38 cm diameter at breast height and 12 m height) may hold up to 1.4 kg of seeds (about 56 million seeds) (Rayachhetry, unpub. data). While massive, synchronous seed release occurs in response to various stresses, some capsules open successively in a non-synchronous manner, resulting in a light but constant seed rain (Woodall, 1982; Hofstetter, 1991). In Florida, capsules contain 200 to 350 seeds each (Meskimen, 1962) and each seed weighs ca. 25 ì g (Rayachhetry, unpub. data). Only about 15% of the canopy-held seeds in Florida are filled (embryonic). Overall, about 9% of seeds are viable and 7% can germinate, suggesting that ca. 2% remain dormant (Rayachhetry et al., 1998). Enforced dormancy under field conditions is suggested by the fact that a small proportion of buried seeds remain germinable for more than two years (Van, unpub. data). Forest fires reduce competition, prepare ash-enriched forest floors, and promote establishment and rapid growth of seedlings, provided the soil remains wet and the canopy is open. Seed germination occurs in both shade and sun, as well as under submerged conditions (Meskimen, 1962; Lockhart, 1995). However, prolonged submergence (six to 12 months) and fire can kill smaller seedlings (Myers, 1975; Woodall, 1981).

Because of the massive seed release from mother trees, extremely dense (more than 250,000/ha of 3to 4 m-tall trees) *M. quinquenervia* stands are common (Hofstetter, 1991; Van *et al.*, 2000). Standing biomass of 129 to 263 metric ton/ha has been reported for *M. quinquenervia* in the United States and Australia (Van *et al.*, 2000). *Melaleuca quinquenervia* is fire adapted (Stocker and Mott, 1981; Ewel, 1986). It has layers of thick, spongy bark; dormant epicormic buds on trunks that regenerate new shoots; and is capable of sprouting from roots (Turner *et al.*, 1998).

Analysis of Related Native Plants in the Eastern United States

The Myrtaceae is a large, diverse plant family with approximately 100 genera and 3,000 species worldwide (Stebbins, 1974). It is almost entirely tropical in distribution. The group achieves maximum diversity in Australia, where several hundred species are known, but it is also quite diverse in the New World tropics. The family was formerly divided into two groups (the Myrtoideae and Leptospermoidae) based upon characteristics of the fruit. The Myrtoideae, which are centered in tropical America, produce berries whereas the Leptospermoideae, which are centered in Australia, produce serotinous capsules. Eight indigenous species of Myrtoideae occur in the continental United States and Florida (Tomlinson, 1980), including the genera Eugenia, Calyptranthes, Psidium, and Myrcianthes, commonly referred to as "stoppers." Some species such as red stopper (Eugenia rhombea Krug and Urban) and long-stalked stopper (Psidium longipes [Berg] McVaugh) are rare and considered endangered. All native Florida species are threatened by loss of habitat to development. At least 30 non-native species of Eugenia (sensu latu), as well as species in other Myrtoideae genera, are cultivated in Florida for their edible fruits and for ornamental uses (Menninger, 1958). Besides M. quinquenervia, about 56 additional Melaleuca species have been imported to Florida, of which at least 16 and 14 species were common in California and Florida, respectively, during the first decade of the 20th century (Dray, pers. comm.). Current status of these additional Melaleuca species in both states is not known. No native species of Leptospermoideae occur in North America. Besides Melaleuca, the only representatives of Leptospermoideae present in Florida are a few species of Australian native Callistemon (bottlebrush, some of which have been recently transferred to the genus *Melaleuca*). These have been widely planted as landscape ornamentals.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Australia is clearly the center of origin for the genus Melaleuca, but a few tropical species within this genus extend into New Guinea, New Caledonia, Malaysia, and Burma (Holliday, 1989; Craven, 1999). The *M. leucadendra* group consists of broad-leaved Melaleuca species, including M. quinquenervia and 14 closely related species (Craven, 1999). This group is widespread along the eastern coast of Australia, from Sydney to Cape York. It also occurs in New Caledonia and the southern parts of Papua New Guinea and Irian Jaya (Blake, 1968). In Australia, M. quinquenervia is more common in the southern part of its range, mainly growing along streams and in swamps (Holliday, 1989), or in seasonally inundated, low-lying areas. Five separate sources (Nice, France; Ventimiglia, Italy; Tamatave, Madagascar; Sydney, Australia; and Burringbar, Australia), mostly botanical gardens or plantations, have been identified for the M. quinquenervia seeds that were introduced into Florida (Dray, pers. comm.).

Areas Surveyed for Natural Enemies

Preliminary surveys to locate biological control agents for M. quinquenervia were conducted in New Caledonia and southeastern Queensland in 1977 (Habeck, 1981). The United States Department of Agriculture, Australian Biological Control Laboratory (USDA ABCL), started a long-term exploration program in 1986. Surveys have been conducted from south of Sydney in New South Wales, along the eastern seaboard of Australia, to Cape Flattery in northern Queensland. Searches for biological control agents on other broad-leaved Melaleuca spp., closely related to M. quinquenervia, also were conducted near Darwin in the Northern Territory, and in southern Thailand. During November 1999, several species in the *M. leucadendra* complex were surveyed for pathogens in southern and northern Queensland and northeastern New South Wales in Australia. A number of microorganisms have been found associated with *M. quinquenervia* in Florida and in Australia.

Natural Enemies Found

More than 450 plant-feeding insect species have been collected from *M. quinquenervia* in Australia, and an additional 100 species have been collected from closely related Melaleuca spp. (Balciunas et al., 1994a, 1995). Of the major herbivores (Table 1), seven species have been intensively studied, but only five have been introduced into domestic quarantine facilities. Only the melaleuca snout beetle (leaf weevil), Oxyops vitiosa Pascoe, and the melaleuca psyllid, Boreioglycaspis melaleucae (Moore), have been released. The bud gall fly, Fergusonina n. sp. Malloch, is currently undergoing host range testing. The melaleuca defoliating sawfly, Lophyrotoma zonalis (Rohwer), is being tested for vertebrate toxicity. The mirid bug Eucerocoris suspectus Distant and the tip wilting bug, Pompanatius typicus Distant, though very damaging (Burrows and Balciunas, 1999) were found to be insufficiently host specific for introduction. Other insects, including a leaf-galling cecidomyiid (Lophodiplosis indentata Gagné), several flower-feeding tortricids (Holocola sp., Thalassinana species group), and the tube-dwelling pyralid moth Poliopaschia lithochlora (Lower), are currently undergoing preliminary host range testing in Australia.

Previously, a few fungal species had been reported from *M. quinquenervia* and its allies in Florida, Australia, and some other parts of the world (Alfieri *et al.*, 1994; Rayachhetry *et al.*, 1996ab, 1997). Four additional fungal species (*Fusarium* sp., *Pestalotiopsis* sp., *Phyllosticta* sp., *Guignardia* sp.) have recently been found to be associated with *M. quinquenervia* and its close relatives in Australia (Rayachhetry, unpub. data).

Host Range Tests and Results

Three herbivorous insect species (O. vitiosa, L. zonalis, and B. melaleucae) have been subjected to intensive host specificity tests. These host range studies have shown O. vitiosa, L. zonalis, and B. melaleucae to be specific to M. quinquenervia. Small amounts of feeding and development through only one generation in the laboratory were found on a few test plant species, mostly Callistemon spp. (Balciunas et al., 1994b; Buckingham, 2001; Center et al., 2000;

Scientific Name	Unofficial Common Name	Impact/Current Research Status				
	Agents Released and Established					
Oxyops vitiosa (Coleoptera: Curculionidae)	Snout beetle	Foliage on growing branch tips grazed; tip dieback/field impact evaluation				
<i>Boreioglycaspis melaleucae</i> (Hemiptera: Psyllidae)	Melaleuca psyllid	Foliage and stems wilt, saplings killed; quarantine studies completed				
Agents Introduced into U.S. Quarantine						
<i>Lophyrotoma zonalis</i> (Hymenoptera: Pergidae)	Melaleuca defoliating sawfly	Complete defoliation of trees; quarantine studies completed, found to be host specific and vertebrate toxicity testing underway				
Fergusonina sp. (Diptera: Fergusoninidae)	Bud-gall fly	Floral and vegetative buds galled; growth and reproduction retarded; further quarantine studies underway				
<i>Eucerocoris suspectus</i> (Hemiptera: Miridae)	Leaf-blotching bug	Young foliage blotched and distorted resulting in leaf drop; attacks bottlebrushes; dropped from further consideration				
Agents under Evaluation in Australia						
<i>Holocola</i> sp., Thalassinana species group (Lepidoptera: Tortricidae)	Inflorescence axis borer	Flower buds aborted; immature flowers and foliage damaged				
<i>Lophodiplosis indentat</i> a (Diptera: Cecidomyiidae)	Pea-gall fly	Young foliage distortion				
Careades plana (Lepidoptera: Noctuidae)	Defoliating noctuid	Stem and branch defoliation				
<i>Paropsisterna tigrina</i> (Coleoptera: Chrysomelidae)	Defoliating chrysomelidae	Stem and branch tip defoliation				
<i>Poliopaschia lithochlora</i> (Lepidoptera: Pyralidae)	Tube-dwelling moth	Shoots webbed; defoliated				
Agents with Questionable Specificity or are Poorly Known						
<i>Pomponatius typicus</i> (Hemiptera: Coreidae)	Tip-wilting bug	Wilting of stem and branch tips; rejected due to low host specificity				
? Acrocercops sp.(Lepidoptera: Gracillariidae)	Leaf blister moth	Young foliage mined and blistered				
<i>Haplonyx multicolor</i> (Coleoptera: Curculionidae)	Flower weevil	Damage of flowers and foliage				
<i>Cryptophasa</i> spp. (Lepidoptera: Oecophoridae)	Branch fork moth	Defoliation; weakening of branch forks				
Rhytiphora sp.(Coleoptera: Cerambycidae)	Stem boring longicorn beetle	Branches and stems killed				
Pergaprapta sp. (Hymenoptera: Pergidae)	Gregarious sawfly	Defoliation of growing branch tips				
<i>Acanthoperga cameroni</i> i (Hymenoptera: Pergidae)	Sapling sawfly	Defoliation of growing branch tips, especially of saplings				

Table 1. Insects under Investigation for Biological Control of Melaleuca quinquenervia

Wineriter and Buckingham, 1999). However, extensive field studies in Australia determined that *Callistemon* spp. are not host plants of *O. vitiosa, L.* zonalis, or *B. melaleucae* (Balciunas et. al., 1994b; Burrows and Balciunas, 1997; Purcell et al., 1997). Currently, federal authorities are preparing biological and environmental assessments for the field release of *B. melaleucae*. Australian host range studies have demonstrated that the bud-gall fly, *Fergusonina* sp., also is highly specific to *M. quinquenervia* and it is undergoing further host specificity testing at the quarantine facilities in Florida.

Botryosphaeria ribis (a canker fungus) and Puccinia psidii (a rust fungus) were evaluated in south Florida as potential *M. quinquenervia* biological control agents. Botryosphaeria ribis appeared to be a plurivorous pathogen (Smith, 1934) that attacked stressed plants (Punithalingham and Holiday, 1973; Rayachhetry *et al.*, 1996c,d), while *P. psidii* attacked vigorously growing *M. quinquenervia* branch tips (Rayachhetry *et al.*, 1997) and had a host range restricted to the family, Myrtaceae (Rayachhetry *et al.*, 2001b).

Releases Made

Of the five insects imported into Florida quarantine, only O. vitiosa and B. melaleucae have been released (Center et al., 2000). Adults and/or larvae of O. vitiosa were released during spring 1997 at both permanently and seasonally flooded habitats. By winter 2000, more than 47,000 adults and 7,000 larvae had been released at more than 97 locations in south Florida. Oxyops vitiosa established at all but the permanently flooded sites. Even small releases of 60 adults successfully produced viable populations when site conditions were favorable (Center et al., 2000). However, populations have dispersed slowly. Ease of establishment and slow dispersal suggested an optimal introduction strategy of numerous small releases at carefully selected but widely dispersed sites. Currently, the distribution of O. vitiosa is limited compared to the vast area occupied by M. quinquenervia. Therefore, concerted establishment and redistribution efforts are ongoing to ensure the widespread colonization of M. quinquenervia in south Florida. Boreioglycaspis melaleucae was first released during Spring 2002 but it is not yet certain whether populations have established.

BIOLOGY AND ECOLOGY OF NATURAL ENEMIES

Oxyops vitiosa (Coleoptera: Curculionidae)

Oxyops vitiosa larvae prefer to feed on relatively new foliage (Fig. 4a), while adults feed on both young (Fig. 4b) and old (Fig. 4c) foliage. The resultant damage stunts growth of saplings and reduces foliage production in older trees. Larvae are most damaging, feeding on one side of a leaf through to the cuticle on the opposite side, which produces a window-like feeding scar (Fig. 4a). This damage may persist for months, ultimately resulting in leaf drop (Fig. 5). Adult feeding on young and mature leaves is characterized by holes (Fig. 4b) and narrow scars along the leaf surfaces (Fig. 4c), respectively. Oviposition occurs mainly during daylight hours from September to March in Florida (Center et al., 2000). Eggs are laid singly, or in small clusters, on the surface of young leaves, usually near their apex, or on stems of young shoots. A hardened black-to-tan coating of frass and glandular materials covers individual eggs. In Florida, larvae are absent or uncommon from April to August unless damage-induced regrowth is present (Center et al., 2000). Pupation occurs in the soil, usually beneath the host plant. Egg-to-adult development requires about 50 days. Females survive up to 10 months and can produce more than 1,000 eggs. Adults can be collected year round.

Boreioglycaspis melaleucae (Homoptera: Psyllidae)

The melaleuca psyllid, *B. melaleucae*, severely damages *M. quinquenervia*, especially in the absence of its predators and parasites. Nymphs are parasitized by *Psyllaephagus* sp. (Hymenoptera: Encyrtidae) and preyed on by coccinellids (Coleoptera) and lygaeids (Hemiptera) in Australia. This psyllid was collected in northern and southeastern Queensland and northern New South Wales during field surveys in Australia. Collection records also exist for Western Australia and the Northern Territory. Psyllids, both adults and nymphs, reportedly feed on phloem sap through the stomata (Clark, 1962; Woodburn and Lewis, 1973); however, nymphs cause the most damage by inducing defoliation and sooty mold growth on excreted honeydew. Populations of *B. melaleucae*



Figure 4a.



Figure 4b.



Figure 4c.

Figure 4. *Oxyops vitiosa* on *Melaleuca quinquenervia*: (a) Two larvae and typical larval feeding damage on a twig tip, note feeding scars on young leaves; (b) Adults aggregated on young tips, note typical adult feeding holes on young leaves; (c) Note an adult and feeding scars on fully mature leaves at the tip of a twig. (Photographs by W. Durden and G. Buckingham.)



Figure 5. Severely defoliated (bare twigs) upper crown of *Melaleuca quinquenervia* trees. Such branch defoliation and twig dieback is caused by severe larval and adult feeding damages. (Photograph by T. Center.)

grow rapidly, causing moderate leaf curling, discoloration, defoliation, and plant mortality.

Adults of *B. melaleucae* mate throughout the day and the male grasps the female with large abdominal claspers (parameres) before mating. Females oviposit on leaves or stems of host plants and lay an average of 78 eggs. Each egg is attached to the leaf by a pedicel that is inserted into the plant tissue to absorb water (White, 1968). Most eggs hatch within 18 days. Nymphs of *B. melaleucae* congregate on leaves and secrete white, flocculent threads, which can completely cover the nymphs. These secretions facilitate easy detection at field sites. Like all psyllids, *B. melaleucae* has five instars (Hodkinson, 1974) and development from egg to adult takes 28 to 40 days. Purcell *et al.*, (1997) present a complete biology of *B. melaleucae*.

Lophyrotoma zonalis (Hymenoptera: Pergidae)

The defoliating melaleuca sawfly, *L. zonalis*, was the most damaging insect observed on *Melaleuca* spp. in Australia. It was collected from Mackay in central Queensland to the Daintree River in north Queensland, and near Darwin in the Northern Territory. Records also indicate its presence in New Guinea (Smith, 1980). Larvae are voracious leaf feeders and dense populations cause complete defoliation. Defoliation stresses trees and reduces flowering during subsequent years (Burrows and Balciunas, 1997). Adults do not feed on the plant tissue. They are frequently observed swarming around the bases of trees.

Larvae burrow into the papery bark of M. *quinquenervia* to pupate, unlike many other pergid sawflies that pupate in soil. It therefore should be an excellent agent for use in wetter areas, where other agents are less effective. Females are parthenogenic, producing all males when unmated, while mated females produce both males and females.

Burrows and Balciunas (1997) provide a detailed description of the life history of L. zonalis. The life cycle from egg to adult takes approximately 12 weeks. Females insert eggs into the tissue along the edges of leaves using their saw-like ovipositors. The subsequent egg batches form a line along the leaf margin, and harden and turn brown with age. Females oviposit up to 140 eggs in their lifetime, which are heavily parasitized in Australia. The neonate larvae feed gregariously, forming a feeding front across the leaf; later instars become solitary feeders. Three unidentified fly species (Diptera: Tachinidae) and one wasp species (Hymenoptera: Ichneumonidae) parasitize larvae. The final instar, or prepupa, does not feed and burrows into the bark of the trunk and lower branches to excavate a chamber in which it enters the pupal stage. In Australia, L. zonalis is mainly found during the summer months and a resting, possibly diapausing, prepupal stage occurs during winter. Larval outbreaks also occasionally occur during cooler months.

The toxic peptides lophyrotomin and pergidin, which have been reported in three other sawflies from around the world (Oelrichs *et al.*, 1999), have recently been detected in *L. zonalis* larvae (Oelrichs, pers. comm.). Consumption of large quantities of larvae of a related sawfly from *Eucalyptus* sp. causes cattle mortality in Australia, although *L. zonalis* has never been implicated in livestock or wildlife poisonings (Oelrichs *et al.*, 1999). Therefore, the decision to release *L. zonalis* in Florida awaits assessment of the risk of this insect to wildlife and livestock.

Fergusonina sp. (Diptera: Fergusoninidae)

The *M. quinquenervia* bud-gall fly, *Fergusonina* sp., forms galls in vegetative and reproductive buds of *M. quinquenervia* in a unique, mutualistic association with nematodes of the genus *Fergusobia* Currie (Nematoda: Tylenchida: Sphaerulariidae). Preliminary data indicate that the nematode initiates gall production (Giblin-Davis *et al.*, 2001). *Fergusonina* sp. have been reared from most broad-leaved *Melaleuca* spp. in Australia, although the flies on each

plant species appear to be unique (Taylor, pers comm.). Galls on *M. quinquenervia* vary greatly in size and color, depending on growth stage and type of buds being attacked, and on developmental stage of the gall. They have the potential to impede branch and foliage growth, and retard flower formation resulting in reduced seed set. These galls also may act as nutrient sinks, reducing plant vigor (Goolsby *et al.*, 2000). However, the gall production is seasonal, with highest densities occurring during periods of maximum leaf bud production, usually during winter and spring (Goolsby *et al.*, 2000). The flies are heavily parasitized by several species of parasitic Hymenoptera in Australia.

Botryosphaeria ribis (Pleosporales: Botryosphaeraceae)

Grossenbacher and Duggar (1911) first described B. ribis from currants (Ribes sp.) in New York. Taxonomy, biology, and ecology of this fungus are discussed in Punithalingam and Holliday (1973), Morgan-Jones and White (1987), and Rayachhetry et al. (1996a). It belongs to a group of fungi that produce conidiospores (asexual spores) in stromatic pycnidia and/or ascospores in ascomata on the surface of stems, leaves, and fruits. The mode of entry into stem tissues is assumed to be through wounds, frost-induced cracks, sun-scorched bark, lenticels, or branch stubs. Stems of healthy plants callus rapidly, and the fungus may remain latent under the callus tissues, causing perennial cankers when trees are stressed. Stems and branches of stressed trees are girdled quickly due to the plants' inability to callus and compartmentalize the fungus. Infected plants may die back, show vascular wilt, or crown thinning. Affected vascular tissues usually appear brown to black in color (Rayachhetry et. al., 1996d).

Puccinia psidii (Uredinales: Pucciniaceae)

Puccinia psidii, commonly known as guava rust, has been reported on 11 genera and 13 species in the family Myrtaceae in Central America, Caribbean Islands, and South America (Laundon and Waterston, 1965; Marlatt and Kimbrough, 1979). In 1996, *P. psidii* was found to attack healthy new growth of *M. quinquenervia* (Rayachhetry *et al.*, 1997). Figueiredo *et al.*, (1984) studied the life cycle of *P. psidii* on *Syzygium jambos* (L.) Alston, and reported three spore stages (uredospore, teliospore, and basidiospore) in its life cycle. Only uredinial pustules have been observed on *M. quinquenervia* in Florida, but other stages also may exist. No alternate host has been discovered and it is assumed to be autoecious (Figueiredo *et al.*, 1984). Guava rust attacks both foliage and succulent stems of vigorously growing *M. quinquenervia* saplings. Rust disease on *M. quinquenervia* is usually severe during winter and spring. Severe infections cause foliage distortion, defoliation, localized swellings on twigs, and tip diebacks (Rayachhetry *et al.*, 2001b).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Oxyops vitiosa is now established at many locations in south Florida where larvae or adults were released; however, rate of spread is limited (Center et al., 2000). Slowly expanding O. vitiosa populations now exist in Dade, Broward, Lee, Collier, Palm Beach, Martin, Monroe, Sarasota, and Glades Counties. Habitats with short hydroperiods, dry winter conditions, and abundant young foliage favor growth and development of O. vitiosa. Oxyops vitiosa populations did not establish in permanently aquatic sites because of the soil requirement for pupation (Center et al., 2000). Dispersal occurs more rapidly at sites where the trees are scattered savannah-like in open areas. Other factors such as geographical location, hydroperiod, wind direction, life stage released, or date of release do not affect the rate of overall dispersal (Pratt, unpub. data). Also, adults seem to move from unsuitable trees (tall, dense stands with a paucity of young foliage) onto trees that provide acceptable foliage (smaller, bushier, open-grown trees with an abundance of young foliage) (Center et al., 2000).

Suppression of Target Weed

Oxyops vitiosa adults feed on both old and new foliage as well as on emerging vegetative and reproductive buds (Fig. 4). Early instars feed only on young succulent foliage, while late instars are less discriminating (Fig. 4a). Adults feed on both young and mature leaves (Figs. 4b, c). Severe adult or larval feeding results in tip dieback and defoliation (Fig. 5). Repeated damage of growing tips removes apical dominance and induces lateral growth from axillary buds. Subsequent new growth acts as a nutrient sink and sustains continual adult and larval weevil populations. Foliar damage, and the subsequent diversion of photosynthetic resources to the development of new foliage, appears to limit reproductive performance of *M. quinquenervia*. In preliminary studies, flowering of severely damaged *M. quinquenervia* trees was reduced more than 90%, (Pratt, unpub. data).

Repeated defoliation weakens the trees' defense mechanisms, predisposing them to attack by other insects and pathogens. As a result, existing populations decline as their regenerative capabilities become reduced. The diverse community of insects that damage M. quinquenervia in Australia probably suppresses the regenerative potential of native melaleuca forests. For example, the number of seed-capsules per unit of infructescense length is three and eight capsules/cm in Australia and Florida, respectively. Similarly, the viability (9.1 vs. 3.3%) and germinability (in 14 days, 7.8 vs. 2.8%) of M. quinquenervia seeds are significantly higher in the United States than in Australia. The reduction in seed production, and thus the invasibility of *M. quinquenervia*, is the primary objective of the biological control program. While removal of existing stands may be best accomplished by other means (herbicides and mechanical removal), a reduction in canopy seed production through biological control should enhance the efficacy of the overall management program (Laroche, 1999).

Recovery of Native Plant Communities

The diversity and abundance of native plant species in areas invaded by *M. quinquenervia* should begin to recover as *M. quinquenervia* canopies open due to crown thinning and/or tree mortality resulting from feeding by biological control agents. Long-term monitoring programs have been initiated by establishing permanent plots in *M. quinquenervia*-infested sites to document such events in dry, seasonally inundated, and aquatic habitats.

Economic Benefits

The containment and/or elimination of M. quinquenervia monocultures should produce economic benefits by sustaining the tourist industry, permitting the recovery of native flora and fauna, decreasing the risk to human health, and reducing the fire hazard to urban areas near highly flammable *M. quinquenervia* stands.

RECOMMENDATIONS FOR FUTURE WORK

Currently, the M. quinquenervia biological control program is focused on procuring additional biological control agents. Additional quarantine space is needed to improve and accelerate host testing of additional agents. Construction of a new facility designed for this purpose began at Fort Lauderdale during December 2001. The primary focus of the Fort Lauderdale Invasive Plant Research Laboratory has been the release of new agents as they become available, and the evaluation of those agents that establish. To combat the M. quinquenervia invasion and successfully reduce its impact, state and federal agencies will need to (1) continue foreign exploration for new biological control agents, with special emphasis on those that will complement the effects of existing agents; (2) continue to evaluate host specificity and efficacy of promising agents; (3) import selected agents into quarantine for further evaluation; (4) accelerate release programs through development of efficient testing facilities and reduction of avoidable delays; (5) develop a thorough understanding of the biology and ecology of the host as well as the candidate biological control agents, both in Florida and Australia, to enhance agent selection and subsequent establishment; (6) acquire necessary permits for field release of the bud-gall fly into M. quinquenervia populations in south Florida; (7) continue to monitor field populations of established agents and redistribute them to new locations as needed; and (8) monitor the impact of released agents at individual plant, community, and landscape scales.

Because *M. quinquenervia* is a large perennial tree, the effect of biological control agents likely will be slow and cumulative over an extended period of time. In addition to *O. vitiosa*, and *B. melaleucae* which have already been released, other insects are either waiting for field-release permission or undergoing evaluation in Australia or in U.S. quarantine. Therefore, evaluation of the performance of released agents in the field and their relationship with predators and pathogens in Florida should continue with special emphasis on (1) measuring changes in the reproductive potential of existing trees and monitoring for signs of population decline and habitat recovery; (2) assessing the impact of predators, parasitoids, and pathogens on the released biological control agent populations; (3) monitoring other plant species to validate host specificity research and determine whether non-target effects occur; and (4) developing and integrating selected fungal agents into the suite of herbivorous biological control agents.

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9 COMMON REED

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PEST STATUS OF WEED

Common reed (Fig. 1), Phragmites australis (Cav.) Trin. ex Steudel, is a widely distributed clonal grass species, ranging all over Europe, Asia, Africa, America, and Australia (Holm et al., 1977). Extensive reed beds are protected in Europe (Tscharntke, 1992) because of their important ecological functions. In contrast, the rapid expansion of *P. australis* in North America, particularly along the Atlantic coast (Chambers et al., 1999), is considered a threat to biodiversity in natural areas (Marks et al., 1994). Peat core analysis (Orson, 1999) shows that P. australis was an uncommon component of marshes in New England several thousand years ago. Recent genetic evidence (Saltonstall, 2002) has now confirmed that a more aggressive genotype has been introduced to North America (Metzler and Rosza, 1987; Tucker, 1990; Mikkola and Lafontaine, 1994; Besitka, 1996, Orson, 1999), probably in the late 1800s along the Atlantic coast (Saltonstall, 2002). The distribution of the native genotypes is not well known but they appear more common in the western part of the continent (Saltonstall, 2002). At present, invasive P. australis occurs throughout the whole of the United States, except Alaska and Hawaii; however, problems caused by non-indigenous P. australis are most severe along the Atlantic coast.

Nature of Damage

Economic damage. Phragmites australis is largely a weed of natural areas and direct economic damage has not been assessed or reported.

Ecological damage. Phragmites australis invasion alters the structure and function of diverse marsh ecosystems by changing nutrient cycles and hydrological regimes (Benoit and Askins, 1999; Meyerson *et al.*, 2000). Dense *Phragmites* stands in North America decrease native biodiversity and quality of



Figure 1. *Phragmites australis* invasion front at the Montezuma National Wildlife Refuge, New York. (Photograph by B. Blossey.)

wetland habitat, particularly for migrating waders and waterfowl species (Thompson and Shay, 1989; Jamison, 1994; Marks *et al.*, 1994; Chambers, 1997; Meyerson *et al.*, 2000). A survey of Connecticut marshes showed that rare and threatened bird species in the area were associated with native, shortgrass habitats and were excluded by *Phragmites* invasion (Benoit and Askins, 1999).

Extent of losses. Lack of long-term data makes quantification of direct losses difficult. At sites where *Phragmites* eradication programs have been instigated, such as Primehook National Wildlife Refuge in Delaware, waterfowl abundance has significantly increased following control procedures (G. O'Shea, pers. comm.). Recovery of bird communities after chemical control of *P. australis* suggests a significant habitat loss due to encroachment by common reed.

Geographical Distribution

Presently, non-indigenous, invasive *P. australis* is most abundant along the Atlantic coast and in freshwater and brackish tidal wetlands of the northeastern United States, and as far south as North Carolina. It occurs in all eastern states and populations are expanding, particularly in the Midwest.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Phragmites australis is a perennial monocot in the family Poaceae, tribe Arundineae (Clayton, 1967). The genus *Phragmites* includes four species, with *P. australis* being distributed worldwide; *Phragmites japonicus* Steudel being found in Japan, China, and eastern areas of Russia; *Phragmites karka* (Retz.) Trin. found in tropical Africa, Southeast Asia, and northern Australia; and *Phragmites mauritianus* Kunth in tropical Africa and the islands of the Indian Ocean (Darlington and Wylie, 1955; Clayton, 1967; Tucker, 1990; Besitka, 1996). The status of the eleven recently discovered native haplotypes (Saltonstall, 2002) needs further evaluation. All species show high phenotypic plasticity making species identification difficult (Clayton, 1967).

Biology

Phragmites australis is a clonal grass species with woody hollow culms that can grow up to 6 m in height (Haslam, 1972). Karyotypic studies in North America have identified different ploidy levels with populations of 3x, 4x, and 6x plants, but with 4x being the dominant chromosome number in modern day populations (Besitka, 1996). Leaves are lanceolate, often 20 to 40 cm long and 1 to 4 cm wide. Flowers develop by mid-summer and are arranged in tawny spikelets with many tufts of silky hair.

P. australis is wind pollinated but self-incompatible (Tucker, 1990). Seed set is highly variable and occurs through fall and winter and may be important in colonization of new areas. Germination occurs in spring on exposed moist soils. Vegetative spread by below-ground rhizomes can result in dense clones with up to 200 stems/m² (Haslam, 1972).

Analysis of Related Native Plants in the Eastern United States

Phragmites australis is a member of the Poaceae with more than 100 genera represented in the northeastern United States alone (Gleason and Cronquist, 1991). The closest related species to *P. australis* is *Arundo donax* L., an invasive introduced species. The most important genera to consider for their wildlife value include species of *Typha*, *Spartina*, *Carex*, *Scirpus*, *Eleocharis*, *Juncus*, *Arundinaria*, and *Calamagrostis*.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Research in North America and Europe began in 1998 with literature and field surveys for potential control agents (Tewksbury *et al.*, 2002)

Area of Origin of Weed

The current distribution of P. australis includes Europe, Asia, Africa, America, and Australia (Holm et al., 1977), however, the origin of the species is unclear. The rapid spread of *Phragmites* in recent years in North America has led wetland ecologists to believe that the species may be introduced. However, Phragmites rhizomes were found in North American peat cores dated 3,000 years old (Orson, 1999). Several different hypotheses have been proposed to explain the recent population explosion in North America, including the introduction of more aggressive European genotypes about 100 years ago (Besitka, 1996; Orson, 1999). The absence of specialized North American herbivores of P. australis in North America and the lack of wildlife use are indications for the introduced status of the species (Tewksbury et al., 2002). Saltonstall (2002) has compared historic and present day populations of P. australis from North America and other continents using advanced genetic techniques. Her results show that present day populations in North America consist of a mixture of eleven non-invasive native North American haplotypes and one distinctive introduced invasive (most likely European) haplotype (Saltonstall, 2002). The status of an additional haplotype (either native or introduced) growing along the Gulf of Mexico is still unresolved (Saltonstall, 2002).

Areas Surveyed for Natural Enemies

In 1997, literature surveys and limited field surveys in the northeastern Unites States began. Work in Europe started in 1998 with additional literature surveys and the estblishment of field sites in Hungary, Austria, Germany, and Switzerland (Schwarzländer and Häfliger, 1999).

Natural Enemies Found

Literature and field surveys (in the northeastern United States and eastern Canada) reveal that currently 26 herbivores are known to attack *P. australis* in North America (Tewksbury et al., 2002). Many of these species were accidentally introduced during the last decades; only five are potentially native (Tewksbury et al., 2002). Only the Yuma skipper, Ochlodes yuma (Edwards) (a species distributed throughout the western United States); a dolichopodid fly in the genus *Thrypticus*; and a gall midge, Calamomyia phragmites (Felt), are considered native and monophagous on P. australis (Gagné, 1989; Tewksbury et al., 2002). The native broad-winged skipper, Poanes viator (Edwards), has recently included P. australis in its diet (Gochfeld and Burger, 1997) and the skipper is now common in Rhode Island (Tewksbury et al., 2002). The dolichopodid fly and the gall midge C. phragmites are widespread in North America but appear to be restricted to native North American haplotypes of *P. australis* (Blossey, unpub. data). The European moth Apamea unanimis (Hübner) was first collected in North America in 1991 near Ottawa, Canada (Mikkola and Lafontaine, 1994). Larvae feed on leaves of P. australis and species of Phalaris and Glyceria. A second European species, Apamea ophiogramma (Esper), was first reported in 1989 from British Columbia, Canada (Troubridge et al., 1992), but it has now been found in New York, Vermont, Quebec, and New Brunswick (Mikkola and Lafontaine, 1994). Additional species such as several shoot flies in the genus Lipara, Dolichopodidae; a rhizome feeding noctuid moth Rhizedra lutosa (Hübner); the gall midge Lasioptera hungarica Möhn; the aphid Hyalopterus pruni (Geoffr.); and the wasp Tetramesa phragmitis (Erdös), Eurytomidae - all appear widespread. The mite Steneotarsonemus phragmitidis (Schlechtendal) was recently discovered in the Finger Lakes Region of New York and the rice-grain gall midge Giraudiella inclusa (Frauenfeld) in Massachusetts, Connecticut, New Jersey, and New York (Blossey and Eichiner, unpub.).

In Europe, at least 140 herbivore species have been reported feeding on *P. australis*, some causing significant damage (Schwarzländer and Häfliger, 1999; Tewksbury *et al.*, 2002). About 50% of these species are considered *Phragmites* specialists (Schwarzländer and Häfliger, 1999) and almost 40% of the species are monophagous. Lepidoptera (45 species) and Diptera (55) are the most important orders. More than 70% of all these herbivores attack leaves and stems of *P. australis*, and only five of the monophagous species feed in rhizomes (Tewksbury *et al.*, 2002). Of the 151 herbivore species known from outside North America, already 21 (13.9%) have been accidentally introduced (Tewksbury *et al.*, 2002).

Host Range Tests and Results

Rhizedra lutosa larvae were exposed to a number of ornamental grasses (Balme, 2000). The larvae did not feed on any of the species tested, and no host specificity screening has been conducted for any other herbivores of *P. australis*.

Releases Made

No deliberate releases have been made, but at least 21 species feeding on common reed have been accidentally introduced to North America (Tewksbury *et al.*, 2002).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The following is a summary of life history and ecology on potential natural enemies associated with *P. australis* in North America and Europe. Species included in this list were selected according to their abundance and potential impact on plant performance. Species marked by an asterix have already invaded North America.

Lipara rufitarsis* Loew, L. similis* Schiner, L. pullitarsis* Doskocil and Chvala, L. lucens* Meigen (Diptera: Chloropidae)

The genus *Lipara* Meigen is restricted to the Palaearctic region, and all nine presently recognized species use *P. australis* as their sole host plant (Beschovski, 1984). The European species *L. lucens*, *L. rufitarsis*, *L. similis*, and *L. pullitarsis* cause more or less distinct apical shoot galls, in which the mature larvae overwinter (Chvala *et al.*, 1974). A single larva develops per shoot (De Bruyn, 1994). All four species are widely distributed through Europe with variable but usually low (5 to 10%) attack rates (Schwarzländer and Häfliger, 1999).

Sabrosky (1958) records 1931 as the first North American record of *L. lucens*, based on material from Connecticut. The same author reports intercepting *L. similis* in New York in a shipment from the Netherlands where dry *Phragmites* stems were used as packaging materials (Sabrosky, 1958). Use of Phragmites as packaging material may be a major mode of introduction for many other insects that overwinter in dry stems of this species. Recent regional surveys in the northeast United States (Tewksbury et al., 2002; Blossey and Eichiner, unpub.) reveal a widespread distribution and high abundance of L. rufitarsis, L. similis (Fig. 2), and L. pullitarsis. However, L. lucens has not been found after the initial record in 1931 and may not be established in North America. Taxonomic identification of adult flies is difficult and the species recorded in 1931 may have been misidentified and may have been L. rufitarsis. Attempts to locate the original specimens have been unsuccessful (Muth, pers. comm.). Attack rates in the northeastern United States, particularly of L. similis, can approach 80% (Balme, 2000; Blossey and Eichiner, unpub.).



Figure 2. Typical sign of attack of all *Lipara* spp. is the wilting of the top leaf. (Photograph by B. Blossey.)

The different *Lipara* species can be best distinguished using criteria of gall morphology and larval overwintering habit. Attack by *L. lucens* causes stunting of 10 to 13 internodes and larvae penetrate the growing point to feed in a gall chamber. Attack by *L. rufitarsis* causes stunting of only five to six internodes with larvae also penetrating the growing point. Attack by *L. pullitarsis* causes stunting of apical internodes and gall formation similar to *L. rufitarsis*, but larvae overwinter above the growing point. Attack by *L. similis* causes only slight alterations of shoot diameters. Similar to *L. pullitarsis*, *L. similis* larvae feed and overwinter above the growing point of attacked shoots. Attack by all *Lipara* species can easily be identified by dried up apical leaves and the lack of inflorescences on infested shoots. Pupation of larvae occurs in early spring and flies emerge in May.

Lasioptera hungarica Möhn (Diptera: Cecidomyiidae)*

Lasioptera hungarica is a univoltine gall midge with P. australis as the only recorded host plant (Skuhrava and Skuhravy, 1981). The species appears to be more common in eastern and southern Europe (Schwarzländer and Häfliger, 1999). Shoots infested by L. hungarica show no obvious signs of damage; however, they often break in strong winds at the site of attack, suggesting a weakening of stem tissues. Larvae overwinter in the stem, and 30 to 300 yelloworange larvae often can be found in a single internode. The species is easily identified by its association with a black fungal mycelium (genus Sporothrix) (Skuhrava and Skuhravy, 1981) that fills the internode (Fig. 3). Oviposition by females also infects the stem with fungal spores, providing food for the developing larvae. Lasioptera hungarica was recognized in North America in 1999 (Tewksbury et al., 2002) but the species is widespread throughout the northeastern United States (Blossey and Eichiner, unpub.).



Figure 3. Larvae of *Lasioptera hungarica*. Note the black mycelium of the associated fungus. (Photograph by P. Häfliger.)

Chaetococcus phragmitis Marchal (Homoptera: Pseudococcidae)*

The legless reed mealybug, *Chaetococcus phragmitis* (Fig. 4), has recently been found in Delaware, Maryland, New Jersey, southern New York (Kosztarab, 1996; Krause, 1996), Virginia and Connecticut (Blossey and Eichiner, unpub.), and Rhode Island (Tewksbury *et al.*, 2002). Native to central Europe, Armenia, Azerbaijan, and the Mediterranean region (Ben-Dov, 1994), this mealybug is only known to feed on *Phragmites* and *Arundo* species (Kosztarab, 1996). In North America, *C. phragmitis* is regionally very common (Krause, 1996). The mealybugs feed and overwinter under leaf sheaths.



Figure 4. Overwintering *Chaetococcus phragmites* under leaf sheaths of the host plant (partially removed). (Photograph by B. Blossey.)

Rhizedra lutosa (Hübner) (Lepidoptera: Noctuidae)*

The rhizome feeding noctuid moth *Rhizedra lutosa* (Fig. 5) was first reported in 1988 from New Jersey (McCabe and Schweitzer, 1991). It was subsequently found in the Catskills in New York in 1991 (Mikkola and Lafontaine, 1994) and by 1999 was widespread in Rhode Island, Connecticut, Massachusetts, New York, and as far west as Ohio (Tewksbury *et al.*, 2002). This moth overwinters as eggs deposited on *Phragmites* leaves. Larvae hatch in spring, enter newly

growing *Phragmites* shoots, and feed in the rhizome. Attack by larvae results in shoot death, visible as dying yellow shoots in the middle of the growing season. Larvae complete development by July or August and pupate in the soil; adults fly in the fall. Attack rates appear low (Balme, 2000) and further work is needed to assess the potential of this species as a biological control agent.



Figure 5. Adult *Rhizedra lutosa* moth. (Photograph by P. Häfliger.)

Archanara geminipuncta (Haworth) (Lepidoptera: Noctuidae)

This shoot-boring moth has been extensively researched in Europe because of the damage it does to reed beds. Larvae mine the shoots in spring and early summer; adults fly in the summer and eggs overwinter. Mined portions of shoots and the growing point wilt after attack. A single larva needs several shoots to complete development, and attack rates of more than 50% of stems are common. Attack by this shootboring moth can reduce shoot height by 50 to 60% and result in significant reed dieback.

Phragmataecia castaneae (Hübner) (Lepidoptera: Cossidae)

This large moth needs two years to complete its development, which occurs at the base of the shoot and in the rhizomes. Moths fly in summer and females lay 200 to 400 eggs. Larvae may move from shoot to shoot as they look for new food during their development. Larvae can be found in both dry reed stands and those that are permanently flooded.

Chilo phragmitella (Hübner) (Lepidoptera: Pyralidae)

Like *P. castaneae*, this species mines shoots and roots of *Phragmites*. Larvae are active in the summer; older larvae mine deeper parts of the rhizome and are difficult to detect. Infested shoots remain small and wilt.

Schoenobius gigantella (Denis and Schiffermüller) (Lepidoptera: Pyralidae)

Larvae of this moth mine shoots of flooded *Phragmites* below the water level, causing considerable damage. Attacked shoots wilt and break apart. Little is known about the life history of the species, but it is assumed that larvae need two years to complete development. Adults fly in the summer.

Platycephala planifrons (Fabricius) (Diptera: Chloropidae)

Platycephala planifrons (Fig. 6) attacks *Phragmites* shoots early in the year leading to severe stunting of attacked stems by killing the growing point. *Platycephala planifrons* was one of the most damaging species found during surveys in Europe. Attack can cause biomass reductions of >50%. Females fly in the summer and are long lived. Eggs are laid in late summer. Larvae hatch in late summer, feed for a limited period, and overwinter.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

No deliberate introductions of biological control agents have been made. The diversity of accidentally introduced *Phragmites* herbivores is highest closest to New York City (Blossey and Eichiner, unpub.). This suggests that a major area for the introduction of arthropods is the harbor. Various introduced species associated with *Phragmites* appear to be spreading from New York City along highways, rivers, and the coastline.



Figure 6. Adult *Platycephala planifrons* fly on *P. australis* stem. (Photograph by P. Häfliger.)

Suppression of Target Weed

No work on evaluating the effects of these European herbivores on *Phragmites* has yet been done in North America. However, the recent discovery of several such species in the northeast provides an opportunity to measure the influence of these organisms on *Phragmites* performance.

RECOMMENDATIONS FOR FUTURE WORK

Genetic analysis (Saltonstall, 2002) has confirmed the presence of native North American genotypes of *P. australis*. Promising biological control agents have been identified in Europe and their impact and host specificity need to be determined experimentally. Native North American genotypes of *P. australis* do exist, therefore it will be extremely important to assess whether the potential control agents show any preferences among different genotypes. The fact that some native North American herbivores appear restricted to native *P. australis* genotypes and that some accidentally introduced European insect herbivores do not attack native North American genotypes

(Blossey, unpub. data) is some indication that genotype-specific biological control may be possible. However, detailed investigations as to preference and performance of potential biological control agents on native North American and introduced European genotypes have to be conducted.

A large number of European herbivorous insects that are specific to P. australis have become accidentally established in North America. Some of these insects species are widespread and abundant in the northeastern United States. However, we do not know their full distribution, habitat requirements, or potential control value. In particular, gall flies in the genus Lipara and the rhizome-feeding moth R. lutosa are widespread, although only the Lipara species reach high abundances. These observations should form the basis for a more intensive analysis of the ecology and impact of these species and their potential to control the spread or reduce existing invasive populations of P. australis. It needs to be determined why R. lutosa does not build up to higher population levels and whether the attack by the gall flies or R. lutosa can stop the spread of Phragmites or weaken existing stands. Before any of these species may be used as biological control agents, their host specificity or impact on native P. australis must be determined.

We plan to establish a web-based system to collect information from land managers about the distribution of the various reed insects already present and spreading within the United States. The web site will feature pictures and drawings of the accidentally introduced insects and their feeding damage. For most of these organisms, their gross appearance or damage is distinctive, allowing non-entomologists to participate in data collection. This system will allow the production of distribution maps, and potentially will be able to track the spread of these organisms across the continent.

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10 OLD WORLD CLIMBING FERN

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PEST STATUS OF WEED

Old World climbing fern, *Lygodium microphyllum* (Cav.) R. Br. (Lygodiaceae) (Fig. 1), is an aggressive invasive weed of moist habitats in southern Florida (Pemberton and Ferriter, 1998). This rapidly spreading weed colonizes new areas without the need of habitat disturbance and frequently completely dominates native vegetation. Herbicidal and mechanical controls are expensive, temporary solutions, and are damaging to non-target plants. The fern, first found to be naturalized in 1965, has become one of the most dangerous weeds in southern Florida.



Figure 1. *Lygodium microphyllum* showing sterile leaflets with entire margins and fertile leaflets with sporangia-bearing teeth. (Photograph by R. W. Pemberton.)

Nature of Damage

Economic damage. Although primarily a weed of natural areas, *L. microphyllum* infests residential land-scapes, horticultural nurseries, and other managed

lands near infested natural vegetation. Current control costs for chemical control of *L. microphyllum* range from \$325 to \$1,250/ha (D. Thayer, pers. comm.). But for areas that are hard to reach, such as the *L. microphyllum* infestations on the Loxahatchee National Wildlife Refuge in Florida, the cost for a single application was \$3,750/ha in 2000, and since the fern has regrown the infestations were retreated in 2001 (M. Bailey and W. Thomas, pers. comm.).

Ecological damage. Lygodium microphyllum's ability to grow up and over trees and shrubs and to run horizontally allows it to smother whole communities of plants (Figs. 2 and 3) reducing native plant diversity. It is difficult for other plants to grow through the thick fern mats (up to 1 m thick). Lygodium microphyllum is common in bald cypress (Taxodium distichum [L.] Richard) stands, but also infests pine flatwoods, wet prairies, saw grass (Cladium jamaicense Crantz) marshes, mangrove communities, Everglades tree islands, and disturbed areas. Some Everglades tree islands are so completely blanketed by the fern that it is not possible to see trees and other vegetation beneath the fern mat (Fig. 3). Lygodium microphyllum also threatens rare plants. In Loxahatchee Slough in Palm Beach County, Florida, the fern is an "imminent danger" to Tillandsia utriculata L. and other rare bromeliads (Craddock Burks, 1996). Infestations of this fern alter the impact of fire, which is a naturally occurring element and a management tool in many Florida communities (Roberts, 1998). Thick skirts of old fronds enclose trees and serve as ladders that carry fire into tree canopies. Trees that can withstand ground fires are killed when fire is brought into the canopy. Fires that usually terminate at the margins of cypress sloughs during the wet season can burn into and through cypress sloughs infested with L. microphyllum. Portions of burning fern also can break free and spread fire to new areas. Lygodium



Figure 2. Lygodium microphyllum blanketing an Everglades tree island in Loxahatchee National Wildlife Refuge, Florida. (Photograph by Amy Ferriter, South Florida Water Management District, West Palm Beach.)



Figure 3. Adult of *Cataclysta camptozonale*, an Australian pyralid moth currently under study as potential biological control agent of *Lygodium microphyllum*. (Photograph by Christine Bennett, Florida Biocontrol Lab, USDA, ARS, Florida Division of Plant Industry, Gainesville.)

microphyllum appears to be long-lived and persistent, and can occupy a large proportion of suitable habitats in a relatively short time. The fern is classified as a Category I invasive species (the most invasive species) by the Florida Exotic Plant Pest Council (Langeland and Craddock Burks, 1998).

Extent of losses. It is hard to quantify the extent of the losses due to Old World climbing fern. The explosive growth and rapid spread of the fern are relatively recent. It was first collected from Jonathan

Dickinson State Park in Palm Beach County in 1966 (Beckner, 1968), and by 1993, it was present on 493 ha (11%) of the park and the Loxahatchee National Wild and Scenic River (Roberts, 1998). In 1995, the weed was present on 6,800 ha (12%) of the Loxahatchee National Wildlife Refuge (Palm Beach Co.), where it was undetected in 1990 (S. Jewel, pers. comm.). The land area infested by this fern is estimated (from aerial surveys) to have increased 150% between 1997 and 1999 (A. Ferriter, pers. comm.). Present losses due to this weed are bad, yet modest compared to potential losses unless effective controls can be found and implemented soon.

Geographical Distribution

In the United States. Lygodium micophyllum is a subtropical and tropical plant that requires shallow aquatic habitats or moist soils. At present, L. *microphyllum* is limited to the southern third of the Florida peninsula from Brevard and Highlands County south. The area with the lowest winter temperatures currently infested is Polk and Highlands Counties (ca. 28°N) in south-central Florida. These areas are in the USDA Plant Hardiness Zone 9B (minimum of 3.9 to 6.6°C) (Cathey, 1990). Because Zone 9B extends up the eastern coast to the Georgia border (ca. 30°N), the weed may well be able to colonize this area. Zone 9B extends to just above Tampa on the west coast of Florida. If spores of the fern are carried across the Gulf of Mexico to the southern coast of Texas and Mexico, the weed could establish in those areas because of suitable climates and habitats. If it establishes in Mexico, it could spread south to much of wet tropical America. Lygodium microphyllum also is naturalized to a limited extent in Jamaica and Guyana (Pemberton and Ferriter, 1998), so the opportunity for it to spread within the Caribbean and other tropical portions of the Americas already exists.

Native range. Lygodium microphyllum has an exceptionally large native range, occurring in much of the moist Old World tropics and subtropics (Pemberton, 1998). The fern's temperate limits are between 28°S and 29°S in Australia and South Africa, and 25° N and 27°N in Assam (northeastern India) and the Ryuku Islands (the southwestern most part of Japan). It spans more than half of the world's circumference from 18°E in Senegal to 150°W in Tahiti. In Africa, *L. microphyllum* ranges from Senegal south and east through most of West Africa to Zaire,

then south to Angola, east to East Africa, and then south to South Africa. In Asia, the fern is distributed from India and Nepal, east through much of Southeast Asia, and north through the warmer provinces of southern China to Taiwan and Okinawa. It also occurs throughout many of the Southeast Asian islands to Australia and, in the Pacific, east to Tahiti.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The correct name of Old World climbing fern is L. microphyllum (Alston and Holttum, 1959; Hanks, 1998), but the species is occasionally referred to as Lygodium scandens (L.) Sw., particularly in older works. As many as 40 species have been placed in the genus Lygodium (Mabberley, 1997), but a recent revision has reduced this number to 26 (Hanks, 1998). All but two species are from areas with tropical or subtropical climates. The genus Lygodium has usually been placed in the Schizaeaceae, a small primitive family that also includes the genera Actinostachys, Schizaea, Anemia, and Mohria (Prantl, 1881; Holttum, 1973; Hanks, 1998). Since Lygodium is unique morphologically, it is sometimes interpreted to comprise its own monogeneric family, the Lygodiaceae (Bierhorst, 1971; Wagner and Smith, 1993). The relationship of the Schizaeaceae (Lygodiaceace s.s.) to other groups of ferns is unclear (Smith, 1995).

Lygodium microphyllum is a distinctive fern in North America. This vine has pinnately compound fronds (pinnules), except the sterile fronds (pinnae), which have entire margins. Lygodium japonicum (Thunberg ex. Murray) Swartz, another invasive species in the southeastern United States, has twice pinnately compound fronds with sterile fronds that have toothed margins. Lygodium palmatum (Bernh.) Sw., a temperate native member of the genus living from Appalachia north to New England, has palmately compound fronds. Lygodium microphyllum has been placed, based on morphology, in the subgenus Volubilia; the native L. palmatum in the subgenus Palmata; and L. japonicum in the subgenus Flexuosa (Prantl, 1881; Hanks, 1998).

Biology

The biology of *L. microphyllum* is not well studied. The fern is a long-lived perennial vine. The aerial vines are actually very long leaves with a stem-like rachis and leaflet-like pinnae and pinnules comprising the photosynthetic tissue. The plant bears both fertile leaflets with sporangia bearing teeth along the edge of the blade, and sterile leaflets with entire margins. The true stems are underground rhizomes. These vines can be 30 m in length. Growth and sporulation appear to occur all year. The fern produces large numbers of spores; more than 800 spores/m³/ hour were trapped in one Florida infestation (Pemberton and Ferriter, 1998). Spores can germinate in six to seven days (Brown, 1984). Dried spores taken from the plants have germinated after two years (Lott and Pemberton, unpub.). The life cycle of L. *microphyllum* is the same as with other ferns. The spores require moist conditions to germinate and grow into small, liverwort-like gametophytes. Male and female organs are produced on the same gametophytes and fertilization occurs when the swimming spermatozoid swims from the male organ to a female organ to penetrate the ovule. Fertilization gives rise to the familiar large leafy fern, which is the sporophyte stage. The fern spreads locally by vegetative growth and over long distances by wind-borne spores. The plant can grow in standing water and wet soils, and either in full sun or shade.

Analysis of Related Native Plants in the Eastern United States

In addition to *L. palmatum* (discussed above), there are West Indian *Lygodium* species that are being considered in the biological control program because of the proximity of this region to southern Florida. *Lygodium volubile* Sw., which occurs in Cuba and other areas of the West Indies, belongs to the same subgenus Volubilia as *L. microphyllum. Lygodium cubense* Kunth. (a Cuban endemic), *Lygodium venustum* Sw. (found in the West Indies), and *Lygodium oligostachyum* (Willd.) Desv. (endemic to the Dominican Republic and Haiti) (Prantl, 1881; Hanks, 1998) all belong to the subgenus Flexuosa.

Except for L. palmatum, the only native North American plants that have been considered related to L. microphyllum are three species of Anemia, one species of Actinostachys, and one species of Schizaea (Wagner and Smith, 1993; Nauman, 1993; Mickel, 1993). Anemia mexicana Klotzsch occurs in southwest Texas and northern Mexico. Anemia adiantifolia (L.) Swartz is locally common in Florida and the West Indies. Anemia wrightii Baker in Hooker and Baker is a tiny rare fern limited to lightly shaded solution holes and limestone sinks in southern Florida and the West Indies. Both Florida Anemia species are broadly sympatric with L. microphyllum. Schizaea pusilla Pursh is found in the northeastern part of North America. Actinostachys pennula (Swartz) Hooker is a widely distributed species in tropical America whose only known North American population is on Everglades tree islands that are being overgrown by L. microphyllum.

The relationships among the genera of the Schizaeaceae s.l. are unclear (Smith, 1995). Recent molecular research (*rbcL*) on the phylogeny of ferns found that *Lygodium*, *Actinostachys*, and *Anemia* have more intrageneric distance than occurs between most fern families (Hasebe *et al.*, 1995). The research also showed the family to be very isolated, with more intrafamilial distance between it and other fern families than occurs between most fern families (Hasebe *et al.*, 1995). The molecular data and the antiquity of the Schizaeaceae (*Anemia* spores are known from the Cretaceous [Smith, 1995]), suggest that the family arose earlier than other fern groups.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

While the native range of *L. microphyllum* is well defined, it is very large and the area(s) of origin of the plants that have become invasive in Florida is unknown. To attempt to identify the region(s) of origin of the Florida plants, collections of Florida material and material from many different parts of the native range are being made for genetic comparison. The weed is of horticultural origin in Florida (Pemberton and Ferriter, 1998). It was recognized to be a potential problem not long after it was found to be naturalized (Nauman and Austin, 1978).

Areas Surveyed for Natural Enemies

A preliminary survey for the natural enemies of *Lygodium* spp. was made in Japan, northern Taiwan, and Hong Kong during the autumn of 1997 by R. Pemberton. *Lygodium japonicum*, the only *Lygodium* in Japan, was common in central and western Honshu, including Tokyo. *Lygodium microphyllum* was uncommon in northern Taiwan; only one population was found. In Hong Kong, *L. microphyllum*, *L. japonicum*, and *Lygodium flexuosum* (L.) Swartz were examined. *Lygodium microphyllum* occurred in small patches, a few meters wide, along streams and on hillsides in heavy soils. The discovery of various pyralid moths attacking the plants helped secure funding for the project.

Much of the exploratory effort for Lygodium natural enemies is being carried out by J. Goolsby and T. Wright. This effort began in 1998 and is focused on *L. microphyllum* and other *Lygodium* spp. (L. japonicum, L. flexuosum, and Lygodium reticulatum Schkuhr, Farnkr.) in Southeast Asia and Australia. Lygodium microphyllum is widely distributed throughout the wet tropics and subtropics of Australia and Southeast Asia. Within Australia areas in New South Wales, Queensland, the Northern Territory, and Western Australia were explored. In southeast Asia, areas in Indonesia, Malaysia, Singapore, and Thailand were surveyed. Several trips have been made to each of the collection locations to capture the seasonal diversity of herbivores, and more than 250 sites have been visited. In these areas, L. microphyllum is not weedy and is associated with a complex of insects, mites, and pathogens.

Lygodium microphyllum and Lygodium smithianum Pres. were surveyed in West Africa (Benin, Ghana, and Cameroon) by R. Pemberton in 1999. West Africa is at the western edge of L. microphyllum's huge Old World distribution. The plant was found in both swamps and in diverse terrestrial habitats in high rainfall areas. The plant often was common, but not abundant or dominant. Two short visits were made by cooperators to a L. microphyllum population in Natal South Africa, near the plant's southern latitudinal limit.

Natural Enemies Found

More than 18 species of herbivores have been collected from *L. microphyllum* (Table 1). The pyralid moth *Neomusotima conspurcatalis* Warren is the most

Name	Collection Locations	Host Plant	
<i>Cataclysta camptozonale</i> (Hampson) Lepidoptera: Pyralidae	Australia (Queensland)	L. microphyllum L. reticulatum	
Neomusotima conspurcatalis Lepidoptera: Pyralidae	Australia (Queensland and Northern Territory), Indonesia, Malaysia, Singapore, Thailand, Hong Kong	L. microphyllum	
<i>Neomusotima fuscolinealis</i> Yoshiyasu Lepidoptera: Pyralidae	Japan	L. japonicum	
<i>Musotima</i> sp. Lepidoptera: Pyralidae	Malaysia, Singapore, Thailand	L. microphyllum	
<i>Callopistria</i> spp. Lepidoptera: Noctuidae	Australia (Northern Territory), Thailand, Indonesia, Malaysia, Singapore	L. microphyllum	
Lepidoptera: Limacodidae	Thailand	L. microphyllum	
Archips machlopis Meyrick Lepidoptera: Tortricidae	Thailand	L. microphyllum	
Lepidoptera: Tortricidae	Malaysia, Singapore	L. microphyllum	
Stem-borer Lepidoptera: Pyralidae	Singapore	L. microphyllum L. flexuosum	
<i>Neostromboceros albicomus</i> (Konow) Hymenoptera: Tenthridinidae	Malaysia, Singapore, Thailand, Vietnam	L. flexuosum	
<i>Metriona</i> sp. Coleoptera: Chrysomelidae	Australia (Northern Territory)	L. microphyllum	
<i>Endelus</i> sp. Coleoptera: Buprestidae	Singapore	L. microphyllum	
<i>Manobia</i> sp. Coleoptera: Chrysomelidae	Thailand	L. flexuosum	
<i>Lophothetes</i> sp. Coleoptera: Apionidae	Palau (Arakabesang ls.)	L. microphyllum	
Hemiptera: Miridae	Australia (Northern Territory)	L. microphyllum	
<i>Acanthuchus trispinifer</i> (Fairmaire) Homoptera: Membracidae	Australia (Queensland, Northern Territory)	L. microphyllum	
Thrips: Thysanoptera	Malaysia, Thailand	L. microphyllum	
<i>Floracarus</i> sp. Acarina: Eriophyidae	Australia, Indonesia, Malaysia, Singapore, Thailand	L. microphyllum	

Table 1. Herbivores Collected from Lygodium spp. in Asia and Australia

widely distributed, followed by an eriophyid mite in the genus *Floracarus*. Most efforts to locate natural enemies have focused on the above-ground portions of the fern. Searching methods have included visual inspection, beating trays, and black-light trapping.

In South Africa, few natural enemies were found. In West Africa, the most damaging and common natural enemy of *L. microphyllum* was a *Tenuapalpis* mite (Tenuapalpidae), which caused brown, channel-like scars on the leaves. The mite also commonly fed on *Nephrolepis* ferns, which indicated a undesirably wide host range; *Nephrolepis* ferns are a modern group of ferns whereas *Lygodium* ferns are an ancient group. The paucity of natural enemies associated with *Lygodium* in Africa may relate to the time of year that the surveys were made, or to the low diversity of *Lygodium* species on the continent. Only two species of *Lygodium* occur there, compared to about a dozen species in southeast Asia, where many natural enemies have been found.

A rust fungus, *Puccinia lygodii* (Har.) Arth., native to South America and naturalized in the United States, has recently been found infecting *L. japonicum* in northern Florida (Rayachhetry *et al.*, 2001). The rust is not known to occur in the region infested by *L. microphyllum* and its capability to infect *L. microphyllum* is unknown. It is a glasshouse pest of ornamental *Lygodium* (Jones, 1987), and may have a role in *L. microphyllum* control (Pemberton, 1998).

Host Range Tests and Results

Host specificity testing schemes based on plant family affiliations, as employed for weedy flowering plant, are not suitable for use with weedy ferns because of the lack of agreement on fern families, even in recent publications. Recent molecular work (Hasebe, 1995) has helped to identifying more natural groupings of ferns. Nevertheless, fern genera are usually the reliable taxa used to orient host specificity testing. Because of the relatively modest number of genera of ferns in Florida and the southeastern United States, it is possible to test representatives of most genera. The most difficult species to evaluate are the 40 species of ferns considered threatened or endangered in Florida. Most all of these ferns are neotropical species reaching the northern limits of their ranges in southern Florida. Permits from federal, state, and local governments are needed to collect small numbers of representative species of each genus of rare ferns. Because of the taxonomic isolation of the genus Lygodium, we expect to find specialist natural enemies with host ranges limited to the genus.

For the moth species currently being evaluated, host range tests have been designed to measure the oviposition behavior of the adult and the suitability of the test ferns for development of the immature stages. No-choice sleeve cage tests are being used to determine oviposition responses of the adults. Oviposition in sleeves is recorded daily, along with hatching and mortality of immature stages. In many cases, adult moths do not oviposit on test plant species. For these species, naïve neonate larvae are placed on test plants to determine their ability to feed and develop. For larger larvae, which are big enough to crawl between test plants in a choice test, simultaneous presentation of cut foliage from several test plant species will be used to determine the ability of larger larvae to choose plant species best suited for completion of their development.

Cold-temperature tests will be used to determine the critical lower thermal limit for survival of the target herbivores. Because the geographical range of *L. microphyllum* is from 28°N to 28°S, specialist herbivores of this fern also will be tropical or subtropical species. In cases where development of these herbivores occurs on temperate species, such as *L. palmatum* in North America, the lower thermal limit of the herbivore could reduce the risk to such nontarget species. We do not expect tropical or subtropical biological control agents to tolerate winter temperatures found in the southern part of *L. palmatum*'s range.

Releases Made

No releases of any agents have been made against Old World climbing fern in the United States as of 2000.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Cataclysta camptozonale (Hampson) (Lepidoptera: Pyralidae)

Cataclysta camptozonale (Fig. 4) has been collected from subtropical south Queensland to tropical north Queensland. In northern Queensland, it has been collected from both *L. microphyllum* and *L. reticulatum.* Heavy damage to *L. microphyllum* has been noted despite high levels of predation and egg parasitism (Goolsby, unpub.). Larvae skeletonize *L. microphyllum* leaves, sometimes consuming much of the new growth. In laboratory cultures, larvae consume all the foliage, and scarify the stems, which kills the plants.

Developmental studies of *C. camptozonale* were conducted on two hosts, *L. microphyllum* and *L. japonicum*. Females laid an average of 25 eggs either singularly or in clusters on the upper surface of mature pinnae. Longevity of adult females was 6.2 days. Development time from egg to adult was 44 days at 24°C on both plant species. *Cataclysta camptozonale* appears to have four larval instars. Pupae can be sexed based on the presence of a slit in the middle of the second to last tergite in males only. The sex ratio of



Figure 4 Larva of *Cataclysta camptozonale* feeding on *Lygodium microphyllum*. (Photograph by Christine Bennett, Florida Biocontrol Lab, USDA, ARS, Florida Division of Plant Industry, Gainesville.)

the laboratory colony used in this test was slightly female biased with a male:female ratio of 1:1.3.

Preliminary host range tests have started with *C. camptozonale* in the laboratory. Fifteen fern species have been tested in no-choice tests. Thus far it appears that *C. camptozonale* larvae develop only on *Lygodium* spp., including the North American endemic *L. palmatum*. Further testing is underway to determine the host range and critical minimum survival temperature of this moth.

Neomusotima conspurcatalis (Lepidoptera: Pyralidae)

Neomusotima conspurcatalis has been collected from many locations in northern Australia and the wet tropics of southeast Asia. Larvae defoliate leaves and skeletonize *L. microphyllum* in a manner similar to *C. camptozonale*. To determine whether *N. conspurcatalis* might be a complex of species, we used molecular genetic methods to analyze the DNA of populations from different areas. Molecular sequencing of the mitochondrial D2 gene showed an exact match between the specimens from Australia and southeast Asia. This indicates that both populations are likely to be the same species.

Fecundity, longevity, and host range of this species appear to be very similar to that of *C. camptozonale*. *Neomusotima conspurcatalis* has only been collected in tropical regions thus far. The geographical distribution of this moth seems to indicate that it is not tolerant of the cooler winters of the subtropics; however, further studies are planned to determine the exact critical low temperature.

Musotima sp. (Lepidoptera: Pyralidae)

Musotima sp. has been collected in Thailand, Malaysia, and Singapore, but only on *L. microphyllum*. It appears to be restricted to areas with tropical climates to a greater degree than either *C. camptozonale* or *N. conspurcatalis*. The moth is currently being described by Alma Solis (ARS-Systematic Entomology Laboratory, Beltsville, Maryland).

Although little is known so far, preliminary studies in quarantine indicate that adults of this species live up to 10 days, pupal development requires eight days, and the sex ratio favors females (m:f, 1:1.5). Larvae are vigorous defoliators of *L. microphyllum*, although the damage is less pronounced in the field, presumably due to parasitism and predation. The species also completes its life cycle on *L. palmatum* and *L. japonicum*.

Floracarus sp. (Acarina: Eriophyidae)

Field collections in the Brisbane area have documented the damage caused by the mite *Floracarus* sp. (Eriophyidae) (Fig. 5) on *L. microphyllum*. Feeding by the mite on the new growth causes the pinnule (leaflet) margins to curl. It also appears that mite feeding causes disease transmission, because the feeding is associated with a black streaking and necrosis of the leaflets. Similar damage has been noted in southeast Asia as well. Fungi were isolated from the necrotic patches associated with the mite damage. The causal agent was identified as *Botryospheria* sp., which is believed to be a secondary pathogen, associated with leaf damage.



Figure 5. Leaf galls on *Lygodium microphyllum* caused by an eriophyid gall mite *Floracarus* sp., a candidate biological control agent of the fern. (Photograph by John Goolsby, Australian Biological Control Laboratory, USDA-ARS, Brisbane.)

We intend to compare mite populations from Australia with those from southeast Asia, using molecular DNA tools. Analysis of the DNA (D2 gene) should indicate whether there are several species feeding on *Lygodium* in different parts of its range. Danuta Knihinicki of New South Wales Agriculture identified the mite as *Floracarus* sp. and intends to describe it as a new species. Field studies are continuing to determine the life cycle and host range of the mite. Preliminary testing indicates that this mite is highly specific to *L. microphyllum*.

RECOMMENDATIONS FOR FUTURE WORK

The biological control program against Old World climbing fern began in 1997. Although promising natural enemies have been located, none have been fully tested and none released. For this reason and because large areas of *L. microphyllum*'s native range are unexplored, surveys to locate additional natural enemies will continue in southern China, various Pacific islands, Irian Jaya, New Caledonia, and India. In addition to surveying for herbivores attacking *L. microphyllum* and other *Lygodium* spp. in the weed's native range, surveys of neotropical *Lygodium* species will be made to find natural enemies not previously associated with the weed.

Molecular phylogenetic studies are planned that will attempt to match the genotype of the *L. microphyllum* population in Florida with populations from around the world. More than 30 samples of *L. microphyllum* from Florida and various parts of its native range have been collected. Matching the invasive population with its source population should lead us to the natural enemies which with the greatest affinity for the Florida genotype. This research also will allow us to determine the degree of relatedness of species within the genus. Several subgenera have been established based on morphology. We intend to look for congruency in placement of the species in subgenera with molecular-based phylogenies. Understanding which species are most closely related to *L. microphyllum* (in the same subgroup) will allow us to develop the most meaningful host plant test list. This is especially important since many species of *Lygodium* are neotropical and could potentially be affected by introduction of biological control agents to Florida.

The climatic factors that influence distribution of potential agents also must be investigated. Because *L. palmatum* occurs in temperate areas of North America, it should not be at risk from importation of agents that have tropical or subtropical origins. Laboratory tests to establish the critical thermal limits of potential agents are planned.

More than two hundred field sites in Australia and Southeast Asia across a wide range of climates, soil types, and nutrient regimes have been surveyed for natural enemies. Lygodium microphyllum cannot be described as weedy in any of these locations. Yet, it is not apparent from field surveys which agent(s) most restrict population growth of this fern. Field studies are planned to determine the regulatory effects of the key agents on L. microphyllum. Floracarus sp. appears to be associated with leaf necrosis and defoliation. We intend to investigate the role of this mite in promoting infections by plant pathogens. Pathogens and insects also may be associated with the rhizome of the fern. Methods must be developed to identify rhizome natural enemies and determine if they reduce the growth of the plant.

Although current research is focused on *L.* microphyllum, *L. japonicum* could become a part of the program in the future. This invasive fern is naturalized in the United States from Texas to the Carolinas and southward to central Florida. Its more temperate distribution would require the use of biological control agents more tolerant of cold climates than those needed for *L. microphyllum*. Use of such coldhardy agents might place the native species *L. palmatum* at risk. Additional information on these ferns is available in the *Lygodium* Management Plan for Florida (Ferriter, 2001).

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11 PURPLE LOOSESTRIFE

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PEST STATUS OF WEED

Purple loosestrife, *Lythrum salicaria* L., (Fig. 1) is a weed of natural areas and its spread across North America has degraded many prime wetlands resulting in large, monotypic stands that lack native plant species (Thompson *et al.*, 1987; Malecki *et al.*, 1993). Established *L. salicaria* populations persist for decades, are difficult to control using conventional techniques (chemical, physical, and mechanical), and continue to spread into adjacent areas (Thompson *et al.*, 1987). Purple loosestrife has been declared a noxious weed in at least 19 states.

Nature of Damage

Economic damage. With the exception of reduced palatability of hay containing purple loosestrife and reduction of water flow in irrigation systems in the West, purple loosestrife does not cause direct economic losses. Indirect losses accrue due to reductions in waterfowl viewing and hunting opportunities.

Ecological damage. The invasion of L. salicaria alters biogeochemical and hydrological processes in wetlands. Areas dominated by purple loosestrife (Fig. 2) show significantly lower porewater pools of phosphate in the summer compared to areas dominated by Typha latifolia L. (Templer et al., 1998). Purple loosestrife leaves decompose quickly in the fall resulting in a nutrient flush, whereas leaves of native species decompose in the spring (Barlocher and Biddiscombe, 1996; Emery and Perry, 1996; Grout et al., 1997). This change in timing of nutrient release at a time of little primary production results in significant alterations of wetland function and could jeopardize detritivore consumer communities adapted to decomposition of plant tissues in spring (Grout et al., 1997).



Figure 1. Purple loosestrife stand. (Photograph by B. Blossey.)



Figure 2. Wetland dominated by purple loosestrife. (Photograph by B. Blossey.)

Specialized marsh birds such as the Virginia rail (*Rallus limicola* Vieillot), sora (*Porzana carolina* L.), least bittern (*Ixobrychus exilis* Gmelin), and American bittern (*Botaurus lentiginosus* Rackett), many of which are declining in the northeastern United States (Schneider and Pence, 1992), avoid nesting and foraging in purple loosestrife (Blossey et al., 2001a). Black terns (Clidonias niger L.), once a common breeding species at the Montezuma National Wildlife Refuge in upstate New York, declined and became locally extinct by 1987. The local extinction coincided with a population explosion of purple loosestrife from few individuals in 1956 to a coverage of more than 19% of the total area (600 ha), representing 40% of the emergent marsh habitat in 1983 (T. Gingrich, pers. comm.). Another wetland specialist, the marsh wren (Cistothorus palustris Wilson), was conspicuously absent in purple loosestrife-dominated wetlands but used adjacent cattail marshes (Rawinski and Malecki, 1984; Whitt et al., 1999). The federally endangered bog turtle (Clemmys muhlenbergi Schoepff) loses basking and breeding sites to encroachment of purple loosestrife (Malecki et al., 1993).

Purple loosestrife is competitively superior over native wetland plant species (Gaudet and Keddy, 1988; Weiher et al., 1996; Mal et al., 1997). The species is dominating seedbanks, particularly in areas with established purple loosestrife populations (Welling and Becker, 1990; 1993). The fact that expanding purple loosestrife populations cause local reductions in native plant species richness has been demonstrated by the temporary return of native species following the suppression of *L. salicaria* through use of herbicide (Gabor et al., 1996). However, without the continued use of herbicides, purple loosestrife re-invades and re-establishes dominance within a few years (Gabor et al., 1996). In areas where the distributions of L. salicaria and of the native winged loosestrife, Lythrum alatum Pursh., overlap, the taller, more conspicuous purple loosestrife reduces pollinator visitation to L. alatum resulting in significantly reduced seed set of L. alatum. (Brown, 1999).

Extent of losses. Direct losses are difficult to quantify due to lack of long-term monitoring programs and data.

Geographical Distribution

Lythrum salicaria now occurs in all states of the United States, except Florida, Alaska, and Hawaii, and in nine Canadian provinces. The abundance of L. salicaria varies throughout this range with populations in all but the eastern United States (the oldest infested area) still expanding, In the Northeast and Midwest, a significant portion of the potentially available habitat has been invaded.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Purple loosestrife is a member of the Lythraceae (the Loosestrife family), with highly variable growth form and morphology. Main leaves are 3 to10 cm long and can be arranged opposite or alternate along the squared stem and are either glabrous or pubescent. The inflorescence is a spike of clusters of reddishpurple petals (10 to15 mm in length). Flowers are trimorphic with short, medium, and long petals and stamens. Many ornamental varieties have been developed, some through introgression with the native L. alatum (Ottenbreit and Staniforth, 1994). Until recently, Lythrum virgatum L. was treated as a separate species also introduced from Europe but the species is now considered a synonym of L. salicaria (Ottenbreit and Staniforth, 1994). Further details can be found in Mal et al., (1992).

Biology

Purple loosestrife needs temperatures above 20°C and moist open soils for successful germination. Seedlings grow rapidly (>1 cm/day) and plants can flower in their first growing season. Established plants can tolerate very different growing conditions, including permanent flooding, low water and nutrient levels, and low pH. Plants can grow in rock crevasses, on gravel, sand, clay and organic soils. Plants develop a large, laterally branching rootstock with starch as the main form of nutrient storage (Stamm-Katovitch et al., 1998). Mature plants can develop rootstocks of heavier than 1 kg and can produce more than 30 annual shoots reaching a maximum height of more than 2 m. Plants are long lived and mature plants may produce more than 2.5 million seeds annually, which remain viable for many years. Spread to new areas occurs exclusively by seed, which is transported mainly by water but also adheres to boots, waterfowl and other wetland fauna.

Analysis of Related Native Plants in the Eastern United States

The Lythracea belong to the order Myrtales of which four families (Lythraceae, Thymelaceae, Onagraceae, and Melastomataceae) are native to much of North America. Within the Lythraceae, 12 species (excluding *L. salicaria*) belonging to the genera *Ammannia*, *Cuphea, Decodon, Lagerstroemia, Lythrum, Rotala*, and *Didiplis (Peplis)* occur in the northeastern Unites States (Gleason and Cronquist, 1991). With the exception of *Didiplis diandra* (Nutt.), water purslane, all species of the Lythraceae covered by Gleason and Cronquist (1991) were used in the host specificity testing (Blossey *et al.*, 1994a, b; Blossey and Schroeder, 1995).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Lythrum salicaria has distribution centers in Europe and Asia. The European distribution extends from Great Britain across western Europe into central Russia with the 65th parallel as the northern distribution limit (Tutin et al., 1968). Purple loosestrife is common throughout central and southern Europe and along the coastal fringe of the Mediterranean basin. In Asia, the main islands of Japan are the core of the species native range, with outlying populations extending from the Amur River south across the lowlands of Manchuria and other parts of China to Southeast Asia and India (Hultén and Fries, 1986). Lythrum salicaria was introduced to North America in the early 1800s in ship ballast, wool, and most likely also as an ornamental or medicinal herb (Thompson et al., 1987).

Areas Surveyed for Natural Enemies

Research in Europe began in 1986 with field surveys for potential control agents. By 1992, field surveys for natural enemies were conducted in Finland, Sweden, Norway, Denmark, Germany, Switzerland, Austria, and France, extending earlier observations (Batra *et al.*, 1986). These surveys covered 140 different sites and an area from the northernmost distribution in central Finland to the Mediterranean basin (Blossey, 1995b). Additional surveys were conducted in North America from Maryland to Nebraska (Hight, 1990).

Natural Enemies Found

No native or accidentally introduced herbivores with the potential for control of *L. salicaria* were found in North America (Hight, 1990). More recently, several native pathogens have been evaluated for their potential as biological control agents (Nyvall, 1995; Nyvall and Hu, 1997). Surveys in Europe identified more than 100 different insect species most commonly associated with purple loosestrife (Batra *et al.*, 1986), but only nine species were evaluated in more detail (Blossey, 1995b).

Host Range Tests and Results

Of the nine potential control agents identified in Europe, six species were tested for their host specificity, against 48 test plant species in 32 genera (for a complete list of test plants taxonomically associated, associated wetland plants, and important agricultural plants see Blossey et al., 1994b). This selection was based on literature reports of their specificity, their distribution and availability in the field, and initial observations of their impact on purple loosestrife performance. The selected species were the root-mining weevil, Hylobius transversovittatus Goeze; two leaf beetles, Galerucella calmariensis L. and Galerucella pusilla Duftschmidt; a flower-feeding weevil, Nanophyes marmoratus Goeze; a seed-feeding weevil, Nanophyes brevis Boheman; and a gall midge, Bayeriola salicariae Gagné.

Host specificity tests identified two native North American plant species, Decodon verticillatus (L.) Ell. (swamp loosestrife) and L. alatum as potential hosts for the Galerucella leaf beetles (Blossey et al., 1994b) and with less probability for H. transversovittatus. (Blossey et al., 1994a). Both plant species are members of the family Lythraceae and therefore closely related to L. salicaria. The flower and seed feeding weevils N. marmoratus and N. brevis were entirely restricted to L. salicaria (Blossey and Schroeder, 1995). The gall midge B. salicariae attacked and successfully completed larval development on L. alatum, Lythrum californicum Torr. and Gray and Lythrum hyssopifolia L. although attack rates were much lower than on L. salicaria (Blossey and Schroeder, 1995).

Releases Made

Based on results indicating a potential wider host range, the gall midge B. salicariae was not proposed for introduction (Blossey and Schroeder, 1995). After review by the Technical Advisory Group, it was determined that further invasion by L. salicaria is considered a greater threat to the native L. alatum and D. verticillatus than potential attack by the leaf beetles or the root feeder, and releases were approved. Initial introductions in eastern North America occurred in Virginia, Maryland, Pennsylvania, New York, Minnesota, and southern Ontario in August, 1992 (Hight et al., 1995). Predictions that at high population densities beetles might nibble at other species (Blossey et al., 1994a, b; Blossey and Schroeder, 1995) were confirmed (Corrigan, 1998; Blossey et al., 2001b), but attack was transient and restricted to newly emerging beetles.

Approval to introduce the flower-feeding weevil *N. marmoratus* was granted followed by introductions in New York and Minnesota in 1994. Additional releases occurred in New Jersey in 1996. The seed-feeding weevil *N. brevis*, while approved for introduction, was not released into North America, due to the presence of a nematode infection. This infection appeared benign for *N. brevis*, however, due to the potential for non-target effects of the nematode after introduction into North America, only disease free specimens should be introduced, which, at present, effectively precludes the introduction of *N. brevis*.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Galerucella calmariensis and G. pusilla (Coleoptera: Chrysomelidae)

Galerucella calmariensis (Fig. 3) and *G. pusilla* are two sympatric species that occur throughout the European range of purple loosestrife (Palmén, 1945; Silfverberg, 1974) and share the same niche on their host plant (Blossey, 1995a). With some experience adults can be identified to species; however, eggs and larvae are indistinguishable. The two introduced species easily can be confused with other North American *Galerucella* species (see Manguin *et al.*, 1993 for descriptions of all five species in the genus *Galerucella* known from North America).



Figure 3. Mating pair of *Galerucella calmariensis.* (Photograph by B. Blossey.)

Adults overwinter in the leaf litter and emerge in early spring synchronized with host plant phenology. Adults feed on young plant tissue causing a characteristic "shothole" defoliation pattern. Females lay eggs in batches of two to 10 on leaves and stems from May to July. First instar larvae feed concealed within leaf or flower buds; later instars feed openly on all aboveground plant parts. Larval feeding strips the photosynthetic tissue off individual leaves creating a "window-pane" effect by leaving the upper epidermis intact. Mature larvae pupate in the litter beneath the host plant. At high densities (>2 to 3 larvae/cm shoot), entire purple loosestrife populations can be defoliated (Fig. 4). At lower densities, plants retain leaf tissue but show reduced shoot growth, reduced root growth, and fail to produce seeds (Blossey 1995a, b; Blossey and Schat, 1997). Both species are usually



Figure 4. Defoliated purple loosestrife plants. (Photograph by B. Blossey.)

univoltine, although a second generation may occur in some parts of North America. Adults are mobile and possess good host finding abilities. Peak dispersal of overwintered beetles is during the first few weeks of spring. New generation beetles have dispersal flights shortly after emergence and are able to locate patches of host plants as far away as 1 km (Grevstad and Herzig, 1997).

Hylobius transversovittatus (Coleoptera: Curculionidae)

In the spring, overwintered H. transversovittatus adults (Fig. 5) appear shortly after L. salicaria shoots begin to grown. The largely nocturnal adults (10 to 14 mm) consume foliage and stem tissue; oviposition begins approximately two weeks after adults emerge from overwintering and lasts into September (Blossey, 1993). Females lay white, oval-shaped eggs in plant stems or in the soil close to the host plant. First instar larvae mine the root cortex and older larvae subsequently enter the central part of the rootstock where they feed for one to two years. Development time from egg to adult is dependent upon environmental conditions (temperature, moisture) and time of oviposition (Blossey, 1993). Pupation chambers are found in the upper part of the root and adults emerge between June and October and can be long-lived (several years).



Figure 5. *Hylobius transversovittatus* adult. (Photograph by B. Blossey.)

Adult feeding is of little consequence; however, larval feeding can be very destructive (Fig. 6) (Nötzold *et al.*, 1998). With increasing attack rates, larval feeding reduces shoot growth, seed output, and shoot and root biomass, and can ultimately result in plant mortality (Nötzold *et al.*, 1998). Attack rates vary widely with rootstock age and size (up to 1 larva/ 10 g of fresh root weight) and up to 40 larvae have



Figure 6. Destroyed rootstock (due to *Hylobius transversovittatus* larval feeding). (Photograph by B. Blossey.)

been found per rootstock (Blossey, 1993). Large rootstocks can withstand substantial feeding pressure and several larval generations will be necessary before significant impacts can be expected.

In Europe, the weevil occurs in all purple loosestrife habitats, except permanently flooded sites (Blossey, 1993), from southern Finland to the Mediterranean and from western Europe through Asia. Experiments have shown that adults and larvae can survive extended submergence. However, excessive flooding prevents access to plants by adults and will eventually kill developing larvae. Aside from this restriction, the species appears quite tolerant of a wide range of environmental conditions. Information on movements of *H. transversovittatus* is sparse because of its nocturnal nature and secretive habits during daylight hours. The most likely time to find adults is at night using a flashlight or on overcast days with light rain. Adults move primarily by walking, but dispersal flights of newly emerged adults have been reported (Palmén, 1940).

Nanophyes marmoratus (Coleoptera: Curculionidae)

Overwintered adults of *N. marmoratus* (1.4 to 2.1 mm) (Fig. 7) appear on purple loosestrife in mid to late May in upstate New York. The beetles start feeding on the youngest leaves. As soon as flower buds develop, beetles move to upper parts of flower spikes where they mate and feed on receptacles and ovaries. Oviposition starts soon thereafter and continues into August. Eggs are laid singly into the tips of flower buds before petals are fully developed. Larvae first consume stamens and, in most cases, petals, followed by the ovary. Mature larvae use frass to form pupa-



Figure 7. Nanophyes marmoratus adult. (Photograph by B. tion chambers herefore) bottom of the bud. Attacked buds remain closed and are later aborted. The new generation beetles appear mainly in August and feed on the remaining green leaves of purple loosestrife before overwintering in the leaf litter. Complete development from egg to adult takes about 1 month. There is one generation a year. Adult and larval feeding causes flower-bud abortion, thus reducing the seed output of *L. salicaria*. Attack rates can reach more

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

All four introduced species have successfully established in North America. The two Galerucella species are established in Maine, Massachusetts, Connecticut, Rhode Island, Vermont, New Jersey, New York, New Hampshire, Maryland, Delaware, Virginia, West Virginia, Pennsylvania, Ohio, Indiana, Tennessee, Michigan, Illinois, Wisconsin, Minnesota, Kansas, and Iowa. The species have spread up to 5 km from the original release sites and G. calmariensis appears to be more successful than G. pusilla. The secretive nature of H. transversovittatus makes assessments of its status difficult. Releases have occurred throughout the United States but establishment (attacked roots) is confirmed only for Colorado, Maryland, Pennsylvania, New York, Indiana, Minnesota, New Jersey, Michigan, and Virginia. The flower-feeding weevil now occurs in New York, New Jersey, Colorado, and Minnesota, and populations are expanding.

Suppression of Target Weed

At several release sites complete defoliation of large purple loosestrife stands (many hectares) has been reported with local reductions of more than 95% of the biomass (Fig. 8). Such outcomes are currently restricted to some of the earlier release sites but similar observations have been made in Rhode Island, Connecticut, New York, Indiana, Michigan, Illinois, Minnesota, and Canada.



Figure 8a.



Figure 8b.

Figure 8. Purple loosestrife before (a) and after (b) suppression. (Photograph by B. Blossey.)

Recovery of Native Plant Communities

A standardized long-term monitoring program has been developed to follow the development of wetland plant populations. Presently, it is too early to assess results, other than limited observations at the most advanced release sites. For example, at a release site in Illinois, several native plant species were rediscovered after suppression of purple loosestrife.

than 70%.

Similar results and a resurgence of cattails and other wetland plants have been observed at several release sites in New York. Further long-term data are needed to evaluate changes in plant communities.

Economic Benefits

The successful control and further implementation of biological control has resulted in reductions of herbicide purchases.

RECOMMENDATIONS FOR FUTURE WORK

At present, the focus in the purple loosestrife biocontrol program is on evaluation of releases using the standardized monitoring protocol. A second focus is the continued mass production of beetles to make control agents available to interested agencies or private citizens. The development of an artificial diet for the root-feeding weevil *H. transversovittatus* is anticipated to accelerate the release program and increase establishment rates. Later plans include redistribution of the flower-feeding weevil *N. marmoratus*.

Ongoing research and monitoring programs are testing the assumption of cumulative effects of herbivores. Agent combinations are anticipated to be more destructive to plants than a single species alone (Malecki *et al.*, 1993). However, agent combinations also may impede some species, as even spatially separated herbivores can compete via their common host plant (Masters *et al.*, 1993; Denno *et al.*, 1995). Whether these interactions have any influence on control of *L. salicaria* where both *Galerucella* and *H. transversovittatus* were introduced requires further study.

Results from early release sites indicate that successful suppression of purple loosestrife can be achieved. However, it is not yet clear what type of replacement communities will develop. At many sites, a diverse wetland plant community replaces the once monotypic stands of *L. salicaria*. At several sites, other invasive species such as *Phragmites australis* (Cav.) Trin. ex Steudel (common reed) or *Phalaris arundinacea* L. (reed canary grass) may expand as purple loosestrife is controlled – clearly not a desired result. At yet other sites, dense purple loosestrife litter limits growth of native species. In cooperation with land managers, we are currently investigating means (fire, disking, flooding, mowing, etc.) to accelerate the return of native plant communities. As part of these ongoing evaluations an assessment of the changes in animal communities (birds, amphibians, and insects) as *L. salicaria* is controlled will help evaluate whether invaded and degraded wetlands can be successfully restored

Attack of native parasitoids on *H*. *transversovittatus* larvae in the stems and attack of a nematode on adult *Galerucella* remains at 10% (B. Blossey, unpublished data); however, in some instances native predators appear to limit leaf-beetle population growth in cages (T. Hunt, unpublished data) or at dry sites. In Europe, specialized egg, larval and adult parasitoids can have dramatic impacts (attack rates of up to 90%) on the leaf beetles and flower-feeding weevils. While great care was taken to avoid the introduction of these and other natural enemies from Europe, the impact of native predators on the success of purple loosestrife biocontrol and the contribution of biocontrol agents to the wetland food web dynamics needs to be assessed.

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12 JAPANESE KNOTWEED

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PEST STATUS OF WEED

Japanese knotweed (Fallopia japonica var. japonica [Houtt.] Ronse Decraene) (Fig.1) was introduced to North America in the late 19th century (Pridham and Bing, 1975; Patterson, 1976; Conolly, 1977). It rapidly spread to become a problem weed, mirroring its history in the United Kingdom and Europe where it has been present since the 1840s (Beerling et al., 1994). Fallopia japonica is now officially regarded as the most pernicious weed in the United Kingdom (Mabey, 1998), and it is one of only two terrestrial weeds restricted under the Wildlife and Countryside Act 1981, making it illegal to plant it anywhere in the wild. Fallopia japonica is becoming widely recognized as a problem in the United States and some legislation to control it has been introduced in Washington state, where it is designated for mandatory control where not yet widespread. In Oregon, its planting is prohibited in at least one county (Washington State Department of Agriculture, 1999; Multnomah County, Oregon Land Use Planning Division, 1998). In other states, including Tennessee and Georgia, the recently established Exotic Pest Plant Councils list F. japonica as a species of concern and a "severe threat" (Tennessee Exotic Pest Plant Council, 1996; Murphy,



Figure 1. Fallopia japonica. (Photograph by L. Seiger.)

2000). *Fallopia japonica* is extremely difficult and expensive to control and is regarded as a serious pest by the public and authorities alike, thanks to coverage by the popular press. There are few people who share the fondness for the plant displayed by its 19th century importers.

Nature of Damage

There is little quantitative information available for the United States, but extrapolation from United Kingdom figures will be indicative.

Economic damage. The costs of the Japanese knotweed invasion in the United Kingdom are likely to be in the tens of millions of dollars per year. The main quantifiable cost is that of herbicidal treatment, which is often quoted in the United Kingdom at around \$1.60/m² for a year of repeated spraying of glyphosate (Hathaway, 1999). This does not include the costs of revegetation after herbicide treatment, which would be much greater. It has been estimated that the presence of Japanese knotweed on a development site adds 10% to the total budget, in order to cover removal and legal disposal of the topsoil contaminated with viable root material (T. Renals, pers. comm.). Further costs include repairs of flood control structures (Beerling, 1991a) and the replacement of cracked paving and asphalt through which the plant has grown. For example, one supermarket in the United Kingdom had to spend more than \$600,000 to resurface a new parking lot through which knotweed was growing. As is often the case the social cost is impossible to quantify, but a knotweed invasion can affect regional redevelopment plans and damage the tourism industry through obstruction of roadside vistas and reduced access to rivers.

Costs in the United States are expected to be comparable. Again, costs include control, usually through application of herbicide, direct damage to structures, and indirect damage associated with increased flooding and reduced amenity value of land occupied by Japanese knotweed. It has been estimated that about \$500 million is spent each year on residential exotic weed control in the United States and double that amount is spent on golf courses (Pimentel *et al.*, 2000). To be effective, Japanese knotweed control probably will need to be undertaken on a watershed-wide basis, as is being done with the ecologically similar *Arundo donax* L. in California (D. Lawson, pers. comm.). Additionally, *F. japonica* has recently been found as a crop weed in Missouri, adding agricultural losses as a potential cost attributable to this weed (Fishel, 1999).

Ecological damage. Japanese knotweed spreads quickly to form dense thickets that exclude native species and are of little value to wildlife, leading to it being described as an environmental weed (Holzner, 1982). Beerling and Dawah (1993) point out that "...if maximizing phytophagous insect diversity is considered important on nature reserves then clearly F. japonica represents a threat to the aims of the conservationist." The extensive rhizome system of this weed can reach 15 to 20 m in length (Locandro, 1973) and enables the plant to achieve early emergence and great height, which combine to shade out other vegetation, and reduce native species diversity (Sukopp and Sukopp, 1988). At the end of the season, a mass of dead stems remains that further inhibits native plant regeneration and leaves river banks vulnerable to erosion as well as to flooding (Child et al., 1992). Such flooding facilitates the further spread of propagules downstream in the form of fragments of stem and rhizome that rapidly colonize scoured banks and islands. Additionally, the fibrous stems are slow to decompose and may alter rates of decomposition (Seiger, 1997). Once established, F. japonica is very difficult to eradicate and removal efforts may have further adverse impacts on the soil or other plants. In arid areas of the United States, F. japonica has the potential to have significant detrimental effects in scarce and already stressed riparian systems (Seiger, 1997).

Extent of losses. The damage attributed to *F. japonica* in the United States has not been quantified, but is probably greater than generally recognized. Because this plant invades valuable wetland habitat (a significant portion of which has already been lost), it is of particular concern. Large stands have been noted in western Pennsylvania, in particular along the banks of the Ohio and Allegheny Rivers and on

the islands in these rivers where it occupies hundreds of acres of wetlands, stream banks, and hillsides (Wiegman, pers. comm.). It is present on at least two sites belonging to the Pennsylvania Chapter of The Nature Conservancy (Long Pond in the Poconos and Bristol Marsh, an urban preserve near Philadelphia) and has become a problem in creeks in suburban Philadelphia (Broaddus, pers. comm.). *Fallopia japonica* also is a serious problem in other eastern states, including New York, New Jersey, Maryland, and Virginia, where it spreads primarily along river banks, but also grows in wetlands, waste places, along roadways, and in other disturbed areas (Muenscher, 1955; Conolly, 1977; Beerling, 1990; Mehrhoff, 1997; Virginia Native Plant Society, 1999).

Geographical Distribution

Fallopia japonica has spread through most of North America (Fig. 2) and has been observed as far north as Alaska. Its southern distribution extends into Louisiana in the east and to central California in the west. Found throughout the midwestern and much of the western United States, it is particularly abundant in the eastern United States and in the coastal areas of Washington and Oregon (Patterson, 1976; Locandro, 1978; Pauly, 1986; Seiger, 1997; USDA, NRCS, 1999). Its Canadian distribution includes British Columbia and most of eastern Canada (Seiger, 1997; USDA, NRCS, 1999).



Figure 2. Current distribution of *Fallopia japonica* in North America. (L. Seiger.)

In the United Kingdom, *F. japonica* has spread widely, occurring in more than half of the 10 x 10 km quadrats in the national grid (Biological Records Centre, Monkswood). Stands range in size from individual plants to clumps of more than 500 m² (Palmer, 1990). It also is a concern in several other European countries including France, Germany, the Czech Republic and Norway. Its spread in Europe shows the typical exponential invasion pattern (Pysek and Prach, 1993).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Synonyms of Fallopia japonica var. japonica (Houtt.) Ronse Decraene include Reynoutria japonica Houtt. var. japonica, Polygonum cuspidatum Sieb. and Zucc., Polygonum sieboldii Vriese, and Polygonum reynoutria Makino. Common names include: Japanese knotweed, Japanese bamboo, Mexican bamboo, Japanese fleece flower, donkey rhubarb, Sally rhubarb, German sausage, and pea-shooter plant.

Japanese knotweed was independently classified as *Reynoutria japonica* by Houttuyn in 1777 and as *P. cuspidatum* by Siebold in 1846. It was not until the early part of the 20th century that these were discovered to be the same plant (Bailey, 1990), which is generally referred to as *Polygonum cuspidatum* by Japanese and American authors. Recent evidence vindicates Meissner's 1856 classification as *Fallopia japonica* var. *japonica* (Bailey, 1990). The two most common introduced varieties are *japonica* and *compacta*. I is the former that is the main problematic weed, and where this paper refers to *F. japonica* it implies *F. japonica* var. *japonica*.

Biology

In the United States, *F. japonica* has been observed growing in a variety of soil types, including silt, loam, and sand, and in soils with pH ranging from 4.5 to 7.4 (Locandro, 1973). In areas where *F. japonica* has been introduced, it is found primarily in moist, unshaded habitats. Distribution maps from the United Kingdom show that it is generally associated with regions of high precipitation (Conolly, 1977). However, Locandro (1973) reported it growing on xeric as well as hydric sites in the United States. *Fallopia japonica* requires high light environments and competes effectively for light in such situations. It is found primarily in open sites, and its growth and abundance are depressed in shady sites (Beerling, 1991b; Seiger, 1993). Consequently, it is unable to invade forest (Beerling, 1991b, Seiger, 1993) but the species is present at many forest interior sites in New York, potentially a result of earlier plantings that survived the return of the forest (Blossey, pers. comm.)

After overwintering, shoots appear from underground rhizomes early in the spring around March and April. Rapid growth, which can exceed 8 cm per day (Locandro, 1973), means that full height, which can exceed 4 m, is attained by the early part of summer. Flowering occurs in late August or early September (Fernald, 1950; Muenscher, 1955), leaves senesce after reproduction, and the above-ground parts are killed off by the first frost but stems remain standing into the next growing season.

Although insect pollination, sexual reproduction, and wind dispersal of seed is the dominant method of reproduction and dissemination in its native range, introduced populations rely solely on vegetative means. Seeds can be found, but these rarely germinate in the wild. It has been shown that these populations originate from one male-sterile clone and any seed produced by it must therefore be of hybrid origin (Bailey et al., 1996). These hybrids occur in the United Kingdom in the form of crosses between F. japonica and Fallopia sachalinensis (F. Schmidt ex. Maxim.) Ronse Decraene, which form the hybrid Fallopia x bohemica (Chrtek and Chrtková) J. Bailey (Bailey, 1990). Fallopia japonica also hybridizes with Fallopia baldschuanica (Regel) Holub. (Bailey, 1985, 1988, 1990, 1994). In the United States, hybrids morphologically similar to those between F. japonica and F. baldschuanica have been grown from seeds collected in the field, but seedling establishment has not been observed in the wild (Seiger, 1993). Fortunately, these crosses form a plant with reduced vigor rather than conferring the benefits of both parents, but backcrossing could result in F. japonica regaining the advantages of sexual reproduction.

Since plants can reliably regenerate from less than 5 g of root material, the rhizomes beneath a 1 m² stand of knotweed could produce 238 new shoots (Brock and Wade, 1992). Plants also have been observed to regenerate from internode tissue (Locandro, 1973). Such material can regenerate when buried up to 1 m deep, and shoots have been observed growing through two inches of asphalt (Locandro, 1978; Pridham and Bing, 1975). Dispersal is limited to areas where rhizome fragments can be distributed from existing stands by being washed downstream, or when soil containing rhizomes is transported by humans. *Fallopia japonica* occurs over most of the United States and is increasingly recognized as a major weed.

ANALYSIS OF RELATED NATIVE PLANTS IN THE EASTERN UNITED STATES

Fallopia japonica belongs to the Polygonaceae family of which there are about 49 genera and 1,100 species worldwide. There are approximately 24 genera and 446 species in the United States and Canada, many of which are introduced. Most genera originate in northern temperate regions with only a few from subtropical and tropical areas. The most common genera in the United States are Polygonum, Eriogonum, and Rumex (Zomlefer, 1994). Genera of minor economic importance include Rheum, Fagopyrum, Rumex, and Coccoloba for their agricultural products, and a number of other genera used as ornamentals.

The phylogeny of the Polygonaceae is controversial and some of the genera continue to be disputed. However, a recent study indicates that *Fallopia* is among those genera that are distinct (Mondal, 1997). There are seven species of *Fallopia* recorded in the United States: *Fallopia aubertii* (Henry) Holub, *F. baldschuanica, Fallopia convolvulus* (L.) A. Löve, *F. japonica, F. sachalinensis, Fallopia cilinodis* (Michx.) Holub and *Fallopia scandens* (L.) Holub (Kartesz, 1994; USDA, NRCS, 1999). Only the last two are native species. As discussed elsewhere in this text, hybridization occurs between *F. japonica* and *F. sachalinensis*, and between *F. japonica* and *F. baldschuanica* in the United Kingdom and possibly in the United States.

Members of the Polygonaceae comprise a number of cosmopolitan species widely distributed throughout the eastern United States and elsewhere. Many of these species have important wildlife value. The plants and seeds of various species in the closely related genus *Polygonum* are used by birds and small mammals and, in particular, are an important source of food for ducks. Other species of *Polygonum* provide habitat for invertebrates on which ducks feed. Dense stands of *Polygonum* also are used as cover by various birds, small mammals such as muskrats, and deer. Native species that are particularly important to wildlife include the native species *Polygonum pensylvanicum* L., *Polygonum hydropiperoides* Michx., *Polygonum sagittatum* L., and *Polygonum arifolium* L. All grow as herbaceous plants in wetland habitats. The potential effects on these and other closely related species will have to be considered as part of any biological control program.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Fallopia japonica is native to Japan, China, Korea, and Taiwan (Beerling *et al.*, 1994), while the form *japonica* comes solely from Japan. In Japan, where it is known by the name Itadori, meaning "heals the sick," where it can be found at up to 2,400 m on Mt. Fuji (Maruta, 1983). In the more southerly latitude of Taiwan, the plant grows at altitudes between 2,400 and 3,800 m. Although common on roadsides and riverbanks, it is a natural pioneer of volcanic fumaroles (Hirose and Katajima, 1986), where the soil conditions are extreme. At such sites, it is displaced by other vegetation after 50 years or so (Yoshioka, 1974).

Areas Surveyed for Natural Enemies

So far there have been no comprehensive surveys of natural enemies of Japanese knotweed in the area of origin. However some work has been carried out on groups of natural enemies such as the Lepidoptera (Yano and Teraoka, 1995), and ad hoc collections of fungal pathogens have been made by scientists of CAB International. Emery (1983) made some field observations on natural enemies in the United Kingdom and recorded damage inflicted by the green dock beetle, *Gastrophysa viridula* De Geer, but only after heavy skeletonization of neighboring *Rumex obtusifolius* L. plants. Regional surveys for potential natural enemies were begun in 2000 in the northeastern United States.

Natural Enemies Found

In contrast to the situation in the United Kingdom and United States, damage to *F. japonica* by foliagefeeding invertebrates and pathogens was high in some of the Japanese sites examined by Yano and co-workers in 1991 and 1992 (K. Yano, pers. comm.). At least 12 species of insect herbivores were commonly found on the plant at these sites and many more species of insect herbivores have been recorded on the plant. At least 39 of these are likely to be to be feeding on plant parts other than the flowers (Shaw, 1995).

Stem-mining Lepidoptera, found in the internodal sections of stems of the closely related *F. sachalinensis*, are so numerous that they are regularly used as fishing bait (Sukopp and Starfinger, 1995). Zwölfer (1973) reported complete skeletonization of this plant in the field in 1972, noting that the "apparently specific leaf-feeding chrysomelid beetle *Gallerucida nigromaculata* Baly (Fig. 3) seems to play a role in the natural control of *Polygonum* (*cuspidatum*) and may be a promising candidate for the biological control of *P. cuspidatum* in Europe."



Figure 3. Leaf feeding damage to *Fallopia* sp. in Japan 1999. (Photograph by J. Bailey.)

In Japan, *F. japonica* also is attacked by a suite of fungal pathogens in the field, including *Puccinia polygoni-weyrichii* Miyabe, whose erupting uredinia are shown in Fig. 4. It is apparent that a combination of insect and fungal agents severely damages the plant in its native range, reducing it to an innocuous member of the flora in competition with the other members of the "giant herb" community common in Japan.



Figure 4. *Puccinia* sp. on *Fallopia japonica* in Japan showing urediniospores. (Photograph by R. Shaw.)

Host Range Tests and Results

None have been reported to date.

Releases Made

None have been made to date.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Natural enemy surveys have not yet been completed and thus no information is currently available on the biology of candidate natural enemies.

EVALUATION OF PROJECT OUTCOMES

The biological control of this weed has not yet been attempted, although projects in the United Kingdom and United States are being considered.

RECOMMENDATIONS FOR FUTURE WORK

A proposal by CAB International for a classical biological control research program to assess both arthropod and fungal natural enemies for use against *F. japonica* is currently under consideration by potential sponsors in both the United States and the United Kingdom. The United States funding consortium is being coordinated by the Biological Control of Non-Indigenous Plant Species Program at Cornell University.

Initial surveys of natural enemies already present in the United States will run concurrent with a preliminary survey of natural enemies in Japan, in the area of origin, and establishment of collaborative agreements with suitable scientists in the most appropriate areas. An entomologist and pathologist will carry out this work and produce a report based on the findings. Further surveys and shipments of selected natural enemies to CABI's United Kingdom quarantine facilities for host specificity testing will then pursued, coupled with a long-term field study in the area of origin. Special attention will be paid to those species identified as promising in previous literature studies (Fowler et al., 1991; Greaves and Shaw, 1997; Shaw 1995) and to rhizome feeders that may attack the large underground storage reserves. If release is appropriate, then long-term monitoring programs would be set up to monitor for control levels as well as non-target effects.

Apart from the environmental and financial costs associated with ineffective chemical-based control measures, perhaps the most important aspect of knotweed invasions is the displacement of native plants in riparian situations. These problems are common to several countries, so there are advantages to a collaborative approach to research, as well as the sharing of funding. The target plant in this case is believed to be clonal and, therefore, none of the usual problems associated with a variable target weed population will be experienced. However, since hybridization is already occurring, time is of the essence. The opportunity to investigate both arthropod and fungal agents from the outset rather than one following on from the other, as has often been the case, opens up the exciting field of insect-fungal interactions with regard to weed biological control. Japanese knotweed is certainly a plant for which classical biological control is the only long-term, sustainable solution.

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SECTION III: WEEDS OF PRAIRIES AND GRASSLANDS

Spotted Knapweed Leafy Spurge Cypress Spurge Swallow Worts Canada Thistle Musk Thistle Bull Thistle Slenderflower Thistle Plumeless Thistle

13 SPOTTED KNAPWEED

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PEST STATUS OF WEED

Spotted knapweed, *Centaurea maculosa* Lamarck, is a purple-flowered, herbaceous, perennial weed, living three to five years on average. It infests semiarid range lands in the western United States and roadsides and fields in the eastern part of the country. Infested areas are dominated by the plant, reducing their grazing value and suppressing native plant communities. The plant, originally from Central Asia, has been in North America for over 120 years.

Nature of Damage

Economic damage. Spotted knapweed is a serious problem on rangeland, especially in the western United States. Bucher (1984) estimated that an 800,000 ha infestation in Montana was causing \$4.5 million in annual forage losses, and that invasion of 13.6 million ha of vulnerable rangeland in Montana would cost cattle and sheep ranchers \$155.7 million of gross revenue annually. Hirsh and Leitch (1996) reported that an 800,000 ha infestation of spotted knapweed, in combination with two knapweeds of minor importance in Montana (diffuse knapweed, Centaurea diffusa Lamarck, and Russian knapweed, Acroptilon repens [L] de Candolle) was causing \$14 million in direct negative impacts and \$28 million in indirect effects (i.e., reduced regional economy) to the state of Montana. Harris and Cranston (1979) reported that the 30,000 ha infestation in Canada was reducing forage production more than 88%. In the northeastern and northcentral United States, the plant is primarily a problem of roadsides, fields, and waste areas (Hoebeke, 1993); economic impact of the plant in those regions has not been reported.

Ecological damage. Spotted knapweed reduces livestock and wildlife forage (Thompson, 1996; Watson and Renney, 1974), increases surface water

runoff and soil sedimentation (Lacey *et al.*, 1989), and lowers plant diversity (Tyser and Key, 1988). Spotted knapweed produces an allelopathic compound that reduces germination of some grass species (Kelsey and Locken, 1987).

Geographical Distribution

Spotted knapweed is native to Europe and western Asia but has become widespread in parts of the United States and Canada. The plant occurs throughout the United States except for Alaska, Texas, Oklahoma, Mississippi, and Georgia (USDA, NRCS, 2001). The plant is a serious invader of rangeland in the Rocky Mountain region. In Montana alone, the plant infests an estimated 1.9 million ha of rangeland and pasture (Lacey, 1989). In Canada, the plant is abundant in British Columbia, and is common in Ontario, Quebec, and the Maritimes (Watson and Renney, 1974).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The taxonomy of *C. maculosa* has been detailed by Dostal (1976) and reviewed by Müller *et al.* (1988) and Müller (1989). *Centaurea maculosa* is comprised of several subspecies occurring from western Asia to western Europe. The *C. maculosa* occurring in North America is a short-lived perennial tetraploid (2n=36) that is considered the same as *C. biebersteinii* de Candolle subsp. *biebersteinii* (=*C. micranthos* Gmelin ex. Hayek), a native of western Asia. However, the most widely distributed *C. maculosa* in Europe is the biennial diploid (2n=18) *C. maculosa* spp. *rhenana* (Boreau) Gugler (Dostal, 1976; Müller *et al.*, 1988; Müller, 1989).

Biology

Spotted knapweed is a purple-flowered, herbaceous weed, 30 to125 cm tall, with one to 10 upright stems, and a stout taproot (Fig. 1). The plant is a perennial, living an average of three to five years and frequently up to nine years (Boggs and Story, 1987). The flower heads, enclosed by black-tipped bracts, are borne singly at the terminal ends of branches. Seed is shed immediately upon maturation of the seed head. The plant reproduces solely by seed. Seed production ranges from 5,000 to 40,000 seeds/m² (Sheley *et al.*, 1998). Seeds can survive in the soil for eight or more years (Davis *et al.*, 1993).



Figure 1. Spotted knapweed, *Centaurea maculosa* Lamarck. (Photograph by Jim Story.)

The life history of the plant has been described by Watson and Renney (1974). Seed germination occurs in the fall or early spring, depending upon moisture availability. Seedlings develop into rosettes; plants that have overwintered as rosettes usually produce floral stems the following summer. Stem elongation occurs in June followed by flowering in July and seed dispersal in August.

Spotted knapweed is adapted to a range of habitats and soil types, but is especially well suited to relatively dry sites (Watson and Renney, 1974). In Europe, the plant is most aggressive in the forest steppe but can form dense stands in more moist areas on well-drained soils including gravel, and in drier sites where summer precipitation is supplemented by runoff (Sheley *et al.*, 1998).

Analysis of Related Native Plants in the Eastern United States

The North American plants most closely related to spotted knapweed include safflower (*Carthamus tinctorius* L.) and possibly the two "knapweeds," *Centaurea americana* and *Centaurea rothrockii*. Recent evaluations, however, suggest the latter two plants should be treated as *Plectocephalus americanus* (Nutt.) (Müller-Schärer and Schroeder, 1993). The next closest relatives of spotted knapweed are members of the tribe Cardueae, mainly Carduinae (*Cirsium* and *Cynara* [e.g., artichoke]). There are numerous *Cirsium* species native to North America.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The native range of the spotted knapweed (tetraploid) occurring in North America is eastern Europe and western Asia (Müller *et al.*, 1989).

Areas Surveyed for Natural Enemies

Surveys were conducted throughout Europe and western Asia for natural enemies.

Natural Enemies Found

Schroeder (1985) listed 38 arthropod species that were known to be associated with spotted knapweed in Eurasia. Of these, 12 species were screened and released in North America against the plant (Table 1).

Host Range Tests and Results

The number of plants included in the test plant list for each of the 12 insect species varied, but averaged around 45 test plant species per insect. Most of the plant species used were from the family Asteraceae, but representative species from one or more other families also were often tested. Particular emphasis was placed on plants in the Asteraceae tribe Cardueae which includes the genus *Centaurea*. The test plant list for *Larinus minutus* is presented in Table 2 (Jordan, 1995) because it is fairly representative of the plants tested on all 12 insect species. The only plants of economic importance in North America included in the tests were *Carthamus tinctorius* L. (safflower),

			8	1	1	
Scientific Name	Insect Type	Plant Part Attacked	Where Collected	Date of First U.S. Release	State/Date of Release in Eastern U.S. and Canada	Known Estab. in Eastern U.S. and Canada
<i>Urophora affinis</i> Frauenfeld	Fly (Tephritidae)	Flower head	France, Austria	1973	IN 1997 MD 1983	
					NY 1983	х
					VA 1986	х
					MN 1990	Х
					WI 1991	х
					MI 1994	х
					Quebec 1979 Ontario 1970	х
Urophora	Fly	Flower head	Former USSR	1980	Quebec 1979	х
quadrifasciata	(Tephritidae)	i lo not notad			MD 1983	x
(Meigen)	()				NY 1983	
(Meigen)					VA 1986	х
					MN 1990	x
					WI 1991	x
					MI 1994	x
					IN 1997	x
					IN 1997	*
<i>Terellia virens</i> (Loew)	Fly (Tephritidae)	Flower head	Austria, Switzer.	1992	MN 1994	
<i>Chaetorellia acroloph</i> i White and Marquardt	Fly (Tephritidae)	Flower head	Austria,Switzer.	1992	MN 1996	
Metzneria	Moth	Flower head	Switzer.	1980	MN 1991	
paucipunctella Zeller	(Gelechiidae)	i lower neud	C MILLON	1000	VA 1986	х
<i>Agapeta zoegana</i> L.	Moth (Cochylidae)	Root	Austria, Hungary	1984	IN 1996 MN 1991 WI 1991	x
<i>Pterolonche inspersa</i> Staudinger	Moth (Pterolon- chidae)	Root	Hungary	1988	-	
Pelochrista medullana (Staudinger)	Moth (Tortricidae)	Root	Austria, Hungary	1984	-	
Cyphocleonus achates (Fahraeus)	Weevil (Curculionidae)	Root	Austria, Romania	1988	IN 1996 MN 1994	
<i>Bangasternus fausti</i> Reitter	Weevil (Curculionidae)	Flower head	Greece	1990	MN 1992	
Larinus obtusus Gyllenhal	Weevil (Curculionidae)	Flower head	Romania, Serbia	1992	MN 1995	
<i>Larinus minutus</i> Gyllenhal	Weevil (Curculionidae)	Flower head	Greece, Romania	1991	IN 1996 MN 1994	x x

Table 1. Insects Released in the United States for Biological Control of Spotted Knapweed

Helianthus annuus L., (common sunflower), and Cynara scolymus L. (globe artichoke). None of the insects oviposited or fed on any of these three plants except for Cyphocleonus achates adults which fed slightly on artichoke. The feeding by *C. achates* was not of concern, however, because no eggs were laid on the plant. In general, attack by all of the insects was restricted to the genus *Centaurea*, and usually to

Table 2. Test plant list used for Larinus minutus

FAMILY: ASTERACEAE Tribe: Cardueae Subtribe: Centaureinae Genus: Centaurea Subgenus: Acrolophus Centaurea arenaria Bieb. C. cineraria L. C. diffusa Lamarck Europe C. diffusa USA C. friderici Vis. C. maculosa Lamarck Europe C. maculosa USA C. micranthos S. G. Gmelin C. paniculata L. C. vallesiaca (D. C.) Jordan Subgenus Calcitrapa C. calcitrapa L. C. iberica Trev. Sprengel Subgenus: Cartholepis C. macrocephala Muss. Subgenus: Centaurea C. ruthenica Lamarck Subgenus: Cyanus C. cyanus L. C. montana L. Subgenus: Jacea C. jacea L. C. nigra L. C. nigrescens Willd. C. pannonica (Heuffel) Simonkai C. phrygia Subgenus Lopholoma C. scabiosa L. Subgenus: Phalolepis C. alba L. Subgenus: Psephellus C. dealbata Willd. Subgenus: Seridia C. aspera L. C. napifolia Subgenus: Solstitiaria C. nicaeensis All. C. solstitialis L. other genera: Acroptilon repens (L.) D. C. Carduncellus monspelliensum All. Carthamus tinctorius L. Cnicus benedictus L. Crupina vulgaris Pers. Mantisalca salmantica Brig. and Cavillier Plectocephalus americanus (Nutt.)

Subtribe: Carduinae Arctium lappa L. Carduus acanthoides L. C. nutans L. Cirsium arvense (L.) Scop. C. crassicaule (Greene) Jeps. C. creticum C. undulatum (Nutt.) Spreng. Cynara scolymus L. Galactites tomentosa Onopordum acanthium L. Silybum marianum (L.) Gaertn. Tribe: Anthemideae Achillea millefolium L. Anthemis tinctoris L. Artemisia absinthium L. Chrysanthemum leucanthemum L. Tribe: Astereae Aster novi-belgii L. Solidago canadensis L. Tribe: Calenduleae Calendula officinalis L. **Tribe: Carlineae** Carlina vulgaris L. **Tribe: Cichorieae** Cichorium intybus L. Taraxacum officinale Web. **Tribe Echinopeae** Echinops sphaerocephalus L. **Tribe Heliantheae** Helianthus annuus L. H. decapetatus L. H. tuberosus L. Rudbeckia hirta L. **Tribe: Inuleae** Inula helenium Helichrysum orientale (L.) Gaertn. Tribe: Senecioneae Senecio jacobaea L. FAMILY: CARYOPHYLLACEAE Dianthus superbus Silene vulgaris (Moench) Garcke FAMILY: CHENOPODIACEAE Beta vulgaris L. FAMILY: CISTACEAE Helianthemum vulgare Gaertn. FAMILY: CRUCIFERAE

Brassica oleracea L. FAMILY: DIPSACACEAE

Dipsacus fullonum L.

FAMILY: POLYGONACEAE Rumex acetosa L.

FAMILY: RANUNCULACEAE

Delphinium elatum L.

FAMILY: UMBELLIFERAE

Apium graveolens L. Daucus carota L. the subgenus *Acrolophus*. There has been no report of attack on non-target species by any of the insects since release, although specific surveys have apparently not been conducted.

Releases Made

Of the 12 biological control agent species released against spotted knapweed in the United States, 10 species have been released against spotted knapweed in the eastern United States and five (Table 1) have become established (Hoebeke, 1993; Wheeler, 1995; Mays and Kok, 1996; Wheeler and Stoops, 1996; Lang *et al.*, 1997; Lang, pers. comm.). The root moth, *Pelochrista medullana* (Staudinger) (Lepidoptera: Tortricidae) and the root moth, *Pterolonche inspersa* Staudinger (Lepidoptera: Pterolonchidae) were not released in the eastern United States due to insufficient numbers.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Urophora affinis Frauenfeld (Diptera: Tephritidae)

Urophora affinis is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 2). The fly is distinguished from other knapweed tephritids by the bright yellow spot on its black thorax, the black abdomen, and the light-colored markings on its wings. Collected in France and Austria, the first United States release was made in Montana and Oregon in 1973 (Maddox, 1982).



Figure 2. Urophora affinis Frauenfeld. (Photograph by Robert Richard. USDA, APHIS, PPQ.)

Larval feeding causes the formation of hard, woody galls in the receptacle tissue. The galls divert plant nutrients, resulting in reduced seed production in both attacked and unattacked seed heads on a plant. *Urophora affinis* is currently reducing seed production of spotted knapweed in the Pacific Northwest close to the threshold needed to achieve economic control (Harris and Shorthouse, 1996).

Fly larvae overwinter within galls (one larva per gall) and pupate in May, followed by adult emergence in late June and July. *Urophora affinis* is generally univoltine although a small percentage (approximately 7%) emerge in August and complete a second generation (Zwölfer, 1970; Gillespie, 1983; Story *et al.*, 1992).

Urophora quadrifasciata (Meigen) (Diptera: Tephritidae)

Urophora quadrifasciata is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 3). The fly is distinguished from other knapweed tephritids by its relatively dark body and the dark bands in the shape of the letters "UV" on its wings. The general biology of *U. quadrifasciata* is similar to that of *U. affinis* except that *U. quadrifasciata* forms papery galls in the ovary, attacks larger flower heads than does *U. affinis*, and is generally bivoltine (Harris, 1980; Gillespie, 1983).

Urophora quadrifasciata was introduced into British Columbia in 1972 (Harris, 1980), but not into the United States. However, by the early 1980s, the fly had dispersed into the Pacific Northwest states. Urophora quadrifasciata is now more widely distrib-



Figure 3. Urophora quadrifasciata (Meigen). (Photograph by Robert Richard, USDA, APHIS, PPQ.)

uted than *U. affinis. Urophora quadrifasciata* is common in many areas of the northeast and is very abundant in some areas of upstate New York (Blossey, unpub.data). However, *U. quadrifasciata* numbers remain low in areas where the two *Urophora* spp. coexist.

Metzneria paucipunctella Zeller (Lepidoptera: Gelechiidae)

Metzneria paucipunctella is a small (9 mm), univoltine moth that attacks the flower heads of spotted knapweed (Fig. 4). The moth is tan with small black spots. Originally collected in Switzerland, the moth was introduced into British Columbia in 1973 (Harris and Myers, 1984). Moths collected from British Columbia were subsequently introduced into the United States in Montana in 1980 (Story *et al.*, 1991a).



Figure 4. *Metzneria paucipunctella* Zeller. (Photograph by Robert Richard, USDA, APHIS, PPQ.)

Metzneria paucipunctella overwinters as larvae in seed heads. Pupation occurs in May, followed by adult emergence in June and early July. Young larvae feed on developing seeds while older larvae feed on mature seeds and mine the receptacle. Older larvae bind several seeds together with silk webbing, which prevents dispersal of those seeds at maturity. Due to strong intraspecific competition, only one larva survives per seed head (Englert, 1971). Each larva destroys an average of eight seeds per seed head (Story *et al.*, 1991a). Larvae also will attack and destroy other seed head flies, *Urophora* spp. (Story *et al.*, 1991a). *Metzneria paucipunctella* frequently suffers high overwintering mortality.

Agapeta zoegana L. (Lepidoptera: Cochylidae)

Agapeta zoegana is a small (9 mm), yellow and brown, univoltine moth that attacks the roots of spotted knapweed (Müller *et al.*, 1988) (Fig. 5). Collected in Austria and Hungary, the first United States release of the moth was made in Montana in 1984 (Story *et al.*, 1991b).



Figure 5. Agapeta zoegana L. (Photograph by Jim

Story.) Agapeta zoegana overwinters as larvae in roots. Adult emergence occurs from mid-June to early September. Females begin mating the first night after emergence and begin laying eggs the following evening. Adults live for nine to 11 days and each female lays an average of 75 eggs (up to 290), mostly within a four-day period. Larvae hatch in seven to 10 days and begin mining in the epidermal tissues of the root crown. Older larvae mine in the cortex and endodermis tissues and several larvae may develop in the same root. Agapeta zoegana has one generation per year. Studies in Montana indicate the moth is reducing the biomass of knapweed at some sites (Story et al., 2000). Analyses by Clark et al. (2001a) suggest that probability of A. zoegana establishment at release sites is affected by soil type and the shape (patchy, continuous or linear) of the weed infestation.

Cyphocleonus achates (Fahraeus) (Coleoptera: Curculionidae)

Cyphocleonus achates is a large (19 mm), gray and black mottled weevil that attacks the roots of spotted knapweed (Fig. 6). Collected in Austria and Romania, the first United States release of the weevil was made in Montana in 1988 (Story *et al.*, 1997).



Figure 6. *Cyphocleonus achates* (Fahraeus). (Photograph by CABI Bioscience.)

This univoltine weevil overwinters as larvae in roots. Adults emerge from mid-July to October and live eight to 15 weeks. Each female lays from one to three eggs per day throughout her adult life. Larvae hatch in 10 to 12 days and mine into the root cortex, eventually causing the formation of a conspicuous root gall. Dispersal is slow as adults don't fly (Stinson *et al.*, 1994).

Studies by Clark *et al.* (2001a) suggest that probability of *C. achates* establishment at release sites is affected by elevation, the shape (patchy, continuous or linear) of the weed infestation, and the number of years in which releases are made.

Larinus minutus Gyllenhal (Coleoptera: Curculionidae)

Larinus minutus is a small (4.5 mm) univoltine weevil that attacks flower heads of diffuse and spotted knapweed (Jordan, 1995) (Fig. 7). Collected in Greece and Romania, the weevil was introduced into the United States in Montana, Washington, and Wyoming in 1991 (Lang *et al.*, 1996).



Figure 7. *Larinus minutus* Gyllenhal. (Photograph by Robert Richard, USDA, APHIS, PPQ.)

Weevils overwinter as adults in soil and become active in early June. Eggs are deposited into freshly opened flower heads during late July through early September. Larvae hatch in about three days and immediately feed downwards into the flower head, where they eat seeds and pappus hairs. Larval development is completed in about 28 days followed by a short pupation period (one to two weeks; Jordan, 1995). Adult *L. minutus* emerge from the seed head in late September and October and feed on knapweed leaves for a short period before entering the soil to overwinter.

Larinus minutus has developed large populations on diffuse knapweed in Washington, Montana, and Oregon, but population increase on spotted knapweed has been slow.

Larinus obtusus Gyllenhal (Coleoptera: Curculionidae)

Larinus obtusus is a small (5 mm) univoltine weevil that attacks the flower heads of spotted knapweed (Groppe, 1992). The weevil is slightly larger than *L. minutus*. Collected in Romania and Serbia, *L. obtusus* was introduced into the United States in Montana in 1992 (Story, unpub. data). The insect is established in moderate numbers in Montana.

Adult weevils become active in May and June and eggs are deposited into freshly opened flower heads in July. Larvae hatch in about four days and immediately feed downward into the flower head, where they eat seeds and pappus hairs. Larval development is completed in about 17 days followed by a nine-day pupation period. Adults of the new generation emerge from the seed head in late summer, approximately 30 days after egg deposition. Adults feed on knapweed leaves for a short period before entering the soil to overwinter.

Bangasternus fausti Reitter (Coleoptera: Curculionidae)

Bangasternus fausti is a small (4.5 mm) univoltine weevil that attacks the flower heads of spotted knapweed (Sobhian *et al.*, 1992). The weevil, collected in Greece, was introduced into the United States in 1990 (Rees *et al.*, 1995).

Adults become active in May and June and eggs are deposited (usually singly) on the stems or bracts of flower heads that are 3.0 to 3.5 mm in diameter. Females cover eggs with a black, hard material. Eggs hatch in eight to12 days and larvae tunnel through the stem until they enter the flower head. Larvae from eggs laid on the flower head tunnel directly into the flower head. Once in the flower heads, larvae consume florets and ovules. Adults of the new generation emerge from the seed head in late summer and later enter the soil to overwinter. The period from egg to adult is about 32 days.

Chaetorellia acrolophi White and Marquardt (Diptera: Tephritidae)

Chaetorellia acrolophi is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 8). The fly is distinguished from other knapweed tephritids by having nine black spots on a light-colored thorax, a light-colored abdomen, and light-colored markings on the wings in a "UV" pattern similar to that of *U. quadrifasciata. Chaetorellia acrolophi* was collected in Austria and Switzerland and introduced into the United States in Montana in 1992 (Story, unpub. data). Establishment rates have been very low in most states.



Figure 8. *Chaetorellia acrolophi* White and Marquardt. (Photograph by CABI Bioscience.)

Chaetorellia acrolophi overwinters as larvae in seed heads. Pupation occurs in May, followed by adult emergence in June and early July. Eggs are deposited into unopened flower heads from June to July. Larvae hatch in about four days and immediately travel to the center of the flower head, where they burrow into florets. Older fly larvae attack several young seeds, additional florets, and parts of the seed head receptacle. The fly has two generations per year. Larvae and pupae of the first generation of *C. acrolophi* are white, while second generation larvae and pupae are yellow (Groppe and Marquardt, 1989a).

Terellia virens (Loew) (Diptera: Tephritidae)

Terellia virens is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 9). The fly is distinguished from other knapweed tephritids by its lack of wing markings, its light-colored abdomen, and the faint spots on its light-colored thorax. *Terellia virens*, collected in Austria and Switzerland, was introduced into the United States in Montana in 1992 (Story, unpub. data). Establishment rates have been very low in most states.



Figure 9. *Terellia virens* (Loew). (Photograph by CABI Bioscience.)

The fly overwinters as larvae in seed heads. Pupation occurs in May, followed by adult emergence in June and early July. Eggs are deposited into flower heads that are beginning to open. Larvae hatch in about four days and immediately burrow into young seeds (one larva per seed). Older larvae attack several young seeds and occasionally feed on the seed head receptacle. *Terellia virens* often has two generations, depending upon fall weather (Groppe and Marquardt, 1989b).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Of the natural enemy species released against spotted knapweed in the eastern United States and Canada, the following have been established: *Urophora affinis* (Virginia, New York, Pennsylvania, Minnesota, Wisconsin, Michigan, Quebec); *Urophora quadrifasciata* (Connecticut, Indiana, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, West Virginia, Wisconsin, and Quebec); Metzneria paucipunctella (Virginia); Agapeta zoegana (Minnesota); and Larinus minutus (Indiana, Minnesota) (Hoebeke, 1993; Wheeler, 1995; Wheeler and Stoops, 1996; Mays and Kok, 1996; Lang et al., 1997; Lang, pers. comm.) (Table 1). Except for the two Urophora species, particularly U. quadrifasciata, dispersal of the knapweed agents has been modest. An assessment of the Urophora spp. spread was conducted in Montana (Story et al., 1987).

Suppression of Target Weed

Effects of imported natural enemies on spotted knapweed densities in the eastern United States have not been examined. However, impact information has been collected at sites in the western United States. Studies in Montana indicate that the two Urophora spp. are reducing spotted knapweed seed production by a minimum of 40% (Story et al., 1989), seed reduction by the Urophora spp. is further increased when *M. paucipunctella* is present (Story *et al.*, 1991a), and A. zoegana is significantly reducing the biomass of spotted knapweed at some sites (Story et al., 2000). Spotted knapweed density is significantly reduced at two sites in western Montana where C. achates is well established (Story, unpub. data). Clark et al. (2001b) reported that spotted knapweed stem density, at 13 sites in Montana and adjacent states where U. affinis and one or both root feeding species of natural enemies (A. zoegana, C. achates) were established, declined from about 15 plants per m² in 1991 to1993 to seven plants in 1997 to 1998.

Effects on Native Plants

Neither the impact of these released agents on native, non-target plants, nor the recovery of native plant communities as weed densities decline have been examined.

Economic Benefits

The economic benefits of biological control have not been realized yet, even in the west where some agents have been established for more than 15 years. However, given the reductions in knapweed density recently observed at localized infestations in Montana, economic benefits should be measurable in many states in the near future.

RECOMMENDATIONS FOR FUTURE WORK

Because of the large infestations of spotted knapweed in the west and the wide distribution in the north central and eastern United States, extensive redistribution of established biological control agents is required throughout much of the country. For preventative purposes, releases of the agents should be made in all states having only small populations of the weed.

The potential of most of the agents has not yet been realized in the west due to the large size of the infestations and the agents' modest rate of population increase. The control agents currently established in the United States are probably capable of reducing spotted knapweed densities in most locations.

There will undoubtedly be locations where the biological control agents are not effective. For example, early observations suggest the current complex of biological control agents in North America may not be effective on knapweed growing at higher elevations (>1,800 m). There are several niches on the plant (e.g., meristem, root collar, stems) that are not being exploited by the current agents in North America. If the need for further agents is deemed necessary, exploration for agents should be concentrated in Asia on tetraploid plants, with some emphasis on those agents attacking the currently unoccupied niches and those occurring at higher elevations.

Evaluation of the agents' impact is a priority goal now that some agent populations are reaching high levels at some locations in the west. Evaluation efforts may soon be possible at the smaller infestations in the east, especially in the northcentral states where the root insects, *A. zoegana* and *C. achates*, have been introduced.

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14 LEAFY SPURGE

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PEST STATUS OF WEED

Nature of Damage

Leafy spurge, *Euphorbia esula* L., is an invasive, deeprooted perennial herb that is native to Eurasia (Watson, 1985; Pemberton, 1995). The plant spreads through explosive seed release and vigorous lateral root growth, forming large, coalescing patches that can dominate rangeland, pastures, prairies and other noncrop areas in the Great Plains region of North America (see Fig. 1, a and b, and Fig. 2).

Economic damage. Leafy spurge has infested more than one million hectares in North America since its introduction approximately 200 years ago (Alley and Messersmith, 1985), and threatens to invade more areas (Lacey et al., 1985). All parts of leafy spurge produce milky latex that can cause dermatitis in humans and cattle (Lacey et al., 1985), and can cause death in cattle if sufficient quantities are consumed (Kronberg et al., 1993). Leafy spurge reduces forage production and wildlife habitat, and causes considerable monetary losses to the livestock industry (Messersmith and Lym, 1983; Watson, 1985; Lacey et al., 1985; Nowierski and Harvey, 1988; Bangsund, 1993; Leitch et al., 1994). Cattle carrying capacity in rangeland can be reduced by 50 to 70% (Alley et al., 1984), and in some cases, by 100 percent (Watson, 1985) through loss of grasses from competition, and the tendency of cattle to avoid spurge-infested grass (Lacey et al., 1985; Hein and Miller, 1992; Kronberg et al., 1993). Direct and secondary economic losses from leafy spurge, due to lost cattle production, for the Dakotas, Montana, and Wyoming in 1994 were estimated to approach \$120 million annually (Leitch et al., 1994). In addition, Wallace et al. (1992) estimated nonagricultural losses (e.g., watershed and



Figure 1. (a) Flowering stems of leafy spurge, *Euphorbia esula* L. and (b) dense patch of leafy spurge, *Euphorbia esula* L. (Photograph [a] courtesy of Montana State University Extension Service; and [b] by USDA, ARS.)



Figure 2. Rangeland severely infested by leafy spurge, *Euphorbia esula* L. (Photograph courtesy of USDA, ARS.)

recreation impacts) from leafy spurge at \$10 million annually over the same four-state region. Leafy spurge is much less abundant in the eastern United States, although it can be weedy enough in pastures to require control.

Ecological damage. Although leafy spurge is most commonly associated with more mesic sites, it is adapted to a broad range of habitats, ranging from xeric to riparian sites (Nowierski and Zeng, 1994; Lym 1998; Kirby et al., 2000). The percent cover of grasses and forbs may be significantly reduced at medium to high densities of leafy spurge (Nowierski and Harvey, 1988). Studies by Belcher and Wilson (1989) have shown that native plant species may be severely affected by leafy spurge. Such reductions in native plant diversity also may have a negative impact on wildlife populations (Wallace et al., 1992; Trammell and Butler, 1995). Population declines in a number of native grassland bird species have been documented in the Great Plains Region of North America at sites with moderate to high densities of leafy spurge (D. Johnson, pers. comm.).

Geographic Distribution

Leafy spurge is native to Eurasia and is widely distributed from Spain to Japan (Ohwi, 1965; Radcliff-Smith and Tutin, 1968; Pemberton, 1995). Since the first recording of this weed in North America at Newbury, Massachusetts in 1827 (Britton, 1921), it has become widespread in certain regions of the United States and Canada. Leafy spurge has been recorded in 35 states within the United States, but has yet to be recorded in Oklahoma, Texas, Arkansas, Louisiana, Kentucky, Tennessee, North Carolina, Mississippi, Alabama, Georgia, South Carolina, and Florida (USDA, NRCS, 2001). The most extensive infestations of the weed occur in the northern Rocky Mountain and Great Plains states (Idaho, Montana, Wyoming, North Dakota, South Dakota, Nebraska, and Minnesota), and in the Canadian provinces of British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario (USDA, APHIS, PPQ, CAPS, 1994). In the upper Mississippi River drainage, leafy spurge occurs primarily in riparian habitats (R. Hansen, pers. comm.). In the eastern United States, the plant is an occasional weed of pastures, roadsides, and riparian habitats (R. Hansen, B. Blossey, J. Wickler, and P. Wrege, pers. comm.). The weed can be locally abundant, but usually is limited to discrete patches. Fifteen New York counties were known to be infested with leafy spurge in the early 1980s (Batra 1983).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

In North America, leafy spurge occurs as a complex of forms, species, and hybrids and has been most commonly referred to as *Euphorbia esula* L. (Euphorbiaceae) (Pemberton, 1985). The most problematic type appears to be *E. x pseudovirgata*, which is a hybrid of *E. esula sensu stricto* and *E. waldsteinii* (=*E. virgata*) (Dunn and Radcliffe-Smith, 1980), hereafter referred to as leafy spurge, *E. esula* L. (Harvey *et al.*, 1988). Harvey *et al.* (1988) examined the leaf morphology and triterpenoid composition of leafy spurge accessions from Montana and five related European spurge species and concluded that all the Montana leafy spurge and three of the five European species could not be distinguished from *Euphorbia esula*.

Leafy spurge populations show a high degree of genetic, chemical, and morphological variability, and as a consequence the taxonomic identity of the United States populations and their affinities to other species is unclear (Shulz-Schaeffer and Gerhardt, 1987; Watson, 1985; Harvey et al., 1988; Torell et al., 1989; Nissen et al., 1992; Pemberton, 1995; Rowe et al., 1997). This genetic variability, combined with other traits, including the plant's possession of both sexual and asexual reproduction, a deep underground root system, an ability to infest xeric, mesic, and even hydric sites across a wide range of soil types (Nowierski and Zeng, 1994; Nowierski et al., 1996; Nowierski et al., 2002), along with the existence of many native spurge species (Euphorbiaceae) in North America (Pemberton, 1985), makes both conventional management and classical biological control of this weed complex and potentially difficult (Shulz-Schaeffer and Gerhardt, 1987).

Biology

Leafy spurge is an aggressive, deep-rooted perennial herb that reproduces from seed and from numerous vegetative buds along its extensive vertical and horizontal root system (Watson, 1985). Seeds of leafy spurge are released explosively by dehiscence of the seed capsules, and may be projected up to 4.6 m from the parent shoot (Hanson and Rudd, 1933; Bakke, 1936). Seeds are dispersed by ants, birds, grazing animals, humans, and water (Hanson and Rudd, 1933; Bowes and Thomas, 1978; Messersmith *et al.*, 1985; Pemberton, 1988; Pemberton, 1995). Germination of leafy spurge seed can occur throughout the growing season whenever adequate moisture is available, but the most favorable conditions for germination occur in early spring (Bakke, 1936; Messersmith *et al.*, 1985). The roots of leafy spurge reportedly can reach a depth of 9 m (Best *et al.*, 1980).

Stems of leafy spurge are erect, tough and woody and range from 0.1 to 1.0 m in height (Lacey *et al.*, 1985). The showy yellow-green inflorescences produce an average of 140 seeds per stem. Leafy spurge leaves are highly variable in shape, ranging from broadly linear-lanceolate to ovate (Watson, 1985). Additional details on the morphology and anatomy of leafy spurge can be found in Raju (1985).

Leafy spurge is one of the first plants to emerge in the spring, and its appearance has been recorded as early as March in Iowa and Wisconsin and early April in North Dakota (Messersmith et al., 1985). Vegetative development and stem elongation occurs rapidly as the temperatures increase during late April through early June. The swelling of the stem apex signals initiation of the leafy spurge inflorescence, which occurs approximately one week after stem emergence. The first yellow to yellowish-green bracts appear at the base of the terminal inflorescence from early to late May depending on environmental conditions (Messersmith et al., 1985). The showy yellow bracts of the leafy spurge inflorescence are most visible from late May through June. Flowering in the terminal inflorescence ends between late June and early July. Seed development and maturation continue for approximately one month post flowering. As the plants mature, the stems and leaves often turn from a blue-green to a reddish brown, red, or yellow, either during hot, dry periods after seed production in midsummer or due to senescence in the fall (Messersmith et al., 1985). Plant phenology may vary greatly within and among locations due to local microclimatic differences.

Analysis of Related Native Plants in the Eastern United States

Risks to native plant species as a result of biological control of leafy spurge were analyzed by Pemberton (1985). The analysis was limited to the genus Euphorbia, in the tribe Euphorbieae, subfamily Eurphorbioideae, family Euphorbiaceae (Mabberley, 1997). The genus is divided into five subgenera, four of which are represented in the native flora of the eastern United States. Of the approximately 107 native Euphorbia species in the continental United States and Canada, about 45 occur east of the Mississippi River. These include 23 species in the subgenus Chamaesyce, 13 species in the subgenus Agaloma, and three species in the subgenus Poinsettia. The remaining six species belong to the subgenus Esula, to which leafy spurge belongs. Of these six, four are broadly sympatric with leafy spurge. These are E. commutata Engelm., E. obtusa Pursh, E. purpurea (Raf.) Fern., and E. spatulata Lam. Euphorbia purpurea is the only perennial of these four, and it also is the only rare eastern species growing in the general region where leafy spurge is more common. This perennial species is under review for legally protected status by the U.S. Fish and Wildlife Service (1993). The plant occurs in both dry and moist woods (Gleason and Cronquist, 1963) in Delaware, Maryland, North Carolina, New Jersey, Ohio, Pennsylvania, Virginia, and West Virginia (Federal Register, 1993). There are four other rare species of Euphorbia s.l. east of the Mississippi River, but all occur in Florida (Federal Register, 1993). Euphorbia telephioides Chapm. is formally listed as a threatened species (U.S. Fish and Wildlife Service, 1997) and is a member of the subgenus Esula that is restricted to the Florida panhandle. The other three rare spurges belong to the subgenus Chamaesyce, within the genus Euphorbia. Subgenera of Euphorbia appear to be natural groupings and most Euphorbia-feeding insects that have been evaluated as biological control agents distinguish among subgenera, accepting plants within some subgenera as hosts while rejecting potential host plants found in other subgenera (Pemberton, 1985).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The native range of leafy spurge is Eurasia and extends from Spain to Japan (Ohwi, 1965; Radcliff-Smith and Tutin, 1968; Watson, 1985; Pemberton, 1995). More precise geographic origins for populations invasive in the United States have not been determined. In its native range leafy spurge is typically just a scattered plant in the ecosystem. R. M. Nowierski has observed the occasional use of leafy spurge in flower arrangements in Europe.

Areas Surveyed for Natural Enemies

European surveys for natural enemies of leafy spurge began in the early 1960s by the Commonwealth Institute of Biological Control (CIBC; name subsequently changed to the International Institute of Biological Control [IIBC]; now called CABI-Bioscience), through their European Station in Delémont, Switzerland. In the 1970s, surveys were initiated by the USDA, ARS Biological Control Laboratory in Rome, Italy (which is now the USDA, ARS European Biological Control Laboratory in Montpellier, France). All of the natural enemies released in North America to date against leafy spurge were discovered during these extensive European surveys. Additional surveys for spurge natural enemies, conducted in China from 1987 to the early 1990s, identified additional promising agents, including several Aphthona species that are still under study (Pemberton and Wang, 1989; Fornasari and Pemberton, 1993).

Natural Enemies Found

Manojlovic and Keresi (1997) reported that 121 insect species (23 species of Homoptera, six Heteroptera spp., 37 Lepidoptera spp., four Hymenoptera spp., 14 Diptera spp., and 37 Coleoptera spp.) are able to develop on plants of E. esula, Euphorbia virgata Waldstein-Wartemberg and Kitaibel, and E. cyparissias L. in Europe. Additional discussion of the spurge fauna was provided by Gassmann and Schroeder (1995). Through surveys for natural enemies of leafy spurge conducted by personnel of the IIBC laboratory in Delémont, Switzerland, between 1961 and 1990, two rust species and 39 insect species were found that were thought to be specialized on leafy spurges (Gassmann, 1990). Of these, 22 insect species were screened as potential biological control agents of leafy spurge. Additional insects have been screened by personnel at the USDA, ARS Biological Control of Weeds Laboratory, Rome, Italy; the USDA, ARS Biological Control Laboratories in Albany, California, USA; the Montana State University Insect Quarantine Laboratory, Bozeman, Montana, USA (Pemberton, 1995); and more recently the USDA, ARS Laboratory in Sidney, Montana, USA.

Host Range Tests and Results

See "Host Range Tests and Results" for cypress spurge for details regarding the host range tests for natural enemies attacking both leafy spurge and cypress spurge.

Releases Made

Since 1965, 12 insect species have been released against leafy spurge or cypress spurge in the United States, and 17 species have been released in Canada. The first insect released in the United States against leafy spurge was the spurge hawkmoth, *Hyles euphorbiae* L. (Lepidoptera: Sphingidae) (Figs. 3 and 4), which was first released in Idaho, Montana, Oregon, Utah, and Washington during the mid-1960s (Julien 1987). The release material was collected from an established population on cypress spurge in Braeside, Ontario, from stocks originating from cypress spurge, *Euphorbia cyparissias* L, and *E. seguieriana* Necker, from Switzerland, France, and Germany (Harris, 1984).

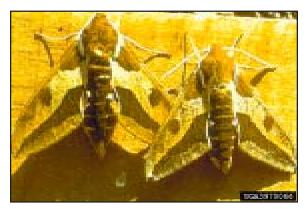


Figure 3. Adults of the leafy spurge hawkmoth, *Hyles euphorbiae* L. (Photograph courtesy of USDA, ARS.)



Figure 4. Larva of the leafy spurge hawkmoth, *Hyles euphorbiae* L. (Photograph courtesy of USDA, ARS.)

Hyles euphorbiae also was the first natural enemy of spurge to be released in the eastern United States beginning in 1978 in New York, with releases directed against both leafy and cypress spurge (Batra, 1983). Although the insect was released against leafy spurge in numerous states (California, Colorado, Idaho, Nebraska, Montana, North Dakota, Nevada, New York, Oregon, Wyoming) from 1964 to 1986, the insect only has become established in New York (Batra, 1983), in Wyoming (Coombs, 2000), and at a number of sites in Montana (R. M. Nowierski, unpub. data). Researchers have attributed the poor rates of establishment of this insect to predation by ants, carabids, and mammalian predators (Harris et al., 1985; R. M. Nowierski, S. J. Harvey, and J. M. Story, unpub. data), and to the possible existence of different moth host races (Harris, 1984).

The clearwing moth, *Chamaesphecia* tenthrediniformis (Denis and Schiffermüller) (Lepidoptera: Sesiidae), was released against leafy spurge in Idaho, Montana, and Oregon during 1975 to 1979. None of the releases resulted in establishment (Pemberton, 1995). This and two other species, *C. hungarica* (Tomala) (Fig. 5) and *C. crassicornis* Bartel (Fig. 6), were released against leafy spurge in the western United States in 1975, 1993, and 1994, respectively. At present, it appears that none of these releases were successful, except for one population of *C. crassicornis*, which has established on leafy spurge in Oregon (Coombs, 2000).

The first coleopteran species released against leafy spurge in the United States was the stem boring beetle, Oberea erythrocephala (Schrank) (Coleoptera: Cerambycidae) (Fig. 7). Releases of the beetle were made in Montana, Oregon, North Dakota, and Wyoming during 1980 to 1986. Additional releases of O. erythrocephala were made by APHIS, PPQ in Colorado, Iowa, Idaho, Michigan, Minnesota, Montana, Nebraska, Nevada, New Hampshire, New Mexico, New York, North Dakota, Oregon, Rhode Island, South Dakota, Utah, Washington, Wisconsin, and Wyoming during 1988 to 1995. Oberea erythrocephala establishment has been documented in Montana (Rees et al., 1986; Hansen et al., 1997), Oregon and Wyoming (Coombs, 2000), North Dakota (Pemberton, 1995), and Colorado and South Dakota (Hansen et al., 1997).



Figure 5. Adult of the clearwing moth, *Chamaesphecia hungarica* (Tomala). (Photograph courtesy of USDA, APHIS.)



Figure 6. Adult of the clearwing moth, *Chamaesphecia crassicornis* Bartel. (Photograph courtesy of USDA, APHIS.)



Figure 7. Adult of the stem boring beetle, *Oberea erythrocephala* (Schrank). (Photograph courtesy of USDA, APHIS.)

Flea beetles in the genus Aphthona have been the most successful biocontrol agents released against leafy spurge in North America. Aphthona abdominalis Duftschmidt (Coleoptera: Chrysomelidae) (Fig. 8), Aphthona cyparissiae (Koch) (Fig. 9), Aphthona czwalinae (Weise) (Fig. 10), Aphthona flava Guillebeau (Fig. 11), Aphthona lacertosa Rosenhauer (Fig. 12), and Aphthona nigriscutis Foudras (Figs. 13 and 14), were first released in the United States in 1993, 1986, 1987, 1985, 1993, and 1989, respectively, and all but A. abdominalis have established in the United States (Pemberton, 1995; Hansen et al., 1997). In 1994 and 1995 USDA, APHIS, PPQ transferred Aphthona beetles from established populations in the western United States to a number of eastern states (Hansen et al., 1997). Releases of individual species or mixed collections of several species (A. flava, A. cyparissiae, A. nigriscutis, A. lacertosa and A. czwalinae) were made in Iowa, New Hampshire, Michigan, Minnesota, New York, and Wisconsin.

The shoot tip gall midge, Spurgia esulae Gagné (Diptera: Cecidomyiidae) (Figs. 15a,b), is the only fly species released against leafy spurge in the United States. Releases were made in Montana, Oregon, North Dakota, and Wyoming during 1985 to 1988, and establishment was later recorded in Montana and North Dakota from these releases (Pemberton, 1995). Additional releases were made by USDA, APHIS, PPQ in Colorado, Idaho, Iowa, Michigan, Minnesota, Montana, North Dakota, Nebraska, Nevada, New Hampshire, New Mexico, New York, Oregon, Rhode Island, South Dakota, Utah, Washington, Wisconsin, and Wyoming from 1988 to 1996 (Hansen et al., 1997). As of 1997, establishment of the midge from these releases has been documented in Colorado, Montana, New York, Oregon, Rhode Island, South Dakota, and Wyoming (Hansen et al., 1997). The midge also has been recorded as established on leafy spurge in Idaho (Coombs 2000).

Informal human transport of leafy spurge biological control agents from Canada to the United States and vice-versa has probably resulted in additional releases (R. Hansen, pers. comm.). In addition, some biological control agents of leafy spurge, such as the tortricid moth *Lobesia euphorbiana* (Freyer), that have been released in Canada but not in the United States, may move into the United States on their own.



Figure 8. Adult flea beetle, *Aphthona abdominalis* Duftschmidt. (Photograph courtesy of USDA, APHIS.)



Figure 9. Adult flea beetle, *Aphthona cyparissiae* (Koch). (Photograph courtesy of USDA, APHIS.)



Figure 10. Adult flea beetle, *Aphthona czwalinae* Weise. (Photograph courtesy of USDA, APHIS.)



Figure 11. Adult flea beetle, *Aphthona flava* Guillebeau. (Photograph courtesy of USDA, APHIS.)



Figure 14. Larvae of the flea beetle, *Aphthona nigriscutis* Foudras. (Photograph courtesy of USDA, APHIS.)



Figure 12. Adult flea beetle, *Aphthona lacertosa* Rosenhauer. (Photograph courtesy of USDA, APHIS.)



Figure 15. (a) Adult of the shoot tip gall midge, *Spurgia esulae* Gagné; (b) shoot tip gall made by midge larvae (inset). (Photograph courtesy of USDA, APHIS.)



Hyles euphorbiae (L.) (Lepidoptera: Sphingidae)

The leafy spurge hawkmoth feeds on the leaves and flowers of *Euphorbia* species in the subgenus *Esula* (Harris, 1984). Adult females lay from 70 to 110 eggs singly or in clusters on the plant surface, and the small black larvae emerge a week or two later depending on temperature. A generation is completed in about six weeks (Pemberton, 1995). Larvae go through a series of color changes as they grow, from black as they first eclose, to greenish-yellow during the next couple of instars, to a showy combination of black,



Figure 13. Adult flea beetle, *Aphthona nigriscutis* Foudras. (Photograph courtesy of USDA, APHIS.)

white, red, and yellow during the last two instars. The larval integument and hemolymph contains triterpenoids derived from feeding on leafy spurge (P. Mahlberg and R. M. Nowierski, unpub. data). Larvae are believed to use these compounds for chemical protection against predators, and field studies in Montana have shown larval predation to be low (N. H. Poritz, R. M. Nowierski, and S. J. Harvey, unpub. data). In contrast, rates of predation on pupae, measured using different levels of exclusion, are high and are most likely due to field mice (Peromyscus spp.) and shrews (R.M. Nowierski, S. J. Harvey, N. H. Poritz, and J. M. Story, unpub. data). High pupal predation by animals may explain the extreme differences in hawkmoth populations among years, as populations of small mammalian predators typically are quite variable over time.

In Montana, hawkmoth larvae are generally present during the last week or so of June and are most abundant the first week of July. Larvae pupate in the soil in July and August and a significant proportion of pupae eclose for a second generation.

Oberea erythrocephala (Coleoptera: Cerambycidae)

The longhorn beetle, *O. erythrocephala*, is native to Eurasia where it feeds within the stems and roots of several *Euphorbia* species. Adults appear in early to mid-summer when spurges are in flower, and feed on the young leaves, flowers, and stem tissue for approximately two weeks before beginning oviposition (Pemberton, 1995; Hansen *et al.*, 1997). Adult beetles girdle the upper part of the stem, chew a hole in it just above the girdle, insert an egg and cover it with latex (Pemberton, 1995; Hansen *et al.*, 1997). Larvae take approximately one month to mine their way down the stem into the crown and roots (Pemberton, 1995). Larvae feed within crowns or roots until March or April and pupate within cells in the root crown in May.

Aphthona spp. (Coleoptera: Chrysomelidae)

The flea beetle genus *Aphthona* (Coleoptera: Chrysomelidae) contains approximately 40 species that are known to feed on leafy spurges (*Euphorbia* spp.) in Europe and Asia (Harris *et al.*, 1985; Fornasari and Pemberton, 1993; Fornasari, 1996). All of the established flea beetle species released against leafy

spurge in the United States are univoltine, with some of the species showing phenological differences in adult emergence during the course of the growing season (Hansen, 1994). Aphthona abdominalis, which has not yet been documented as established in North America, reportedly may produce more than one generation per year (Fornasari, 1996). Early larval instars feed in/on root hairs of the host plant, while later instars feed in/on yearling roots. Larval feeding contributes to leafy spurge mortality by disrupting water and nutrient transport and may provide entry points for pathogenic soil inhabiting fungi (Hansen et al., 1997). Adult flea beetles feed on leaves and flower bracts of leafy spurge. Aphthona species overwinter as larvae, and generally pupate within the spurge roots in late spring to early summer (Rees et al., 1996).

Aphthona cyparissiae (Coleoptera: Chrysomelidae)

The native range of *A. cyparissiae* extends from southern Spain and France through central and eastern Europe to western Russia (Pemberton, 1995). In Eurasia, this species occurs at higher altitudes and in areas with cool, rainy summers (Pemberton, 1995). The species has a relatively broad ecological amplitude and has been recorded from xeric to mesic sandy loam sites in Eurasia (Müller, 1949; Maw, 1981; Fornasari, 1996; Gassmann *et al.*, 1996). However, this species has been less successful in establishing on leafy spurge in the United States than *A. nigriscutis* and *A. lacertosa*.

Aphthona czwalinae (Coleoptera: Chrysomelidae)

This blue-black flea beetle species is native to central and eastern Europe (Germany, Austria, Poland), the lower Danube region, parts of Russia, central Asia, and eastern Siberia (Gassmann, 1984). It is most commonly found at mesic sites where *Euphorbia* is intermixed with other vegetation, and is thought to have the potential to colonize sites such as stream margins, where leafy spurge is often most abundant (Pemberton, 1995). The biology and host range of *A. czwalinae* is similar to that of *A. cyparissiae* and *A. flava*, although it is limited to fewer species in the subgenus *Esula* than the other two species (Gassmann, 1984; Pemberton 1987). Because the releases of *A. czwalinae* have typically been reported as an *A. czwalinae*/*A. lacertosa* mix (Hansen *et al.*, 1997), the actual establishment and impact of this species on leafy spurge in various states in the United States is unclear.

Aphthona flava (Coleoptera: Chrysomelidae)

This flea beetle species is found from northern Italy east and north through the former Yugoslavia, Hungary, Czechoslovakia, Bulgaria, Romania, and Russia (Sommer and Maw, 1982). In Eurasia, this species occurs in xeric to mesic habitats in areas with drier and warmer summers (Pemberton, 1995). Like *A. cyparissiae*, this species has been less successful than *A. nigriscutis* and *A. lacertosa* in establishing on leafy spurge in North America.

Aphthona lacertosa (Coleoptera: Chrysomelidae)

This species is native to Eurasia where it is associated with loamy or loamy-clay soils, in either dry or wet habitats (Gassmann, 1990; Fornasari, 1996; Gassmann et al., 1996; Nowierski et al., 2002). However, Maw (1981) reported that it preferred moist sites. Aphthona lacertosa establishment and its impact on leafy spurge has been greatest at moderately dry to mesic sites in the United States (Rees et al., 1996). Unlike A. nigriscutis, which appears to be restricted to drier sites, A. lacertosa has a broader ecological amplitude and may have greater potential for controlling leafy spurge across a broad range of habitats. Aphthona lacertosa can be distinguished from A. czwalinae by its light-colored hind femur, whereas in A. czwalinae the hind femur is black (A. Gassmann, pers. comm.).

Aphthona nigriscutis (Coleoptera: Chrysomelidae)

This *Aphthona* species is native to Europe and is adapted to drier sites and sandier soils. This species has been most successful in establishing and controlling leafy spurge in dry, open, sandy-loam sites in Canada and the United States (Rees *et al.*, 1996). It generally has done poorly when released in high density leafy spurge infestations occurring in heavier clay soils (R. M. Nowierski, Z. Zeng, and B. Fitzgerald, unpub. data).

Spurgia esula (Diptera: Cecidomyiidae)

This small midge causes shoot-tip galls on leafy spurge, which prevents flowering and thus seed production of the attacked shoot. Spurgia esula is multivoltine and produces two or three generations per year in Montana (Hansen et al., 1997) and up to five generations per year in its native European range (Pecora et al., 1991). This gall midge overwinters as a mature larva and the first adults appear in mid- to late spring. Adult females deposit groups of eggs on leafy spurge leaves, typically near the apical buds (Hansen et al., 1997). Upon eclosion, first instar larvae migrate to leafy spurge buds and begin feeding within the meristematic tissues. Larval feeding causes hypertrophy in the bud tissues and the formation of a bud gall, within which the larvae feed. Larvae require two to four weeks to complete development, depending on environmental conditions (Hansen et al., 1997). Larvae of the non-diapausing summer generation construct silken cocoons inside the bud galls, from which adult flies later emerge. Mature larvae of the diapausing generation exit the galls, drop to the ground, and overwinter in the soil. No major impacts on leafy spurge populations have been reported for this biological control agent. However, Lym (1998) reported greater suppression of leafy spurge when S. esulae was combined with herbicides than when either approach was used alone.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

The spurge hawkmoth, *H. euphorbiae*, is established on spurges in New York (Batra, 1983) and is locally common in the state (B. Blossey, pers. comm.). Coordinated natural enemy releases by the USDA, APHIS, PPQ during the mid 1990s have resulted in the establishment of many biocontrol agents of leafy spurge east of the Mississippi River. Five *Aphthona* species (*A. cyparissiae*, *A. czwalinae*, *A. flava*, *A. lacertosa*, and *A. nigriscutis*) have established in Iowa, Michigan, Minnesota, New York, and Wisconsin (Hansen *et al.*, 1997). The gall midge, *S. esulae*, has established in New York (Hansen *et al.*, 1997), and in Michigan and Wisconsin (R. Hansen, pers. comm.). Oberea erythrocephala has established in Michigan (J. Winklar, pers. comm.) and in Minnesota (R. Hansen, pers. comm.). At present, it is unclear whether any of these agents have established on leafy spurge in New Hampshire. As of 1997, populations of *S. esulae* and the *Aphthona* species in New York were not sufficiently large to provide insects for redistribution (Hansen *et al.*, 1997). But more recently, populations of the *Aphthona* species have reached adequate levels for redistribution in New York (P. Wrege, pers. comm.).

Suppression of Target Weed

The effects of imported natural enemies on leafy spurge densities in the eastern United States have not been formally evaluated, but there is some evidence that the *Aphthona* beetles are having an effect. The beetles have provided control over large areas in Minnesota (R. Hansen, pers. comm.), and are significantly reducing the weed at some sites in Michigan (J. Winklar, pers. comm.) and New York (P. Wrege, pers. comm.). More information is available about the impact of these biological control agents against leafy spurge in the Northern Great Plains region.

Rees et al. (1996) reported that five Aphthona species (A. cyparissiae, A. czwalinae, A. flava, A. lacertosa, and A. nigriscutis) have established to varying degrees on leafy spurge in the United States and Canada, and in a number of cases have significantly reduced spurge density at the release sites (see Figs. 16 and 17). Reductions in leafy spurge stem densities have been attributed to flea beetle feeding by a number of authors (Hansen, 1993; Baker et al., 1996; Lym et al., 1996; Stromme et al., 1996; and Kirby et al., 2000). Stromme et al. (1996) reported that leafy spurge foliar cover decreased from 40 to 1.7%, five years after A. nigriscutis was released near Edmonton, Canada. At two sites in North Dakota, A. nigriscutis and A. czwalinae/A. lacertosa reduced foliar cover of leafy spurge from 45 to 7% over a three year period, and reduced stem densities by nearly forty-fold (Kirby et al., 2000). In other areas, infestations of leafy spurge have been successfully suppressed through a combination of flea beetle herbivory and controlled grazing by sheep (J. Elliott, pers. comm.). Herbicides combined with the leafy spurge flea beetles (A. nigriscutis or A. czwalinae/A. lacertosa) or the gall midge (S. esulae) have controlled leafy spurge better than either method used alone (Lym, 1998).



Figure 16. Leafy spurge infestation on the N-Bar Ranch, Grass Range, Montana 1989, prior to release of the flea beetle *Aphthona nigriscutis* Foudras that same year. (Photograph courtesy of USDA, ARS.)



Figure 17. N-Bar Ranch, Grass Range, Montana leafy spurge site in 1993, four years after release of the flea beetle *Aphthona nigriscutis* Foudras. (Photograph courtesy of USDA, ARS.)

Effects on Native Plants

Neither the impact of introduced biocontrol agents on native, non-target plants nor the recovery of native plant communities following the decline in population levels of leafy spurge (following natural enemy impact) have been reported in the literature. Some leaf feeding by adult *A. nigriscutis* on *Euphorbia robusta* (Engelm.) Small has occurred at one leafy spurge site in Wyoming, and larvae also were found on the roots of this native euphorb (L. Baker, pers. comm.). However, the plant is increasing in abundance at the site due to the beetle's control of leafy spurge (L. Baker, pers. comm.). *Euphorbia robusta* is very closely related to leafy spurge, and prerelease laboratory studies indicated that the plant might become a host of *Aphthona* spp.

Economic Benefits

The economic benefits from the biological control of leafy spurge have not been formerly reported in the literature. However, given the fact that *A. nigriscutis* and *A. lacertosa* have reduced leafy spurge densities at numerous sites in the United States and Canada, this sort of information should be forthcoming.

RECOMMENDATIONS FOR FUTURE WORK

As discussed previously, *A. nigriscutis* and *A. lacertosa* have been the most successful biocontrol agents released against leafy spurge in North America. However, neither of these agents have had a consistent suppressive effect on leafy spurge growing in shaded areas and riparian sites. Hence, additional natural enemy surveys are needed to find specialized natural enemies of leafy spurge that are adapted to such habitats. Pemberton (1995) recommended that only narrow specialists with potential host ranges at or below the level of the subgenus *Esula* should be employed to avoid damage to native North American *Euphorbia* species.

Leafy spurge is currently found in 35 states in the United States (USDA, NRCS) and in all Canadian provinces except Newfoundland (Roslycky, 1972). The potential for further range expansion of this weed warrants the continued redistribution of established biocontrol agents throughout North America. In addition to recent biological control efforts in New Hampshire and New York, biological control programs should be initiated in all other states in the northeast and central United States that have significant infestations of leafy spurge. Before releasing biological control agents in the eastern United States, host specificity data should be obtained for each agent relative to the rare Euphorbia purpurea and the endangered E. telephioides. The abilities of these spurge natural enemies to live in the southern United States, where additional rare Euphorbia occur, also should be considered.

Studies evaluating the effects of natural enemies introduced for the biological control of leafy spurge should be initiated across a wide range of habitat types and geographic areas in the United States. Studies should include the assessment of economic and environmental benefits of biological control, the effect of flea beetles on plant species richness and diversity (including native species), and the assessment of any harmful effects on threatened and endangered *Euphorbia* species. Lastly, integrated weed management strategies need to be developed and implemented on a grander scale to be able to achieve consistent and sustainable management of leafy spurge in North America in the future.

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15 CYPRESS SPURGE

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PEST STATUS OF WEED

Cypress spurge (*Euphorbia cyparissias* L.) (Fig. 1) is a herbaceous European perennial introduced into North America as an ornamental plant in the 1860s (Croizat, 1945). It was widely planted in graveyards and often is called graveyard weed (Muenscher, 1936). The plant escaped cultivation and became established on open ground, particularly in pastures (Stuckey and Pearson, 1973).



Figure 1. *Euphorbia cyparissias* L. in bloom. (Photograph by R. A. Casagrande.)

Nature of Damage

Economic damage. Although cypress spurge is found throughout much of North America, economic losses are primarily restricted to the northeastern United States (USDA, NRCS, 1999; Stahevitch *et al.*, 1988). Cypress spurge is particularly prevalent in Ontario and Quebec (Gassmann, 1985). In the United States, 25 counties have infestations of more than 500 acres and most of these sites are in the northeast (Dunn, 1979). Cypress spurge is listed as a noxious weed in Canada and some New England states (Stahevitch *et al.*, 1988; Torrey, 1999) and it has the potential to

become a major weed in other areas. In 1975, it was found in 26 states; 25 years later it was recorded in 42 states (Dunn, 1979; USDA, NRCS, 1999). At one site in Rhode Island, approximately 70 out of 170 acres of hay meadow were dominated by cypress spurge, making most of the land unfit for cattle and growing hay. Farmers who are unaware of cypress spurge in their hay fields spread the weed when transporting hay infested with cypress spurge seeds. Chemical control of cypress spurge is difficult because of its extensive root system. Plants readily regrow from roots following destruction of above-ground parts, so repeated applications of several herbicides usually are required for control (Pemberton, 1985). Cultivating infested fields can spread cypress spurge by moving root pieces caught on machinery to clean locations where roots produce new plants (Moore and Lindsay, 1953).

All parts of cypress spurge contain a toxic latex (Stephens, 1980) that irritates the eyes, mouth, and gastrointestinal tract and causes dermatitis upon contact in some people (Westbrooks and Preacher, 1986). Most grazing animals avoid cypress spurge. Sheep can browse the plant with no ill effects, but cattle that accidentally ingest it become weak, collapse, and may die (Muenscher, 1964).

Ecological damage. Cypress spurge is primarily found on limestone, sandy, or gravelly soils. It tends to form almost pure stands at open sites and is likely to be responsible for displacement of native species (Moore and Lindsay, 1953; Stuckey and Pearson, 1973). Cypress spurge does not generally occur on intensively cultivated soils, nor is it found in heavily forested areas (Stahevitch *et al.*, 1988). This weed is commonly found along roadsides throughout the northeastern United States, but generally is not considered a problem as it forms an attractive ground cover.

Geographical Distribution

Native to Europe, cypress spurge is found throughout the continent between 40 and 60 °N (Pritchard, 1959). In North America, it is currently found in 42 states and Canada (Dunn, 1979; USDA, NRCS, 1999). It also is an invasive weed in New Zealand (Stahevitch et al., 1988). There are three cytogenetic variants present in Europe - fertile tetraploids (Fig. 2), fertile diploids, and sterile diploids. Fertile tetraploids, the most widely distributed form, are found throughout the range from southern Finland to northern Greece and west from England to as far east as Lake Baikal in central Siberia (Pritchard, 1959). Fertile diploids have a relatively southern distribution (France, Italy, Switzerland, Austria, and the former Yugoslavia), while sterile diploids are found primarily in England (Pritchard, 1959). Only sterile diploids and fertile tetraploids are found in North America (Stahevitch et al., 1988). The sterile diploid was probably intentionally introduced as an ornamental plant in North America and the fertile tetraploid was apparently accidentally introduced. The tetraploid form is considerably more vigorous and weedy than the diploid form (Dunn, 1979; Gassmann and Schroeder, 1995), and this form has been increasing in abundance in North America. Reports of fruiting cypress spurge (fertile tetraploid) were rare in North America from 1910 to 1931, but became more common by 1953 (Deane, 1910; Deane, 1912; Muenscher, 1931; Moore and Lindsay, 1953). In Rhode Island during the spring of 2000, we conducted a survey in 54 cypress spurge stands. Fifty-three out of the 54 stands were comprised of fruiting plants, indicating a predominance of tetraploid cypress spurge in the state.



Figure 2. Close-up of fruiting structure of tetraploid *Euphorbia cyparissias* L. (Photograph by R. A. Casagrande.)

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Cypress spurge is a member of the Euphorbiaceae, or spurge family. Synonyms for E. cyparissias are Galarhoeus cyparissias (L.) Small and Tithymalus cyparissias (L.) Hill. The genus Euphorbia contains about 1,600 species native to Africa, Asia, Europe, and North America (Gassmann et al., 1991). In North America, native or introduced species are found in four subgenera: Agaloma, Chamaesyce, Esula, and Poinsettia (Pemberton, 1984). Cypress spurge and the closely related leafy spurge, Euphorbia esulae L., belong to subgenus Esula (Gleason and Cronquist, 1991). Leafy spurge is another invasive Eurasian species that has caused considerable damage in the north central United States and the Canadian prairies (Gassmann, 1985). Euphorbiaceae typically have a poisonous white sap in all plant parts (Clark and Fletcher, 1909), which appears to be for defensive purposes (Gassmann et al., 1991).

Native Range

According to Stahevitch *et al.* (1988), cypress spurge is found throughout Europe from 60 °N in southern Finland to 40 °N is northern Greece, and ranges from Britain to central Siberia.

Biology

Cypress spurge is a perennial that overwinters as root and crown tissue. The fertile tetraploid also can overwinter as seed. The root system consists of two root types. Young seedlings send out a taproot that is persistent and indeterminate. The taproot may reach lengths of three or more meters and give rise to lateral roots, which produce adventitious buds. In early spring, shoots develop from the crown and buds. Shoots grow in masses and reach about 40 cm in height before flowering in mid-spring. The sterile diploid cypress spurge flowers but does not set seed. The fruit of the fertile form is an explosive capsule that splits open when mature and throws its seed up to five meters (Stahevitch *et al.*, 1988)

Analysis of Related Native Plants in the Eastern United States

There are 107 *Euphorbia* species native to North America, 21 of which are in the subgenus *Esula*

(Pemberton, 1985). In the northeastern United States there are 13 native Euphorbia species, of which three are in the subgenus Esula: Euphorbia commutata Engelm., Euphorbia purpurea (Raf.) Fern., and Euphorbia spatulata Lam. (USDA, NRCS, 1999; Magee and Ahles, 1999) (Table 1). Euphorbia purpurea is listed as a species of concern by the U.S. Fish and Wildlife Service and is under review for protective status. This plant is found in swampy woods in the eastern United States (Pemberton, 1985). The other native Euphorbia species are in one of three other subgenera found in North America: Agaloma, Chamaesyce, or Poinsettia (Gleason and Cronquist, 1991). In addition to cypress and leafy spurge, ten other Euphorbia species in the subgenus Esula have been introduced into the Northeast (USDA, NRCS 1999). Subgenera appear to be natural groupings. Many Euphorbia-feeding insects accept as host plants most of the species in one subgenus and reject species in the other subgenera (Pemberton, 1985).

BACKGROUND INFORMATION ON PEST PLANT

Area of Origin of the Weed

Cypress spurge is believed to be indigenous to western Europe where the fertile diploid form of the plant is found. Fertile diploids occur throughout France and northcentral Spain and also in a narrow band across central Europe (excluding the Alps). Fertile tetraploids probably arose from fertile diploids, enabling the plant to colonize new habitats. Tetraploids apparently replaced diploids in most locations and extended the range of the species to the north and east. Fertile diploids and tetraploids are sympatric in southeastern France and the western Balkans (Pritchard, 1959). The sterile diploid is generally associated with human habitation, suggesting that this form was propagated as an ornamental. Since it is most common in England, it was probably propagated there. The sterile diploid was introduced from England into North America as an ornamental and the fertile tetraploid was apparently accidentally introduced as an ornamental and then escaped gardens and cemeteries (Stahevitch et al., 1988).

Areas Surveyed for Natural Enemies

Cypress spurge and leafy spurge are not serious weeds in Eurasia where they are attacked by a large complex of specialized insects and pathogens (Spencer, 1994). Leafy Spurge has been the target of a biological control program since 1961. Because cypress spurge is closely related to leafy spurge, agents released against leafy spurge also were released against cypress spurge.

Leafy spurge probably originated in northern Caucasus or northern China (Kuzmanov, 1964). However, because of political and financial limitations, surveys were conducted in the most western part of its distribution in Europe. Surveys originally funded by Canada began in 1961 at the International Institute of Biological Control of the Centre for Agriculture and Biosciences International (CABI-IIBC) in Delemont, Switzerland (Gassmann, 1990). Insects were collected from leafy spurge and cypress spurge plants in Italy, Switzerland, Germany, Austria, Hungary, and the former Yugoslavia. From 1980 to 1990 field surveys were expanded in scope to include other common perennial spurges in the subgenus Esula. This was done to enlarge the range of plant habitats from very dry to moist. In particular, Euphorbia seguieriana Necker and Euphorbia lucida Waldstein and Kitaibel were included in the survey. Field surveys were terminated in 1990 (Gassmann and Schroeder, 1995).

Natural Enemies Found

Thirty-nine insect species and two rust fungi were found and considered for the biological control of leafy spurge and 22 of the insects were screened as potential control agents. Originally, the selection was based mainly on agent availability and the damage a single individual caused to plants. This led to a focus on species with large individuals, like the sphingid moth Hyles euphorbiae (L). After several early introductions failed to reduce spurge populations, the strategy shifted towards using a large number of natural enemy species, which cumulatively might inflict greater stress on plants. Since spurge plants can tolerate repeated defoliation whether caused by mowing or herbicides, preference was given to root-feeding chrysomelid beetles in the genus Aphthona instead of leaf-feeding agents (Gassmann and Schroeder, 1995).

There appears to be an evolutionary relationship between *Aphthona* species and spurge. There are 66 known European *Aphthona* species, which have been collected from 33 plant families. Of these 66 species, almost half were found only on *Euphor*-

Table 1. Euphorbia Species in the Northeastern United States

Subgenus	Species	Originª	Form ^ь					States				
Esula	<i>E. commutata</i> Engelm.	Nat.	А									PA
	E. cyparissias L.	Intro.	Ρ	ME	NH	VT	MA	СТ	RI	NY	NJ	PA
	E. epithymoides L.	Intro.	Р							NY		
	E. esula L.	Intro.	Р	ME	NH	VT	MA	СТ		NY	NJ	PA
	E. exigua L.	Intro.	А									PA
	E. falcata L.	Intro.	А									PA
	E. helioscopia L.	Intro.	А	ME	NH	VT	MA	СТ		NY	NJ	PA
	E. lathyris L.	Intro.	A/P				MA	СТ		NY	NJ	PA
	E. lucida Waldst. & Kit.	Intro.	Ρ				MA			NY		PA
	E. paralias L.	Intro.	Ρ									PA
	E. peplus L.	Intro.	А	ME	NH	VT	MA		RI	NY	NJ	PA
	E. platyphyllos L.	Intro.	А			VT	MA			NY		PA
	<i>E. purpurea</i> (Raf.) Fern.	Nat.	Р								NJ	PA
	E. segetalis L.	Intro.	А								NJ	PA
	E. spatulata Lam.	Nat.	А									PA
	E. terracina L.	Intro.	Ρ									PA
Poinsettia	<i>E. dentata</i> Michx.	Intro.	А		NH	VT	MA			NY	NJ	PA
Agaloma	E. corollata L.	Nat.	Ρ		NH	VT	MA	СТ	RI	NY	NJ	PA
	E. ipecacuanhae L.	Nat.	Ρ					СТ		NY	NJ	PA
	E. marginata Pursh.	Nat.	А		NH		MA	СТ	RI	NY	NJ	PA
	<i>E. pubentissima</i> Michx.	Nat.	Ρ		NH							PA
Chamaesyce	E. glyptosperma Engelm.	Nat	А	ME	NH	VT	MA			NY		
	E. humistrata Engelm.	Intro.	А		NH	VT					NJ	
	E. maculata L.	Nat.	А	ME	NH	VT	MA	СТ	RI	NY	NJ	PA
	E. nutans Lagasca	Nat.	А				MA	СТ	RI	NY	NJ	PA
	E. ophthalmica (Pers.) Burch	Nat.	А									PA
	E. polygonifolia L.	Nat.	А	ME	NH		MA	СТ	RI	NY	NJ	PA
	E. prostrata Aiton	Intro.	А				MA					PA
	E. serpens HBK	Intro.	А		NH						NJ	PA
	E. serpyllifolia Pers.	Intro.	А		NH					NY		
	E. strictospora (Engelm.) Small	Intro.	А							NY		
	E. vermiculata Raf.	Nat.	А	ME	NH	VT	MA	СТ	RI	NY	NJ	PA

^a Plant either native (Nat.) or introduced (Intro.) to North America.

^b Plant form either annual (A), perennial (P), or both (A/P).

^c Plant located in Maine (ME), New Hampshire (NH), Vermont (VT), Massachusetts (MA), Connecticut (CT), Rhode Island (RI), New York (NY), New Jersey (NJ), or Pennsylvania (PA).

bia species (Sommer and Maw, 1982). *Aphthona* species are generally adapted to a single subgenus of *Euphorbia* and the host range often is restricted to a few species within a subgenus (Gassmann, 1990). *Aphthona* species found feeding only on plants in the subgenus *Esula* were collected and considered as potential biological control agents.

In addition to *Aphthona* species, a cecidomyiid gall midge, *Spurgia esulae* Gagné, was found on *E. esulae* in Italy (Pecora *et al.*, 1991). *Spurgia esulae* has been recorded in nature only on *E. esulae* (Gagné, 1990).

Host Range Tests and Results

Between 1961 and 1994, tests measuring the host specificity of several species of natural enemies were conducted by the CABI-IIBC (Delemont, Switzerland), and the USDA Agricultural Research Service European Biological Control Laboratory (Montpellier, France). These tests estimated the host range of selected natural enemies to the plant genus level. Insects considered for release in the United States were subjected to a second round of tests at the USDA, ARS laboratory in Albany, California, USA.

Eighteen insects were eventually cleared for release in North America for control of leafy spurge, twelve of which were released in the western United States. Seven of the twelve species released in the western United States also were released in the eastern United States against both leafy and cypress spurge (Table 2). Host specificity results for the seven insects released in the eastern United States are reviewed here.

Aphthona species host specificity. For the first round of host specificity tests, 50 to 56 plant species in 19 to 22 families of plants were selected to test Aphthona species host specificity. Test plants were selected from four categories: 1) plants related to leafy spurge; 2) plants attacked by other species in the genus Aphthona; 3) plants with latex other than Euphorbia; and 4) economically important plants (Sommer and Maw, 1982). Twenty adult Aphthona beetles were placed in cages with five test plant species. Two series of tests were made, one including a control plant (either E. esulae, E. cyparissias, or Euphorbia virgata) Waldstein-Wartemberg and Kitaibel; the second, a no choice test without a control plant. All plants were examined for insect feeding (Gassmann, 1984, 1985, 1990; Sommer and Maw, 1982).

Table 2. Species Released in North America Against
Leafy or Cypress Spurge (1965 to 1994)

Leary of Cypress Spurge (1905 to 1994)							
Species	Canada	Western USA	Eastern USA				
Hyles euphorbiae (L.)	1965	1968	1976				
Chamaesphecia empiformis Esperª	1969	-	-				
Chamaephecia tenthrediniformis (Denis & Schiffermuller)ª	1972	1975	-				
Chamaesphecia hungarica (Tomala)	1991	1993	-				
Chamaesphecia astatiformis (Herrich-Schaffer 1846)	1993	-	-				
Chamaesphecia crassicornis Bartel 1912	1994	1994	-				
Oberea erythrocephala (Schrank)ª	1979	1980	-				
Aphthona cyparissiae (Koch)ª	1982	1986	1995				
Aphthona flava Guill.ª	1982	1985	1995				
Aphthona nigriscutis Foudrasª	1983	1989	1995				
Aphthona czwalinae (Weise)ª	1985	1987	1995				
Aphthona lacertosa (Rosh.)ª	1990	1993	1995				
Aphthona abdominalis Duftschmidt	-	1993	-				
<i>Pegomya euphorbiae</i> (Kieffer)	1988	-	-				
Lobesia euphorbiana (Freyer)ª	1983	-	-				
<i>Minoa murinat</i> a (Scopoli)	1988	-	-				
Spurgia esulae Gagnéª	1987	1985	1995				
Spurgia capitigena (Bremi)ª	1990	-	-				

^a Species released on cypress spurge

To test for larval survival, 50 to 100 newly hatched *Aphthona* sp. larvae were transferred onto stem bases of potted plants. The same plant species used in adult feeding tests were used for larval feeding tests as well as control plants. All plants were later dissected to check host plant acceptance and larval development (Gassmann, 1984, 1985, 1990; Sommer and Maw, 1982).

Testing in the European laboratories showed that the host ranges for the six selected *Aphthona* species examined were restricted to the genus *Euphorbia*. Following the European tests, insects were sent to the USDA, ARS laboratory in Albany, California for the second round of testing. This testing was to determine host range within the genus *Euphorbia*. In Europe, all *Euphorbia* species are in the subgenus *Esula*. In North America there are more than 100 native species representing four subgenera (*Agaloma*, *Chamaesyce*, *Esula*, and *Poinsettia*) (Pemberton, 1985).

Ten native plant species were selected to represent the four different Euphorbia subgenera. For the first four Aphthona species tested, Euphorbia purpurea was selected as a test plant. This plant is native to some mid-Atlantic states and under review for protective status by the U.S. Fish and Wildlife Service. Euphorbia purpurea did not support larval development of any of four Aphthona species tested (Pemberton, 1986, 1987, 1989; Pemberton and Rees, 1990; Spencer and Prevost, 1992). Euphorbia purpurea was not a test plant for the two other Aphthona species because it was decided that E. purpurea did not grow in areas likely to contain leafy or cypress spurge (Gassmann, 1990; Fornasari, et al., 1994). Testing in Albany indicated that all six Aphthona species appear to be restricted to a few species in the subgenus Esula.

Spurgia esulae host specificity tests. Following protocols similar to those used with Aphthona species, the Cecidomyid was tested against 56 plants in 22 families. Test plants included species closely related to Euphorbia and economically important plants such as snow-on-the-mountain, E. marginata; flowering spurge, E. corollata; and fire plant, E. heterophylla. Tests performed in 1982 by the USDA, ARS laboratories in Rome, Italy, indicated that S. esulae could complete its development only on plants in the genus Euphorbia. In 1984, host specificity tests were conducted in Albany, California on 11 native North American Euphorbia species to examine the potential host range of S. esulae in North America. Host specificity testing indicated that S. esulae is able to oviposit and complete its development on a limited number of species in the subgenus *Esula* of the genus *Euphorbia*. Out of 21 North American native *Euphorbia* species in the subgenus *Esula*, seven species were tested for host specificity. Of these seven species, five supported *S. esulae* development (Pecora *et al.*, 1991).

Hyles euphorbiae host specificity tests. The Canadian Department of Agriculture conducted the host specificity tests for the Sphingidae, Hyles euphorbiae (Gassmann and Schroeder, 1995). In no-choice tests, larvae were successfully reared on *E. epithymoides*, *E. lathyris* (subgenus *Esula*), *E. marginata* (Agaloma), but not on the subgenera Poinsettia and Chamaesyce or other plants except for Lythrum salicaria L. (Lythraceae). In Europe, *H. euphorbiae* was primarily found feeding on *E. cyparissias* (cypress spurge), but also was found on *E. esulae*, Euphorbia gerardiana (Jacq.) Fourr., *E. paralias*, and other species in the subgenus *Esula* (Harris, 1999).

Releases Made

Eleven species of European insects were released in North America to control cypress spurge; seven species in the eastern United States and ten in Canada (Gassmann and Schroeder, 1995; Harris, 1999) (Table 2).

The first biological control agent released was *Hyles euphorbiae*, in Canada in 1965. Insects initially did not survive, but a subsequent release in 1966 and 1967 at Braeside, Ontario, did survive. From 1976 through 1982, third and fourth instar larvae collected from Braeside, Ontario were released on cypress spurge or leafy spurge in Virginia, New York, and Maryland (Batra, 1983).

A root-boring insect, *Chamaesphecia* empiformis (Esper) (Lepidoptera: Sesiidae), was released on cypress spurge in Ontario in 1969, but did not establish. Repeated releases of *C. empiformis* in the 1970s as well as another root-boring insect, *Chamaesphecia tenthrediniformis* (Denis and Schiffermüller), on North American leafy spurge, did not result in establishment. It later was determined that these *Chamaesphecia* species are host specific to the European plants *E. esulae* and *E. cyparissias* (Gassmann and Schroder, 1995; Harris, 1999). Between 1982 and 1993, six *Aphthona* species were released on leafy spurge in the Great Plains of the United States. Researchers in Canada released five *Aphthona* species on leafy spurge and four *Aphthona* species on cypress spurge in Ontario and Nova Scotia (*Aphthona cyparissiae* [Koch], *Aphthona czwalinae* (Weise), *Aphthona flava* Guill., *Aphthona nigriscutis* Foudras, *and Aphthona lacertosa* [Rosenhauer].) (Gassmann and Schroeder, 1995; Harris, 1999). *Spurgia esulae* was released in the western United States in 1985. *Spurgia capitigena* (Bremi), another gall midge, was released together with *S. esulae* on leafy spurge and cypress spurge in Ontario (Gassmann and Schroeder, 1995; Julien, 1992).

Five of the Aphthona species (A. cyparissiae, A. czwalinae, A. flava, A. nigriscutis, and A. lacertosa) and S. esulae, increased in the Great Plains to populations large enough to permit collection for redistribution to other states (Figs. 3, 4, 5). Beginning in June 1995, adults of various Aphthona species and galls containing S. esulae were collected in Montana and North Dakota, screened, packaged, and sent by overnight mail to cooperators in New Hampshire, New York, and Rhode Island. Aphthona beetles were released in groups of 500 to 2000 next to marking stakes in one to five acres of cypress or leafy spurge stands. Spurgia esulae was released in bundles of 20 galls at several sites. U.S. Department of Agriculture cooperators in New Hampshire released insects at two leafy spurge and two cypress spurge sites; New York cooperators released insects at two leafy spurge sites in the northeast part of the state; and cooperators in Rhode Island released insects at three cypress spurge sites (Hansen et al., 1997) (Table 3).

During the 1990s two other insects were released on cypress spurge in Ontario, Canada. *Oberea erthrocephala* (Schrank), a root-boring beetle in the family Cerambycidae, became established, but *Lobesia euphorbiana* (Freyer), a leaf-tying moth in the family Tortricidae, did not (Harris, 1999).



Figure 3. Aphthona nigriscutis on Euphorbia cyparissias L. (Photograph by R. A. Casagrande.)



Figure 4. Aphthona flava on Euphorbia cyparissias L. (Photograph by R. A. Casagrande.)



Figure 5. Aphthona lacertosa on Euphorbia cyparissias L. (Photograph by R. A. Casagrande.)

Table 3. Biological Control Agents Released in 1995-
1998 in Northeastern United States

State	County	Species	Year	Status ^a
NH	Carroll	A. czwalinae/ A. lacertosa	1995	Е
		Mixed <i>Aphthona</i> spp.⁵	1995	E
		S. esulae	1995	Е
	Rockingham	A. czwalinae/ A. lacertosa	1995, 96	Е
		S. esulae	1995, 96	NE
NY	Jefferson	A. czwalinae/ A. lacertosa	1995, 96	E (A. flava)
		Mixed <i>Aphthona</i> spp.	1995, 96	Е
		S. esulae	1995, 96	Е
RI	Kent	A. czwalinae/ A. lacertosa	1995	Е
		A. flava	1996	Е
		S. esulae	1995	NE
	Newport	A. cyparissiae	1995	Е
		A. czwalinae/ A. lacertosa	1995, 96, 98	E
		A. flava	1996, 98	Е
		Mixed <i>Aphthona</i> spp.	1995, 98	Е
		E. esulae	1995, 96	Е
	Washington	A. czwalinae/ A. lacertosa	1996	Е
		A. flava	1998	Е

^a Status of biological control agent populations in 2000; E, population(s) established; NE, population(s) not established

^b Two or more of the following species released together: *Aphthona cyparissiae, A. flava,* and *A. nigriscutis*

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Aphthona Species (Coleoptera: Chrysomelidae)

Aphthona species overwinter in the soil as larvae and pupate in spring in pupal cells. Adult beetles emerge in early to mid-summer and feed on spurge. Adult females mate and then lay eggs in small batches in the soil or near the base of spurge shoots. Females oviposit for several months, producing 50 to 300 eggs each. Larvae emerge in about two weeks, burrow into the soil and feed on small roots, moving to larger roots as they mature. Large larvae may burrow in the soil around spurge roots or tunnel inside large roots and root buds. Larval feeding damages spurge plants by disrupting water and nutrient transport and provides entry points for soil inhabiting fungi. Adult feeding may defoliate plants at high beetle densities, but this has little or no impact on plant health (Hansen et al., 1997).

All *Aphthona* species released in northeastern United States are univoltine (Gassmann and Shroeder, 1995). Another species, *Aphthona abdominalis* Duftschmidt, has up to four generations per year in Europe. This species was released in Montana and Colorado, but has not established (Hansen *et al.*, 1997).

Aphthona species are highly specialized and each occupies a specific niche in its native range. Aphthona nigriscutis shows a distinct preference for sandy or gravely sites, while A. cyparissiae prefers sandy loam sites (Gassmann, 1985). Aphthona flava prefers mesic-to-dry habitats and is well adapted to live in alluvial soils above flood lines, as well as in soils of relatively dry, sunny sites. Aphthona flava tolerates light shade and is probably less likely to survive low temperatures than the other species (Sommer and Maw, 1982). Aphthona czwalinae is adapted to mesic habitats with cool summers. Aphthona lacertosa prefers loamy soils and can adapt locally to both dry and wet habitats (Gassmann, 1990).

Spurgia Species (Diptera: Cecidomyiidae)

Spurgia esulae is a multivoltine insect, with two or three generations per year in Montana on leafy spurge and up to five generations per year in Europe. It overwinters in soil as mature larvae and first generation adults emerge in mid to late spring. Females deposit groups of eggs on spurge leaves, near the apical buds, producing 20 to 100 eggs over their one to two day lifespan. First instar larvae migrate to spurge buds and begin feeding within the meristematic tissue. Larval feeding induces hypertrophy in bud tissue and leads to the formation of a gall (Fig. 6). Larvae feed exclusively within gall tissue and complete development in two to four weeks. Mature larvae construct silken cocoons inside galls from which adult flies emerge. Mature larvae of the final generation drop from galls and burrow into the soil to overwinter (Pecora et al., 1991). Spurgia capitigen, released in Canada, has a similar life cycle.

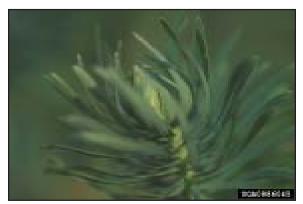


Figure 6. Gall caused by *Spurgia esulae* on *Euphorbia cyparissias* L. (Photograph by H. Faubert.)

Hyles euphorbiae (Lepidoptera: Sphingidae)

Hyles euphorbiae requires 42 to 72 days to complete development and has one or two generations per year. It overwinters as pupae in the soil, from which the moths emerge in spring. Mated females deposit light green, spherical eggs on leaves and bracts of spurge plants, producing up to 150 eggs in a lifetime. The conspicuously colored larvae feed on leaves for several weeks before entering the soil to pupate (Poritz, 1988).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Between 1976 and 1982, *Hyles euphorbiae* was released in Virginia, New York, and Maryland on both cypress spurge and leafy spurge. The only successful release of *H. euphorbiae* in the eastern United States was on cypress spurge in Warren County, New York in 1977. At all other release sites, this insect did not become established (Batra, 1983; Barbosa *et al.*, 1994). The population in Warren Co. increased from 180 to about one million insects within five years and caused defoliation in some areas. Even where insect populations were high, *H. euphorbiae* did not inflict significant damage since spurge plants easily tolerate yearly defoliation (Spencer, 1994).

Research with *H. euphorbiae* halted in the early 1980s due to high insect mortality attributed to predation by several insect species, raccoons, and deer mice. A virus also limited the numbers of *H. euphorbiae* (Batra, 1983).

Insect releases in the 1990s in New York, New Hampshire, and Rhode Island were more successful (Table 3). Where *Aphthona* species were released, sweep-net samples were performed following protocols set up by USDA, APHIS-PPQ (Attavian, 1994). Sweep sampling began the year following release and continued for several field seasons. On each sampling date, four sweeps were made adjacent to the marked release point and at 2, 4, 6, and 8 m from the release point, along each cardinal direction (20 sampling points, 80 sweeps total). A voucher sample was collected and sent to Bozeman, Montana for species verification (Hansen *et al.*, 1997).

In the 1990s, one or more insects became established at each of the northeastern states' release sites. In New York, *A. czwalinae*, *A. lacertosa*, and *A. flava* as well as *S. esulae* became established, while only two individual *A. nigriscutis* or *A. cyparissiae* were recovered as of 1999 (P. Wrege and B. Blossey, pers. comm.). In New Hampshire and Rhode Island, all released species have been recovered. In Rhode Island, *A. flava*, *A. nigriscutis* and *A. cyparissiae* can be found easily, but *A. czwalinae* and *A. lacertosa* are scarcer. In New York on leafy spurge, *A. czwalinae* and *A. lacertosa* have been the species recovered most often, while *A. flava* has been detected less frequently (P. Wrege, pers. comm.). Releases in New Hampshire have not been followed as closely, but all released species have been recovered (J. Weaver, pers. comm.).

In Rhode Island and New York, some Aphthona species increased sufficiently to allow redistribution to other sites infested with cypress spurge. In New York in June of 2000, researchers collected a mix of 10,000 A. czwalinae, A. lacertosa, and A. flava from the two leafy spurge release sites. These insects were distributed to two new leafy spurge infested sites on two dairy farms in New York (P. Wrege, pers. comm.). At one release site in Rhode Island during the summer of 2000, approximately 50,000 A. flava were collected from a small stand of cypress spurge where 500 A. flava were released in 1996. Cypress spurge was swept during 16 collecting visits from June 23 to July 17, 2000. These insects were then released at eight other pasture or hay fields in Rhode Island infested with cypress spurge.

Within farms, *Aphthona* species spread readily on their own. Collecting adult *Aphthona* beetles and redistributing them to areas heavily infested with cypress spurge on the same farm can sped up this natural dispersal of *Aphthona* species.

The gall midge, *S. esulae*, can be found sporadically at New York and New Hampshire release sites and in extremely high numbers at one Rhode Island release site.

In Rhode Island, seven release sites on two farms have realized excellent biological control of cypress spurge, with weed suppression noted the year after releasing insects in many sites (Fig. 7). Six of these releases were with 500 to 1500 adult beetle mixes of *A. flava* and *A. nigriscutis* or *A. nigriscutis* and *A. cyparissiae*. The seventh successful release was a mix of 1,000 *A. czwalinae* and *A. lacertosa*. Most of the suppression at this site may be attributed to feeding from *A. flava* and *A. nigriscutis* since many of these beetles were found at the site one year after *A. lacertosa* and *A. czwalinae* were released. Within three years, *A. flava* and *A. nigriscutis* beetles spread 70 m from their release site.

The second year following release resulted in clearly noticeable suppression at all seven sites in Rhode Island (Figs. 8 and 9), with areas nearly free from spurge extending in a diameter of 3 to 10 m around marking stakes where releases were originally



Figure 7. Aphthona flava defoliating Euphorbia cyparissias L. at URI Alton Jones Campus, June, 2000. (Photograph by H. Faubert.)



Figure 8. "Windmill" release site at Watson Farm, Jamesown, R.I., in 1997. Yellow flowers are *Euphorbia cyparissias* L. (Photograph by H. Faubert.)



Figure 9. "Windmill release site at Watson Farm, Jamestown, R.I., in 2000. Note relative scarcity of yellow flowers of *Euphorbia cyparissias* L. (Photograph by H. Faubert.)

made. *Aphthona* species were numerous on surrounding cypress spurge plants and sweep counts often reached two beetles per sweep, the amount recommended for redistributing the beetles to other locations (Hansen *et al.*, 1997). At all sites where *Aphthona* species established, populations increased sufficiently to allow collecting and redistribution.

The third year after release, weed suppression around release stakes reached 5 to 30 m diameters. *Aphthona* beetles had moved onto other cypress spurge plants and were difficult to find within 10 m of release stakes. At one site, four years after releasing 500 *A. flava*, nearly all the cypress spurge has been suppressed.

Some Rhode Island releases have not been as successful. Releases of mixes of 500 *A. czwalinae* and *A. lacertosa* have provided little or no control after four years. At two sites, *A. flava* and *A. nigriscutis* migrated into the area and are providing control. At another site, cypress spurge is being displaced by another invasive weed, black swallowort, *Vincetoxicum nigrum* (L.) Moench.

Spurgia esulae galls are found in New York, New Hampshire, and Rhode Island, though damage to leafy or cypress spurge is not apparent at this time. The galls are considered a nutrient sink and reportedly kill cypress spurge with repeated heavy attacks (Harris, 1999). An additional benefit of *S. esulae* is reported to be reduced seed production, however, in the northeast United States, the majority of cypress spurge flowering occurs before galls are present each spring. These flowers continue to develop seeds, and galls form on other shoots. No attempt has been made to redistribute *S. esulae* within the Northeast because it does not appear to contribute to biological control of leafy or cypress spurge.

Recovery of Native Plant Communities

Since cypress spurge has been suppressed in Rhode Island pastures, pasture grasses such as timothy and other cool-season perennials have grown back, but so have some other invasive weeds, specifically black swallow-wort and Canada thistle (*Carduus arvensis* [L.]) Robson.

Economic Benefits

At one site in Rhode Island, cypress spurge has been controlled. By 2000, *Aphthona* species were redistributed to eight different farms in Rhode Island. Several of these sites were in hay fields where growers were unaware of cypress spurge problems. These growers had been harvesting cypress spurge infested hay and selling it for animal food or as construction hay, perhaps assisting the spread of cypress spurge to new areas. Introducing *Aphthona* species into these areas may eliminate the need for herbicides to control cypress spurge, could help protect farm animals, and reduce the spread of cypress spurge.

RECOMMENDATIONS FOR FUTURE WORK

In the western United States, future efforts against leafy spurge will concentrate on continued introductions of insects that have not been released at many locations, specifically *A. abdominalis, C. hungarica,* and *O. erythrocephala* (Hansen *et al.,* 1997). Whether or not these species will contribute to biological control of the target weed has yet to be determined.

The Aphthona species presently available in North America provide good control of leafy and cypress spurge in open grassland habitats, but have not been as successful at controlling spurge in highmoisture or shaded habitats. In Rhode Island, the original Aphthona species releases were made on light, sandy soils in full sunlight. In these habitats the insects are succeeding in suppressing cypress spurge. It is unknown how effective these insects will be controlling cypress spurge in other conditions. Perhaps additional biological control agents can be found in Eurasia that are effective against cypress spurge in shaded or wet environments.

In the eastern United States, where future efforts will likely involve redistributing Aphthona species to other infestations of cypress spurge, it is particularly important to locate infestations of the more aggressive form of cypress spurge, the fruiting tetraploid form. This can be accomplished by surveying for cypress spurge in April and May while it is blooming and most easily detected. Once an infestation is located it must be revisited in June to see whether or not cypress spurge seed is present. In a survey conducted in Rhode Island in 2000, 98% of all cypress spurge sampled was the tetraploid form. This is a dramatic change from when Deane (1912) located only three stands of tetraploid cypress spurge in North America. If this switch to tetraploid cypress spurge is occurring throughout the region, there is added impetus to distribute biological control agents of this pest.

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16 Swallow-Worts

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PEST STATUS OF WEED

There are three European species of swallow-worts found in North America: Vincetoxicum nigrum (L.) Moench (black swallow-wort), Vincetoxicum rossicum (Kleo.) Barb. (pale swallow-wort or dog strangling-vine), and Vincetoxicum hirundinaria Medik. (white swallow-wort) (Sheeley and Raynal, Swallow-worts are in the family 1996). Asclepiadaceae. Vincetoxicum nigrum and V. rossicum now are naturalized in northeastern North America, and both are invasive in natural areas and abandoned pastures (Lawlor, 2000). Swallow-worts are found in gardens and fields, along fencerows, roadways, grassy slopes, wooded edges, and streambanks. Tangled masses of swallow-wort vines shade and suppress native plants (Sheeley and Raynal, 1996). In Rhode Island, heavy growth of V. nigrum reduces the effectiveness of electric fences around pastures (Minto, pers. comm.). Loss of native plant species reduces habitat value for wildlife (Christensen, 1998). Vincetoxicum hirundinaria occurs sparsely in the northeast (Gleason and Cronquist, 1963), and Sheeley and Raynal (1996) suggest that this species is not well established in North America.

Nature of Damage

In central New York, V. rossicum forms dense monospecific stands in shrubby areas with a history of disturbance, and in the understory of successional woodlands (Lawlor, 2000). Near Windsor, Vermont, Lawlor (2000) observed V. nigrum out competing a population of a federally endangered endemic species, Jesup's milkvetch, Astragalus robbinsii (Oakes) Gray var. jesupii Egglest. and Sheldon. She also observed that V. rossicum is overgrowing the federally listed Hart's tongue fern, Phyllitis scolopendrium (L.) Newman at Split Rock, near Onadaga, New York. Vincetoxicum rossicum is threatening the only New England population of *Asclepias viridiflora* Raf. in Connecticut, an endangered species in that state (Mehrhoff, pers. comm.).

Loss of native plant species may reduce biodiversity and delay or redirect succession (Lawlor, 2000), as well as reduce the value of habitat to wildlife (Christensen, 1998). Cows and sheep in pastures will eat swallow-worts, and control their growth, but swallow-worts spread rapidly in abandoned pastures in New York (Lawlor, 2000) and Rhode Island (Casagrande, unpubl.). Swallow-worts are important weeds requiring management in tree plantations in New York (Lawlor, 2000), and in Rhode Island nurseries (Casagrande, unpubl.).

Current control measures have not been adequate to alleviate harmful effects of swallow-worts. Lawlor (2000) evaluated a number of control techniques used against V. rossicum. Her recommendations include mowing or hand pulling just as pods are beginning to form to minimize seed production. For herbicidal control, repeated applications are necessary. Christensen (1998) conducted experiments in Ontario to evaluate the effectiveness of herbicide control techniques for V. rossicum. Two applications of glyphosate were necessary (in mid-June and early August) to achieve greater than 90% reduction of V. rossicum. Following treatment with herbicide, another invasive plant, Melilotus alba Medicus (sweet white clover), replaced V. rossicum as the dominant plant. Repeated mowing is not successful in reducing the amount of cover of V. rossicum (Kirk, 1985).

Geographical Distribution

Gray (1868) first reported *Vincetoxicum nigrum* as escaping from gardens in Cambridge, Massachusetts. According to Pringle (1973), Scoggan (1979), and Sheeley and Raynal (1996), the distribution of *V. nigrum* currently extends west from the Atlantic coast to southeastern Ontario and south to southern Pennsylvania and Missouri. There is a record of *V. nigrum* from California in the USDA PLANTS Database (Fig. 1). Swallow-worts are commonly found in pastures and natural sites in these areas.

Vincetoxicum rossicum is distributed from the Atlantic coast west to southern Michigan and northern Indiana, and from southern Ontario, Canada, south through southern Pennsylvania (Pringle, 1973; Scoggan, 1979; Sheeley and Raynal, 1996) (Fig. 2). Moore (1959) reported that *Cynanchum medium* had been collected frequently since 1889 in Ontario, Canada. *Cynanchum medium* is a synonym of *V. rossicum* (Sheeley and Raynal, 1996). Collections of *V. rossicum* have come primarily from roadsides and wild areas (Sheeley and Raynal, 1996).

Vincetoxicum hirundinaria was first recorded in North America in Gray's Manual (Robinson and Fernald, 1908) as Cynanchum vincetoxicum. There are records of V. hirundinaria from New York, Michigan, and Montreal. The USDA PLANTS Database has only the New York record for the United States (Fig. 3). However, there are no reports of wellestablished populations of V. hirundinaria in North America (Sheeley and Raynal, 1996).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Swallow-worts are members of the family Asclepiadaceae. The generic placement of the European and North American swallow-wort species is dynamic. The generic names Cynanchum and Vincetoxicum have been applied in North American and European literature. Black swallow-wort has been known as Cynanchum nigrum (L.) Pers. or Vincetoxicum nigrum (L.) Moench. (Kartesz and Gandhi, 1991). We use the scientific nomenclature of Sheeley and Raynal (1996) for the three swallowwort species introduced into North America: Vincetoxicum nigrum, Vincetoxicum rossicum, and Vincetoxicum hirundinaria. Recent molecular evidence indicates that both Vincetoxicum and Cynanchum are valid genera and that the European species presently in the northeastern United States are all in the genus Vincetoxicum (W. D. Stevens, pers. comm.). These are apparently the only three species of Vincetoxicum present in North America. In Europe, there are 18 native species of Vincetoxicum (with

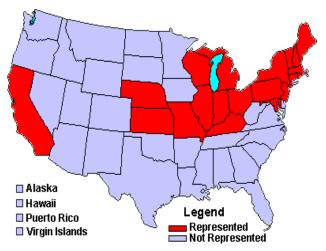


Figure 1. Distribution of *Vincetoxicum nigrum* in the United States. (USDA PLANTS Database.)



Figure 2. Distribution of *Vincetoxicum rossicum* in the United States. (USDA PLANTS Database.)

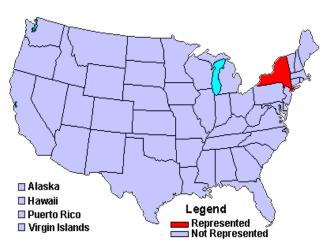


Figure 3. Distribution of *Vincetoxicum hirundinaria* in the United States. (USDA PLANTS Database.)

nine subspecies of *V. hirundinaria*) and one native species of *Cynanchum* (*C. acutum* L.) (Heywood, 1972) (Table 1).

Biology

Swallow-worts are herbaceous perennials in the family Asclepiadaceae that grow into twining vines (Fig. 4). In one season a vine can grow 1 to 2 m. In New York, flowering begins in late May, peaks in mid-June and ends in mid-July (Lumer and Yost, 1995). Flowers (Fig. 5), which have the scent of rotting fruit, each remain open for six to eight days. The fruit pods (Fig. 6) release seeds from mid-August to early October (Lumer and Yost, 1995). *Vincetoxicum nigrum* spreads clonally from deep rhizomes (Lumer and Yost, 1995). *Vincetoxicum rossicum* moves into new

Table 1. Native Cynanchum and Vincetoxicum Species in Europe (Heywood, 1972)

Species	Native	Main Countries / Area
Cynanchum acutum L.	Yes	Albania, Bulgaria, France, Greece, Italy, Romania, Portugal, Spain, Yugoslavia, S. Russia
Vincetoxicum canescens (Willd.) Decne	No (from S.W. Asia)	Greece
V. fuscatum (Hornem.) Reichenb.	Yes	Albania, Bulgaria, Greece, Yugoslavia, S. and E. Russia, Turkey
V. <i>hirundinaria</i> subsp. <i>adriaticum</i> (G. Beck) Markgraf	Yes	N. W. Yugoslavia
<i>V. hirundinaria</i> subsp. <i>contiguum</i> (Koch) Markgraf	Yes	W. Yugoslavia
V. hirundinaria subsp. hirundinaria	Yes	All Europe except Portugal and Spain
V. <i>hirundinaria</i> subsp. <i>intermedium</i> (Loret and Barr.) Markgraf	Yes	S. France, N. E. Spain
V. <i>hirundinaria</i> subsp. <i>jailicola</i> (Juz.) Markgraf	Yes	S. Ukraine
<i>V. hirundinaria</i> subsp. <i>lusitanicum</i> Markgraf	Yes	N. W. Portugal, N. Spain
<i>V. hirundinaria</i> subsp. <i>nivale</i> (Boiss. and Heldr.) Markgraf	Yes	Balkan
<i>V. hirundinaria</i> subsp. <i>stepposum</i> (Pobed.) Markgraf	Yes	C. and S. Russia, Ukraine
V. huteri Vis. and Ascherson	Yes	Albania, Yugoslavia
V. juzepczukii (Pobed.) Privalova	Yes	S. Ukraine
V. nigrum (L.) Moench	Yes	France, Italy, Portugal, Spain
V. pannonicum (Borhidi) J. Holub	Yes	Hungary
V. rossicum (Kleopow) Barbarich	Yes	Ukraine, S. E. Russia
V. scandens Sommier and Levier	Yes	S. and E. Ukraine, S. Russia
V. schmalhausennii (Kusn.) Markgraf	Yes	S. Ukraine
V. speciosum Boiss. and Spruner	Yes	Albania, Bulgaria, Greece, Yugoslavia, Turkey
<i>V. vincetoxicum</i> subsp. <i>cretaceum</i> (Pobed.) Markgraf	Yes	S. E. Russia, S. and E. Ukraine



Figure 4. *Vincetoxicum nigrum* vine on pasture fence. (Photograph by H. Faubert.)



Figure 5. *Vincetoxicum nigrum* flower. (Photograph by R. A. Casagrande.)



Figure 6. *Vincetoxicum nigrum* seed pod. (Photograph by R. A. Casagrande.)

sites by seed (Christensen, 1998). Like other members of the family Asclepiadaceae, these species have parachute-lifted seeds that are carried by wind. *Vincetoxicum rossicum* is very successful in areas of shallow soil over limestone bedrock (Lawlor, 2000). Swallow-worts growing in shaded areas have thinner stems and tendrils; larger, darker, thinner leaves; fewer roots; and fewer, paler flowers than plants growing in sunny areas (Christensen, 1998).

Analysis of Related Native Plants in the Eastern United States

There are no native species in the genus *Vincetoxicum* in North America. There are fourteen species of native plants listed in the genus *Cynanchum* in the United States (The Biota of North America Program, 2001) (Table 2). Most have a very limited distribution; nine of the fourteen have been recorded in only one state. One species, *Cynanchum laeve* (Michx.) Pers., is found in 26 states. The family Asclepiadaceae in North America includes more than 80 species of milkweeds, in the genus *Asclepias* (USDA, NCRS, 1999). *Asclepias syriaca* L., common milkweed, is a preferred food source for larvae of the monarch butterfly (*Danaus plexippus* L.) (Hartzler and Buhler, 2000).

Haribal and Renwick (1998) found that female monarch butterflies (Fig. 7) oviposit on black swallow-wort (*V. nigrum*) in choice tests in the laboratory; however, resulting larvae were not able to complete development on this plant. Dacey and Casagrande (pers. obs.) found that monarchs readily oviposit on *V. nigrum* in the laboratory and in large cages in the field. In both cases, when monarchs were given a choice of ovipositing on common milkweed (*A. syriaca*) or black swallow-wort, they laid approximately 25% of their eggs on the swallow-wort, and all of the resulting larvae died. Dacey and Casagrande (pers. obs.) found eggshells as evidence of monarch oviposition on black swallow-wort in uncaged field populations of swallow-wort and milkweed.

It is not clear what impact *V. nigrum* may be having on populations of monarch butterflies in nature. Haribal and Renwick (1998) note that in some locations in the United States, *V. nigrum* has replaced much of the native vegetation, including the *Asclepias*

Species	Common Name	States
Cynanchum angustifolium Pers.	Gulf Coast swallow-wort	AL, FL, GA, LA, MS, NC, SC, TX
C. arizonicum (Gray) Shinners	Arizona swallow-wort	AZ, NM
C. barbigerum (Scheele) Shinners	Bearded swallow-wort	ТХ
C. blodgettii (Gray) Shinners	Blodgett's swallow-wort	FL
<i>C. laeve</i> (Michx.) Pers.	Honeyvine	AL, AR, DE, FL, GA, IA, ID, IL, IN, KS, KY, LA, MD, MI, MS, NC, NE, NY, OH, OK, PA, SC, TN, TX, VA, WV
C. ligulatum (Benth.) Woods.	Mexican swallow-wort	AZ
C. maccartii Shinners	Maccart's swallow-wort	ТХ
C. northropiae (Schlechter) Alain	Fragrant swallow-wort	FL
C. pringlei (Gray) Henrickson	Pringle's swallow-wort	ТХ
C. racemosum (Jacq.) Jacq.	Talayote	ТХ
<i>C. racemosum</i> var. <i>unifarium</i> (Scheele) E. Sundell		ТХ
C. scoparium Nutt.	Leafless swallow-wort	FL, GA, MS, SC
C. utahense (Engelm.) Woods	Utah swallow-wort	AZ, CA, NV, UT
C. wigginsii Shinners	Wiggins' swallow-wort	AZ

Table 2. Native Cynanchum Species in North America

spp., hosts for monarch butterfly larvae. Milkweeds are used as host plants by at least eight other native North American insects (Arnett, 1985; Palmer, 1985; McCauley, 1991). There is no literature on whether these native insects are able to successfully use *Vincetoxicum* species as host plants or whether, as with monarchs, they are threatened by these invasive plants.



Figue 7. Monarch butterfly (*Danaus plexippus* L.). (Photograph by J. Dacey.)

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Vincetoxicum nigrum is native to southwestern Europe; *V. rossicum* is found in the Ukraine and southeast Russia; and *V. hirundinaria* is distributed throughout Europe (Heywood, 1972).

Areas Surveyed for Natural Enemies in North America

Only one insect, the tarnished plant bug (*Lygus lineolaris* [Palisot de Beauvois]), has been reported feeding on *Vincetoxicum* species in North America (Lawlor, 2000), but damage was minimal. Sheeley (1992) noted the lack of herbivores and pathogens in swallow-wort stands in upstate New York. Christensen (1998) also found no evidence of herbivory or disease in swallow-worts in Ontario. Christensen suggests that the toxic substances in swal-

low-worts repel herbivorous insects. It appears that none of the natural enemies known to be associated with swallow-wort in Europe have been accidentally established in North America.

Natural Enemies Found in Europe

There are several potential biological control agents associated with V. hirundinaria in Europe. In western and central Europe, two chrysomelids, Chrysochus asclepiadeus Pallas and Chrysomela aurichalcea ssp. bohemica Mann, are reported as specialists on V. hirundinaria (Mohr, 1966; Dobler et al., 1998). The Russian literature indicates that there are several other species of chrysomelid beetles that feed on Vincetoxicum species in Russia and central Asia (Izhevski, pers. comm.). Five other species of specialist insects herbivorous on V. hirundinaria have been reported in Europe: the noctuid moth Abrostola asclepiadis (Denis and Schiff.) (Forare, 1995); two gall midges, Contarinia vincetoxici Kieffer and Contarinia asclepiadis (Giraud), which feed, respectively, on the flowerbuds and the pods of V. hirundinaria (Buhr, 1965); and two other seed-feeding species, the tephritid fly Euphranta connexa (Fabricius) (Solbreck and Sillen-Tullberg, 1986) and the lygaeid bug Lygaeus equestris (L.) (Kugelberg, 1977; Solberg and Sillén-Tullberg 1990). One weevil, Otiorhynchus pinastri Herbst, is believed to be monophagous on V. hirundinaria in Europe (Dieckmann, 1980; Kippenberg, 1981). The insect fauna of V. nigrum and V. rossicum in Eastern Europe and in Russia is confounded by the plant synonymy at both the specific and generic level. The potential for finding herbivores of swallow-worts seems great given the number of Vincetoxicum species recorded in Eurasia.

Two pathogens of *Vincetoxicum* spp. are recorded in the literature; *Peridermium pini* (Pers.) Lev., a stem rust that alternates between pine and other plants such as *Vincetoxicum* spp. and *Paeonia* spp. (Gibbs *et al.*, 1988), and *Cronartium asclepiadeum* (Willdenau) Fries (Gaumann, 1959).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Little is known on the biology and ecology of natural enemies of swallow-worts. Some information is available on the following species.

Abrostola asclepiadis Schiff. (Lepidoptera: Noctuidae)

In Finland, Sweden, and Denmark, the larva of the noctuid moth A. asclepiadis is monophagous on V. hirundinaria (Forare, 1995). Adults fly in June and July. Development from egg to pupa takes about six weeks, leaving time for only one generation per year in Sweden. Further south in Europe, more than one generation occurs (Forare, 1995). Female moths can lay at least 255 eggs on the undersurface of V. hirundinaria leaves. Small shaded patches of host plants receive higher egg densities than large exposed ones (Forare, 1995). First and second instar larvae feed day and night, moving very little from where the eggs were deposited. Larger larvae are nocturnal and actively search for foliage, feeding mainly at the top of plants. Larvae complete development in August or September and pupate in the soil.

Generalist predators and parasitoids cause most of the mortality of A. asclepiadis eggs in Scandinavia. Ants are the primary generalist predators, but chrysopid larvae, anthocorid bugs, and mites also have been observed feeding on A. asclepiadis eggs (Forare, 1995). Species of Trichogramma (Trichogrammatidae) and Telenomus (Scelionidae) parasitize A. asclepiadis eggs. First and second instars are attacked by the same predators as the eggs. Ants and predaceous pentatomid bugs attack larger larvae. Egg and larval predation are important in reducing the population size of A. asclepiadis (Forare, 1995). This is the primary reason why this insect has very little effect on its host plant population, although occasionally there are small outbreaks of the species, which may cause local defoliation (Forare, 1995).

Euphranta connexa (Fabr.) (Diptera: Tephritidae)

Larvae of the fly, *Euphranta connexa*, feed on the seeds within the developing pods of *V. hirundinaria*, attacking 50 to 100% of the pods. Pods attacked by *E. connexa* usually have most seeds destroyed and even undamaged seeds are more susceptible to fungal pathogens. *Euphranta connexa* is monophagous on *V. hirundinaria* and only has one generation per year. The polyphagous ichneumonid *Scambus brevicornis* (Gravenhorst) parasitizes *E. connexa* in Sweden, but does not appear to regulate its density (Solbreck and Sillen-Tullberg, 1986).

Lygaeus equestris (L.) (Heteroptera: Lygaeidae)

Lygaeus equestris is a seed-feeding bug that feeds on a number of plant species, but prefers V. hirundinaria. Both nymphs and adults of L. equestris feed on seeds of V. hirundinaria. Lygaeus equestris adults hibernate in crevices in rock walls and buildings from late August through late April or May (Solbreck and Sillén-Tullberg, 1990). In Sweden, it appears to have no serious natural enemies. Weather conditions and food resources limit the populations of L. equestris (Kugelberg, 1977).

Natural Enemies Subjected to Host Range Tests

No natural enemies of *Vincetoxicum* species have been subjected to host range screening.

Releases Made

No natural enemies of *Vincetoxicum* species have been released in North America.

RECOMMENDATIONS FOR FUTURE WORK

It is commonly recognized that invasive non-indigenous plants can displace native plants, sometimes also affecting populations of native animals that use these plants for food or shelter. Swallow-worts, which often grow as vines on other plants, are very effective competitors, often warranting control measures on this basis alone. Black swallow-wort is apparently unusual, however, in effectively serving as a sink for monarch butterfly eggs. These important native insects are stimulated to oviposit on swallowwort, but larvae cannot survive. It is not known how many other native North American insects might also unsuccessfully (or successfully) use this new plant as a host. Laboratory and field cage studies, followed by field surveys in eastern United States, are needed to determine if this plant has the potential to harm populations of other native insects in addition to the monarch butterfly. Such research would also provide information on the effects of native insects on swallow-worts.

European research will lead to a better understanding of the potential for classical biological control of swallow-worts in North America. Swallowworts are not considered weeds in Europe, presumably because of the complex of insects that feed upon them. There is a high probability that European herbivores can be found with the genus-level host specificity that would be required for consideration for North American introduction. European research will involve detailed literature and herbarium survey for distribution and taxonomy of Vincetoxicum herbivore records. Surveys for insects herbivorous on Vincetoxicum species should be conducted in western Europe, the Balkans, and southern Russia. All natural enemies found should be identified and evaluated. Once promising natural enemies are identified, biological studies and preliminary host range testing with critical North American Asclepiadaceae species will be needed. Host use evolution has been shown in the Chrysochus milkweed beetles in behavioral studies and population genetics (Dobler and Farrell, 1999). Parallel studies could be applied to the chrysomelids and other natural enemies associated with Vincetoxicum in Europe.

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17 CANADA THISTLE

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PEST STATUS OF WEED

Canada thistle, *Cirsium arvense* (L.) Scop. (Fig. 1), is a vigorous, competitive weed that occurs in a wide range of habitats and is difficult to control due to its ability to regrow from its extensive, deep creeping root system (Nadeau and Vanden Born, 1989).



Figure 1. Canada thistle [*Cirsium arvense* (L.) Scopoli]. (Photograph by L. M. Dietz.)

Nature of Damage

Economic damage. Canada thistle causes extensive crop yield losses through competition and, perhaps, allelopathy (Stachon and Zimdahl, 1980) (Fig. 2). The prickly mature foliage also is thought to reduce productivity of pastures by deterring livestock from grazing. Canada thistle is the species most frequently declared noxious under state or provincial weed control legislation in the United States and Canada (Skinner *et al.*, 2000). It is listed as a noxious weed under



Figure 2. Canada thistle [*Cirsium arvense* (L.) Scopoli] infestation in canola (*Brassica rapa* L.). (Photograph by A. S. McClay.)

state weed control legislation in Delaware, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, North Carolina, North Dakota, Ohio, Oklahoma, Pennsylvania, South Dakota, and Wisconsin (USDA, NRCS, 1999).

Ecological damage. Canada thistle can be an invasive species in some natural communities, including prairie potholes and wet or wet-mesic grasslands in the Great Plains and sedge meadows in the upper Midwest (Nuzzo, 1997). It usually is a problem in disturbed areas and moister sites. Canada thistle was among the most prevalent weeds on Conservation Reserve Program (CRP) land in Minnesota, occurring in 65 to 75% of CRP fields throughout the state. Canada thistle ground cover in these fields frequently reached 50 to 75%, giving rise to concern about seed dispersal into neighboring agricultural land (Jewett *et al.*, 1996). It was ranked as "urgent" for control in a review of exotic plants at Pipestone National Monument, Minnesota (Hiebert and Stubbendieck, 1993).

Extent of losses. A density of 20 Canada thistle shoots per m² caused estimated yield losses of 34% in barley (O'Sullivan *et al.*, 1982), 26% in canola (O'Sullivan *et al.*, 1985), 36% in winter wheat

(McLennan *et al.*, 1991), and 48% in alfalfa seed (Moyer *et al.*, 1991). Densities of Canada thistle in field infestations can reach 173 shoots per m² (Donald and Khan, 1996).

Geographical Distribution

Canada thistle occurs in all eastern U.S. states south to Kansas, Arkansas, Tennessee, and North Carolina, but it is sparsely distributed south of latitude 37° N (USDA, NRCS, 1999). The main areas of occurrence are the northeastern, mid-Atlantic, Great Lakes, and northern Great Plains states. In a survey in Maryland, Canada thistle was found in about 17% of suitable sites in the eastern and central part of the state, but only 10% of sites further west (Tipping, 1992).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Canada thistle is a member of the genus *Cirsium*, subtribe Carduinae, tribe Cardueae, and family Asteraceae (Bremer, 1994). It differs from most other *Cirsium* species by its dioecious flowers, and from most native North American members of the genus by its extensive creeping roots and small, numerous flower heads borne on branched stems. Several varieties have been described based on variations in leaf shape and degree of spininess.

Biology

The biology of Canada thistle was extensively reviewed by Moore (1975), Donald (1994), and Nuzzo (1997). It is a perennial herb with an extensive creeping root system that can give rise to new shoots from adventitious root buds. The stems usually die back over winter and new shoots are produced each spring from old stem bases or root buds. Canada thistle is almost perfectly dioecious and can produce abundant seeds, which are dispersed by wind (Lloyd and Myall, 1976). It is a long-day plant, requiring a photoperiod of at least 14 to 16 hours (depending on ecotype) for flowering to be induced (Hunter and Smith, 1972). It occurs in a wide range of habitats and soil types.

Analysis of Related Native Plants in the Eastern United States

The genus Cirsium is a large one, with 92 native species in North America, of which 20 occur in the U.S. states that fall wholly or in part east of the 100th meridian (USDA, NRCS, 1999). One of these, Cirsium pitcheri (Torrey) Torrey and Gray, is listed as threatened under the Endangered Species Act. This species occurs in sand dunes along the shores of the Great Lakes in Illinois, Indiana, Michigan, Wisconsin, and Ontario. Phylogenetic studies of North American and Eurasian Cirsium species are needed to elucidate relationships among species in the genus and to provide a basis for planning host-specificity tests and interpreting resulting data. Studies have been initiated using the external transcribed spacer (ETS) region of ribosomal DNA to develop a phylogeny for North American and selected Eurasian Cirsium species (D. Kelch, pers. comm.).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Canada thistle was among the first 19 weed species selected as targets for biological control when the USDA Rome Laboratory was established in 1959 (Schroeder, 1980). However, most host specificity testing of agents for Canada thistle was conducted from 1961 to 1984 by staff of Agriculture Canada or by the International Institute of Biological Control (now CABI Bioscience) working with Canadian funding. The agents released in the United States have been those that became available as a result of the Canadian program, the results of which were reviewed by Schroeder (1980), Peschken (1984a), and McClay et al. (2001). Most releases in the eastern United States were made by USDA, ARS staff at the Beltsville Agricultural Research Center; some studies also were carried out by staff of the Maryland Department of Agriculture. Biological control of Canada thistle in New Zealand has been reviewed by Jessep (1989).

Area of Origin of Weed

Canada thistle is native to Europe, parts of North Africa, and Asia south to Afghanistan, Iran and Pakistan, and east to China. Its exact center of origin within the native range is not known, although it is suggested by Moore (1975) to be in southeastern Europe and the eastern Mediterranean area.

Areas Surveyed for Natural Enemies

Extensive surveys of natural enemies of Canada thistle and other Cardueae species in western Europe were carried out starting in 1959. Other surveys have been carried out in Japan, Iran, and northern Pakistan (Schroeder, 1980), and in China (Wan and Harris, unpub. data). Further surveys in southern Russia, central Asia, and China are currently under way (Gassmann, unpub. data). In addition to surveys specifically carried out for biocontrol purposes, the general European entomological literature contains much information on insects associated with Canada thistle (e.g., Redfern, 1983; Stary, 1986; Volkl, 1989; Freese, 1994; Berestetsky, 1997; Frenzel *et al.*, 2000). The phytophagous insects associated with Canada thistle in Poland are listed by Winiarska (1986).

Natural Enemies Found

Surveys by Zwölfer (1965a) in Europe found 78 species of phytophagous insects feeding on Canada thistle. Of these, six are reportedly monophagous, five are found on Canada thistle and a few related species, 26 are oligophagous on plants in the same subtribe, and the remaining 42 are less specific and of no interest for biological control (Schroeder, 1980).

A number of European insects and pathogens attacking Canada thistle have been accidentally introduced into North America, and some of these have been studied as potential biological control agents. The leaf-feeding tortoise beetle Cassida rubiginosa Müller (Coleoptera: Chrysomelidae) occurs widely in the eastern United States, south to Virginia and west to southern Michigan and Ohio, and in Canada (Ward and Pienkowski, 1978a). The seed-feeding Larinus planus (F.) (Coleoptera: weevil Curculionidae) was found by Wheeler and Whitehead (1985) to be well established in Pennsylvania, Maryland, Ohio, and New York, with the earliest records dating from 1968 in Ohio. It has also been collected from Indiana and West Virginia (C. W. O'Brien, pers. comm.). The seed-head fly Terellia ruficauda (F.) (=Orellia ruficauda F.) (Diptera: Tephritidae) is distributed across Canada, and presumably also occurs widely in the eastern United States. A survey showed it to be present in South Dakota (R. Moehringer, S. Dakota Dept. of Agriculture, pers. comm.), and specimens are known from Michigan. The root-feeding weevil *Cleonis pigra* (Scopoli) (Coleoptera: Curculionidae) occurs in New York, Pennsylvania, Michigan, Indiana, Ontario, and Quebec (O'Brien and Wibmer, 1982; Anderson, 1987; C. W. O'Brien, per. comm.). The rust *Puccinia punctiformis* (Strauss) Röhling is widespread in North America.

A phytopathogenic bacterium, *Pseudomonas* syringae pv. tagetis (Hellmers 1955) Young, Dye and Wilkie 1978, causing apical chlorosis, has been isolated from Canada thistle. Field tests of applications of this bacterium in a commercial corn field resulted in 57% mortality of Canada thistle as well as damage to several other weedy Asteraceae species. A surfactant is required to allow penetration of the Canada thistle cuticle by the bacterium. Further work on formulation of this agent is under way (Johnson *et al.*, 1996). The bacterium occurs in Maryland (P. Tipping, pers. comm.).

One species which was introduced as a biological control agent for *Carduus* species, the seed-head weevil *Rhinocyllus conicus* (Frölich) (Coleoptera: Curculionidae), also is recorded attacking Canada thistle (Rees, 1977; Youssef and Evans, 1994). This species is widespread in the eastern United States, and has been found attacking Canada thistle in Maryland (P. Tipping, pers. comm.).

Host Range Tests and Results

In the earlier part of the period 1961 to 1984, host specificity testing for agents attacking Canada thistle was focused on assessing potential risks to economic species of Cardueae, of which the two most important are safflower (*Carthamus tinctorius* L.) and globe artichoke (*Cynara scolymus* L.). In later studies, some native North American *Cirsium* species also were tested, but potential impacts of most agents on native non-target *Cirsium* species were not assessed in detail.

The leaf-feeding beetle *Altica carduorum* Guérin-Méneville (Coleoptera: Chrysomelidae) is known in the field in Europe mainly from Canada thistle, with a single record of adults from *Carduus* pycnocephalus L. (Zwölfer, 1965a). The host specificity of a population of *A. carduorum* from Switzerland was studied by Harris (1964), using starvation tests with adults and larvae. First instar larvae complete development only on *Cirsium*, *Carduus*, and *Silybum* species. Adults feed readily on all *Cirsium* species tested, which included only two North American species, but their feeding rate is highest on Canada thistle. Similar results were obtained by Karny (1963) and Zwölfer (1965b).

More recently, the host specificity of a biotype of A. carduorum from Xinjiang, China, was assessed by Wan et al. (1996), who found that in no-choice tests this beetle can complete development on 18 Cirsium species (mostly North American) and Silybum marianum (L.) Gaertner. A risk analysis approach, however, predicted that North American Cirsium species would be safe from attack in the field because host selection requires a series of sequential steps, with the native species being less preferred than C. arvense at each stage (Wan and Harris, 1997). It also was suggested that the insect is monophagous in the field because host finding is dependent on aggregation to substances from wounds and feces specific to C. arvense (Wan and Harris, 1996). As the Xinjiang biotype was not approved for field release in North America, it has not been possible to test these predictions in the field.

The only known field host plant of the weevil Ceutorhynchus litura (F.) (Coleoptera: Curculionidae) in Europe is Canada thistle, except for three collections from Carduus defloratus L. in Switzerland (Zwölfer and Harris, 1966). Ceutorhynchus litura was screened by Zwölfer and Harris (1966), who found that feeding, oviposition, and larval development are restricted to species in the genera Cirsium, Carduus, and Silybum. Normal larval development occurs on all Cirsium species tested, including three native North American species. Ceutorhynchus litura was approved for release in Canada and the United States based on its lack of attack on economic Cardueae species. In a more recent European field survey of seven Cirsium and Carduus species by Freese (1994), C. litura was found only in Canada thistle.

The stem- and petiole-galling fly Urophora cardui (L.) (Diptera: Tephritidae) is reported in the field in Europe only from Canada thistle (Zwölfer, 1965a) and the closely related species *Cirsium setosum* von Bieberstein (sometimes treated as a synonym of *C. arvense*) (Frenzel *et al.*, 2000). It was screened by Peschken and Harris (1975) against 14 other European Cardueae species and against 11 species, mainly economically important plants, in other tribes and families. In these tests, consistent oviposition was seen only on Canada thistle, with occasional oviposition on *Cirsium vulgare* (Savi) Ten. and *Carduus acanthoides* L.

Host specificity tests on the weevil *L. planus* were conducted by McClay (1989), who found that *L. planus* will not feed on ornamental or economic species in the tribe Cardueae and that Canada thistle is preferred over other *Cirsium* species for feeding and oviposition. These tests suggested that small-flowered *Cirsium* species were more suitable as hosts than native *Cirsium* species, which generally have larger flower heads. However, Louda and O'Brien (2002) found L. planus reducing seed production of the large-flowered native Cirsium undulatum (Nutt.) Spreng. var. tracyi (Rydb.) Welsh in Colorado, indicating that redistribution of this insect poses greater risks to native species than was previously believed.

Cassida rubiginosa is recorded from numerous species of *Arctium*, *Carduus*, *Cirsium*, *Silybum*, *Onopordum*, and *Centaurea*. In feeding tests, adults and larvae accept species from all these genera, as well as from globe artichoke (Zwölfer and Eichhorn, 1966; Zwölfer, 1969). Spring and Kok (1997) found that *C. rubiginosa* shows no oviposition preference between Canada thistle and *Carduus thoermeri* Weinmann; however, mortality of immature stages is lower on Canada thistle. They also observed adults, larvae, and egg masses on burdock, *Arctium minus* (Hill) Bernhardi, in the field, and reared *C. rubiginosa* from egg to adult on this species.

Host specificity testing also was conducted on the lace bug *Tingis ampliata* Herrich-Schäffer (Hemiptera: Tingidae) (Peschken, 1977a) and the leaf beetle *Lema cyanella* (L.) (Coleoptera: Chrysomelidae) (Peschken and Johnson, 1979; Peschken, 1984b). *Tingis ampliata* was never released in North America because of concerns about possible attack on globe artichoke, *Cynara scolymus* L. Limited releases of *L. cyanella* have been made in Canada but no further releases or redistribution are planned (McClay, unpub. data). *Cleonis pigra* attacks numerous species of Cardueae in Europe, and is an economic pest of globe artichoke (LaFerla, 1939; Zwölfer, 1965a; Batra *et al.*, 1981). *Terellia ruficauda* has been reared from six *Cirsium* species in Europe (Zwölfer, 1965a).

Releases Made

Information on releases of biological control agents against Canada thistle was obtained from the literature and, for the period between 1981 and 1985, from the USDA, ARS database on natural enemy releases in the United States (ROBO at http://www.ars-grin.gov/nigrp/robo.html). There undoubtedly have been many additional releases that have not been published; for example, 18 releases of *C. litura* and 12 of *U. cardui* were made in the eastern part of South Dakota between 1987 and 1984, and *L. planus* and *C. rubiginosa* also have been released in this area (R. Moehringer, S. Dakota Dept. of Agriculture, pers. comm.).

Releases of *A. carduorum* began in 1966, using material from Switzerland via Canada, and were made in Delaware, Indiana, Maryland, Minnesota, New Jersey, South Dakota, and Wisconsin; in 1970, material from France was released in Maryland, New Jersey, and South Dakota (Julien and Griffiths, 1998). Two releases of *A. carduorum* from a population collected near Rome, Italy, were made in Maryland in 1982.

Releases of *C. litura* began in 1971 (Julien and Griffiths, 1998). This weevil was released in Maryland on 16 occasions from 1982 to 1985 and at one site in New York State in 1984. Most of these releases were made using material imported from Bavaria, Germany, but four releases were made with material from established field populations in Montana.

Urophora cardui was released on nine occasions in Maryland between 1981 and 1984, mostly using material from field collections near Vienna, Austria. Two releases of *U. cardui* from this source also were made in Iowa in 1982 and 1985. Another series of four releases totaling 4,400 adults from the population in British Columbia, Canada, was made in 1985 in Virginia (Kok, 1990).

Cassida rubiginosa was moved from northern Virginia to a southwestern area of the state where it previously had not occurred (Ward and Pienkowski, 1978a).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Altica carduorum Guérin-Méneville (Coleoptera: Chrysomelidae)

This species has a Mediterranean and partly Atlantic distribution in Europe (Zwölfer, 1965b). A closely related species, *Altica cirsicola* Ohno, occurs in China and Japan (Laroche *et al.*, 1996); however, RAPD fingerprinting (a DNA identification method) showed that a population from Xinjiang in western China was *A. carduorum* (Wan and Harris, 1995). Thus the distribution of *A. carduorum* extends from the Mediterranean and eastern Europe, through Kazakhstan, Kirghizia and Tadzhikistan to western China (Wan and Harris, 1995).

In Switzerland, overwintering adults of A. carduorum begin to appear on foliage of Canada thistle in mid-April and oviposition starts in early May. Larvae are present on the leaves from mid-May through late July. Newly emerged adults feed heavily on foliage in August and September before leaving the plant to seek overwintering sites (Zwölfer, 1965b). Females oviposit on the underside of Canada thistle leaves, usually laying about 12 eggs per day. Under laboratory conditions, eggs hatch in about 11 days, larval development requires about one month, and pupa develop to adults in 10 to 11 days. Larvae feed on the undersurface of leaves, producing "windows" of clear epidermis. Adult feeding damage is evenly dispersed over the whole plant; heavy adult feeding can cause the collapse of plants both in the laboratory and in the field (Karny, 1963).

Cassida rubiginosa Müller (Coleoptera: Chrysomelidae)

This univoltine shield beetle feeds on foliage of several Cardueae species, both as adults and larvae. In Virginia, adults appear in late winter and oviposit, mainly on the underside of thistle leaves, from mid-March to early July. Eggs are laid in oothecae containing about five eggs. Development from egg to adult requires 435 degree-days above a threshold of 10.4°C. New generation adults begin to appear in late spring and can be found on plants up to November. Females produce an average of 815 eggs under laboratory conditions (Ward and Pienkowski, 1978a). In the field, C. rubiginosa is attacked by several larval parasitoids including Tetrastichus rhosaces (Walker) (Hymenoptera: Eulophidae) and Eucelatoriopsis dimmocki (Aldrich) (Diptera: Tachinidae) (Ward and Pienkowski, 1978b). However, Ang and Kok (1995) felt that parasitism did not limit C. rubiginosa populations in Virginia. Tipping (1993) found that adults released on Canada thistle in Maryland remained in close proximity to the release point and that most oothecae were laid within 1.6 m of the release point. Parasitism in this study was 10.5%, with the most common parasitoid being E. dimmocki. Larvae and pupae are heavily predated by larvae of Coccinella septempunctata L. (Coleoptera: Coccinellidae) in Maryland (P. Tipping, pers. comm.). Spring and Kok (1999) found about 21% overwintering survival of adult C. rubiginosa.

Ceutorhynchus litura (F.) (Coleoptera: Curculionidae)

This stem- and root-mining weevil occurs in France, Switzerland, Austria, Germany, Britain, and southern Scandinavia (Zwölfer and Harris, 1966) (Fig. 3). Females oviposit into the mid-veins of rosette leaves of Canada thistle leaves in spring. Eggs are laid in groups of one to five in a cavity made with the rostrum in the underside of a young leaf. Larvae hatch after five to nine days and mine down through the vein into the base of the stem and upper tap root (Fig. 4). There they form a feeding tunnel that may cause the stem to become somewhat inflated into an indistinct gall. Mature larvae leave the stem and pupate in a cocoon of soil particles, from which they emerge in late summer (Zwölfer and Harris, 1966; Peschken and Beecher, 1973). Adults overwinter in the soil or leaf litter.

Cleonis pigra (Scopoli) (Coleoptera: Curculionidae)

Adults of this large weevil emerge from overwintering sites in May and feed on Canada thistle foliage in June and July. The females oviposit into the lower portions of Canada thistle stems. The larvae mine down through the stem base into the root, which develops a spindle-shaped gall around the feeding site. Pupation occurs in the root, and adults emerge in late summer or fall (Anderson, 1956).



Figure 3. *Ceutorhynchus litura* (F.) adult. (Photograph by A. S. McClay.)



Figure 4. *Ceutorhynchus litura* (F.) larva in stem base of Canada thistle.. (Photograph by A. S. McClay.)

Larinus planus (F.) (Coleoptera: Curculionidae)

Adults of this weevil (Fig. 5) feed on Canada thistle foliage, but generally cause little damage. Females oviposit into the unopened flower buds, where larvae feed on the developing achenes and receptacle tissue. Larvae pupate in a cocoon formed of chewed host plant tissue (Fig. 6.). Only one larvae can complete development in each head. Adults emerge in late summer and overwinter in the litter (McClay, 1989).

Puccinia punctiformis Strauss (Röhling) (Uredinales: Pucciniaceae)

This fungus is an autecious brachycyclic rust that produces systemic infections on the spring-emerging shoots of Canada thistle. Systemically infected shoots are pale and die before flowering, but spermogonia and uredosori are formed before plant death. Later in the season, infection of other shoots by uredospores leads to local infection followed by



Figure 5. *Larinus planus* (F.) adult. (Photograph by A. S. McClay.)



Figure 6. *Larinus planus* (F.) larva in seed head of Canada thistle. (Photograph by A. S. McClay.)

the formation of teliospores in autumn (Van Den Ende et al., 1987). Teliospores are responsible for the systemic form of infection (Van Den Ende et al., 1987; French and Lightfield, 1990). Germination of teliospores is stimulated by volatile compounds from germinating Canada thistle seeds and root cuttings (French et al., 1988; French et al., 1994). The germination rate of teliospores is highest in the temperature range of 10°C to 15°C (Frantzen, 1994). Systemic infection may be induced in the laboratory in root buds or seeds inoculated with teliospores (French and Lightfield, 1990; French et al., 1994), but it is not yet clear how root infection from teliospores could take place in the field (French et al., 1994). Systemically infected shoots are taller than uninfected ones but fail to flower and their root biomass is reduced (Thomas et al., 1994). Cumulative mortality of infected shoots in a field study in Maryland was 80% compared with less than 10% for healthy shoots (Tipping, 1993).

Terellia ruficauda (F.) (Diptera: Tephritidae)

Ovipositing females of this fly select female Canada thistle flower heads one day away from blooming. Eggs are laid between immature florets and the larvae feed on developing achenes through a hole drilled in the pericarp. Third instar larvae form cocoons of pappus hairs in which they overwinter; pupation and emergence take place in the spring (Lalonde and Roitberg, 1992).

Urophora cardui (L.) (Diptera: Tephritidae)

This univoltine stem-galling fly oviposits in the axillary buds of Canada thistle (Fig. 7). The eggs hatch in seven to 10 days. Larvae induce development of multi-chambered galls in the form of a swelling in the stem up to 23 mm in diameter (Lalonde and Shorthouse, 1985) (Fig. 8). Pupation and overwintering occur in the gall, from which adults emerge in early summer. Larvae in the galls are preyed on by birds, ants, and an unidentified mite (Acari: Pyemotidae) in Maryland (P. Tipping, pers. comm.).



Figure 7. *Urophora cardui* (L.) adult. (Photograph by A. S. McClay.)



Figure 8. *Urophora cardui* (L.) galls on stem of Canada thistle. (Photograph by A. S. McClay.)

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

There is no evidence that A. carduorum has become established in the United States. Peschken (1977b) attributed the failure of this species to establish in Canada to predation. Ceutorhynchus litura is reported to be established in Maryland, North Dakota, South Dakota, and Virginia (Julien and Griffiths, 1998; P. Tipping, pers. comm.). Urophora cardui is reported to be established in Maryland and Virginia (Julien and Griffiths, 1998), although the species is probably not currently established in Maryland (P. Tipping, pers. comm.). Galls of *U. cardui* were found at all Virginia field sites visited in 1986 but at only two sites in 1987; however, numbers of galls had increased at these two sites in 1987 (Kok, 1990). No recoveries are recorded in Virginia since 1987. Urophora cardui is common along the Hudson River and in other areas in New York state (B. Blossey, pers. comm.). Its establishment status in Iowa is unknown. C. rubiginosa became established in southwestern Virginia and has persisted there for more than 20 years (Ang and Kok, 1995).

Suppression of Target Weed

There has been little work done to evaluate the effectiveness of biological control agents for Canada thistle in the eastern United States. Using Canada thistle root cuttings transplanted to caged field plots, Ang *et al.* (1995) showed that feeding by *C. rubiginosa* significantly reduced biomass and survival of Canada thistle. The effects of *C. rubiginosa* were stronger than those of plant competition from tall fescue (*Festuca arundinacea* Schreb.) and crownvetch (*Coronilla varia* L.). Similar results were obtained by Bacher and Schwab (2000) in Switzerland.

Forsyth and Watson (1986) evaluated the stress inflicted on Canada thistle by four insect species and one pathogen in Québec, Canada. The seed head predator *O. ruficauda* reduced seed production by about 22%. Root mining by *C. pigra* sometimes killed plants. Main shoot galling by *U. cardui* reduced plant height and number of flowers, but side-shoot galling had less impact. Reports of the impact of *C. litura* have been varied. Based on field sampling, Rees (1990) suggested that this species had a significant impact on survival of Canada thistle in Montana. Peschken and Derby (1992), however, found in controlled experiments that combined attack by this species and *U. cardui* had no significant effect on most performance parameters of Canada thistle. The impact of biological control of Canada thistle in terms of economic benefits or recovery of native plant communities has not been evaluated.

RECOMMENDATIONS FOR FUTURE WORK

Future Needs for Importation or Evaluation

The impact of currently established agents needs to be evaluated by controlled experimental methods, preferably using naturally-occurring densities of agents in field weed stands (McClay, 1995). The extent of non-target damage from the currently established agents also need to be further assessed. Such damage has been shown repeatedly for the seed weevil R. conicus, released as a biocontrol agent for Carduus and Silybum species (Rees, 1977; Louda, 1999; Herr, 2000). As with R. conicus, most of the agents released against Canada thistle have laboratory host ranges that include many native Cirsium species, but it is not known whether any of these native species are in fact being damaged, or are at risk of damage, in the field. Information on this would provide a valuable test of the reliability of laboratory host-range tests in predicting non-target utilization in the field.

The European range of Canada thistle has been extensively explored for potential biocontrol agents, and it seems unlikely that there are promising agents yet undiscovered in this region. Further exploration in Central Asia and China may identify other possible candidate agents, and such exploration is planned (A. Gassmann, pers. comm.).

Other Comments

Canada thistle may be a difficult target for biological control for two reasons. Firstly, it is a significant agricultural weed in its native range in Europe (Schroeder *et al.*, 1993), suggesting that its natural enemies there are not very effective in limiting its population density, at least under agricultural conditions. There has been little study of the impact of herbivory on natural populations of Canada thistle in Europe; however, Edwards *et al.* (2000) found that exclusion of insects with chemical pesticides had no effect on recruitment or density of Canada thistle in cultivated soil or grassland in southern England. Secondly, Canada thistle is congeneric with a large number of native North American Cirsium species, raising concerns about non-target damage to native species by introduced biological control agents (Louda, 1999; Louda and O'Brien, 2002). Although some phytophagous insects associated with Canada thistle, such as U. cardui, appear to be virtually monophagous, others have a broad host range within the genus Cirsium and also will accept species of Carduus or related genera. In the past, several agents have been approved for release against Canada thistle on the basis of host specificity tests that would not be considered sufficient justification for release today.

Future progress in classical biological control of Canada thistle will depend on the identification of new, adequately host specific herbivores from its native range, and will require improvements in hosttesting procedures to allow better prediction and evaluation of non-target impacts.

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18 MUSK THISTLE (NODDING THISTLE)

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PEST STATUS OF WEED

Musk thistle, *Carduus nutans* L., is an invasive weed that has become widespread in the contiguous states of the United States. It is a highly competitive weed of Eurasian origin that has replaced much of the native vegetation in pastures and disturbed areas (Surles et al., 1974; Kok, 1978a,b).

Nature of Damage

Economic damage. Musk thistle invades pastures, rangeland, and forest lands, and areas along roadsides, railroad right-of-ways, waste areas, and stream banks. In agricultural systems, the invasive nature and prolific seed production of musk thistle result in large populations of the weed, which compete with crops for space, nutrients, and light. Thus, infestations may reduce productivity of pasture and rangeland by suppressing growth of desirable forage plants, as well as preventing livestock from eating plants growing in the vicinity of thistles due to the sharp spines on their stems, leaf margins and blooms (Trumble and Kok, 1982; Desrochers et al., 1988a). In the northeastern United States, the highest economic losses due to musk thistle infestations occur on fertile soils formed over limestone.

Ecological damage. Musk thistle generally does not pose a great threat to high-quality natural areas, although it has been known to invade native and restored grasslands despite the presence of dense, native prairie vegetation. Musk thistle may retard natural secondary succession processes. Because musk thistle is unpalatable to wildlife and livestock, selective grazing leads to severe degradation of native meadows and grasslands as grazing animals focus their foraging on other plants, giving musk thistle a competitive advantage. Successful biological control of musk thistle (Kok and Surles, 1975) is often accompanied by increased growth and coverage of pasture grasses such as fescue (*Festuca arundinaria* Schreb.) and orchard grass (*Dactylis glomerata* L.), or less desirable plants such as spotted knapweed (Kok and Mays, 1991).

Extent of losses. The rate of expansion of musk thistle populations in North America has been very rapid since the mid-1950s, when it was first recognized as a weed (Dunn, 1976). A single musk thistle per 1.49 m² can reduce pasture yields by 23%. In Canada, stands of 150,000/ha have been observed (Desrochers *et al.*, 1988a). Direct losses are difficult to quantify due to lack of long-term monitoring programs and data.

Geographical Distribution

Musk thistle was first reported in the United States in 1953 at Harrisburg, Pennsylvania (Stuckey and Forsyth, 1971). In the 1970s, the musk thistle complex (see Taxonomy for definition) has been found in at least 3,068 counties in 42 of the mainland states, with 12% of those counties rating their infestations as economically severe (Dunn, 1976). Musk thistle is declared a noxious weed in some 20 states, including Illinois, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, Nebraska, North Carolina, Ohio, Oklahoma, and Pennsylvania (USDA, NRCS, 1999). Thus, musk thistle extends from the east to west coast in both the deciduous forest and prairie biomes. It grows from sea level to about 2,500 m elevation. It prefers moist alluvial soils but will grow in eroded uplands without difficulty.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The C. nutans complex in North America has been treated either as one species with four subspecies (subsp. nutans, subsp. leiophyllus [Petrovic] Stoj. and Stef., subsp. macrolepis [Peterm.] Kazmi, and subsp. macrocephalus [Desf.] Nyman), or as three species: Carduus nutans with two subspecies (subsp. nutans and subsp. macrolepis), C. thoermeri Weinm., and C. macrocephalus Desf. (McCarty, 1978; Desrocher et al., 1988b). Recent work by Desrochers et al. (1988b) has supported the existence, in Canada, of only two closely related groups of taxa referred to as subsp. nutans and subsp. leiophyllus. Carduus thoermeri Weinm. and C. nutans subsp. leiophyllus refer to the same taxon. In North America, C. nutans ssp. macrocephalus has only been collected from the United States. Carduus nutans ssp. nutans is distinguished from ssp. leiophyllus by its moderate to dense pubescence on leaves and phyllaries, by its generally smaller head diameter (1.5 to 3.5 cm in subsp. nutans and 1.8 to 4.5 cm in subsp. leiophyllus) and by the shape of its phyllary. In subsp. nutans, the lower portion of the phyllary is more or less equal to the upper portion, while in subsp. Leiophyllus, the lower portion is distinctly narrower than the upper portion. The two subspecies also can be separated by their flavonoid compounds. Carduus nutans subsp. macrocephalus differs from subsp. nutans by a wider head diameter and phyllaries. It also differs from subsp. leiophyllus by being pubescent on leaves and phyllaries, and by having phyllaries that have the lower portion more or less equal to the upper portion. Hybridization between C. nutans and Carduus acanthoides L. also has been reported (Warwick et al., 1990). Presumably, the distribution of subsp. nutans in the United States is similar to its distribution in Canada, where it is mainly distributed in the eastern part of the country, while only subsp. leiophyllus and subsp. macrocephalus are present in the Great Plains (McGregor, 1986).

Biology

The biology of musk thistle has been reviewed by Desrochers *et al.* (1988a). *Carduus nutans* L. is a herbaceous biennial though occasionally it becomes a



Figure 1. Musk thistle rosette. (Photograph by L.-T. Kok.)



Figure 2. Musk thistle in bloom. (Photograph by L.-T. Kok.)

winter annual. It is 20 to 200 cm tall, with a long, fleshy taproot. The taproot is large, corky, and hollow near the surface of the ground. One or more highly branched stems grow from a common rootcrown. Musk thistle grows in all soil textures, although the soils must be well drained. Leaves are dark green with light green midribs with a white margin (Fig. 1). The plant blooms in May and June. The showy flowers (Fig. 2) are terminal, large, solitary, and nodding (slightly bent). They are deep rose to violet or purple in color. The seeds are straw colored and do not have a light requirement for germination, but are affected by temperature. Higher germination rates occur at temperatures between 20 and of vernalization, a minimum of 40 days below 10 °C for flowering. It does not reproduce vegetatively and is propagated by seeds dispersed primarily by wind. Most seeds are deposited within 50 m of the release point and less than 1% are blown farther than 100 m (Smith and Kok, 1984). Up to 11,000 achenes may be produced per individual with as many as 1,500 seeds per flower head. Seed viability remains high for more than ten years.

Analysis of Related Native Plants in the Eastern United States

There are no native North American species in the genus Carduus. Carduus nutans belongs to the tribe Cardueae (family Asteraceae) which is largely an Old World group. The tribe is further divided into four subtribes (Echinopsidinae, Carlininae, Carduinae, and Centaureinae) including some 13 genera in North America (Bremer, 1994; USDA, NRCS, 1999). From these, only three contain native species - Centaurea (two species, subtribe Centaureinae), Saussurea (seven species, subtribe Carduinae, but the position of the genus in the tribe remains uncertain), and Cirsium (subtribe Carduinae). The genus Cirsium includes about 100 native species, of which 21 species occur in the eastern United States. One of these, Cirsium pitcheri (Torr. ex Eat.) Torr. and Gray, is listed as threatened under the Endangered Species Act. This species occurs in sand dunes along the shores of the Great Lakes in Illinois, Indiana, Michigan, Wisconsin, and Ontario.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Musk thistle was among the first 19 weeds selected for biological control when the USDA overseas laboratory was established at Rome, Italy in 1959. In the early 1960s, staff of the USDA intensively surveyed *Carduus* spp. in Italy, whereas the Commonwealth Institute of Biological Control (now CABI Bioscience), funded by Canada Department of Agriculture, extended the survey area across Europe from western France to eastern Austria on more than 30 species in the subtribe Carduinae. The history of biological control of thistles was reviewed by Dunn (1978) and by Schroeder (1980).

Area of Origin of Weed

The genus *Carduus* is native to the Eastern Hemisphere, where its distribution extends over Europe, central Asia, and East Africa. Franco (1976) recognized 48 species in *Flora Europaea*. Several taxa have been reported in North America and separated into three groups: the slender-flowered thistles (*Carduus tenuiflorus* Curt. and *Carduus pycnocephalus* L.), the small-flowered thistles (*Carduus acanthoides* L. and *Carduus crispus* L.), and the large-flowered thistle (*Carduus nutans s.l.*). Southern Europe is considered to be the center of origin for *Carduus* because of the many endemic *Carduus* species found there.

Areas Surveyed for Natural Enemies

Areas surveyed included southern England, France, Austria, Germany, Italy and the northern part of the former Yugoslavia (Zwölfer, 1965; Boldt and Campobasso, 1978). Other surveys have been carried out in Pakistan, Iran, and Japan (Schroeder, 1980).

Natural Enemies Found

Some 130 insect species have been recorded on C. nutans s.l. in Europe (Zwölfer, 1965; Boldt and Campobasso, 1978). In Italy alone, 109 species from six orders and 33 families fed or reproduced on musk thistle. Some 25 species were reported to be broadly oligophagous on plants in the subtribe Carduinae (Table 1), and only very few were considered to have a host range restricted to plants in the genera Carduus, Cirsium, and Silybum, or to be monophagous. Since there was no concern about non-target impact on native thistles in the earliest phase of the program, oligophagy on several thistle species in the genera Carduus, Cirsium, and Silybum was considered as an advantage and only those species recorded as economic pests were eliminated from further consideration. After a few other candidate biological control agents had been discarded on the grounds that they did little damage to the target weeds, fewer than 10 species were considered as potential biological control agents of Carduus species and bull thistle, Cirsium vulgare (Savi) Tenore. Preference was given to seed

 Table 1. Oligophagous Arthropods (Restricted to Carduinae) Recorded on Selected European Thistles (With Contributions from A. McClay)

Insect Species	Carduus nutans s.l.	Carduus acanthoides	Carduus tenuiflorus/ pycnocephal- us	Cirsium vulgare	Cirsium arvense	Food Niche
DIPTERA						
Agromyzidae						
Agromyza n.sp.nr. reptans	b					Leaf miner
Liriomyza soror Hendel					а	Leaf miner
<i>Melanagromyz</i> a <i>aeneoventris</i> (Fallen)	d	d		d	d	Stem
Phytomyza cardui Hering				а		Leaf miner
Anthomyiidae						
Pegomya nigricornis (Strobl)			С			Stem?
Cecidomyiidae						
Clinodiplosis cirsii Kieffer					а	Flower head
<i>Jaapiella cirsiicola</i> Rübsammen				а	а	Flower head
<i>Macrolabis cirsii</i> Rübsammen					а	Flower head
Syrphidae						
<i>Cheilosia albipila</i> (Meigen)	d	d		d	d	Root collar
C. corydon (Harris)	b released		c released			Root collar
C. cynocephala Loew	b					Root collar
Tephritidae						
Orellia winthemi Meigen		а				Flower head
Tephritis hyoscyami L.	а	а				Flower head
T. cometa (Loew)					а	Flower head
Terellia serratulae L.	a b (1)	а	a c	а		Flower head
T. ruficauda Fabricius					a (2)	Flower head
Urophora cardui (L.)					a d released	Stem gall
<i>U. sibynata</i> Rondani	b					Flower head
U. solstitialis (L.)	a b released	a released	С			Flower head
<i>U. stylata</i> Fabricius	b	а		a released	а	Flower head
<i>Xyphosia miliaria</i> Schrank	a b			а	а	Flower head

Insect Species	Carduus nutans s.l.	Carduus acanthoides	Carduus tenuiflorus /pycnocephal- us	Cirsium vulgare	Cirsium arvense	Food Niche
COLEOPTERA						
Apionidae						
Apion carduorum Kirby	a b	а	а	а	а	Root collar/stem
A. gibbirostre Gyllenhal	d	d			d	Root collar/stem
A. onopordi Kirby	d			d	d	Root collar/stem
Curculionidae						
Ceuthorhynchidius horridus (Panzer)	a released	a released	С		а	Root collar/stem?
C. urens Gyllenhal					а	Root collar/stem?
<i>Ceutorhynchus litura</i> Fabricius					a d released	Root collar/stem
C. trimaculatus Fabricius	a b (1)		a c	d		Root collar/leat buds
Cleonus piger Scopoli	а	а		а	a (2)	Root collar/ stem
Larinus cynarae Fabricius	b					Flower head
L. jaceae Fabricius	а	а	С			Flower head
<i>L. planu</i> s (Fabricius)	а	а	а	а	a (2)	Flower head
<i>L. turbinatus</i> Gyllenhal				а	а	Flower head
<i>Lixus cardui</i> Olivier	a b	а	a c		а	Stem
L. elongatus Goeze	a b d	a d	a c	a d	а	Stem
Rhinocyllus conicus Frölich	a b released	a released	a c released	а	а	Flower head
Cerambycidae						
Agapanthia dahli Richter		d				Stem
Chrysomelidae						
<i>Altica carduorum</i> Guérin- Méneville					a released	Leaf
A. cirsii Israelsen					а	Leaf
Cassida deflorata Suffrian			a c		а	Leaf
<i>C. rubiginosa</i> Müller	a b		а	а	a (2)	Leaf
Lema cyanella (L.).					a (1)	Leaf
Psylliodes chalcomera (Illiger)	b released		С			Leaf buds/leaf
Sphaeroderma testaceum Fabricius	a b			а	а	Leaf

Table 1. Oligophagous Arthropods (continued)

Table 1. Oligophagous Arthropods (continued)

Insect Species	Carduus nutans s.l.	Carduus acanthoides	Carduus tenuiflorus /pycnocephal- us	Cirsium vulgare	Cirsium arvense	Food Niche
LEPIDOPTERA						
Cochylidae						
Aethes badiana Hübner				а		Root/stem?
A. cnicana Westwood				а		Root/stem?
Lobesia fuligana Haworth					а	Stem
Noctuidae						
Gortyna flavago Den. & Schiff.		d				Root
<i>Porphyrinia purpurina</i> Den. & Schiff.	b			а	а	Root crown/stem
Olethreutidae						
<i>Epiblema pflugiana</i> (Haworth)	b					Root crown/leaf
Pyralidae						
<i>Myelois cribrumella</i> (Hübner)	d	а		d		Stem/flower head
Sesiidae						
Euhagena palariformis (Lederer)					f	Root
HETEROPTERA						
Lygaeidae						
<i>Tingis ampliat</i> a Herrich- Schäffer				а	а	Leaf
T. cardui L.	a b	а	а	а	а	Leaf

Insect Species	Carduus nutans s.l.	Carduus acanthoides	Carduus tenuiflorus /pycnocephal- us	Cirsium vulgare	Cirsium arvense	Food Niche
HOMOPTERA						
Aphididae						
Aphis acanthi Schrank					а	?
Brachycaudus cardui (L.)	b g			g	g (2)	Leaf/stem/ root
Capitophorus braggi Gyllenhal					a (2)	Leaf/stem
<i>C. carduinus</i> Walker	a g (2)	а		a g	g (2)	Leaf/stem
<i>C. flaveolus</i> Walker		а			а	?
Chomaphis cirsii Börner					а	?
Dactynotus aeneus HRL.	a g	а			g	Leaf/stem
<i>D. cirsi</i> i HRL					a g (2)	Leaf/stem
Psyllidae						
Trioza agrophila Loew					а	?
ACARINA						
Eriophyidae						
<i>Aceria anthocoptes</i> (Nalepa)					e (2)	Flower/leaf
a = from Zwölfer (1965) ar s-Germany, Austria, n b = from Boldt and Campo c = from Goeden (1974) ar d = from Freese (1993). Su e = from Petanovic <i>et al.</i> 19	oorthern forme obasso (1978). 1d Dunn (1978 rvey area: Gen	r Yugoslavia, 'n Survey area: Ita). Survey area: I many	-Italy ly	ngland, France	,	

Table 1. Oligophagous Arthropods (continued)

e = from Petanovic et al. 1997. Survey area: Yugoslavia

f = from Tosevski (pers. com). Survey area: Turquey

g = from Redfern (1983). Survey area: western Europe

(1) studied but not released in the United States

(2) accidental introduction in the United States (from Maw, 1976; Story et al., 1985; Julien and Griffiths, 1999 ; http://www.sel.barc.usda.gov/acari/content/eriophyoidea.html)

feeding insects for biological control of *Carduus* spp. and bull thistle because these weeds are short-lived species and reproduce by seeds. In contrast, defoliating beetles were selected for the perennial thistle *Cirsium arvense* (L.) Scop. (see Chapter on Canada thistle).

In 1964, the seed-feeding weevil Rhinocyllus conicus (Frölich) was the first insect selected for biological control of Carduus species. Zwölfer (1971) believed that because of R. conicus' high egg potential and a tendency to disperse its eggs, this weevil should exert strong pressure on its host plant, especially after the weevil was released from limitation by its coevolved competitors and parasitoids. Shortly after biological studies had started with R. conicus, the rosette weevil Trichosirocalus horridus (Panzer) and the two rosette beetles Ceutorhynchus trimaculatus (F.) and Psylliodes chalcomera (Illiger) also were considered because they occupy different food niches and have different phenologies. Concern about non-target impact was increasing and, in the early 1980s, permission for field release of C. trimaculatus and P. chalcomera was denied. Consequently, more specific species were selected to complement the impact of R. conicus and T. horridus. The syrphid root-crown fly Cheilosia corydon (Harris) has the same feeding niche as *T. horridus* but it has a different phenology. The seed-feeding tephritid fly Urophora solstitialis (L.) was selected for biological control of C. acanthoides because R. conicus was not well synchronized with this thistle in many parts of North America (Surles and Kok, 1977). Later, Dunn and Campobasso (1993) showed that native North American Cirsium species were not exploited by P. chalcomera under field test conditions, and this flea beetle was finally released in the United States in 1997. Thistle insects discovered in Asia have not been exploited yet. The host specificity of Terrelia serratulae L., a trypetid fly from Pakistan, has been examined (Baloch and Khan, 1973), but it has not been considered further.

Host Range Tests and Results

Rhinocyllus conicus (Frölich). Field host records for the seed-feeding weevil *R. conicus* in Europe include thistles in several genera in the subtribe Carduinae (*Carduus*, *Cirsium*, *Sylibum*, and *Onopordum*)(Zwölfer and Harris, 1984). The plant species tested in the screening trials in the 1960s included primarily agricultural crops and horticultural

species in the Asteraceae family, plus a few European thistles. Since the cultivated plants tested (Cynara scolymus L., Carthamus tinctorius L., Helianthus annuus L., Lactuca sativa L.) were not used by the weevil, and the potential use of native North American Cirsium species was not a concern at that time, R. conicus was approved and released in Canada (in 1968) and in the United States (in 1969). Feeding by R. conicus on native Cirsium species in North America was first reported by Laing and Heels (1978) and Rees (1978). Rhinocyllus conicus has been reported in flowerheads of nearly 20 native Cirsium spp. in the west and in the central plains and mountains (Louda, 2000). Genetic variation among populations of R. conicus does exist, but its role in host plant use is not well understood. The concept of host races associated with the main thistle species in Europe (Zwölfer and Preiss, 1983) has been challenged recently (Klein and Seitz, 1994; Briese, 1996).

Trichosirocalus horridus (Panzer). Field records of the rosette weevil *T. horridus* in Europe include a few genera in the subtribe Carduinae (*Carduus*, *Cirsium*, *Onopordum*, and *Galactites*). Host range studies were carried out in the late 1960s and early 1970s (Ward *et al.*, 1974; Kok, 1975). As for *R. conicus*, the plant species tested included cultivated plants and a few European thistles. Some larval feeding occurred on lettuce (*L. sativa*), cauliflower (*Brassica oleracea* L.) and artichoke (*C. scolymus*), but none of these species supported normal larval development. Preferred hosts were species of *Carduus*, *Cirsium*, and *Onopordum*. *Trichosirocalus horridus* has only occasionally been reported to feed and develop on native North American thistles (McAvoy *et al.*, 1987).

Cheilosia corydon (Harris). In Europe, the rootcrown fly C. corydon has been reared from Carduus nutans s.l., Carduus crispus L., and Carduus pycnocephalus L., and rarely from Cirsium vulgare, Cirsium eriophorum (L.) Scop., and Cirsium palustre (L.) Scop. In laboratory tests, larvae survived on all six Carduus species tested as well as on the native North American species, Cirsium crassicaule (Greene) Jeps. None of the other nine Cirsium species (including six native North American species) were suitable for C. corydon development. In field trials in Italy, oviposition was recorded on Carduus nutans but not on the seven native Cirsium species tested (Rizza et al., 1988).

Ceutorhynchus trimaculatus (Fab.). Field records of this thistle-rosette weevil in Europe include

Carduus spp., *Cirsium* spp., *Onopordum* spp., *Silybum marianum* (L.) Gaertn., and *Galactites tomentosa* Moench (Boldt *et al.*, 1980). *Ceutorhynchus trimaculatus* was found to complete development on artichoke (*C. scolymus*) and several *Cirsium* species in quarantine screening tests (Kok *et al.*, 1979, 1982; Kok and McAvoy, 1983). In field tests carried out in Italy in 1984 and 1985, larvae of *C. trimaculatus* were found on all three North American native *Cirsium* spp. exposed, but not on artichoke (Dunn and Campobasso, 1993).

Psylliodes chalcomera (Illiger). Under experimental conditions, adult feeding, oviposition, and larval development by this thistle-rosette weevil occurred on European *Carduus* and *Cirsium* species (Dunn and Rizza, 1977). Adult feeding and oviposition, but no larval development, were recorded on artichoke under no-choice conditions. In field tests carried out in Italy between 1987 and 1989, this flea beetle did not use any of the three North American *Cirsium* species offered (Dunn and Campobasso, 1993).

Puccinia carduorum Jacky. This rust has been accidentally introduced to North America and also was the first plant pathogen tested and released in the United States for biological control of musk thistle. In greenhouse tests, limited infection occurred on some species of Cirsium, Cynara, Saussurea, and Sylibum, but older plants were resistant. Attempts to maintain P. carduorum on 22 native North American species of Cirsium and C. scolymus failed. Musk thistle was the only host that became severely diseased (Politis et al., 1984; Bruckart et al., 1996). No rust development was observed on any of the nontarget plants (10 North American Cirsium spp. and artichoke) in a field trial carried out in 1988 in Virginia (Baudoin et al., 1993). Puccinia carduorum has not been reported from native North American Cirsium species. It has spread rapidly in the eastern United States and was found in Missouri in 1994 (Baudoin and Bruckart, 1996). It can be transmitted by the thistle insects R. conicus, T. horridus, and Cassida rubiginosa Müller (Kok and Abad, 1994).

Releases Made

Information in this section is from Rees *et al.*, 1996; Julien and Griffiths, 1999; and shipment records of L. T. Kok.

Rhinocyllus conicus. Introductions of *R. conicus* from eastern France via Canada began in 1969 in the

United States with releases in Virginia, California, Montana, and Nebraska. Following excellent results in Virginia, weevils were collected in Virginia and released in most of the thistle-infested 48 contiguous states. These included Alabama, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, Tennessee, Texas, West Virginia, and more recently in the southern states of Alabama, Georgia, and North Carolina.

Trichosirocalus borridus. This species was first released in Virginia in 1974 (Kok and Trumble, 1979). Weevils collected from Virginia were subsequently released in many other states, including Alabama, Colorado, Georgia, Illinois, Indiana, Kansas, Kentucky, Maryland, Montana, North Carolina, Oklahoma, Tennessee, Texas, Washington, Wyoming, several western states, and also in Argentina and Canada.

Cheilosia corydon. This fly has been released in low numbers in Maryland, New Jersey, Montana, Nevada, Oregon, and Texas.

Urophora solstitialis. This species was released in 1996, only in Montana.

Ceutorbynchus trimaculatus: This species was not released because it feeds and develops on native *Cirsium* species (Kok *et al.*, 1979, 1982; Kok and McAvoy, 1983).

Psylliodes chalcomera. This species was released in 1997, in Kansas and Texas (DeQuattro, 1997).

Puccinia carduorum. This pathogen was deliberately introduced in Virginia in 1987 (Baudoin *et al.*, 1993), but had been accidentally introduced to North America before 1987 (Julien and Griffiths, 1999).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Rhinocyllus conicus (Coleoptera: Curculionidae).

The biology of this seed-feeding weevil has been described by Zwölfer and Harris (1984). Following adult emergence from overwintering sites in litter and sheltered areas, mating and oviposition occur in spring and early summer. In Virginia, overwintered adult weevils (Fig. 3) were observed to become active in mid-to-late April (Surles and Kok, 1977). Eggs are laid externally on bud bracts (Fig. 4), either individually or in small clusters of two to five eggs. Caps



Figure 3. *Rhinocyllus conicus* adult. (Photograph by L.-T. Kok.)



Figure 5. *Rhinocyllus conicus* larva feeding on receptacle of thistle head. (Photograph by L.-T. Kok.)



Figure 7. *Rhinocyllus conicus* pupa. (Photograph by L.-T. Kok.)

of masticated host plant material, which appear as "warts," cover and protect the eggs from predation. Larvae hatch after six to nine days and bore through the bracts into the receptacle. Larvae feed on both the developing receptacles (Fig. 5) and the florets, pushing out characteristic tufts of hair from an in-



Figure 4. *Rhinocyllus conicus* eggs on thistle head. (Photograph by L.-T. Kok.)



Figure 6. Tufts of hair arising from *R. conicus* infested thistle head. (Photograph by L.-T. Kok.)



Figure 8. Thistle head showing pupation chambers of *R. conicus.* (Photograph by L.-T. Kok.)

fested head (Fig. 6), and sometimes the supporting peduncle under the head. Four larval instars complete development in about four to six weeks (Rowe and Kok, 1985). Larval feeding induces the formation of a gall-like callus of modified parenchyma tissue that provides the larvae with additional food and shelter (Shorthouse and Lalonde, 1984). Larval survivorship is strongly density-dependent, suggesting intraspecific competition causes much of the observed larval mortality (> 80%) within heavily infested inflorescences (Zwölfer, 1979). In North America, R. conicus has acquired a large number of parasitoids, but levels of parasitism are low (Rees, 1977; Goeden and Ricker, 1977, 1978; Puttler et al., 1978; Dowd and Kok, 1981, 1982, 1983; Smith and Kok, 1983). The pupal period is seven to 10 days, and pupae (Fig. 7) usually are found from mid-June through July. A partial second generation may be found in late August and September. Adults usually remain within pupation cells (Fig. 8) for several more weeks, before emerging to disperse to overwintering sites in litter. Phenology and life-cycle details vary geographically according to local climate. Zwölfer and Harris (1984) indicated that a partial second generation could occur for individuals that complete development early, if the photoperiod exceeds 16 hours.

Trichosirocalus horridus (Coleoptera: Curculionidae).

This rosette weevil has a single generation per year. Eggs are laid on the lower side of leaves along the midrib and the primary veins and hatch in about 13 days. Larvae migrate down the petiole to rosette crowns to feed soon after hatching. Mature larvae abandon the plant and enter the soil near the roots where they create pupation cells, made from silk and soil particles (Kok et al., 1975). In Virginia, oviposition occurs from mid-December until early April, and larvae are found in rosettes from late December (first instars) through late May (third instars) (Trumble and Kok, 1979). Trichosirocalus horridus may overwinter as an adult, egg, or larva (Kok and Mays, 1989). Teneral adults appear from mid-May through June and aestivate in July through September. This life cycle is similar to that of T. horridus in southern Europe, although the climatic conditions in southwestern Virginia resemble conditions of central Europe, where the life history of *T. horridus* is substantially different. In central Europe, oviposition of T. horridus occurs from the middle of May through June. Pupation occurs in July and August, and adults emerge in September and overwinter.

Cheilosia corydon (Diptera: Syrphidae)

In southern Europe, adults of this root-crown fly emerge at the end of February or March, and eggs are laid from mid-March to mid-April. Larvae feed in thistle crowns and large flower-bearing stems. Eggs are laid on young leaves in the center of the thistle rosette and young shoots. Newly hatched larvae mine directly into tender, young shoots. As shoots grow, the second and third instars mine up and down the stems. There are three larval instars. In May, larvae tunnel into the shoot base and the root. Pupation occurs in November (Rizza *et al.*, 1988). *Cheilosia corydon* has one generation per year.

Ceutorhynchus trimaculatus (Coleoptera: Curculionidae)

This rosette weevil has one generation per year. Adults emerge at the end of April and feed on the leaves of new rosettes or mature plants for three to four weeks. At the end of May, weevils enter the soil to aestivate. Adults gradually become active again in autumn and feed on the leaves of young rosettes. Oviposition starts in November and continues through March or April. Larvae feed gregariously, boring into leaf buds or growing tips, and moving down into the crown. Pupation occurs in the soil (Boldt and Campobasso, 1981; Kok and McAvoy, 1983).

Psylliodes chalcomera (Coleoptera: Chrysomelidae)

In southern Europe, adults of this thistle-rosette flea beetle emerge in early June, feed heavily on maturing *Carduus* plants, and begin aestivation during late June. Aestivation ends in early November. Oviposition takes place between January and June. Eggs are laid at the base of plants or into soil adjacent to plants. Larvae feed on leaf buds and on young rosette leaves. Larvae mature in mid-May, and pupate in the soil nearby. In the laboratory, some females are long-lived and go through two aestivation and two oviposition periods (Dunn and Rizza, 1976).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents (from Julien and Griffiths, 1999)

Rhinocyllus conicus. Establishment of this seed-feeding weevil has been confirmed in Iowa, Illinois, Kansas, Kentucky, Maryland, Minnesota, Missouri, North Dakota, South Dakota, Pennsylvania, Tennessee, Texas, New York, and Virginia as well as in several western states. In recent years, it also has become established in the southern states of Georgia (Buntin *et al.*, 1993) and North Carolina (McDonald and Robbins, 1993). In Virginia, dispersal was only 1.6 km three years after release, but after six years, both eggs and adults were detected 32 km from the original release site (Kok and Surles, 1975).

Trichosirocalus horridus. Establishment of the rosette weevil was confirmed within two years of its release in Virginia study sites, and weevil populations had reached high levels by the third year. The weevil was found 27 km from release sites four years after initial introduction. By 1981, T. horridus was well established in the immediate release area and covered approximately 609 km². By 1985, the weevil had extended its range to 4,345 km² despite having had to move across forested areas where no thistles occur as well as areas with low thistle populations. Dispersal by flight probably occurs after aestivation during late summer or early fall (McAvoy et al., 1987). Trichosirocalus horridus also is established in North Carolina (McDonald and Robbins, 1993), Kansas, Maryland, Missouri, and several western states.

Cheilosia corydon. Establishment has not been confirmed.

Urophora solstitialis. Establishment has not been confirmed.

Psylliodes chalcomera. Establishment has not been confirmed.

Puccinia carduorum. This species is established in Virginia and Missouri (Baudoin *et al.*, 1993; Baudoin and Bruckart, 1996) and was recorded in Wyoming in 1996.

Suppression of Target Weed

Rbinocyllus conicus. Effects of the weevil on *C. nutans* in Virginia were not apparent until 1973, after a steady increase in weevil densities. By 1974, 16 out of 20 releases resulted in successful establishment, and six showed more than 75% reduction in thistle density (Surles *et al.*, 1974; Kok 1978a, b). Establishment rates were better for spring releases of reproductive adults than summer releases (Kok, 1974). At one location, 90% of the plants were heavily infested, and in 1975 all but one of the 11 plots showed at least 90% reduction in thistle density (Kok and Surles, 1975; Kok and Pienkowski, 1985). Biological control is usually achieved in five to six years (Kok and Surles, 1975; Kok, 1986; Kok and Mays, 1991) [Figs. 9, 10]. Decrease in thistle density was slower at sites



Figure 9. Musk thistle site before *R. conicus* release. (Photograph by L.-T. Kok)



Figure 10. Musk thistle site five years after *R*. *conicus* release. (Photograph by L.-T. Kok)

with little competing vegetation. Grass competition was found to be important in restricting thistle growth and keeping weed population levels low. Control by *R. conicus* is enhanced when combined with proper land management, especially prevention of overgrazing.

Trichosirocalus horridus. Damage results from larval feeding on meristematic tissues in the rosette, resulting in crown tissue necrosis. Cartwright and Kok (1985) found that C. nutans changed its growth pattern in response to feeding by T. horridus. Infested plants produced more stems and a larger crown than uninfested plants, which did not produce multiple stems in this study. Large thistles were stimulated by weevil damage to produce larger stems and more capitula, but small and medium thistles were shorter and produced fewer seeds and capitula than uninfested thistles. Response of thistles also is influenced by larval density (Sieburth et al., 1983). In Virginia, a 96% reduction of musk thistle density occurred at two of three study sites within six years of initial releases (Kok, 1986). The collapse of thistle populations after three years of heavy weevil attack was not unusual, as pasture plants re-established and reduced thistle recruitment. The extent of thistle reduction caused by *T. horridus* varies. If weevil populations are large and grass competition is strong, thistle densities can be reduced dramatically. Suppression of musk thistle growth is greatest when the two weevils (*R. conicus* and *T. horridus*) act in conjunction with plant competition. Tall fescue grass (*Festuca arundinacea* Schreb.) together with thistle weevils suppressed musk thistle growth more quickly than the use of thistle weevils alone (Kok *et al.*,1986).

RECOMMENDATIONS FOR FUTURE WORK

The musk thistle program has been reassessed recently (Nechols, 2000). For a long time, the debate has focused on the effect of the biological control agents on the population level of the target thistle and the degree of their non-target feeding. Of the five insects approved for release, two have established with certainty - the seed head weevil, R. conicus, and the rosette weevil, T. horridus. Long-term impact studies conducted in Virginia (Kok, 1986; Kok and Mays, 1991) suggest that the two weevils are capable of exerting some control of C. nutans, although experimental data are generally lacking from most of the other states. Thus, long-term experiments are needed in which post-dispersal seed mortality, various levels of plant competition, and the impact of both weevils (alone and combined) are considered.

Both the seed head and the rosette weevils have relatively broad host ranges. In addition to various exotic thistles, R. conicus feeds and develops in nearly 20 native North American Cirsium species, and in some cases, heavy infestations cause significant reduction in seed (Louda, 2000). There is considerable controversy over whether or not biotypes R. conicus (or other thistle head insects like U. solstitialis, reviewed by Gassmann and Louda, 2000) might exist, each with a somewhat narrower host range. The existence or absence of such biotypes has important implications in the biological control program against C. nutans and other exotic thistles in North America. This controversy might be due in part to the lack of an accepted definition of the term itself, but the existence of weevil biotypes with inherited differences in their ability to use different hosts still needs to be demonstrated. Genetic variation occurs in *R. conicus* reared from different thistle species (Unruh and Goeden, 1987), but the extent to which this genetic variation drives host selection and acceptance is unknown. Rather, the evidence available to date suggests that the phenology of thistle species in the subtribe Carduinae plays a major role in their exploitation by *R. conicus*. Therefore, the redistribution of *R. conicus* in areas where the weevil has not spread naturally should not be considered without an ecological assessment of the targeted area.

In contrast to R. conicus, Trichosirocalus horridus has been reported only occasionally from native North American Cirsium species (McAvoy et al., 1987). In light of available evidence to date, two questions need to be considered. (1) Is intensive exploitation of native thistles by T. horridus just a matter of time even though it has not been commonly found on non-target weeds after 25 years of release? (2) Is the exploitation of native Cirsium by R. conicus the result of the broad diet of the weevil, or the combination of phenology, host plant affinities, and other biological characteristics? The availability of reproduction sites (synchronization with flowering periods of "any" thistles) rather than preference, weevil aggregation, or altered competitive ability of R. conicus in the flower heads of thistles may play an important role in the exploitation of native Cirsium species by R. conicus (Gassmann and Louda, 2000). If this is the case, it follows that insects with biological characteristics different from those of R. conicus, such as T. horridus, will not necessarily exploit native North American Cirsium species in the same way as R. conicus.

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19 BULL THISTLE (SPEAR THISTLE)

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PEST STATUS OF WEED

Bull thistle, *Cirsium vulgare* (Savi) Tenore, is an invasive thistle from Eurasia, found throughout the United States and in Canada from Newfoundland to British Columbia. It is capable of invading fields, pastures, wastelands and along roadsides, but will not survive in cultivated fields.

Nature of Damage

Economic damage. Bull thistle occurs in overgrazed pastures, where heavy infestations can exclude livestock from infested areas. It also is common along roadside and vacant fields.

Ecological damage. Although bull thistle is a problem predominantly in disturbed areas, it also can be found in natural areas. The basal rosette may grow to nearly 1 m in diameter before bolting, and, once established, bull thistle outcompetes native plant species for space, water, and nutrients.

Geographical Distribution

Bull thistle was introduced into the eastern United States several times during the 19th century. It is now established in all 48 contiguous states as well as Alaska and Hawaii (USDA, NRCS, 1999). It has been designated as a noxious weed in Maryland, Pennsylvania, Minnesota, Iowa, Oregon, and Colorado.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Bull thistle differs from Canada thistle, *Cirsium avense* (L.) Scop., in that leaves are pubescent on both sides, while those of Canada thistle are not pubescent on top, and may or may not be so on the underside. Flower bracts of bull thistle have spines, in con-

trast to those of Canada thistle. Leaves are covered with coarse hairs on the upper surface of the leaf blade, and are woolly below. Long spines extend from the leaf blade at the midrib and at each lobe. The leaf bases extend downward on the stem forming long wings.

Biology

Bull thistle is a biennial species that reproduces by seed. The root system consists of several primary roots each with several smaller lateral roots. It does not reproduce by vegetative means. Bull thistle is erect and bushy in appearance, up to 2 m high, and has many spreading branches (Fig. 1). Stems are erect, stout, often branched, and hairy. Leaves are green on the upper side, with woolly gray hairs on the underside, and end in long, pointed, yellow spines. The compact large purple flower heads (2.5 to 5.0 cm in diameter) are borne singly at the tip of a stem (Fig. 2), each producing up to 250 light straw-colored seeds. Mature plants can produce up to 4,000 seeds



Figure 1. Bull thistle stand. (Photograph by L.-T. Kok.)

per plant. Bull thistle grows best on nitrogen-rich, neutral soils with moderate moisture (Klinkhamer and de Jong, 1993). It is not typically found on sand or on soils with high humus content and is absent from pure clay soils. Establishment is promoted by soil disturbance, which increases nutrient, water, and light availability to seedlings and reduces the vigor of competing vegetation (Randall, 1994). Bull thistle does not grow well in shade and drought. Phenolic acids inhibit competing plants through allelopathic effects or serve as a defense, coupled with spines, against herbivory (Klinkhamer and de Jong, 1993).



Figure 2. Bull thistle bloom, close up. (Photograph by L.-T. Kok.)

Analysis of Related Native Plants in the Eastern United States

Cirsium vulgare belongs to the tribe Cardueae (family Asteraceae), which is largely an Eastern Hemisphere group. The tribe is further divided into four subtribes (Echinopsidinae, Carlininae, Carduinae, and Centaureinae) including some 13 genera in North America (Bremer, 1994; USDA, NRCS, 1999). Only three of these 13 genera include species native to North America: (1) *Centaurea* (two species; subtribe Centaureinae), (2) *Saussurea* (seven species; assigned to the subtribe Carduinae, but the position of the genus in the tribe remains uncertain), and (3) *Cirsium* (subtribe Carduinae). The genus *Cirsium* includes about 100 native species, of which a few are threatened or endangered plants in the United States (*Cirsium fontinale* [Greene] Jepson var. *fontinale*, *Cirsium fontinale* [Greene] Jepson var. *obispoense* J. T. Howell, *Cirsium hydrophilum* [Greene] Jepson var. *hydrophilum*, *Cirsium pitcheri* [Torr. ex Eat.] Torr. and Gray, and *Cirsium vinaceum* Woot. and Standl.).

Some 20 native Cirsium species occur in the eastern United States: C. altissimum (L.) Hill, C. canescens Nutt., C. carolinianum (Walt.) Fern and Schub., C. discolor (Muhl. ex Willd.) Spreng., C. drummondii Torr. and Gray, C. engelmannii Rydb., C. flodmanii (Rydb.) Arthur, C. hilii (Canby) Fern., C. horridulum Michx., C. lecontei Torr. and Gray, C. muticum Michx., C. ochrocentrum Gray, C. nuttalii DC., C. pitcheri (Torr. ex Eat.) Torr. and Gray, C. pumilum (Nutt.) Spreng., C. repandum Michx., C. texanum Buckl., C. turneri Warnock, C. undulatum (Nutt.) Spreng., and C. virginianum (L.) Michx. (USDA, NRCS, 1999). Of these, C. pitcheri is listed as threatened under the Endangered Species Act. It occurs in sand dunes along the shores of the Great Lakes in Illinois, Indiana, Michigan, and Wisconsin.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Cirsium vulgare is a native of Europe, western Asia, and North Africa.

Areas Surveyed for Natural Enemies

Bull thistle was not considered a priority species when the thistle biological control program started in the early 1960s. However, it was included in the extensive surveys of natural enemies of Canada and musk thistle started in Europe in 1961 by the Commonwealth Institute of Biological Control (now CABI Bioscience), funded by Canada Department of Agriculture. Surveyed areas included southern England, France, Austria, Germany, northern Italy, and the northern part of the former Yugoslavia (Zwölfer, 1965).

Natural Enemies Found

More than 40 species have been recorded on bull thistle by Zwölfer (1965), of which 15 were reportedly broadly oligophagous on plants in the subtribe Carduinae (see Table 1 in the chapter on musk thistle). Only the seed-feeding fly, *Urophora stylata* Fabricius, has been selected and released for biological control of bull thistle. With the exception of *T. horridus*, none of the insect species released against *Cirsium arvense* or those used against *Carduus* species have been used for bull thistle.

Host Range Tests and Results

Oviposition and larval development of *U. stylata* were observed on the target host plant and on *Onopordum acanthium* L. in experimental host range studies carried out in the early 1970s. Oviposition, but no larval development was recorded on *Arctium tomentosum* Miller and *Carduus acanthoides* L. European field records include *Carduus acanthoides*, *Cirsium arvense*, *Cirsium pannonicum* (L.f.) Link, and *Cirsium canum* (L.) All. (Zwölfer, 1972).

Releases Made (from Julien and Griffiths, 1999)

Urophora stylata was released in Maryland and Washington in 1983, and was followed by releases in Colorado, Oregon, Montana, and California.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Urophora stylata (Diptera: Tephritidae)

The adult fly (Fig. 3) lays eggs in the closed flower buds. Gall tissue is formed around each larva separately (Zwölfer, 1972). The gall starts to form around the immature achene and the adjacent region of the receptacle begins to swell. Mature larvae (Fig. 4) overwinter within the flowerheads of bull thistle. Pupation occurs in May and adults emerge in June.



Figure 3. *Urophora stylata* adult. (Photograph by Peter Harris.)



Figure 4. *Urophora stylata* larva. (Photograph by Peter Harris.)

EVALUATION OF PROJECT OUTCOMES

Establishment of *U. stylata* in Maryland has not been confirmed, but this species is established in the western United States, with 60 to 90% of seed heads infested in some areas (Julien and Griffiths, 1999).

Trichosirocalus horridus has been released on bull thistle in Wyoming, but the establishment of the weevil has not been confirmed. Following initial releases on *Carduus acanthoides* in Virginia, some 20% of the bull thistle plants within the release areas also were exploited by this rosette weevil (McAvoy *et al.*, 1987).

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20 SLENDERFLOWER THISTLE (WINGED SLENDER OR SEASIDE THISTLE)

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PEST STATUS OF WEED

Nature of Damage

Like many other *Carduus* species, slenderflower thistle, *Carduus tenuiflorus* Curtis, is associated with pastures, disturbed areas, and vacant lots. Invasion is favored by annual burning of pastures. The thistle protects forage from grazing and is a competitive weed in improved pastures.

Geographical Distribution

Slenderflower thistle occurs in Pennsylvania, New Jersey, and Texas but the most serious infestations occur in California, Oregon, and Washington (USDA, NRCS, 1999). The closely related species, Italian thistle, *Carduus pycnocephalus* L., is known from New York, Alabama, and South Carolina in the eastern United States.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Carduus tenuiflorus is very similar to *C. pycnocephalus*, and the two species are sometimes treated together. Flowering stems are single or multiple from the base, branched, strongly ribbed, and slightly woolly. Spiny wings are continuous on stems to the base of the flower heads, but are discontinuous on *C. pycnocephalus*. The flower heads of *C. tenuiflorus* occur in clusters of five to 20, whereas those of *C. pycnocephalus* are in smaller clusters. The slender flower heads are less than 2 cm long, and lack stalks. Rosette and stem leaves are deeply lobed with numerous spines along the margin.

Biology

Carduus tenuiflorus is a winter annual, sometimes a biennial. Plants can grow from 0.3 to 2.0 m tall. It prefers soils of moderate to high fertility, in areas with moderate rainfalls.

Analysis of Related Native Plants in the Eastern United States

See this section in the chapter on musk thistle.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

As pointed out by Dunn (1978), the oldest document relating to biological control of Carduus thistle was a USDA note from 1956 regarding the abundance of C. pycnocephalus and C. tenuiflorus in California. The program against this species began in 1959, with the establishment of the USDA overseas laboratory in Rome, Italy. Thistle insect surveys by USDA staff in Italy initially focused on C. pycnocephalus but later were extended to C. tenuiflorus and Carduus nutans L. During the surveys on the latter two species, it was found that musk thistle supported a larger complex of insects than the other Carduus species, and work was subsequently concentrated on musk thistle. Slenderflower thistle also was included in the survey of European thistles carried out by the Commonwealth Institute of Biological Control (now CABI Bioscience) in the 1960s and funded by the Canada Department of Agriculture (Zwölfer, 1965). Major surveys for natural enemies of C. pycnocephalus were conducted also by Goeden (1974) in central and southern Italy, and in Greece during 1971 and 72.

Area of Origin of Weed

The native range of slenderflower thistle is western and southern Europe and the Mediterranean area, extending northward to Scandinavia.

Areas Surveyed for Natural Enemies

Areas surveyed included southern England, France, Austria, Germany, Italy, the northern part of former Yugoslavia, and Greece (Zwölfer, 1965; Goeden, 1974; Dunn, 1978).

Natural Enemies Found

Most of the C. tenuiflorus and C. pycnocephalus populations sampled by Zwölfer (1965) were in western and southern France, respectively. Altogether, some 15 oligophagous insect species were recorded on C. tenuiflorus and C. pycnocephalus in Europe (see Table 1 in the chapter on musk thistle). Although concern about the invasiveness of slenderflower thistles was the reason for the initiation of the Carduus biological control program in North America, attention soon was redirected to musk thistle. No biological control agent was specifically targeted for slenderflower thistle. Populations of the seed-feeding weevil R. conicus (from C. pycnocephalus in Italy) and the rootcrown fly C. corydon have been released against C. tenuiflorus and C. pycnocephalus in the United States. The host range and biology of the two species are described in the chapter on musk thistle.

Host Range Tests and Results

See the chapter on musk thistle.

Releases Made (from Julien and Griffiths, 1999)

Rhinocyllus conicus. Releases of this seed-feeding weevil originating from Italy were made on *C. tenuiflorus* in 1973 in California and Oregon only. Releases have been made on *C. pycnocephalus* as well.

Cheilosia corydon. This thistle rosette fly from Italy was released in 1990 in Maryland and New Jersey, as well as in Montana and Oregon. The fly also has been released on *C. pycnocephalus* in Oregon.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

See the chapter on musk thistle.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents (from Rees *et al.*, 1996; Julien and Griffiths, 1999)

Rhinocyllus conicus. This weevil (Fig. 1) has become established and contributed to the control of slenderflower thistle in Oregon, especially in unburned areas.

Cheilosia corydon. Establishment of this fly has not been confirmed.

Puccinia carduorum. This rust (Fig. 2) has been accidentally introduced in North America. It is recorded on *C. tenuiflorus* in California and Oregon. *Puccinia carduorum* is native to the Mediterranean area but also is reported from Bulgaria and Romania. The fungus was imported from Turkey by the USDA for host range tests at the Foreign Diseases–Weed Research Laboratory in Frederick, Maryland (Politis and Bruckart, 1986). It also was tested and released for musk thistle control in 1992 (Baudoin *et al.*, 1993).



Figure 1. *Rhinocyllus conicus* adult and eggs on thistle head. (Photograph by L.-T. Kok.)



Figure 2. *Puccinia carduorum* infested thistle leaf. (Photograph by L.-T. Kok.)

(For details, see the chapter on musk thistle). The disease appears first as tiny yellow specks. In several days, rust pustules containing thousands of spores become visible (Figs. 3, 4).



Figure 3. Close up of *Puccinia carduorum* infection. (Photograph by L.-T. Kok.)

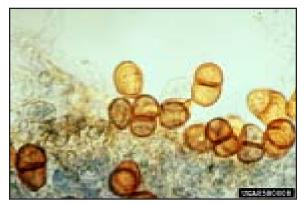


Figure 4. Urediniospores and teliospores of *Puccinia carduorum*. (Photograph by L.-T. Kok.)

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21 PLUMELESS THISTLE (CURLED THISTLE, BRISTLY THISTLE)

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PEST STATUS OF WEED

Plumeless thistle, *Carduus acanthoides* L., is an introduced Eurasian noxious weed in pastures, rangelands, croplands, and along highways in 19 of the contiguous states in the United States (Frick, 1978). *Carduus acanthoides* and *Carduus nutans* L. in the northeastern United States often occupy the same habitats, such as overgrazed pastures and disturbed roadsides, and these species sometimes occur as mixed stands.

Nature of Damage

Economic damage. Plumeless thistle prefers fertile soils developed over limestone, but it is highly adaptable and can even grow in shallow soil, emerging from stone quarries. Infestations of plumeless thistle reduce productivity of pastures and rangeland by suppressing growth of desirable vegetation and preventing livestock from eating plants growing in the vicinity of thistle stands (Desrochers *et al.*, 1988). It is very persistent and has the ability to regenerate because of the longevity and large number of seeds that it produces.

Ecological damage. Plumeless thistle generally does not pose a great threat to high quality areas although it may retard natural secondary succession. Just like musk thistle, livestock avoid it. Selective grazing and the indirect effects of herbicides used for its control result in bare ground that is ideal for its seed germination the following season.

Extent of losses. Carduus acanthoides stands of 90,000 plants per ha were observed in permanent pasture in southern Ontario and parts of Quebec. Such dense infestations are not uncommon in the United States (Desrochers *et al.*, 1988) and result in substantial loss of grazing areas for livestock. As thistles are not subjected to grazing or other stress, they easily outcompete forage grasses to become the dominant

vegetation in areas where they have become established. In time, they can spread to dominate entire fields (Kok, unpub.). No documentation is available of the effect of plumeless thistles in agricultural crops because such areas are usually plowed under during cultivation.

Geographical Distribution

The earliest collections of *C. acanthoides* were made at Camden, New Jersey in 1878, and in Virginia in 1926 (Frick, 1978; Kok and Mays, 1991). In the 1940s, plumeless thistle was reported to occur from Nova Scotia to Nebraska, and south to Virginia and Ohio. Later, the weed was reported from the Canadian provinces of Nova Scotia, Quebec, Ontario, and British Columbia. The distribution of *C. acanthoides* in the United States is not as great as that of the *C. nutans* group. It is most widespread in the northeastern United States and in several central and western states (USDA, NCRS, 1999). *Carduus acanthoides* has been declared a noxious weed in Maryland, Minnesota, Nebraska, North Carolina, South Dakota, Virginia, West Virginia, and six western states.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Carduus acanthoides belongs to the small-flowered (sub-globose) group of *Carduus* species and is close to *Carduus crispus* L. The red to purple flowers (13 to 25 mm in diameter) of plumeless thistle are usually about one-third to one-half the size of musk thistle flowers. Flowers may be single or in clusters, are erect on stems, and usually do not droop or nod. Unlike musk thistle, flower stems are branched, with spiny wings extending to the flower heads. Three forms of plumeless thistle have been described, the most common in Virginia being *C. acanthoides* var. *acanthoides* (Kok and Mays, 1991). Hybridization between *C. acanthoides* and *C. nutans* has been reported (referred to as *C. x orthocephalus* Wallr.). Flowers of the hybrids are larger than the typical capitula of plumeless thistle, but smaller than capitula of musk thistle (Kok, unpub.).

Biology

Carduus acanthoides is an annual or biennial, reproducing by seed. In the rosette stage (Fig. 1), it may be mistaken for musk thistle. The taproot is large and hollow near the ground surface. The stem is erect, branched, and has spiny wings. The plant is 20 to 150 cm tall (Fig. 2). Leaves are hairy on the undersides and are narrower, more deeply lobed, and finely divided than those of C. nutans. Carduus acanthoides generally blooms from May to July, but this varies with environmental conditions. The reddish-purple flowers are about 20 mm in diameter (Fig. 3). Seeds are oblong, striate, and slightly curved. The seeds are about one-third the size of musk thistle seeds. Literature on plumeless thistle is much less extensive than that for musk thistle, but the biology, ecology, history, introduction, and control of both thistles are quite similar. However, plumeless thistle is more tolerant of herbicides and requires a higher rate of application. Like C. nutans, plumeless thistle does not have specific climatic requirements. In the northeastern United States, it is associated with fertile soils formed over limestone. Plumeless thistle tends to occupy drier, better-drained sites than C. nutans within the same pasture. It overwinters either as seeds or rosettes. The many flower heads of plumeless thistle enable it to flower more continuously than C. nutans, e.g., between June and October in southern Ontario, and between June and August in Virginia. A typical plant produces 35 to 60 capitula. Mean seed set averages 56 to 83 seeds per seed head for C. acanthoides and 165 to 256 for C. nutans. Germination occurs mainly in the spring and fall, with resulting plants acting either as winter annuals or as spring or fall biennials (Desrochers et al., 1988).

Analysis of Related Native Plants in the Eastern United States

See this section in the chapter on musk thistle.



Figure 1. Plumeless thistle rosette. (Photograph by L.-T. Kok.)



Figure 2. Plumeless thistle stand. (Photograph by L.-T. Kok.)



Figure 3. Plumeless thistle bloom, close up. (Photograph by L.-T. Kok.)

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

The biological control of *Carduus* spp. started when the USDA overseas laboratory was established at Rome, Italy in 1959. It began with a search of natural enemies in Europe in 1963 (Andres and Kok, 1981). *Carduus acanthoides* was not a primary target weed in the genus *Carduus*. However, this species was included in the European survey carried out by the Commonwealth Institute of Biological Control (now CABI Bioscience) in the 1960s and funded by Canada Department of Agriculture (Zwölfer, 1965).

Area of Origin of Weed

The native distribution of plumeless thistle is Europe and Asia. It is very common in eastern parts of Europe, but absent from most of southwestern and northern Europe (see also this section in the chapter on musk thistle).

Areas Surveyed for Natural Enemies

Areas surveyed included southern England, France, Austria, Germany, northern Italy, and the northern part of the former Yugoslavia (Zwölfer, 1965).

Natural Enemies Found

Most of the *C. acanthoides* populations sampled by Zwölfer (1965) were in southern Germany and eastern Austria. More than 30 insect species were recorded on the target plant. Of these, 15 species were reported to be broadly oligophagous on plants in the subtribe Carduinae (see Table 1 in the chapter on musk thistle). In Europe, fewer phytophagous insect species have been reported from plumeless thistle than from musk thistle. This is probably due to the much smaller geographical distribution of the former species and the lower level of sampling effort directed against plumeless thistle.

The biological control agents that had been selected primarily for musk thistle, i.e., the seed-feeding weevil, *Rhinocyllus conicus* (Frölich) and the rosette weevil, *Trichosirocalus horridus* (Panzer), were used at the same time against plumeless thistle. Attack rates by *R. conicus* on plumeless thistle appear to be low in North America, as they are in Europe, probably because the weevil is poorly synchronized with the plant phenology (Surles and Kok, 1977). Because of increasing concern about effects on nontarget species, a more specific agent, the seed-feeding fly *Urophora solstitialis* (L.), was selected in the mid-1980s and released against plumeless thistle. Shortly after, this fly also was used for musk thistle (see also this section in the chapter on musk thistle).

Host Range and Biology

The seed-feeding insects, *R. conicus* and *U. solstitialis*, and the rosette weevil *T. horridus* have been released against plumeless thistle.

Rhinocyllus conicus and *Trichosirocalus horridus.* The host range and biology of these two species released as biological control agents are described in this section in the chapter on musk thistle. The adult of *T. horridus* is a brown weevil of 3.9-4.3 mm in length (Fig. 4). Newly eclosed larvae burrow down the petiole into the growth point. Deterioration of plant tissues due to larval feeding results in blackened necrotic tissues (Fig. 5). There are three larval instars (Kok *et al.*, 1975). Heavy feeding by mature larvae (Fig. 6) can cause collapse and death to young rosettes (Fig. 7).

Urophora solstitialis L. (Diptera: Tephritidae). Literature data include a large number of misleading host records for this species in the tribe Cardueae. Field surveys in Europe indicate that the seed-feeding fly U. solstitialis (Fig. 8) is restricted to the genus Carduus. In laboratory tests, oviposition and larval development occurred on the three Carduus species tested, on one (Cirsium heterophyllum [L.] Hill) out of four Cirsium species tested, on one (Arctium lappa L.) out of two Arctium species tested, and on one (Centaurea montana L.) out of 10 Centaurea species tested (Moeller-Joop and Schroeder, 1986; Moeller-Joop, 1988). This seed-feeding fly overwinters as a fully developed larva in capitula (Fig. 9). The adults then emerge in mid-spring. Adults live for several weeks and lay their eggs in the tubes of developing single florets inside flower buds. Newly hatched larvae mine through tubes and ovules down into the receptacle, inducing a gall. Most larvae developing from eggs laid early in the season pupate and produce a second generation. The proportion of larvae developing to form a second generation declines as the season progresses, and larvae developing late in the season all enter diapause (Moeller-Joop and Schroeder, 1986; Woodburn, 1993).



Figure 4. *Trichosirocalus horridus* adult. (Photograph by L.-T. Kok.)



Figure 6. Close up of *T. horridus* larva (third instar). (Photograph by L.-T. Kok.)



Figure 8. *Urophora solstitialis* adult. (Photograph by Peter Harris.)

Releases Made (from Rees *et al.*, 1996; Julien and Griffiths, 1999)

Rhinocyllus conicus. Introductions of *R. conicus* from eastern France via Canada began on *C. acanthoides* in 1969 in Virginia (Surles *et al.*, 1974). Releases were made also in Maryland, Pennsylvania, Idaho, Washington, and West Virginia.



Figure 5. Necrosis of rosette due to feeding of *T. horridus* larvae. (Photograph by L.-T. Kok.)



Figure 7. Collapse of thistle rosette infested by *T. horridus* larvae. (Photograph by L.-T. Kok.)



Figure 9. *Urophora solstitialis* larva. (Photograph by Peter Harris.)

Trichosirocalus horridus. The weevil originating from Italy was first released on *C. acanthoides* in Virginia in 1974 (Trumble and Kok, 1979). After establishment in Virginia, adult weevils were collected from sites in Virginia and released in Kansas, Maryland, Missouri, New Jersey, West Virginia, and several western states, as well as in Canada and Argentina. Urophora solstitialis. This fly was released in Maryland in 1993.

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents (from

Julien and Griffiths, 1999)

Rhinocyllus conicus. This seed-feeding weevil is established in Virginia (Surles *et al.*, 1974), Maryland, Pennsylvania, Idaho, Washington, and West Virginia.

Trichosirocalus horridus. Establishment of this rosette weevil has been confirmed in Kansas, Maryland, Missouri, and Virginia, but not in New Jersey. In a study conducted in Virginia from 1976 to 1978, establishment was confirmed at two of seven release sites. By1981, the weevil was established at six of these seven sites, and by 1985 it became established in more than 20 sites (Kok and Mays, 1991). In southwest Virginia, 20% of the *C. acanthoides* plants were infested by the weevil in 1985 compared with 54% of *C. nutans*. In sites with mixed stands of musk and plumeless thistles, musk thistle was preferred over plumeless thistle when weevil populations were low. As the *T. horridus* populations increased, plumeless thistle was subjected to increased attack.

Urophora solstitialis. This seed-feeding fly is not established.

Suppression of Target Weed

Rhinocyllus conicus. Rhinocyllus conicus provides only partial control of *C. acanthoides* because the ovipositional period of the weevil only coincides with the development of the terminal thistle buds, and not that of the lateral buds (Surles and Kok, 1977). The suppressive effect of this weevil is reduced by the long flowering period of plumeless thistle compared with musk thistle. According to Rowe and Kok (1984), females of *R. conicus* survive longer on plumeless thistle than on musk thistle, and peak oviposition on plumeless thistle is delayed about two weeks, suggesting a possible adaptation of *R. conicus* to plumeless thistle.

Trichosirocalus horridus. Damage to C. acanthoides by T. horridus is caused by larvae feeding on rosette meristematic tissues and results in crown tissue necrosis. Infested plants produced a greater number of stems per plant, but 50% fewer heads than the non-infested plants (Cartwright and Kok, 1985). Studies in Virginia showed that large weevil populations and grass competition together could have a large effect on thistle densities (Figs. 10 and 11). As larval infestation increases, the stressed thistles become less dominant and more susceptible to competition by pasture grasses, which increase in vigor and density. In 1981, thistle reduction ranged from 11.6 to 80.9% at five sites with T. horridus, versus an 11.6% increase at one site where T. horridus was not established. At two sites, a reduction in thistle density of more than 80% was found to be due in part to the additional presence of R. conicus and improved pasture vigor (Kok, 1986). By 1990, despite occasional resurgence of thistles in some years, plumeless thistle density was very low, with reductions of the original density ranging from 87 to nearly 100%. Thus, the collapse of plumeless thistle was evident after 10 to 12 years following weevil releases (Kok and Mays, 1991).



Figure 10. Plumeless thistle stand before release of *T. horridus*. (Photograph by L.-T. Kok.)



Figure 11. Plumeless thistle stand eight years after release of *T. horridus*. (Photograph by L.-T. Kok.)

Recovery of Native Plant Communities and Economic Benefits

The main replacement vegetation at the five sites after collapse of plumeless thistle in Virginia was dense stands of desirable pasture grasses like tall fescue (*Festuca arundinaria* Schreb.), orchard grass (*Dactylis* glomerata L.), and bluegrass (*Poa* spp.) (Kok and Mays, 1991).

RECOMMENDATIONS FOR FUTURE WORK

There are some indications that *T. horridus* may be a good biological control agent for plumeless thistle, alone or in combination with *R. conicus* and grass competition (Kok *et al.*, 1986; Kok and Mays, 1991). The impact by thistle weevils can be greatly enhanced when the insects are used in conjunction with tall fescue grass (Kok *et al.*, 1986). Thus, redistribution of this rosette weevil to other infested areas is being continued. Potential feeding on non-target plants, however, deserves further attention. (See also this section in the chapter on musk thistle.)

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SECTION IV: WEEDS OF OLD FIELDS AND PASTURES

Multiflora Rose Tropical Soda Apple, Wetland Nightshade, and Turkeyberry Brazilian Peppertree

22 MULTIFLORA ROSE

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PEST STATUS OF WEED

Multiflora rose, *Rosa multiflora* Thunberg ex. Murray, is a non-indigenous rosaceous plant that is native to East Asia (Japan, Korea, and eastern China) (Fig. 1). It has been introduced into North America many times since the late 1700s as garden plants and as root stock for ornamental roses. Rehder (1936) found it listed in the second edition (1811) of the *Catalog of the Elgin Botanic Garden* in New York. Before its weedy characteristics were well understood, it was widely planted in the 1940s to 1960s in the eastern United States as a wildlife plant for erosion control and as a living fence. The hypanthia often are used for tea as a source of vitamin C. It has been declared a noxious weed in at least ten states (Amrine and Stasny, 1993).

Nature of Damage

Economic damage. Lost pasturage in many states, especially states with hilly terrain and pastures on steep slopes, has resulted in significant reduction in potential beef production. This thorned bramble now infests more than 45 million acres throughout the eastern United States (Underwood et al., 1996). Chalamira and Lawrence (1984) reported that multiflora rose was the highest priority agricultural problem in West Virginia. Experimental multiflora control programs in West Virginia during 1980 and 1981 indicated that more than 36,500 hectares were heavily infested and that a ten-year eradication program using herbicides would cost more than \$40 million (Williams and Hacker, 1982). Similar burdens and costs were reported from neighboring states; to date, multiflora has been declared a noxious weed in Illinois, Iowa, Kansas, Maryland, Missouri, Ohio, Pennsylvania, Virginia, Wisconsin, and West Virginia (Amrine and Stasny, 1993).



Figure 1. Multiflora rose. (Illustration by Rae Chambers, Pennsylvania State University.)

Ecological damage. Multiflora rose has invaded a large number of habitats, from hillside pastures, fence rows, right-of-ways, and roadsides to forest edges and the margins of swamps and marshes (Scott, 1965). A single, vigorous, mature plant can produce up to half a million achenes (seeds) annually. Where plants have become well established, a huge seed bank develops that can continue to produce seedlings for at least twenty years after removal of mature plants. Severe multiflora rose infestations have lowered land values for agriculture, forestry, and recreation (Underwood *et al.*, 1996). Since the 1960s, multiflora rose has become one of the most noxious weeds in the eastern United States. It is especially troublesome in regions with steep slopes, which prevent access by tractors or mowers for cutting this weed. Multiflora rose forms dense, impenetrable thickets in many regions of the eastern United States. At least ten states have passed noxious weed laws against it, and it is illegal to plant it in many areas (Amrine and Stasny, 1993; Fawcett, 1980; Klimstra, 1956; Kriebel, 1987; Williams and Hacker, 1982; Underwood *et al.*, 1996). Many state publications and web sites list cultural and chemical methods for controlling multiflora rose, but biological control has been a neglected management option (Lingenfelter and Curran, 1995; Underwood and Stroube, 1986; Underwood *et al.*, 1996).

Extent of losses. In West Virginia, projected costs to farmers for controlling multiflora rose from 1981 to 1982 exceeded \$40 million (Williams and Hacker, 1982); at today's rates, this cost would exceed \$48 million. Similar costs accrue to most eastern states and control costs continue to rise as this noxious weed continues to spread.

Geographical Distribution

In eastern North America, multiflora rose is abundant from the Great Plains (where the species has been planted as wind breaks) to the east coast. It occurs from northern Texas, Arkansas, Mississippi, Alabama, and Georgia in the south, north to the New England coast, central New York, southern Michigan, Wisconsin, and Minnesota. It occurs only as plantings south of central Georgia, probably because of the lack of cold temperatures needed to stimulate seed germination. The plant's northern distribution is limited by its sensitivity to severe cold temperatures.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Multiflora rose is in the Subfamily Rosoïdeae, Tribe Roseae. *Rosa* is the only known genus in the tribe. The most closely related plants are members of the tribes Potentilleae (Sections Rubinae, Potentillinae, Dryadinae), Cercocarpaceae, Ulmariëae, and Sanguisorbeae. The most common genera that would be most closely related to *Rosa* are *Rubus*, *Potentilla*, *Fragaria*, *Geum*, *Dryas*, *Adenostema*, *Purshia*, *Cercocarpus*, *Alchemilla*, *Agrimonia*, and *Poterium*.

Multiflora rose was first described from Japan. It is a stout, thorny, diffusely branched, perennial shrub with numerous arching stems (canes) arising from the crown; plants may reach 3 m height and 6.5 m diameter. Twigs are reddish to green, 1.5 cm in diameter and armed with numerous, recurved thorns; thornless clones occur sparsely throughout the eastern United States. Leaves are odd-pinnately compound, 8 to 11cm long, divided into five to 11 sharply toothed, ovate to oblong leaflets. Basal petioles are 1.0 to1.3 cm long and have finely dissected, usually glandular stipules. Large clusters of showy, fragrant, white to pink 2.5 cm flowers occur in dense to sparse panicles that appear in late May or June. Panicles contain six to 100 (average of 63) hypanthia or hips that are glabrous to pubescent, develop during the summer, and become bright red by mid-September; hips contain an average of seven (one to 21) achenes. Hypanthia become soft after frost and eventually become leathery, remaining on the plant through the winter. Achenes are yellowish to tan, somewhat irregular in shape, about 2 to 4 mm long by 2 mm wide, and enclosed in sharp spicules. Winter-feeding birds often consume fruits by January. Seeds are attacked by the rose seed chalcid, Megastigmus aculeatus var. nigroflavus Hoffmeyer (Hymenoptera: Torymidae) in many areas (see below).

Biology

Each cane on a large plant may contain 40 to 50 pannicles. Each pannicle can contain as many as 100 hypanthia or hips (average of about 50) and each hip, an average of seven seeds (range of one to 22). Thus each large cane can potentially produce up to 17,500 seeds. Seeds remain viable for a number of years (Evans, 1983; Underwood et al., 1996). We have found as many as 90% of the seed to be viable, in the absence of drought, stress, and seed chalcids. The abundant floral production of this plant may be the result of the plant's evolution in the presence of its seed predator, the multiflora rose seed chalcid, Megastigmus aculeatus var. nigroflavus Hoffmeyer (Hymenoptera: Torymidae). In Asia, the chalcid may infest 95% of the achenes or seeds (Weiss, 1917). The chalcid reproduces by parthenogenesis (female:male ratio is 200:1), possibly a mechanism to match the huge resource (Shaffer, 1987). Multiflora rose is moderately winter-hardy, tolerant to many North American insects and diseases, and grows rapidly into dense thorny thickets favorable for many species of

wildlife. Its abundant fruits are food to deer and birds. The flowers produce large amounts of golden, sweettasting pollen that can be harvested by fitting bee hives with pollen traps (Amrine unpublished). The plant has a vigorous root system capable of checking erosion, and if carefully planted and mechanically trimmed, multiflora rose can make living fences capable of restraining some species of livestock (Dugan, 1960). It is still planted as a living fence in southern Delaware to separate herds of horses. Because of these traits, multiflora rose was widely planted throughout the eastern United States from the 1930s until the 1960s as living fences, for erosion control, and to protect and feed native wildlife. In West Virginia, more than 14 million plants were planted in the 1940s to 1960s (Dugan, 1960), and in North Carolina, more than 20 million were planted (Nalepa, 1989). Only a few states (e.g., Kentucky) refused to promote this plant. Consequently, many areas of Kentucky are relatively free of the weed. Since the plant was distributed as rooted cuttings and not from seed, no seed chalcids were distributed.

Some early experiments were conducted to show that spread of multiflora seed by birds was minimal. However, the birds chosen were chickens, doves, pigeons, turkeys, and their relatives—all of which have gizzards containing stones that grind seeds. Songbirds were not tested as potential seed dispersers. Robins, mockingbirds, starlings, red-winged blackbirds, and other species feed heavily on multiflora rose hips in fall and winter, and, because of the numerous spicules in each hip, seeds pass rapidly through their digestive tracts and remain intact. Passage of seeds through digestive tracts of songbirds increases the germination rate, while bird feces provides fertilizer to seedlings (Lincoln, 1978; Scott, 1965).

Analysis of Related Plants in the Eastern United States

According to the Synonymized Checklist of the Vascular Flora of the United States, Puerto Rico, and the Virgin Islands and the Texas A&M University Bioinformatics Working Group on the Rosaceae (part of BONAP, theBiota of North America Program), there are 82 species or subspecies of roses that are either native to the eastern United States, have escaped from cultivation, or are grown in gardens. In addition, there are some 8,000 registered cultivars of roses, worldwide, with many new ones registered annually. The following is a list of roses occurring in this region:

- <u>1. Rosa acicularis Lindl.</u> Cinnamomeae DC. Prickly rose. (native) Eurasia and North America, Zone 4.
- <u>2. Rosa acicularis ssp. acicularis</u>. (native) Alaska, Eurasia, zone 4.
- 3. Rosa acicularis ssp. sayi (Schwein.) W. H. Lewis. (native) Alaska through Canada, south to West Virginia, Texas and New Mexico (mountains), Zone 5. Occasionally found at higher altitudes and farther north. Synonymy: Rosa acicularis var. bourgeauiana (Crépin) Crépin, Rosa acicularis var. sayana Erlanson, Rosa bourgeauiana Crépin, Rosa collaris Rydb., Rosa engelmannii S. Wats., Rosa sayi Schwein.
- <u>4</u>. <u>Rosa x alba L. (pro sp.) [arvensis x gallica]</u>. European hybrid. Zone 5, mountains and far north.
- <u>5. Rosa arkansana Porter</u>. Cinnamomeae DC. (native). Prairie rose. New York to Alberta, south to Texas.
- <u>6. Rosa arkansana var. arkansana</u> (native). Known locally as prairie rose. From Wisconsin and Minnesota to Colorado and Kansas; rocky slopes. Synonymy: *Rosa lunellii* Greene, *Rosa rydbergii* Greene.
- 7. Rosa arkansana var. suffulta (Greene) Cockerell.(native). Known locally as sunshine rose. New York west to Alberta, south to the District of Columbia, Indiana, Wisconsin, Missouri, Kansas, Texas, and New Mexico. Synonymy: Rosa alcea Greene, Rosa conjuncta Rydb., Rosa pratincola Greene, Rosa suffulta Greene, Rosa suffulta var. relicta (Erlanson) Deam.
- <u>8. Rosa banksiae Aiton</u>. Non-indigenous rose from China, grown in Georgia. Apparently, it has not escaped.
- <u>9. Rosa blanda Aiton</u>. Cinnamomeae DC. (native). Smooth rose. Newfoundland to Maryland and West Virginia, west to Kansas and Montana.
- 10. Rosa blanda var. blanda Aiton. (native). Distribution same. Synonymy: Rosa blanda var. carpohispida Schuette, Rosa rousseauiorum Boivin, Rosa subblanda Rydb., Rosa williamsii Fern.

- <u>11. Rosa blanda var. glabra Crépin</u>. (native). Maine south to New York, west to Minnesota. Synonymy: *Rosa johannensis* Fern.
- <u>12. Rosa blanda var. glandulosa Schuette</u> (native). Indiana.
- 13. Rosa blanda var. bispida Farw. (native). Maryland and Indiana.
- 14. Rosa x borboniana Desportes (pro sp.) [chinensis x damascena]. Bourbon rose. Non-indigenous hybrid. New York, South Carolina and Louisiana.
- 15. Rosa bracteata J. C. Wendl. Bracteatae <u>Thory</u>. Known as Chickasaw or Macartney rose. Non-indigenous rose from China. Found in Zone 7, in Texas, Louisiana, Georgia, and other southern states north to Virginia and Kentucky.
- 16. Rosa canina L. Caninae DC. Dog rose. Nonindigenous rose from Europe and West Asia; Maine south to Alabama, west to Arkansas, Kansas and Wisconsin; western distribution is Washington and Idaho to Utah and California, Zone 4. Present in the CalFlora Database (California distribution map). Synonymy: Rosa canina var. dumetorum Baker.
- <u>17. Rosa carolina L. Carolinae Crépin</u>. (native). Carolina rose, pasture rose. Nova Scotia to Florida, west to Nebraska and Texas.
- 18. Rosa carolina var. carolina L. (native). Common in the east where it is known as the pasture rose. Synonymy: Rosa carolina var. glandulosa (Crépin) Farw., Rosa carolina var. grandiflora (Baker) Rehd., Rosa carolina var. obovata (Raf.) Deam, Rosa serrulata Raf., Rosa subserrulata Rydb., Rosa texarkana Rydb.
- 19. Rosa carolina var. deamii (Erlanson) Deam. (native). Indiana.
- 20. *Rosa carolina* var. *sabulosa* Erlanson. (native). Indiana.
- <u>21. Rosa carolina var. setigera Crépin.</u> (native). New Hampshire, Vermont and Maine. Known locally as prairie rose, climbing rose.
- 22. Rosa carolina var. villosa (Best) Rehd. (native). Maine south to Georgia west to Minnesota and Texas. Synonymy: Rosa carolina var. lyonii (Pursh) Palmer and Steyermark, Rosa lyonii Pursh, Rosa palmeri Rydb.

- 23. Rosa centifolia L. Cabbage rose. Non-indigenous rose from Europe; grown by rosarians for attar of rose, an essential oil in the petals. New York and Connecticut south to New Jersey, west to Missouri and Wisconsin. Synonymy: Rosa centifolia var. cristata Prev., Rosa centifolia var. muscosa (Ait.) Ser.
- **24.** *Rosa chinensis* Jacq. Chinese rose, pygmy rose, fairy rose. Non-indigenous rose from China, grown in Zone 7. Arkansas and Mississippi.
- 25. Rosa cinnamomea L. Cinnamomeae DC. Cinnamon rose. Non-indigenous rose from Eurasia; escaped in North America, Zone 5; Maine south to Virginia, northwest to Wisconsin.
- 26. <u>Rosa x damascena P. Mill. (gallica x</u> <u>moschata</u>). Damask rose. Introduced from Asia Minor; sporadic: New York, Michigan, Missouri and North Carolina. major source of attar of roses. Synonymy: *Rosa* x *bifera* (Poir.) Pers.
- 27. Rosa x dulcissima Lunell (pro sp.) (blanda x woodsii). Hybrid rose with native parents; Wisconsin and Iowa west to the Dakotas.
- 28. Rosa dumetorum Thuill. Corymb rose. Introduced from the Mediterranean region, Zone 6; Kentucky. Synonymy: Rosa corymbifera Borkh.
- 29. Rosa eglanteria L. Caninae DC.- Sweetbrier. Known locally as: sweetbrier. Naturalized from Europe into most of North America, Zone 6. Present in the CalFlora Database (California distribution map). Synonymy: *Rosa rubiginosa* L.
- <u>30. Rosa foliolosa Nutt. Ex. Torr. and Gray</u>. (native). Known locally as leafy rose or white praire rose. Kansas and Arkansas to Texas, Zone 6. Synonymy: *Rosa ignota* Shinners.
- <u>31. Rosa gallica L.</u> Gallincanae DC. French rose. Non-indigenous rose from Europe and west Asia; used to produce attar of roses. Naturalized in North America, Zone 6; Maine south to South Carolina west to Louisiana and Wisconsin.
- <u>32. Rosa gallica var. gallica L.</u> Same distribution as gallica.
- <u>33. Rosa gallica var. officinalis Thory Missouri</u> and Michigan.

- 34. Rosa x harisonii Rivers; also Rosa Harison's Yellow (foetida x spinosissima). A hybrid rose planted by the pioneers where they settled.
- <u>35. Rosa x housei Erlanson (pro sp.) (acicularis</u> <u>x blanda).</u> A hybrid rose; New York, Michigan and Wisconsin.
- <u>36. Rosa hugonis Hemsl.</u> Father Hugo's rose, golden rose of China. Non-indigenous rose from China. Cultivated in northeast North America.
- <u>37. Rosa indica L.</u> Cyme rose. Non-indigenous rose from South Asia; escaped in Puerto Rico.
- 38. Rosa laevigata Michx. Cherokee rose. Nonindigenous rose from China; naturalized in southern United States, Zone 7; North Carolina south to Florida, west to Texas. State flower of Georgia. It has weedy propensities.
- 39. Rosa majalis J. Herrm. Double cinnamon rose. Non-indigenous rose from Europe. Southern New England west to Ohio and Wisconsin. Synonymy: Rosa cinnamomea sensu L. 1759, non 1753.
- <u>40. Rosa manca Greene.</u> Mancos rose. Non-indigenous rose from Europe; Colorado, Utah and Arizona.
- 41. Rosa micrantha Borrer ex Sm. Caninae DC. Small-flower sweetbrier. Non-indigenous rose from Europe, naturalized in North America; most eastern states and the Pacific Northwest.
- 42. Rosa moschata J. Herrm. Musk rose. Nonindigenous rose from southern Europe, northern Africa and western Asia; naturalized in North America, Zone 7; Mississippi and Illinois.
- 43. Rosa multiflora Thunb. ex Murr. Synstylae DC. Multiflora rose, rambler rose. Non-indigenous rose from Japan, Korea and east China-All eastern states west to Texas, Nebraska and Minnesota; also in Washington and Oregon. Synonymy: Rosa cathayensis (Rehd. and Wilson) Bailey.
- <u>44. Rosa nitida Willd.</u> Carolinae Crépin. (native). Shining rose. Newfoundland to Connecticut and Ohio, Zone 4.
- <u>45. Rosa nutkana K. Presl.</u> (native). Nootka rose. Found from California to Alaska, northern Rocky Mountains.

- 46. Rosa nutkana var. hispida Fern. (native). Colorado north to Montana west to Nevada, Oregon and Washington. Synonymy: Rosa anatonensis St. John, Rosa caeruleimontana St. John, Rosa jonesii St. John, Rosa macdougalii Holz., Rosa megalantha G. N. Jones, Rosa spaldingii Crépin, Rosa spaldingii var. alta (Suksdorf) G. N. Jones, Rosa spaldingii var. hispida (Fern.) G. N. Jones, Rosa spaldingii var. parkeri (S. Wats.) St. John.
- <u>47. Rosa nutkana var. muriculata (Greene) G.</u> <u>N. Jones.</u> (native); Washington, Oregon and California.
- 48. Rosa nutkana var. nutkana K. Presl. (native); Washington, Oregon, California, andWyoming. Synonymy: Rosa durandii Crépin
- 49. Rosa nutkana var. setosa G.N. Jones. (native); Washington and California.
- 50. *Rosa obtusiuscula* Rydberg. (native). Appalachian valley rose. Found in Tennessee.
- 51. *Rosa odorata* (Andr.) Sweet. Tea rose. Nonindigenous rose from China; one of the parents of tea roses. Found in Pennsylvania, Louisiana and Utah.
- 52. *Rosa* x *palustriformis* Rydb. (pro sp.) [*blanda* x *palustris*]. Hybrid rose with native parents; Maine to Wisconsin, south to Ohio.
- 53. Rosa palustris Marsh. Carolinae Crépin. (native) Swamp rose. A common native rose, found in marshy locations from Nova Scotia to Minnesota, south to Florida and Texas. Synonymy: Rosa floridana Rydb., Rosa lancifolia Small, Rosa palustris var. dasistema (Raf.) Palmer and Steyermark.
- 54. Rosa x rehderiana Blackb. [chinensis x multiflora]. Polyantha rose. A hybrid non-indigenous rose, similar to multiflora, but canes less than three feet, low and spreading. New York and Louisiana.
- 55. Rosa rubrifolia Vill. Red-leaf rose. Non-indigenous rose from central Europe; Zone 2; Illinois, Maine, Massachusetts, New York and South Carolina. Synonymy: Rosa glauca Pourret.
- 56. Rosa x rudiuscula Greene (pro sp.) (arkansana x carolina). Hybrid with native parents; Ohio to Oklahoma, north to Wisconsin.

- 57. Rosa rugosa Thunb. Cinnamomeae DC. Rugose rose. Non-indigenous rose from China and Japan; it has escaped along the northeast coast, especially in Maine and Long Island, New York. Commonly grown in gardens. Sometimes weedy.
- 58. Rosa sempervirens L. Evergreen rose. Nonindigenous rose from southern Europe, North Africa; Zone 7; escaped in Puerto Rico.
- 59. Rosa serafinii Viviani. Non-indigenous rose from the Mediterranean region; apparently has not escaped.
- <u>60. Rosa setigera Michaux.</u> Synstylae DC. (native). Climbing rose, prairie rose. A common rose, found from Ontario to Kansas, south to Florida and Texas.
- <u>61. Rosa setigera var. setigera Michaux.</u> (native). Synonymy: *Rosa setigera* var. serena Palmer and Steyermark. Same distribution as setigera.
- 62. Rosa setigera var. tomentosa Torr. and Gray. (native). Known locally in Texas as fuzzy rose. Same distribution as setigera.
- <u>63. Rosa spinosissima L.</u> Pimpinellifoliae DC. Scotch rose. Non-indigenous rose from Europe; Found in Virginia and Tennessee west to Kansas, north to Wisconsin and Maine. Synonymy: *Rosa pimpinellifolia* L.
- 64. Rosa spinosissima var. spithamea S. Wats. Non-indigenous rose from Europe. Synonymy: Rosa spithamea var. solitaria Henderson
- <u>65. Rosa stellata Woot.</u> (native). Desert rose. Found in New Mexico and southern Texas.
- <u>66. Rosa stellata ssp. abyssa A. Phillips.</u> (native). Found in Arizona. Synonymy: *Rosa stellata* var. *abyssa* (A. Phillips) N. Holmgren
- 67. Rosa stellata ssp. mirifica (Greene) W. H. Lewis. (native). Known locally as desert rose; found in Texas and New Mexico.
- 68. Rosa stellata ssp. mirifica var. erlansoniae W. H. Lewis. (native). Found in Texas and New Mexico.
- 69. Rosa stellata ssp. mirifica var. mirifica (Greene) Cockerell. (native). Found in Texas and New Mexico. Synonymy: Rosa mirifica Greene.
- <u>70. Rosa stellata ssp. stellata Woot.</u> (native). Found from Texas west to Arizona.

- 71. Rosa tomentosa Sm. Caninae DC. Whitewoolly rose. Non-indigenous rose from Europe and west Asia; apparently has not escaped. Synonymy: Rosa tomentosa var. globulosa Rouy.
- 72. Rosa villosa L. Apple rose. Non-indigenous rose from Europe and west Asia; apparently has not escaped. Fruit is eaten and used in drinks.
- 73. Rosa virginiana P. Mill. Caroninae Crépin. (native). Virginia rose. Newfoundland, south to upland Georgia, Alabama and Tennessee, west to Missouri and Illinois.
- 74. Rosa virginiana var. lamprophylla (Rydb.) <u>Fern.</u> (native). Found in Connecticut north to Maine.
- 75. Rosa virginiana var. virginiana P. Mill. (native). Same as virginiana.
- <u>76. Rosa wichuraiana Crépin.</u> Synstylae DC. Memorial rose. Non-indigenous from east Asia; naturalized in North America, Zone 6, New York and Connecticut south to Florida and Mississippi west to Illinois.
- 77. Rosa woodsii Lindl. Cinnamomeae DC. (native). Wood's rose. A native rose found from western Ontario and Wisconsin to British Columbia, south to Nebraska, New Mexico, west Texas (mountains), and northern Mexico.
- 78. Rosa woodsii var. glabrata (Parish) Cole. (native). California. Synonymy: Rosa mohavensis Parish
- 79. Rosa woodsii var. gratissima (Greene) Cole. (native). California and Nevada. Synonymy: *Rosa gratissima* Greene
- <u>80. Rosa woodsii var. ultramontana (S. Wats.)</u> Jepson. (native). Washington east to Montana south to New Mexico and California. Synonymy: Rosa arizonica Rydb., Rosa arizonica var. granulifera (Rydb.) Kearney and Peebles, Rosa covillei Greene, Rosa lapwaiensis St. John, Rosa pecosensis Cockerell, Rosa ultramontana (S. Wats.) Heller, Rosa woodsii ssp. ultramontana (S. Wats.) Taylor and MacBryde, Rosa woodsii var. arizonica (Rydb.) W. C. Martin and C. R. Hutchins, Rosa woodsii var. granulifera (Rydb.) W. C.Martin and C. R.Hutchins.

- <u>81. Rosa woodsii var. woodsii Lindl.</u> (native). Montana south to New Mexico east to Texas and Wisconsin. Synonymy: Rosa adenosepala Woot. and Standl., Rosa fendleri Crépin, Rosa hypoleuca Woot. and Standl., Rosa macounii Greene, Rosa neomexicana Cockerell, Rosa standleyi Rydb., Rosa terrens Lunell, Rosa woodsii var. adenosepala (Woot. and Standl.) W. C. Martin and C. R. Hutchins, Rosa woodsii var. fendleri (Crépin) Rydb., Rosa woodsii var. hypoleuca (Woot. and Standl.) W. C. Martin and C. R. Hutchins, Rosa woodsii var. hypoleuca (Woot. and Standl.) W. C. Martin and C. R. Hutchins, Rosa woodsii var. hypoleuca (Woot. and Standl.) W. C. Martin and C. R. Hutchins, Rosa woodsii var. macounii (Greene) W. C. Martin and C. R. Hutchins.
- 82. Rosa xanthina Lindl. Hemsl. Non-indigenous rose from north China and Korea; Zone 6; South Carolina. Synonymy: Rosa hugonis
- 83. Rosa yainacensis Greene, (native). Cascade rose. Washington to California.

None of the above roses are known to be rare or endangered; many have ranges restricted to mountains, to the northern regions, to marshes, to deserts or to the west. Several introduced roses have become noxious weeds. The Macartney rose (Rosa bracteata Wendland) was imported into Texas from eastern Asia and has become a noxious weed along the Gulf Coast, infesting more than 500,000 acres of productive grasslands in 40 southeastern Texas counties (Scott, 1965). The Cherokee rose (Rosa laevigata Michaux), another introduced plant from China (however, the State Flower of Georgia), became a severe weed in the Black Belt region (several counties characterized by rich, dark soil) in central Alabama. Land covered by the weed in nine counties could have produced 1.5 million pounds of beef annually, if in productive pasture (Scott, 1965). Rosa canina L., a native of Europe and west Asia, has been introduced into most of the eastern United States; it is widely dispersed and occasionally found to be abundant, but has shown no weedy propensity in the east. The large hips of *R. canina* are valued by natural food enthusiasts. Rosa eglanteria L., another native of Europe has become widely dispersed in the United States; it is very weedy in New Zealand. Rosa rugosa Thunb., another non-indigenous rose from China, has been introduced throughout the eastern US; this species is commonly cultivated as an ornamental species rose; it has escaped and become abundant along the northeast coast, especially in Long Island, New York (Amrine, pers. observ., 2001) and Maine (Peck, 2001).

Common native roses in eastern North America include the prickly rose, *Rosa acicularis* Lindl. (in mountains and northern regions), the smooth rose (*Rosa blanda* Aiton), the prairie rose (*R. setigera*), the swamp rose (*Rosa palustris* Marsh), the Virginia rose (*R. virginiana*) and the pasture rose (*Rosa carolina* L.). None of these native roses have become weeds except in rare instances. Abundant natural controls and seed predators probably prevent them from becoming weeds. The introduced roses, *Rosa eglanteria* L., *R. canina*, and *R. rugosa*, all ornamental species, have escaped and are commonly found in many areas, but have not been observed to be significant weeds.

Related Species

Only the genus Rosa occurs in the tribe Roseae. The most closely related plants are members of the tribes Potentilleae (Sections Rubinae, Potentillinae, Dryadinae), Cercocarpaceae, Ulmariëae, and Sanguisorbeae. Thus, genera most closely related to Rosa are Rubus (blackberries, raspberries, brambles; probably more than 75 species occur in eastern North America), Potentilla (cinquefoil, 15 species), Fragaria (strawberries, five species), Geum (avens, 10 species), Dryas (mountain avens, two species in western North America), Adenostema (chamise, ribbonwood; two species in California), Purshia (antelope bush, two species in western North America), Cercocarpus (mountain mahogany, five species in western North America), Alchemilla (lady's mantle, parsley-piert; three to four naturalized species in eastern North America), Agrimonia (beggar-ticks, about 10 species in eastern North America), Poterium (burnet, one species naturalized in eastern North America) and Filipendula (meadowsweet, two or three native or naturalized species in eastern North America). Some of the Rubus are occasionally attacked by the rose stem girdler, Agrilus aurichalceus aurichalceus Redtenbacher; none of the other arthropods or diseases affecting multiflora rose, discussed herein, occur on any of these related plants.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

As mentioned above, *R. multiflora* originated in eastern Asia. It is native to Japan, Korea and northeast China and a wide variety of other deciduous-forest podzol areas of eastern Asia that are similar to those of the eastern United States (Good, 1964). It also occurs in similar areas of Europe.

Areas Surveyed for Natural Enemies and Natural Enemies Found

Hindal and Wong (1988) surveyed West Virginia for arthropods and diseases occuring on multiflora rose. They found several insects and diseases, of which the following were noted: the rose seed chalcid, Megastigmus aculeatus var. nigroflavus Hoffmeyer (Hymenoptera: Torymidae), introduced from Japan; a native raspberry cane borer, Oberea bimaculata Olivier (Coleoptera: Cerambycidae); a native tortricid hip borer, Grapolita packerdi Zeller (Lepidoptera: Tortricidae); a native powdery mildew (Sphaerotheca sp.); several native fungi that cause cankers (species of Epicoccum, Leptosphaeria, Phoma, and Phomopsis); and several introduced European stem gall forming species, from which bacteria were cultured that were similar to Agrobacterium tumefasciens (E. F. Sm. et Towns.) Conn. Of these, only the seed chalcid appeared to present any possibility of significant biological control. Mays and Kok (1988) found the seed chalcids in roses in Virginia, and Shaffer (1987) reported finding the seed chalcid in all counties of West Virginia that were surveyed as well as in Indiana, Kentucky, Maryland, Ohio, and Pennsylvania. To our knowledge, no surveys have been conducted for natural enemies of multiflora rose in eastern Asia. Consequently, surveys of natural enemies associated with this rose in its native range and compilation from the literature of its known natural enemies, both typical early steps of most plant biological control projects, have not been done.

Host Range Tests and Results

Results of host range tests for the eriophyid mite Phyllocoptes fructiphilus Keifer (vector of rose rosette disease [RRD]) and the rose rosette disease virus are given in Tables 1 through 3. Most native roses in the midatlantic region have been tested and can not be infected with RRD; all are excellent hosts for the mite. Most ornamental roses are capable of sustaining the mite and of being infected by RRD. Many cultivars are very susceptible to RRD and these are indicated in the tables in bold type. Only members of Rosa can be infected with RRD or serve as hosts for the mite. A large number of other rosaceous plants have been tested for RRD susceptibility and mite acceptance. All tests, including backgrafts to multiflora rose, have been negative. None of the other rosaceous plants support the mite. A number of grafted rosaceous plants have been grown at the West Virginia University Horticulture Farm since 1989; to date, none have shown any symptoms of RRD and backgrafts have been negative. The rose seed chalcid has only been found in seed from multiflora rose; apparently differences in the hips and/or times of flowering prevent the chalcid from successfully developing in seeds of other roses.

Releases Made

To our knowledge, no intentional releases were made of any of the insects, mites, or pathogens discussed in the following section; all are either native North American species or, as in the case of the rose stem girdler and the multiflora rose seed chalcid, were accidentally introduced. Rose rosette disease has been transmitted to target multiflora roses by grafting and by mite releases in Iowa and West Virginia (Amrine and Stasny, 1993; Epstein and Hill, 1994b, 1995b; Amrine et al., 1995; Epstein, 1995; Epstein et al., 1997). Because of the susceptibility of many ornamental roses to RRD and P. fructiphilus (Tables 1 and 3), this work has been opposed by the American Rose Society and by rosarians in general (Obrycki, 1995; Philley, 1995; Peck, 2001; Pagliai, pers. comm.). However, augmentation research has provided valuable information on the potential spread of RRD. Experi-

Table 1. Occurrence of Rose Rosette Disease in Species (italics) and Ornamental
Roses (varieties in bold are very susceptible) (alphabetical by species or
variety, *R*. ignored).

Rosa species or Cultivar	Citation	Location	Susceptible (S), Resistant (R) or Tolerant (T)
Alba Maxima	19	Manassas, Virginia	S
American Pillar (Rambler)	18	Alabama	S
<i>R. arkansana</i> Porter = <i>suffulta</i> Greene	1, 7, 8, 9	Nebraska	Т
R. banksiae Aiton	15	Georgia	S
Belle of Portugal (CL)	6	California	S
Bibi Mazoon (SH)	15	Tennessee	S
Black Jade (HT)	11	Missouri	S
Bonica	13, 17, 18	lowa	R (mites)
Buff Beauty (hybrid musk)	18	South Carolina	S
Cara Mia (HT)	10	West Virginia	S
R. canina	1, 7, 8, 9, 10	Nebraska (1,7)	S
		Manitoba (1)	S
		California (8,9)	S
		Indiana (10)	S
Cherry Meidiland (SH)	15	Tennessee	S
Chicago Peace (HT)	11, 14	Missouri	S
Chrysler Imperial (HT)	11, 17	Missouri, Iowa	S
Climbers	7	Nebraska	S
Color Magic	13	lowa	S
Comtessa de Cayla	15	Alabama	S
Constance Spry (climbing shr.)	18	Georgia	S
Crystalline (HT)	15	Tennessee	S
Double Delight (HT)	15	Tennessee	S
Dr. Huey (CL)	15	Tennessee	S
<i>R. dumetorum</i> Thuill (= <i>corymbifera</i> Borkh.)	7, 8, 9	Nebraska	S
R. eglanteria	1, 7, 8, 9	Nebraska	S
R. eglanteria stock w/ hybrids	1	Nebraska	S
English Perfume (HT)	15	Tennessee	S
Europeana (FL)	15	Tennessee	S

Table 1. Occurrence of Rose Rosette Disease in Species (italics) and Orna	nental
Roses (varieties in bold are very susceptible) (alphabetical by spe	cies or
variety, R. ignored) (continued).	

Rosa species or Cultivar	Citation	Location	Susceptible (S), Resistant (R) or Tolerant (T)
Etna	19	Manassas, Virginia	S
First Prize (HT)	15	Tennessee	S
Florabundas	1, 15	Nebraska	S
Fourth of July	15	Georgia	S
Fragrant Cloud (HT)	11	Missouri	S
Francisco Juranville	15	Alabama	S
French Lace (G)	11, 14	Missouri	S
R. gallica L.	1	Nebraska	S
Garden Party (HT)	11, 14	Missouri	S
	15	Tennessee	S
Gertrude Jeckyl (SH)	15	Tennessee	S
Gold Medal (G)	11, 12, 14	Missouri	S
Graham Thomas (Engl. R.)	11, 14	Missouri	S
Grandifloras	1	Nebraska	S
Great Scott (HT)	18	West Virginia	S
Gros Choux d'Hollande	19	Manassas, Virginia	S
Henri Martin	19	Manassas, Virginia	S
R. hugonis Hemsl.	1, 7, 8, 9	Nebraska	S
		California	S
Hybrid Teas	1	Nebraska	S
Hybrid Musk	18	Georgia	S
lpsilante-Gallica	15	Tennessee	S
Irresistable (M)	15	Tennessee	S
Jean Camiole (M)	1	Missouri	S
Jeanne LaJoie (C-MR)	18	West Virginia	S
Jennifer Heart (HT)	11	Missouri	S
Kathleen Harrop	19	Manassas, Virginia	S
Lady Banksia (species rose)	18	South Carolina	S
La Noblesse	19	Manassas, Virginia	S
Loving Touch (M)	11	Missouri	S
Lynn Anderson	15	Tennessee	S

Table 1. Occurrence of Rose Rosette Disease in Species (italics) and Ornamental
Roses (varieties in bold are very susceptible) (alphabetical by species or
variety, R. ignored) (continued).

Rosa species or Cultivar	Citation	Location	Susceptible (S), Resistant (R) or Tolerant (T)
Maiden's Blush	19	Manassas, Virginia	S
Mme Alfred Carriere (noisette)	18	Alabama	S
Mary rose	15	Alabama	S
Mermaid	15	Alabama	S
Mons.Tillier	15	Texas	S
R. montezumae Hum. & Bonpl.	7,8	California	S
Mr. Lincoln (HT)	11,14	Missouri	S
R. multiflora Thunb.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15, 18	Arkansas (4)	S
		California (6,8,9)	S
		Georgia (18)	S
		Illinois (10)	S
		Indiana (10)	S
		Kentucky (10)	S
		Missouri (2,3)	S
		Nebraska (1,7)	S
		Oklahoma (2)	S
		Tennessee (15)	S
		Texas (15)	S
		West Virginia (10)	S
Napoleon	15	Alabama	S
New Dawn	15	Alabama	S
	19	Washington (D.C.)	S
R. nutkana Presl.	6	California	S
R. odorata (Andr.) Sweet.	6	California	S
Old Blush Climber	15	Alabama	S
Old Fashioned Roses	7	Nebraska	S
Olympiad	14	California?	S

Table 1. Occurrence of Rose Rosette Disease in Species (italics) and Ornamer	ıtal
Roses (varieties in bold are very susceptible) (alphabetical by species	or
variety, R. ignored) (continued).	

Rosa species or Cultivar	Citation	Location	Susceptible (S), Resistant (R) or Tolerant (T)
Ornamental Roses	2, 3, 4, 6, 15	Alabama (15)	S
		Arkansas (4)	S
		California (6)	S
		Georgia (15)	S
		Kansas (2)	S
		Missouri (2, 3)	S
		Oklahoma (2)	S
		Tennessee	S
		Texas (15)	S
		Virginia (15)	S
Othello (Engl. Rose)	11, 14	Missouri	S
Peace	17	lowa	S
Perfume Delight (HT)	15	Tennessee	S
Petite Orleanaise	19	Manassas, Virginia	S
Pink Peace (HT)	11, 14	Missouri	S
R. pisocarpa Gray	6	California	S
Properity	18	Georgia	S
Ragged Robin (China Rose)	6	California	S
Red Cascade (CM)	15	Georgia	S
Red Meidiland	13, 14	Missouri	S
Rina Hugo (HT)	15	Tennessee	S
Rose de Rescht (PT)	15	Tennessee	S
<i>R. rubrifolia</i> Vill.	6, 7, 8, 9	California (6-9)	S
		Wyoming (6)	S
Salet	19	Manassas, Virginia	S
Seven Sisters (hybrid multifl.)	15	Tennessee	S
Simply Irresistable (FL)	15	Tennessee	S
R. soulieana Crep.	1	Nebraska	S
R. spinosissima var. altaica (L.) Rehd.	1,8,9	Nebraska (1)	S
		California (8, 9)	S

Table 1. Occurrence of Rose Rosette Disease in Species (italics) and Ornamenta	ıl
Roses (varieties in bold are very susceptible) (alphabetical by species o	r
variety, R. ignored) (continued).	

Rosa species or Cultivar	Citation	Location	Susceptible (S), Resistant (R) or Tolerant (T)
Starry Night (shrub rose)	18	South Carolina	S
Sun Flair (G)	11,14	Missouri	S
The Bishop	19	Manassas, Virginia	S
The Fairy (P)	15	Tennessee	S
The Squire (SH)	18	West Virginia	S
Turner's Crimson Rambler	15	Tennessee	S
Veteran's Honor (HT)	15	Tennessee	S
<i>R. villosa</i> L. (= R. <i>pomifera</i> J. Herrm.)	7, 8, 9	Nebraska (1, 7)	S
		California (8,9)	S
White Masterpiece (HT)	18	West Virginia	S
R. wichurana Crépin (RB)	15	Tennessee	S
William Lobb	19	Manassas, Virginia	S
R. woodsii Lindl.	1,7,8,9	Nebraska (1, 7)	т
		California (8, 9)	S
R. woodsii var. ultramontana (Wats.) (= R. gratissima Greene)	5, 8, 9	California	S
Resistant Species, Varieties			
R. arkansana Porter	16	lowa	R
R. blanda Aiton	16	lowa	R
R. californica Cham. & Schon.	6	California	R
R. palustris Marsh.	10	West Virginia	R
<i>R. setigera</i> Michx.	10, 16	West Virg., Iowa	R
R. spinosissima L.	6,7	Nebraska (7)	R
		California (6)	R

Citations: 1) Allington *et al.*,1968, 2) Crowe, 1983, 3) Doudrick and Millikan, 1983, 4)
Gergerich and Kim, 1983, 5) Keifer, 1966, 6) Thomas and Scott, 1953, 7) Viehmeyer, 1961, 8) Wagnon, 1966, 9) Wagnon, 1970, 10) Amrine *et al.*, 1995, 11) Finkes, 1991, 12) Worden, 1988, 13) Epstein and Hill, 1998, 14) Sauer, 2001, 15) Peck, 2001, 16)
Epstein and Hill, 1994, 17) Epstein and Hill, 1999, , 18) Peck 2002, 19) Higgins 2001.

Abbreviations: CL = Large-flowered climber, CM = Climbing miniature, Engl. R. = English rose, FL = Floribunda, G = Grandiflora, HT = Hybrid Tea, M = Miniature, P = Pollyanna, PT = Portland rose, RB = Rambler, SH = Shrub; R = Resistant, S = Susceptible, T = Tolerant.

Disease.		
Thomas & Scott, 1953	Holodiscus discolor	Cream Bush (grafting only)
	Fragaria chiloensis	Beach Strawberry
	Prunus ilicifolia	Holly-leaved Cherry
Doudrick, 1984	Malus pumila	Apple (grafting only)
	Prunus besseyi	Sandcherry
	P. persica atropurpurea	Peach
	P. serrulata	Japanese Cherry
	P. tomentosa	Nanking Cherry
	Pyrus communis	Pear
	Cydonia oblonga	Common Quince
	Gomphrena globosa	(Amaranthaceae)
	Vinca rosea	(Apocynaceae)
	Chenopodium quinoa	(Chenopodiaceae)
	Cucurbita pepo	(Cucurbitaceae)
	Cucuminus sativus	(Cucurbitaceae)
	Phaseolus vulgaris	(Leguminaceae)
	Vigna unguiculata	(Leguminaceae)
Amrine et al., 1990, 1995	Malus x-domestica	Apple
	P. persica atropurpurea	Peach
	Fragaria virginiana	Strawberry
(grafting and challenged with	Rubus sp.	Blackberry and Raspberry
P. fructiphilus grown on RRD	Sorbus americana	Mountain Ash
symptomatic <i>R. multiflora</i>)	Pyrus communis	Pear
	Prunus avium	Cherry
	Prunus communis	Plum
	Prunus serotina	Black Cherry
	Prunus armeniaca	Apricot

Table 2. List of Plants Tested for Susceptibility to Infection by Rose Rosette Disease.

Results: NONE of the above plants were successfully infected with RRD; Amrine and Stasny (unpublished) showed that back grafts were negative.

Plant Species	Common Name	P. fructiphilus*	P. adalius*
COMMERCIAL FRUIT:			
Fragaria virginiana	Strawberry	0	0
Malus x-domestica	Apple	0	1
Prunus armeniaca	Apricot	0	1
P. avium	Cherry	1	1
P. domestica	Plum	0	0
P. persica	Peach	1	1
Pyrus communis	Pear	0	0
Rubus sp.	Wild Blackberry	0	0
Rubus sp.	Cultivated Blackberry	0	0
Rubus sp.	Wild Raspberry	0	0
ORNAMENTAL TREES:			
Prunus serotina	Black Cherry	0	1
Sorbus americana	Mountain Ash	0	1
SPECIES ROSES:			
Rosa bracteata	McCartney Rose	1	2
R. canina	Dog Rose	2	2
R. carolina	Pasture Rose	1	2
R. fendleri	Wild Rose-Midwest	2	2
R. multiflora	Multiflora Rose	2	2
R. palustris	Swamp Rose	2	2
R. setigera	Prairie Rose	2	2
R. woodsii	Mountain Rose	2	2
ORNAMENTAL ROSES:			
	'Cherish' (florabunda)	2	2
	'Climbing Blaze' (climbing rose)	2	2
	'Headliner' (hybrid tea)	2	2
	'Orange Sunblaze' (miniature)	2	2
	'Queen Elizabeth' (grandiflora)	2	2
	'Red Rascal' (shrub rose)	2	2

Table 3. Rosaceous Pants Tested for host preference/acceptance by *Phyllocoptes fructiphilus* and *Phyllocoptes adalius*

0- mites lived less than 3 days (unsuitable).

1- mites lived for a week without laying eggs (unsuitable).

2- mites laid eggs (suitable).

mental increase of the rose seed chalcid was successful in West Virginia; infestation increased in one season from 3.2 to 77.5% (see section on multifloral rose seed chalcid under Biology and Ecology of Key Natural Enemies).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Four agents have been found in the United States that show potential for biological control of multiflora rose. These are a "virus" that causes rose rosette disease, an eriophyid mite (*P. fructiphilus*) that transmits this virus, a seed chalcid (*M. aculeatus* var. *nigroflavus*) that lays its eggs in rose hips and whose larvae feed on immature seeds, and a stem girdler (*Agrilus aurichalceus aurichalceus* Redtenbacher [Coleoptera: Buprestidae]) that kills multiflora rose canes.

Rose Rosette Disease and *Phyllocoptes fructiphilus* Keifer (Acari: Eriophyidae)

Rose rosette disease was first found in California, Wyoming, and Manitoba, Canada in 1941. It was found to occur on ornamental roses and on Rosa woodsii Lindl., the common rose in Rocky Mountain uplands and the western plains from Minnesota to British Columbia, south to California, Arizona, and Mexico (Liberty Hyde Bailey, 1976). Rose rosette disease produces symptoms in R. woodsii but does not kill the plant (Allington et al., 1968). It was found in Nebraska in 1961 (Viehmeyer, 1961), in Kansas in 1976, in Missouri in 1978, and in Arkansas and Oklahoma in 1982 (Crowe, 1983). It was found in Kentucky and Indiana in 1986 (Hindal et al., 1988). Brown (1995) published a U.S. map showing RRD's known distribution as far east as Ohio, Pennsylvania, Tennessee, and West Virginia in 1994. This native pathogen has caused a fatal epidemic in Rosa multiflora from the Great Plains as far east as Berks County, Pennsylvania and Queen Annes County, Maryland, in the Delmarva peninsula (Fig. 2) (Amrine and Stasny, 1993; Epstein and Hill, 1995a, 1999).

Rose rosette disease is a mite-transmitted, graftable "virus" that produces fragments of doublestranded RNA in rose tissue (Frist, pers. comm.; Di *et al.*, 1990; Hill *et al.*, 1995). Various structures found in electron microscope micrographs have been tentatively identified as the agent (Gergerich and Kim, 1983), but none have been conclusively proven to be the agent. It has not yet been taxonomically charac-

terized (Epstein and Hill, 1999). Symptoms of RRD in multiflora rose include red, purplish or dark green veinal pigmentation (Fig. 3); production of bright red lateral shoots (Fig. 4); enlarged stems and stipules; dense, yellowish, dwarfed foliage; and premature development of lateral buds producing many compact lateral branches forming "witches' brooms" (Figs. 5 and 6) (Amrine and Hindal, 1988; Epstein et al, 1993; Epstein and Hill, 1999). Symptomatic canes are cold sensitive and usually die at temperatures below -10°C. Symptoms on ornamental roses include a yellow mosaic pattern on leaves, greatly increased thorniness of stems (Fig. 7), clumped and wrinkled foliage, and witches' brooms; however, the bright red lateral shoots and vein mosaic seen in multiflora rose do not usually occur except on a few varieties (Thomas and Scott, 1953; Allington et al., 1968; Amrine and Hindal, 1988; Epstein et al., 1993; Epstein and Hill, 1998, 1999,).

Rose rosette disease is transmitted by the eriophyid mite, P. fructiphilus (Figs. 8, 9, and 10), which develops in high numbers on shoots of RRD-infected multiflora roses and other rose species (Amrine et al., 1988). Phyllocoptes fructiphilus was first described from Rosa californica Cham. et Schlechtend. in California by Keifer (1940). Since that date, it often has been found associated with RRD in roses throughout the United States (Amrine and Stasny, 1993; Epstein and Hill, 1994b; Epstein and Hill, 1995a, 1999; Amrine et al., 1995; Amrine, 1996). The mite often occurs in the absence of the virus, producing no visible symptoms on rose plants. It only develops on tender, rapidly growing tissue and is aerially disseminated (Zhao 2000). Doudrick (1984) and Doudrick et al. (1983) claimed that *Phyllocoptes* fructiphilus could not transmit RRD to multiflora roses. They conducted transmission tests by transferring mites from field collected symptomatic plants onto the foliage of greenhouse plants. Amrine et al. (1988) conducted transmission tests on large plants trimmed to the crown, transplanted to greenhouse mist beds and obtained 100% transmission in 17 days when mites were applied to the tips of new, rapidly growing shoots. These experiences show that transmission can be very difficult if mites are applied to older, slower growing plants; it also probably explains the slow rate of spread of RRD since 1989, since most of West Virginia has endured varying states of drought since that time. Return of moister conditions may result in more rapid spread of RRD.

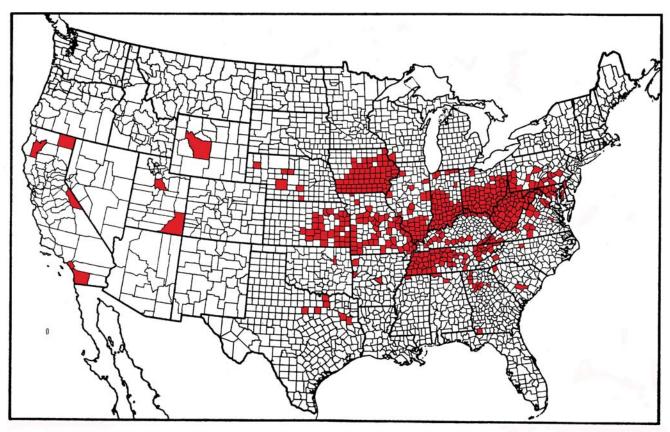


Figure 2. Map of the known distribution of Rose Rosette Disease in the USA; Virginia data from A. Boudoin (2002), J. Amrine, and A. Peck (2002); Maryland data from Tipping & Sindermann (2000), and J. Amrine; data for North Carolina, South Carolina and Georgia from A. Peck (2002).



Figure 3. Rose rosette; irregular reddening of leaf caused by RRD. (Photograph by Jim Amrine.)



Figure 4. Bright red RRD shoots emerging in the spring. (Photograph by Jim Amrine.)



Figure 5. Witches broom of RRD (yellow stems) on multiflora rose, heavily affected by powdery mildew. (Photograph by Jim Amrine.)



Figure 7. Cara-Mia ornamental rose: diseased stem on left with an enlarged thorny stem; normal stem and flower on right (Photograph by Jim Amrine.)



Figure 9. *Phyllocoptes fructiphilus,* dorsal shield of female showing the distinctive pattern that identifies this mite (SEM) (Photograph by West Virginia University Anatomy Department.)



Figure 6. RRD-symptomatic inflorescence (red pannicle) on multiflora rose, accompanied by normal flowers on healthy foliage (a separate plant) (Photograph by Jim Amrine.)

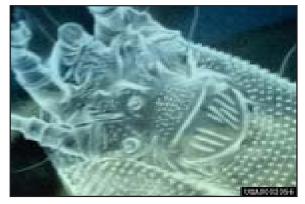


Figure 8. *Phyllocoptes fructiphilus,* ventral surface near head end as seen by the scanning electron microscope; the mite is about 50 microns wide at the genital coverflap. (Photograph by West Virginia University Anatomy Department.)

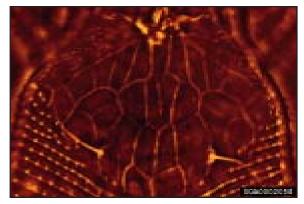


Figure 10. *Phyllocoptes fructiphilus,* dorsal shield of female as seen in the light microscope, using phase contrast microscopy. (Photograph by Jim Amrine.)

Phyllocoptes adalius Keifer is a mite very similar to *P. fructiphilus* and also occurs on many roses in the eastern United States; *P. adalius* occurs as a vagrant, usually on the underside of mature leaf blades of many species and varieties of roses. It has been thoroughly tested as a vector, but can not transmit RRD (Kharboutli, 1987; Kassar and Amrine, 1990; Amrine *et al.*, 1995). Rose rosette disease was first found in West Virginia in 1989, and spread throughout the state by 2000 (Brown and Amrine, unpub.). Several predators, a parasitic fungus, and drought appear to have affected field populations of *P. fructiphilus* in West Virginia and may have slowed the spread of RRD.

Rose rosette disease can also be transmitted by grafting, and experiments in Iowa have shown that this approach can be used to augment the virus in dense stands of multiflora rose (Epstein and Hill, 1994b; Epstein and Hill, 1995b, 1995d, 1998, 1999; Epstein et al., 1997). Obrycki et al. (2001) are conducting new trials of RRD releases and augmentation in southern Iowa to reduce multiflora rose in pastureland. They indicate that releases will not be made in areas with ornamental roses. Much of this work has been opposed by the American Rose Society and by rosarians in general (Harwood, 1995; Obrycki, 1995; Philley, 1995; Peck, 2001; Sauer, 2001; Pagliai, pers. comm.). However, augmentation research by Epstein et al. has provided valuable information on the potential spread of RRD from multiflora to ornamental roses.

Mites overwinter as adult females on living, green rose tissue (Amrine and Hindal, 1988; Amrine et al., 1995). In early spring, the mites move from wintering sites (clumps of overwintering foliage, loose bark on live stems, old or loose bud scales, etc.) onto developing shoots to lay eggs. A favorite oviposition site is between the stem and basal petiole of young leaves appressed to stems. Females live about 30 days and lay about one egg per day. Eggs hatch in three to four days and the development of each immature stage (protonymph and deutonymph) requires about two days (Kassar and Amrine, 1990; Kassar, 1992). Thus, in warm weather, one generation may be produced per week. Development is continuous throughout the season until weather turns cold in the fall and mites seek protective wintering sites on the plants. Overwintering mites will die if host canes die, as they require green stem or leaf tissue.

In May, 1987, Amrine et al. (1990) began a longterm study at Clifty Falls State Park in Madison, Indiana. The site was heavily infested with both healthy and RRD-symptomatic multiflora roses. A total of 180 multiflora rose plants were marked and visited monthly during the growing season for the next five years. The initial average density was 1,200 plants per acre and, at the beginning of the study, 30% of plants were symptomatic and 1% had been killed by RRD. The infection increased each year and leveled off to 94% by September 1991 with a mortality of 88%. The average longevity of infected plants was 22.4 months (range three to 48 months). Mite populations were 14 times larger on symptomatic plants compared to healthy plants in 1987 and 1988. Mite populations were low and sporadic in April and gradually increased to peak abundance by September in most years. At peak abundance, nearly all RRD-symptomatic plants (98%+) were infested with mites. The average number of mites per symptomatic shoot in September of each year (1987 to 90) was 112, 30, 112, and 6.6 respectively (mite density on healthy plants was usually below 10 per shoot). The low average number in 1988 (30) resulted from a severe drought that killed mites on desiccated foliage. The low fall density in 1990 (6.6) resulted from unusually cold weather in December 1989 (-31°C), which killed nearly all above ground RRD-symptomatic canes and thus killed most of the overwintering mites. By the end of the study (1994), 97% of the marked plants were dead or symptomatic and the density of live multiflora roses had dropped to about 800 per acre, many of which were new, small plants.

As of 2001, RRD was present in multiflora roses in all counties in West Virginia and was found as far east as Berks County, Pennyslvania, Queen Anne and Talbot Counties, Maryland and Manassas Battlefield, Virginia (Fig. 2). The disease is probably present in Delaware, New Jersey, New York, and other eastern states. It is likely that RRD will be present throughout the eastern United States within ten years. RRD will have a very significant effect on multiflora rose populations, potentially reducing numbers by 90% or more throughout the region. In each local area, the RRD epidemic is likely to continue until multiflora rose stands are killed. Young seedlings will then sprout and reach moderate size before RRD again reinfects the stand. In Madison, Indiana, for example, a survey in 1994 found that while more than 97% of the original large plants had died of RRD, the infection rate of the abundant, newly sprouted plants was only 20 to 25%. The low percent infection rate reflects the slow build up of the infection in new plants. A visit to Clifty Falls State Park on 26 May 2002 revealed an estimated density of 200-400 multiflora roses per acre with an infestation of 60% RRD. Much of the original grassland has become early stage forest, which will shade future germinating seed and the resulting plants. As another example, RRD was first discovered in Monongalia County, West Virginia in 1989; as of July 2001, the average infection rate throughout the county was 10 to 20%. We expect to see infection rates equivalent to Madison, Indiana (30%) within five more years.

A serious limitation to the use of RRD as a biological control agent is its ability to infect ornamental roses. Many species and varieties of roses are susceptable to the vector and to RRD (Tables 1 and 3). However, other plants in the Rosaceae have been found to be immune to the RRD agent (Table 2). Rose breeders and gardeners throughout the eastern United States will need to reduce local stands of multiflora rose for a one or two mile radius in order to lower the risk of infestation by airborne mites, which transmit RRD. Thomas and Scott (1953), Allington et al. (1968), Amrine et al. (1995), and Epstein and Hill (1998, 1999) listed varieties and cultivars of ornamental roses that are particularly susceptible to RRD and its vector (also, see listings in bold type in Table 1). Avoiding planting of these varieties can help reduce injury to adjacent ornamental roses. Peck (2001) listed Cygon 2E (citing work by Dr. George Philley, Plant Pathologist, Texas A&M, Overton, Texas) as a treatment for protecting ornamental roses; other chemicals such as Avid (abamectin) may prove effective in controlling the mites. Thomas and Scott (1953), Allington et al. (1968), and Amrine et al. (1995) discussed varieties of roses resistant to RRD. This information can be used to incorporate resistance into new rose varieties.

Multiflora Rose Seed Chalcid, *Megastigmus aculeatus* var. *nigroflavus* Hoffmeyer (Hymenoptera: Torymidae)

The multiflora rose seed chalcid (*M. aculeatus* var. *nigroflavus*) is a light, yellowish-brown, small torymid (chalcidoid) wasp about 2 to 3 mm long (Fig. 11). It was reported in the United States from New

Jersey in 1917, where it caused high mortality of multiflora rose seed imported from Japan for rootstock for ornamental roses (Weiss, 1917). Milliron (1949) reported that the rose seed chalcid was established in several mid-Atlantic states. Scott (1965) found large numbers of the rose seed chalcid at the Patuxent National Wildlife Refuge near Washington D.C. with infestation rates as high as 95%. Mays and Kok (1988) surveyed for the multiflora rose seed chalcid in Virginia in 1985 and 1986 and found average infestation rates of 26.5% (range of 2 to 59%) and 23.9% (range of 2 to 52%). Nalepa (1989) found the chalcid throughout North Carolina; with an average infestation rate of 63%. She also found two possible parasites of the seed chalcid in low numbers, Eurytoma sp. (Hymenoptera: Eurytomidae) (n=11) and Eupelmus rosae Ashmead (Hymenoptera: Eupelmidae) (n=4), out of 4,295 chalcids reared. Amrine and Stasny (1993) surveyed multiflora rose seed (Figs. 12 and 13) in West Virginia in 1984 and 1985 and found an average of 49.7% (range 0 to 100%) of viable seed infested with the chalcid. A survey of 16 sites from Maryland, Missouri, Oklahoma, Pennsylvania, Tennessee, Texas, and Virginia in 1984 to 1985 found an average infestation rate of 46.7 % (range of 0 to 95%).

The seed chalcid oviposits in the developing receptacle just after petal-fall in June (Fig. 14). Eggs hatch and larvae (Fig. 15) develop in the ovules beginning in mid-August, consuming and killing the seeds. Larvae mature in late September and enter diapause. In winter, larvae may die if exposed to temperatures below -20°C for 12 hours, and mortality reaches 20 to 80% if temperatures fall below -26°C for more than 24 hours. Seed chalcids in rose hips near the ground and in other protected sites survive low temperatures better than those in hips on exposed canes. Larvae in scattered seeds on the ground survive low winter temperatures if the ground is covered by snow. By late May, larvae transform to pupae. At about petal fall (early to mid-June in West Virginia), adult wasps chew their way out of the seed, emerge, mate and begin oviposition into immature rose hips. Most females are parthenogenic but will mate if males are available. The sex ratio was 0.5% males or about one male to 200 females.

Shaffer (1987) found that seed chalcids have limited ability to fly to newly established rose plantings. Most dispersal is by movement of infested seed by birds; seed chalcids rapidly pass the gut unharmed if



Figure 11. The multiflora rose seed chalcid, *Megastigmus aculeatus* var. *nigroflavus* Hoffmeyer; three females in a dissecting tray; the left female is about 2 mm long. (Photograph by Jim Amrine.)



Figure 12. Hypanthia or hips of multiflora rose. (Photograph by Jim Amrine.)



Figure 13. A dissected hip of multiflora rose: the *soft* fruit shell is on the right (typical of mid-November), five normal-sized seed are at the upper left, and three dwarf seed, representing unpollinated ovules at the lower left; note the abundant, sharply tapered fibers that are always present in the hip; they irritate the digestive tract of song birds, causing the seed to move quickly through the gut in just a few hours. (Photograph by Jim Amrine.)



Figure 14. Ovipositing female rose seed chalcid, inserting her ovipositor near the edge of the dried inflorescence. (Photograph by Jim Amrine.)



Figure 15. Dissected seeds showing larvae and a pupa of the chalcid that were inside (May). (Photograph by Jim Amrine.)

the seed are eaten by song birds such as robins and mockingbirds (Balduf, 1959; Lincoln, 1978; Nalepa, 1989, Amrine unpubl.). Multiflora roses planted in the eastern United States were set out as rooted cuttings, not planted from seeds. Thus chalcids were not disseminated when plants were initially established. Two or three decades are likely to be required, without active dissemination by humans, before the seed chalcid reaches all multiflora rose stands in the eastern United States.

Research suggests that the seed chalcid can quickly infest multiflora rose stands once it has reached them. For example, in 1988 two 30m rows of multiflora roses, each containing 50 plants, were set out as rooted cuttings in test plots in West Virginia. The plants first bloomed in 1989 and produced abundant seed in 1990 and 1991 (12 samples; 20 hips each produced an average of 125.3 seed per sample; 90.3% were viable). In November 1991, 3.2% (range of 0 to 14%) of seeds in the plot were infested with seed chalcids. Multiflora roses growing within 500 m of the plot had an infestation rate of 74.1% (range of 64 to 79%). The seed chalcids likely had reached the new plantings in droppings of birds that fed on the hips produced in 1990. In fall 1991, numbers of seed chalcids in the plot were augmented by placing about 1,500 rose hips (average of seven seeds per hip), which had an infestation rate of 79%. In December 1992, the seed infestation rate in the plot reached 77.5% (20 samples; 20 hips each; range of 57 to 93%).

Suggestions that this seed chalcid will infest the seed of other roses seem unfounded. Torymid infestation of seeds of R. setigera, R. palustris, R. carolina, or Rosa canina L., in our study sites over the past 15 years have not been observed. Balduf (1959) reported rearing a dark form of Megastigmus aculeatus from Rosa eglanteria and R. virginiana; these were not reported to be Megastigmus aculeatus var. nigroflavus Hoffmeyer. Only R. multiflora seems to be susceptible, either because of timing of bloom (late May to early June for multifloras in West Virginia versus July for the others), or because the fruits of other roses are too large or thick for the chalcids' ovipositors to penetrate. Of 31 states in the eastern United States sampled by the author, the chalcid was found in all except Florida, Louisiana, Mississippi, Texas, and northern New England. It will continue to spread by feeding birds until all stands of multiflora roses are infested. Weiss's report (1917) about seed from Japan having 95% infestation indicates the probable potential for this seed chalcid to infest the seed of multiflora rose.

It is virtually certain that RRD will greatly reduce the density of multiflora rose. No multifloras have been found that are resistant to the disease (Amrine et al., 1990, Amrine and Stasny, 1993; Epstein and Hill, 1998). The reduced populations of multiflora rose remaining after the RRD epidemic are likely to be infested by the seed chalcid at the same rate (90 to 95%) as plants in Korea and Japan. Multiflora rose will then be another occasional plant in the environment, and not the noxious weed that it is today. We estimate that this scenario will transpire within the next three to five decades. Farmers and others wanting eradication of multiflora rose desire human intervention to increase the rate of spread of the disease, the mite and the torymid into uninfested areas. However, rosarians desire that all augmentation work with RRD and the mite cease.

Rose Stem Girdler, *Agrilus aurichalceus* Redtenbacher (Coleoptera: Buprestidae)

Synonyms for this species include Agrilus viridis L., Agrilus viridis var. fagi Ratz., Agrilus communis var. rubicola Abeille, Agrilus rubicola Abeille, and Agrilus politus Say. Many reports of this insect in Rubus (brambles) were made under the name Agrilus ruficolis (Fabricius), the red-necked cane borer, whose symptoms are nearly identical. The two beetles are distinctive and easily separated. This small brownishgolden, metallic buprestid beetle is about 5 to 9 mm long (Fig. 16). It is a non-indigenous species from Europe that has been established throughout eastern North America and is abundant at several sites in Delaware, Indiana, Maryland, Ohio, Pennsylvania, Virginia, and West Virginia. It caused a small degree of control of multiflora rose in Ohio and West Virginia (Amrine and Stasny, 1993). All plant tissue beyond the point where the stem is girdled was killed, including developing rose hips and seeds. Borers overwinter in the previous year's canes, pupate in April, and emerge as adults in May. Douglas and Cowles (2001) state that development may require two seasons, which is contrary to all other reports. Adults can be found on multiflora rose foliage in sunny mornings. Females oviposit on the bark of new canes in May and June. Larvae hatch and burrow under the bark, moving upward from the oviposition site (Fig. 17). The initial burrowing does not kill the cane but by late July the infested stems begin to wilt, and by August-September, canes beyond the girdle die and appear as brown "flags" on rose bushes (Figs. 18-19.)

The largest infestation we observed was a site with 20% of canes infested (Fayette County, Ohio, 1988). Large numbers of larvae were found to be parasitized; 22 parasitic wasps emerged from 45 canes held for the emergence of 23 beetles. These parasites were Ptinobius magnificus (Ashmead) (Pteromalidae)(determined by E. E. Grissell), Eurytoma magdaldis Ashmead (Eurytomidae) (new host record, determined by E. E. Grissell), Leluthia astigma (Ashmead) (Braconidae) (determined by P. M. Marsh), Metapelma schwarzi (Ashmead) (Eulophidae) (new host record, determined by M. E. Schauff), and Tetrastichus agrili Crawford (Eulophidae) (determined by M. E. Schauff). The last was most abundant. Because of relatively low inci-



Figure 16. The rose stem girdler, *Agrilus aurichalceus aurichalceus*; a mating pair on a multiflora rose leaflet (May); the male is the smaller, upper beetle. (Photograph by Jim Amrine.)



Figure 18. A 'flag' or dead stem caused by the break of a cane at the girdle produced by the rose stem girdler (August) (Photograph by Jim Amrine.)

dence and high parasitization, we believe that this insect will have only minor importance as a biological control agent of multiflora rose.

Amrine and Stasny (1993) found girdled rose stems on *Rosa multiflora* only. Douglas and Cowles (2001) report that it occurs on *R. rugosa* and *R. hugonis* in Connecticut. *Agrilus aurichalceus aurichalceus* often was found attacking canes of *Rubus* (blackberries, raspberries, brambles) (Hutson, 1932; Mundinger, 1941; Davis, 1963). Brussino and



Figure 17. A girdled multiflora rose cane caused by the larva of the rose stem girdler (August); the oviposition site is at the right edge of the girdle; the cane will probably die distal to the girdle. (Photograph by Jim Amrine.)



Figure 19. Close up of girdle and broken cane caused by the rose stem girldler. (photograph by Jim Amrine.)

Scaramozzino (1982) reported it attacking *Rubus* fruticosus L., *Rubus caesius* L., and *Rosa idaeus* L. in Piedmont, Italy, where it also attacked *Rosa alpina* L., *R. canina*, *Rosa damascena* Mill., and *R. rugosa*. It has also been listed as attacking *Ribes*, *Grossularia*, *Crataegus*, and *Prunus* in North America and Europe (Garlick, 1940; Rejzek, 2001); however, these records are in error, and probably represent different species of *Agrilus* (Brussino and Scaramozzino, 1982).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

All four agents have been well established in the eastern United States and should eventually be found in all dense stands of the weeds. Rose rosette disease and *Phyllocoptes fructiphilus* have been found as far east as Berks County, Pennsylvania, Queen Anne and Talbot Counties, Maryland, and Manassas Battlefield, Virginia. Careful surveys would probably find both agents as far east as New Jersey and southern New York. The rose seed chalcid has been found in 30 eastern states, and it probably is found in all regions where multiflora rose has become established. The rose stem girdler also is found in most areas of eastern North America and in Utah.

Suppression of Target Weed

Amrine et al. (1990) showed that RRD and P. fructiphilus have excellent potential to reduce multiflora rose. Rate of infection of 180 marked plants in Clifty Falls State Park increased from 30% in 1986 to 94% in 1990. Mortality of marked roses increased from 2% to 94% in the same period. However, germination by the vast seed burden replaces most roses killed by RRD. When seed chalcids significantly infest multiflora seed, then reduction will become apparent. This RRD epidemic has now reached equivalent levels in many parts of West Virginia, and it is expected that in the next decade, similar reduction of dense stands of multiflora rose will occur. The rate of infestation of the rose seed chalcid is increasing in all areas surveyed. In some areas of West Virginia, rates of seed infestation now exceed 80% (Amrine, unpub.).

Recovery of Native Plant Communities

In Clifty Falls State Park, multiflora rose was not replaced by native plant species, but by another invasive exotic plant, Japanese honeysuckle (*Lonicera japonica* Thunb.). This weed has covered nearly all of the old dead roses and has invaded nearly every part of the park (as of 1994). In many areas of West Virginia, multiflora rose has been replaced by the noxious weeds, Tatarian honeysuckle (*Lonicera tatarica* L.), autumn olive (*Elaeagnus umbellata* Thunb.), Japanese honeysuckle, and Japanese knotweed (*Polygonum cuspidatum* Siebold et Zucc.). If the alien invasive weeds can be controlled or eliminated, then native vegetation should recover.

Economic Benefits

Millions of dollars now spent annually by farmers in many eastern states to control multiflora rose will be saved when the plant is eventually controlled. In West Virginia, during 1980 and 1981, more than 36,500 hectares were heavily infested with multiflora and a ten-year eradication program using herbicides was estimated to cost more than \$40 million (Williams and Hacker, 1982). The same or increased acreage is now infested, and allowing for inflation this cost has probably doubled. However, monetary savings will be slow to develop because of the slow natural spread of both the epidemic and biological control agents.

RECOMMENDATIONS FOR FUTURE WORK

Much work remains to be done to survey for the distribution and intensity of infection/infestation of RRD and P. fructiphilus in multiflora roses. The RRD epidemic in multiflora rose stands is expected to increase greatly over the next few decades. Studies and data are not available showing potential recovery of pastureland/farmland and savings involved; this work should be done in areas where significant mortality due to RRD has occurred (Missouri, Illinois, Indiana). Dense stands of multiflora rose will need to be controlled to prevent infection of ornamental roses with RRD. To quote R. Hartzler, "reduction of multiflora rose densities should be a common goal for rose growers and landowners" (Obrycki et al., 2001). Horticulturalists need to breed RRD-tolerant or RRD-resistant roses (Zary, 1995). The rose seed chalcid, now found throughout the eastern United States, should be intentionally released in areas wherever infestation rates are below 50 to 60%. Risk to other rose species from this seed chalcid appears to be minimal, but host range studies should be conducted to confirm the chalcid¢s suspected high specificity. This insect's high potential to reduce seeding of multiflora rose justifies its increased distribution. Even if not deliberately spread, its range will increase by birds. Eventually, multiflora rose will be reduced to low levels, occurrence of RRD will become minimal, as in California, Wyoming and Utah, where it originated, and problems for farmers and rosarians alike should be greatly reduced.

ACKNOWLEDGEMENTS

I would like to dedicate this chapter to the memory of Professor Dale F. Hindal, West Virginia University Plant Pathologist, recently deceased. Our discussion of this possible research at a football brunch in 1985 began our work with multiflora rose, RRD, Phyllocoptes fructiphilus, and Megastigmus nigroflavus. His insights, humor, deep knowledge of plant pathology and entomology, and excellent teaching ability launched our adventures into this work. I also express my gratitude to the many acarologists, rosarians, plant pathologists, agronomists, and others who have shared important information regarding the mites, multiflora rose, the seed chalcid, the rose stem girdler and other arthropods discussed in this chapter. This work could not have been done without the expert assistance of my assistant, Terry Stasny. Much of our research was supported financially by the West Virginia Department of Agriculture; all of our research was conducted as part of Hatch Project 317, the Davis College of Agriculture, Forestry and Consumer Sciences, at West Virginia University.

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23 TROPICAL SODA APPLE, WETLAND NIGHTSHADE, AND TURKEY BERRY

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PEST STATUS OF WEEDS

Nature of Damage

Three non-native species of the genus *Solanum* are considered invasive weeds of agricultural and natural areas in Florida (Langeland and Burks, 1998). Tropical soda apple, *Solanum viarum* Dunal, is more widely recognized as a problem than either wetland nightshade, *Solanum tampicense* Dunal, or turkey berry, *Solanum torvum* Swartz, because it has spread rapidly throughout the southeastern United States after establishing in Florida (Westbrooks, 1998). Tropical soda apple and wetland nightshade were discovered in Florida in the early 1980s and therefore are relatively new introductions. Turkey berry was introduced into Florida more than a century ago but its invasive potential was not recognized until recently (Langeland and Burks, 1998).

All three *Solanum* spp. are on the Federal and Florida Noxious Weed Lists (USDA-APHIS-PPQ, 1999; FDACS, 1999), and are listed as Category I invasive species by the Florida Exotic Pest Plant Council (FLEPPC, 1999). Category I plants "are non-native species that have invaded natural areas, and are displacing native plants or are disrupting natural community structure and function" (FLEPPC, 1999). Although it is unclear why these non-native solanaceous plants have become invasive weeds, lack of host-specific natural enemies in the southeastern United States may have afforded a competitive advantage over native species.

Economic damage. Tropical soda apple typically invades improved pastures, which reduces livestock carrying capacity (Fig. 1). Foliage and stems are unpalatable to livestock, and dense stands of this

prickly shrub deny cattle access to shaded areas, which results in heat stress (Mullahey *et al.*, 1998). Stocking rates are drastically reduced and pasture production declines if tropical soda apple is left uncontrolled (Mullahey *et al.*, 1993). In pastures, tropical soda apple forms monocultures that shade out bahiagrass, *Paspulum notatum* Fluegge, a valuable forage species of South American origin. Bahiagrass does not tolerate shade well and productivity declines when it is forced to compete with tropical soda apple. In 1993, a survey of beef cattle operations in south Florida determined the total area of pastureland infested as 157,145 ha, twice the infestation present in 1992 (Mullahey *et al.*, 1994a).



Figure 1. Pasture infested with tropical soda apple, *Solanum viarum* Dunal, in Hendry County, Florida, United States. (Photograph courtesy of Jeff Mullahey.)

Tropical soda apple also serves as a reservoir for various diseases and insect pests of solanaceous crop plants (McGovern *et al.*, 1994ab). At least six plant viruses (cucumber mosaic virus, potato leaf-roll virus, potato virus Y, tobacco etch virus, tomato mosaic virus, and tomato mottle virus) and the potato fungus Alternaria solani Sorauer use tropical soda apple as a host and are vectored during the growing season to cultivated crops (McGovern et al., 1996). In addition, the following major crop pests utilize tropical soda apple as an alternate host: tobacco hornworm, Manduca sexta (L.); tomato hornworm, Manduca quinquemaculata (Haworth); Colorado potato beetle, Leptinotarsa decemlineata (Say); tobacco budworm, Helicoverpa virescens (Fabricius); tomato pinworm, Keiferia lycopersicella (Walsingham); green peach aphid, Myzus persicae (Sulzer); silverleaf whitefly, Bemisia argentifolii Bellows and Perring; soybean looper, Pseudoplusia includens (Walker); and southern green stink bug, Nezara viridula (L.) (Habeck et al., 1996; Medal et al., 1999b; Sudbrink et al., 2000).

Turkey berry usually invades disturbed sites such as pastures, roadsides, damp waste areas, and forest clearings (Fig. 2), and is frequently cultivated as a yard plant in South Florida for its bitter-tasting fruits (Morton, 1981; Westbrooks and Eplee, 1989). Recent studies indicate that turkey berry is potentially poisonous to animals (Abatan *et al.*, 1997), and possibly carcinogenic to humans (Balachandran and Sivaramkrishnan, 1995).



Figure 2. Turkey berry, *Solanum torvum* Swartz, growing next to a pasture in south Florida, United States. The light green turkey berry dwarfs the cow in the foreground. (Photograph courtesy of Mike Bodle.)

Ecological damage. In addition to causing economic problems, tropical soda apple reduces the biological diversity in natural areas by displacing native plants and disrupting the ecological integrity. The plant invades hammocks, ditch banks, and roadsides, where it out competes native plants (Langeland and Burks, 1998). Wooded areas comprise about 10% of the total land infested by tropical soda apple in Florida. Affected woodlands include oak and cabbage

palm hammocks (tree islands surrounded by contrasting vegetation types) and cypress heads (domeshaped tree islands with tallest trees in the center dominated by cypress, *Taxodium* spp.) (Tomlinson, 1980). Prickles on the plants create a physical barrier to animals, preventing them from passing through the infested area. Tropical soda apple also interferes with restoration efforts in Florida by invading tracts of land that are reclaimed following phosphate-mining operations (Albin, 1994).

Unlike tropical soda apple and turkey berry that are invasive in upland sites, wetland nightshade typically invades regularly flooded wetlands (Coile, 1993; Wunderlin *et al.*, 1993; Fox and Bryson 1998). Approximately 200 to 300 ha of riparian and marsh habitats in southwest Florida have been invaded by wetland nightshade. Once established, it forms large, tangled, dense stands along river margins (Fig. 3), cypress swamps, open marsh, and relatively undisturbed wetlands where it displaces more desirable native species such as pickerelweed, *Pontederia cordata* L. (A. M. Fox, pers. obser.).



Figure 3. Infestation of wetland nightshade, *Solanum tampicense* Dunal, along riverbank in southwest Florida, United States. (Photograph courtesy of Alison Fox.)

The occurrence of turkey berry as a serious weed problem in seven different countries (Holm *et al.*, 1979) is perhaps the most compelling evidence foretelling its eventual impact on Florida's native plant communities. According to Gordon and Thomas (1997), the best predictor of invasiveness is whether the plant is invasive elsewhere in a similar climate.

Extent of losses. In 1994, production losses to Florida cattle ranchers attributed to tropical soda apple infestations were estimated at \$11 million annually (Cooke, 1997), or about 1% of total Florida

beef sales. Economic losses from heat stress alone were estimated at \$2 million because cattle avoid woods infested with tropical soda apple that provide shade during the summer months (Mullahey *et al.*, 1998).

Production losses were calculated based on several assumptions, including one cow or calf unit per 1.6 ha (4 acres), 50% steer/50% heifer calf crop, and March 1994 market prices for a 500 lb. calf. The number of ha that can be used for production is reduced by the percentage of ha infested with tropical soda apple. The number of calves that could have been produced is likewise reduced because of the decrease in carrying capacity.

Tropical soda apple has been identified as a host for six plant viruses that infect important vegetable crops (McGovern et al., 1994a, 1994b, 1996). Annual sales from vegetable production in Florida approach \$1.7 billion. Transmission of the viruses identified in tropical soda apple could represent a significant loss in revenue to vegetable growers. The tomato mosaic virus, which is causing millions of dollars in losses to Florida tomato growers, uses tropical soda apple as a reservoir host (Mullahey et al., 1996). Current practices for managing tropical soda infestations also are expensive. Herbicide applications combined with mechanical control (mowing) cost an estimated \$185 per ha for dense infestations of tropical soda apple (Mislevy et al., 1996; Sturgis and Colvin, 1996; Mislevy et al., 1997).

The ability of wetland nightshade to form dense thickets that are difficult for other species to penetrate suggests this noxious weed has the potential to invade and alter many of Florida's wetland habitats as well as impede access to and use of water resources (Fox and Wigginton, 1996; Fox and Bryson, 1998).

Geographical Distribution

Tropical soda apple was first discovered in Glades County, Florida in 1988 (Mullahey *et al.*, 1993, 1998). Initially, the incidence of this plant in Florida was highest in the southern half of the state with infestations concentrated north and west of Lake Okeechobee. Statewide, the total area infested by tropical soda apple in 1990 was approximately 10,000 ha; in 1993, 162,000 ha; and by 1995, the infested area increased to approximately 0.5 million ha (Mullahey, 1996; Mullahey *et al.*, 1998). Tropical soda apple now occurs throughout the state in pastures, natural ecosystems, citrus (*Citrus* spp.), sugar cane (*Saccharum* officinarum L.), sod fields, ditch banks, and roadsides.

After establishment was confirmed in Florida, tropical soda apple quickly spread to Alabama, Georgia, Louisiana, Mississippi, North Carolina, Pennsylvania, South Carolina, Tennessee, and Puerto Rico (Bryson *et al.*, 1995; Akanda *et al.*, 1996; Westbrooks and Eplee, 1996; Mullahey *et al.*, 1998). Initial introduction of tropical soda apple into North America probably occurred from seed adhering to people's shoes or it escaped from cultivation (J. J. Mullahey, pers. comm.).

Rapid spread of tropical soda apple throughout the southeastern United States (Fig. 4) occurred inadvertently through the cattle industry (Westbrooks, 1998). The number of infested acres in Georgia, Mississippi, and Alabama was directly related to the number of cattle imported from Florida (Bryson *et al.*, 1995). Extremes in temperature and photoperiod will not prevent tropical soda apple from spreading into adjacent states (Patterson *et al.*, 1997). Tropical soda apple also has invaded other regions outside the United States including the Caribbean, Mexico, Africa, India, Nepal, and China (Chandra and Srivastava, 1978; Coile, 1993; Wunderlin *et al.*, 1993).

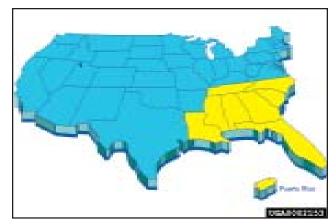


Figure 4. Distribution of tropical soda apple, *Solanum viarum* Dunal, in the United States. Infested region indicated in yellow. (Data from Westbrooks, 1998.)

Wetland nightshade was originally recorded from the Dry Tortugas in 1974 (Langeland and Burks, 1998) and in mainland Florida in 1983 (Fig. 5) (Wunderlin *et al.*, 1993; Fox and Bryson 1998). The largest infestation of wetland nightshade, approximately 60 ha, occurs in southwest Florida (Fox and Wigginton, 1996; Fox and Bryson, 1998). Turkey berry was first collected in Columbia County, Florida, in 1899, and has been reported in at least nine counties in peninsular Florida (Langeland and Burks, 1998; J. P. Cuda, pers. comm.), and a new infestation was discovered recently in Glades county (J. J. Mullahey, pers. comm.) (Fig. 5). Turkey berry also is considered a weed in 32 countries and is particularly invasive in parts of Australia and South Africa climatically similar to Florida (Holm *et al.*, 1979).



Figure 5. (a) Distribution of wetland nightshade, *Solanum tampicense* Dunal, (left-hand map) and (b) distribution of turkey berry, *Solanum toroum* Swartz, (right-hand map) in Florida, United States. Infested counties indicated in yellow. (Data from Wunderlin *et al.*, 1998.)

BACKGROUND INFORMATION ON PEST PLANTS

Taxonomy

Tropical soda apple, turkey berry, and wetland nightshade are members of the prickly Solanum subgenus Leptostemonum (Nee, 1991). Tropical soda apple (also called sodom apple, yu-a, or tutia de vibora in Argentina, and joa bravo or joa amarelo pequeno in Brazil) belongs to the section Acanthophora. This section includes 19 species characterized by prickly stems, lobed or dented prickly leaves with only simple hairs on the upper surface, and a chromosome number 2n=24 (22 in Solanum mammosum L.). Solanum chloranthum DC, Solanum viridiflorum Schlechtendal, and Solanum khasianum Clarke var. chatterjeeanum Sen Gupta are synonyms of Solanum viarum (tropical soda apple) (Nee, 1991). Solanum acanthoideum Jacquin, a species thought to be native to South Africa, is probably synonymous with S. viarum (tropical soda apple) (T. Olckers, pers. comm.).

Turkey berry (also known as susumber, gullybean, Thai eggplant, or devil's fig) is placed in the section *Torva* (D'Arcy, 1972). This section contains approximately 35 species with turkey berry designated as the type species (D'Arcy, 1972; M. Nee, pers. comm.). Langeland and Burks (1998) list *Solanum ferrugineum* Jacquin and *Solanum ficifolium* Ortega as synonyms of *S. torvum* (turkey berry).

Wetland nightshade (or aquatic soda apple, sosumba, ajicón, huistomate, huevo de gato) belongs to the section Micracantha that contains approximately 25 species including Solanum lanceifolium Jacquin (D'Arcy, 1972; M. Nee, pers. comm.). The close similarity of wetland nightshade to the latter species created some identification and nomenclatural problems (Coile, 1993; Wunderlin et al., 1993; Fox and Bryson, 1998). Solanum quercifolium Miller and Solanum houstonii Martyn are regarded as valid synonyms of S. tampicense (wetland nightshade) (Wunderlin et al., 1993; Langeland and Burks, 1998). Solanum houstonii Dunal is occasionally included in the synonymy of wetland nightshade, but S. houstonii Dunal is considered an invalid name because it is a later homonym of S. houstonii Martyn (Wunderlin et al., 1993).

Biology

Tropical soda apple can be "distinguished in Florida from other prickly Solanum spp. by its straight prickles, mixture of stellate and simple hairs with and without glands, clearly petioled leaves with a velvety sheen, terminal (white flowers with recurved petals), and yellow berries that are dark-veined when young." (Langeland and Burks, 1998) (Fig. 6). The plant is readily identified by its immature fruits, which are pale green with dark green veins, and resemble immature watermelons. Tropical soda apple can grow from a seed to a mature plant in 105 days (Mullahey and Cornell, 1994). Petioles and leaves are heavily armed with long straight prickles on leaf veins when exposed to full sunlight, but prickles are fewer in number and less developed on shaded plants (Gandolfo, 1997). Flowers and fruits are produced primarily from September through May in the United States and from November to April (spring to midfall) in Argentina (Gandolfo, 1997), with few fruits developing during summer months. A single plant produces about 150 fruits per year. Each mature fruit contains about 400 reddish brown seeds that are moderately flattened and are enveloped in a mucilaginous layer containing the glycoalkaloid solasodine.



Figure 6a.



Figure 6b.



Figure 6c.

Figure 6. Tropical soda apple, *Solanum viarum* Dunal; (a) juvenile plant; (b) typical flower; (c) mature fruits. (Photographs courtesy of Jeff Mullahey.)

Rapid spread of tropical soda apple in the southeastern United States is associated with the plant's tremendous reproductive potential, and highly effective seed dispersal mechanisms. Tropical soda apple also is capable of regenerating vegetatively from its extensive root system (Mullahey and Cornell, 1994; Akanda et al., 1996). One plant can produce on average 45,000 seeds with 70% viability (Mullahey and Colvin, 1993; Mullahey et al., 1997). In one growing season, a single plant can yield enough viable seed to produce 28,000 to 35,000 new tropical soda apple plants. Seeds will not germinate inside the fruit and must be removed from the fruit to dry (aging process) before germination can occur (Akanda et al., 1996). Seed germination occurs following exposure to favorable conditions and is enhanced by scarification (Mullahey et al., 1993). Approximately 20% of the annual seed crop is dormant (Akanda et al., 1996). Seed can remain dormant for months, although average period of dormancy is one month (Pingle and Dnyansagar, 1980). Seed viability increases with fruit diameter, not ripeness (J. J. Mullahey, pers. comm.).

Foliage of tropical soda apple is unpalatable to livestock but cattle and wildlife (deer, raccoons, feral hogs, birds) ingest the fruits and spread the seeds in their droppings (Mullahey et al., 1993; Akanda et al., 1996; Brown et al., 1996). The rapid spread of tropical soda apple is often associated with soil disturbance (Mullahey et al., 1993). Disking a field, cattle congregating around a feeder, cleaning of ditch banks, or feral hogs rooting in a field provide a favorable environment for tropical soda apple establishment and growth. Standing water will stress the plant and even cause death, but once the area begins to dry out new plants will emerge from the seed banks (Mullahey et al., 1993). Cypress heads will harbor tropical soda apple in the center of the head until completely flooded by summer rains that cause the plants to dieback to the outer, drier areas. As water in the cypress head recedes during winter months, tropical soda apple re-infests the inner regions of the cypress head.

Moving water, seed-contaminated hay, grass seed, sod, and machinery also contribute to spreading the plant. In an attempt to alleviate this problem in sod farms, the Florida Department of Agriculture and Consumer Services began charging a fee to sod farmers to certify sod as free of tropical soda apple (Mullahey *et al.*, 1998).

Tropical soda apple contains the glycolalkaloid solasodine in the mucilaginous layer surrounding the plant's seeds (Chandra and Srivastava, 1978). Solasodine, a nitrogen analogue of diosgenin, is used in the production of steroid hormones. These steroids have been useful in treatment of cancer, Addison's disease, rheumatic arthritis, and in production of contraceptives. Maximum content of solasodine in tropical soda apple fruits occurs when fruits change color from green to yellow (Kaul and Zutshi, 1977). Although intensively cultivated as a source of solasodine in Mexico and India (Sahoo and Dutta, 1984), propagation of tropical soda apple for the glycoalkaloid has significantly declined or ceased altogether in these two countries. Apparently, another solanaceous plant was discovered that contains higher levels of solasidine (J. J. Mullahey, pers. comm.).

Solasodine is poisonous to humans with symptoms appearing after consumption of the fruits; a lethal dose requires approximately 200 fruits (Frohne and Pfander, 1983). Mature fruits have a sweet smell similar to a plum or apple when the berry is opened, but the coated seed has a bitter taste (J. J. Mullahey, pers. comm.). Apparently, bitter taste does not prevent wildlife and cattle from consuming the fruits.

Turkey berry can be recognized in Florida "... by its treelike habit, (very few) stout prickles, clearly petioled leaves with dense stellate hairs (on both leaf surfaces and on the stem), numerous bright white flowers followed by yellow grape-sized berries, and glandular hairs on the flower stalks. . ." (Langeland and Burks, 1998) (Fig. 7). This prickly shrub can grow up to 3 m in height (Ivens *et al.*, 1978), and forms thickets by sprouting from lateral rhizomes. Turkey berry produces flowers and fruits year-round in tropical and subtropical regions (Adams, 1972), and the seeds are probably bird dispersed (D'Arcy, 1974). The plant is capable of growing in a variety of habitats ranging from wetlands to rocky hillsides (Adams, 1972).

Wetland nightshade is characterized "... by its (recurved prickles on the lower surface leaf veins, straight hairs on the upper surface leaf veins) and clusters of up to 11 pea-sized red berries (with no dark markings when green); its petioled longer-than-wide, deeply sinuate leaves; its pubescence of stellate hairs only (no straight or glandular hairs); and its clambering, almost vinelike habit. . ." (Langeland and Burks, 1998) (Fig. 8). The plant will thrive under conditions ranging from full shade to full sunlight but flowers and fruits prolifically from May to



Figure 7a.





Figure 7. Turkey berry, *Solanum torvum* Swartz; (a) juvenile plant; (b) flowers and unripe fruits. (Photographs courtesy of Nancy Coile.)

January when exposed to the sun (Fox and Wigginton, 1996; Fox and Bryson, 1998). New stems sprout annually from the woody base of the plant and adventitious roots form at the leaf axils. Wetland nightshade can tolerate frost and temporary high water conditions but not permanent flooding. Seeds withstand freezing and drying periods for up to 12 months with little loss in viability (Fox and Wigginton, 1996). More than 90% of the fresh seeds of wetland nightshade will germinate under suitable conditions. In riparian habitats, dispersal of seeds and stem fragments probably occurs downstream (Fox and Wigginton, 1996; Fox and Bryson, 1998).

A comprehensive list of vegetative and reproductive characteristics used to distinguish the three non-native species from other prickly solanums occurring in the southeastern United States was compiled by Fox and Bryson (1998).



Figure 8a.



Figure 8b.

Figure 8. Wetland nightshade, *Solanum tampicense* Dunal; (a) stem and leaves with recurved prickles; (b) cluster of berries and typical leaf. (Photographs courtesy of Alison Fox.)

Analysis of Related Native Plants in the Eastern United States

The genus *Solanum* contains more than 30 species that are indigenous to the United States, 27 of these occurring in the southeast (Soil Conservation Service, 1982). The potato tree, *Solanum donianum* Walpers, is found only in the Florida Keys and is listed as a threatened species in Florida (Coile, 1998). Another species potentially at risk is *Solanum pumilum* Dunal, a native plant closely related to *Solanum carolinense* L., once thought to be extinct but now known from a few locations on rock outcroppings in Alabama (M. Nee, pers. comm.) and Georgia (J. Allison, pers. comm.). The genus and family (Solanaceae) also contain economically important ornamental (e.g., petunias) and crop plants closely related to tropical soda apple, wetland nightshade, and turkey berry (Bailey, 1971). Economically important crop species such as pepper (Capsicum), tomato (Lycopersicon), tobacco (Nicotiana), eggplant, and potato (both, Solanum spp.) are valuable cash crops that contribute significantly to North American agriculture. In 1991, the combined economic value for production of solanaceous crop plants in Florida alone was reported to be approximately \$950 million (Capinera et al., 1994). Clearly, insects or pathogens introduced from the native ranges of the three exotic solanums must be target specific to minimize risk of damage to crops or non-target species (Louda et al., 1997; USDA, APHIS, PPQ, 2000).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Tropical soda apple is native to South America and wetland nightshade to the Caribbean and Central America (Wunderlin *et al.*, 1993), whereas turkey berry is a pantropical weed (D'Arcy, 1974). Tropical soda apple is endemic to southeastern Brazil, northeastern Argentina, Paraguay, and Uruguay (Nee, 1991), and is not considered an important weed in Brazil and Paraguay (Medal *et al.*, 1996). This suggests the plant is regulated by several factors in its native range (possibly natural enemies) that were excluded when tropical soda apple was introduced into Florida in the mid-1980s.

Wetland-nightshade is native to southern Mexico, Guatemala, Belize (Gentry and Standley, 1974), and the Caribbean region (Sauget and Liogier, 1957). It probably also has spread into other areas including the northern part of South America.

The area of origin for turkey berry has not been resolved. It is thought to have originated in either West Africa (Ivens *et al.*, 1978), Central/South America and the Caribbean region (Morton, 1981), or Asia (Medal *et al.*, 1999).

Areas Surveyed for Natural Enemies

Field surveys for native pathogens with potential as biological control agents for tropical soda apple were made in Florida (McGovern *et al.*, 1994ab; Charudattan and DeValerio, 1996; Charudattan *et al.*, 2001). Also, several natural enemies associated with silverleaf nightshade, *Solanum elaeagnifolium* Cavanaugh (Goeden, 1971; Olckers, 1996) were collected in south Texas to determine whether they would accept the non-native solanums as novel hosts (Cuda *et al.*, 1998, 2002). Silverleaf nightshade is native to the southern United States, Mexico, and Argentina (Goeden, 1971; Boyd *et al.*, 1983), and belongs to the same infrageneric group (subgenus *Leptostemonum* Dunal) as the three invasive *Solanum* species (D'Arcy, 1972).

A field survey for natural enemies of tropical soda apple in Brazil and northeastern Paraguay in June 1994 identified sixteen insect herbivores and several pathogens (Mullahey *et al.*, 1994b; Medal *et al.*, 1996). Additional exploratory surveys for insect natural enemies were carried out in northeastern Argentina, Brazil, southeastern Paraguay, and Uruguay (Gandolfo, 1997; Olckers *et al.*, 2002).

Natural Enemies Found

More than 75 species of insects were collected from tropical soda apple in the United States (Sudbrink *et al.*, 2000). Field surveys in Florida isolated more than 45 pathogens from the foliage, stems, and roots, including fungal isolates of *Alternaria*, *Colletotrichum*, *Curvularia*, *Fusarium*, *Helminthosporium*, *Phomopsis*, *Verticillium*, and bacterial isolates of *Ralstonia* (= *Pseudomonas*) solanacearum (E. F. Smith) Yabuuchi and *Pseudomonas syringae* van Hall pathovar tabaci (Charudattan and DeValerio, 1996). A strain of the tobacco mild green mosaic virus (TMGMV U2) was recently tested in greenhouse and field trials, and found to be lethal to tropical soda apple (Charudattan *et al.*, 2001).

The gall-making nematode *Ditylenchus phyllobius* (Thorne) Filipjev (Parker, 1991) and the defoliating leaf beetles *Leptinotarsa defecta* (Stål) and *Leptinotarsa texana* (Schaeffer) (Jacques, 1988) were screened as potential "new associates" of the nonnative solanums (Cuda *et al.*, 1998, 2002). These species severely damage their natural host plant silverleaf nightshade, but do not harm economically important solanaceous crops (Olckers *et al.*, 1995). Although silverleaf nightshade is reported from Florida (Wunderlin *et al.*, 1998), its natural enemies do not occur there (Esser and Orr, 1979; Jacques, 1985). However, climate models indicate their potential to persist in Florida if tropical soda apple, turkey berry, or wetland nightshade were suitable host plants.

The tingid Corythaica cyathicollis (Costa) and the membracid Amblyophallus maculatus Funkhonser were the two most common insects found during surveys on tropical soda apple in Brazil and Paraguay (Medal et al., 1996). Leaf-feeding beetles of the genera Metriona, Gratiana, and Platyphora as well as the nymphalid butterfly Mechanitis lysimnia Fabricius severely defoliate the plant in its native range (Medal et al., 1996; Gandolfo, 1997). The defoliating leaf beetles Metriona elatior Klug and Gratiana boliviana (Spaeth) are both promising candidates because they complement each other (D. Gandolfo, pers. comm.). Metriona elatior prefers larger plants in shaded areas whereas G. boliviana favors plants growing in open areas. The flower bud weevil Anthonomous tenebrosus Boheman, collected during surveys in Argentina and Brazil (Gandolfo, 1997), is another promising biological control candidate attacking the flower buds, which reduces seed production.

Host Range Tests and Results

In a host range trial using 31 *Solanum* spp. and five strains of *R. solanacearum*, all test plant species were either mildly or highly susceptible to one or more strains of the bacterium (Charudattan and DeValerio, 1996). This finding suggests that if *R. solanacearum* is developed commercially as a bioherbicide for use against the non-native solanums, the potential for non-target damage due to drift must be considered.

The nematode *D. phyllobius*, a species collected from silverleaf nightshade, failed to induce leaf or stem galls on either tropical soda apple or wetland nightshade (Cuda *et al.*, 1998); turkey berry was unavailable for testing.

Leptinotarsa defecta did not feed and develop on any of the three invasive species tested, but *L. texana* may have some potential as a control agent for turkey berry (Cuda *et al.*, 2002). Development and reproduction of *L. texana* on turkey berry were comparable with its normal host plant silverleaf nightshade, and larvae did not exhibit a feeding preference when given a choice between the two species in paired plant tests (Cuda *et al.*, 2002). In screening tests with the nymphalid butterfly *M. lysimnia* conducted in Argentina, it was found that this insect was not sufficiently host specific to warrant further consideration as a biological control agent (Gandolfo, 1997).

The leaf-feeding tortoise beetle *M. elatior* exhibited a broad host range under laboratory conditions (Hill and Hulley, 1996; Medal *et al.*, 1999b), but this insect fed and oviposited only on tropical soda apple in surveys and open field experiments conducted in the insect's native range (Medal *et al.*, 1999a; Olckers *et al.*, 2002). Contradictory results obtained with critical solanaceous test plants may be explained by the conditions under which the screening studies were conducted (Medal *et al.*, 1999ab).

Gratiana boliviana, another leaf-feeding chrysomelid beetle, developed completely albeit poorly on eggplant and three South American Solanum spp. in no choice laboratory feeding trials (Gandolfo, 1998; Gandolfo et al., 2000ab; Medal et al., 2002). However, surveys and open field experiments conducted in Argentina, Brazil, Paraguay, and Uruguay since 1997 clearly demonstrate that G. boliviana does not attack eggplant in South America, even when tropical soda apple plants are growing intermixed or adjacent to egg plant fields (Gandolfo, 1999; Medal et al., 1999a; Gandolfo et al., 2000ab; Olckers et al., 2002; Medal et al., 2002). Apparently, the high density of stellate trichomes on the leaves of eggplant act as a physical barrier to the neonates of G. boliviana (Gandolfo, 1998; Gandolfo, 2000).

Releases Made

No insect natural enemies have been released for classical biological control of tropical soda apple in the United States as of March 2002. An application for permission to release *M. elatior* against tropical soda apple in the United States was submitted to the Technical Advisory Group for Biological Control Agents of Weeds (TAG) in October 1998, but the request for release from quarantine was denied because of the perceived risk to eggplant. The TAG recommended additional field-testing in South America to resolve discrepancies that often occur between laboratory and open field tests.

A request for the release of *G. boliviana* from quarantine was submitted to the TAG in April 2000 (Medal *et al.*, 2000). The TAG recommended that *G. bolviana* be approved for use as a biological control agent of tropical soda apple in April 2002. The release of this insect for classical biological control of tropical soda apple is anticipated in the Spring of 2003.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Pathogens

Ralstonia solanacearum is a ubiquitous soil-borne bacterium that is pathogenic to tropical soda apple (Charudattan and DeValerio, 1996). Chlorosis, necrosis, systemic wilting, and rapid plant mortality characterize the disease. *Ralstonia solanacearum* can survive in the soil for a long time even in the absence of a host. As a soil-borne pathogen, *R. solanacearum* does not spread readily unless contaminated soil and tools, infected plant parts, or contaminated irrigation water are involved. The bacteria can survive for several years in certain types of soils. However, use of resistant crop varieties, proper sanitation, rotation with nonhost crops, soil solarization, or soil fumigants can control the disease.

The U2 strain of the tobacco mild mosaic virus causes foliar lesions, systemic necrosis of the petioles, and systemic wilt of tropical soda apple plants within 14 days post-inoculation (Charudattan *et al.*, 2001). Unlike the U1 strain that induces only mosaic or mottle symptoms, the U2 strain causes hypersensitive mortality of tropical soda apple (Charudattan *et al.*, 2001).

Leptinotarsa texana (Coleoptera: Chrysomelidae)

The biology of *L. texana* on silverleaf nightshade was recently summarized by Olckers *et al.* (1995). In the laboratory, females laid clusters of 20 to 40 eggs on the lower leaf surfaces (Fig. 9), while in the field egg batches may exceed 100 eggs. The cream-colored eggs of *L. texana* are larger than the yellow eggs of *L. defecta*. Females, which live longer than males, may oviposit more than 2,000 eggs in their life span of three to four months in the laboratory. Adults readily cannibalize each others eggs, especially under crowded conditions in cages.

Larvae hatch after four to five days and consume the eggshells before feeding on the plant. Larvae feed in groups, and pass through four instars in 10 to 14 days. Mature larvae burrow into the soil to pupate; adults emerge 10 to 14 days later.



Figure 9. Adult and egg mass of *Leptinotarsa texana* (Schaeffer) on silverleaf nightshade, *Solanum elaeagnifolium* Cavanaugh. (Photograph courtesy of Gary Bernon.)

Larvae of *L. texana* have orange head capsules from the third instar onwards and are easily differentiated from *L. defecta* larvae, which have black head capsules. The period from larval eclosion to adult emergence in these trials was 22 to 26 days. Adults commence feeding immediately after emergence and are able to oviposit after seven to 10 days. Adults of *L. texana* have four black stripes along each elytron (Fig. 9), and easily are distinguished from *L. defecta* adults, which have two elytral stripes. The adults undergo a reproductive diapause before winter, burrowing into the soil as the plants senesce in autumn, and emerge the following spring. Adult quiescence is induced by poor host plant quality, particularly senescing leaves rather than photoperiod.

Metriona elatior (Coleoptera: Chrysomelidae)

The biology of *M. elatior* was studied on *S. sisymbriifolium* by Hill and Hulley (1996) and on tropical soda apple by Gandolfo (1997). Adults have a nearly circular body shape (Fig. 10). Pronotum and elytra are mostly green, but occasionally are pale red. Ventrally, the body is shiny black with a pale reddish or greenish lateral margin on the posterior abdominal segments; legs are shiny black.

Females deposit 31 to 109 egg masses, each containing 5 to 13 eggs, on lower surfaces of leaves. Larvae hatch in six or seven days at 25°C. First instars feed individually on the same leaf where the egg mass was deposited. There are five instars, and the pale yellow larvae carry the exuviae and feces dorsally. At high densities, larvae can induce leaf abscission. Mature larvae stop feeding and attach themselves to the lower surface of a leaf with an abdominal secre-



Figure 10. Adults of *Metriona elatior* Klug feeding on leaf of tropical soda apple, *Solanum viarum* Dunal. (Photograph courtesy of Julio Medal.)

tion to pupate. Pupae are yellow and black in color, and the duration of the pupal stage is five to eight days. Development from the egg to the adult stage is completed in approximately 35 days.

Gratiana boliviana (Coleoptera: Chrysomelidae)

Gandolfo (1998) and Gandolfo et al. (2000b) studied the biology of G. boliviana. Adults of G. boliviana are elliptical in shape and light green in color (Fig. 11a). Females produce an average of 300 eggs during their lives, deposited individually on the leaves or petioles. Eggs are white initially but turn light green during incubation. Larvae hatch within five to seven days at 25°C. There are five instars and the larvae usually feed on the underside of younger leaves (Fig. 11b). The larval stage is completed in 15 to 22 days. Like *M. elatior*, the larvae carry the exuviae and feces on their backs. Mature larvae cease feeding, and attach themselves by the last abdominal segment to the underside of the leaves near the insertion of the petiole to pupate. Pupae are green and flex their bodies when disturbed. The pupal stage usually lasts 6 to 7 days.

Anthonomus tenebrosus (Coleoptera: Curculionidae)

The anthonomine weevil *A. tenebrosus* was collected on tropical soda apple during initial surveys in Argentina and Brazil, but was misidentified as *Apion* sp. (Gandolfo, 1997). Adults are black (Fig. 12), approximately 2 mm in length, and feed on tender shoots, buds and flowers of tropical soda apple. The larvae destroy the contents of the flower buds as they



Figure 11a.



Figure 11b.

Figure 11. *Gratiana boliviana* (Spaeth) shown with feeding damage on leaves of tropical soda apple, *Solanum viarum* Dunal; (a) adult, (b) larvae. (Photographs courtesy of Julio Medal.)



Figure 12. *Anthonomus tenebrosus* Boheman, flower bud weevil of tropical soda apple, *Solanum viarum* Dunal. (Photograph courtesy of Stephan McJonathan.)

develop and pupate inside the buds. This type of damage can inhibit fruit production, which reduces spread of the plant. There are no previous host records for this species but a close relative (Anthonomus sisymbrii Hustache) that is known from S. sisymbriifolium (Clark and Burke, 1996), also attacks tropical soda apple (Olckers et al., 2002). The specimens collected on tropical soda apple were tentatively identified as A. tenebrosus as some specimens seem to fall somewhere between A. tenebrosus and A. sisymbrii (W. E. Clark, pers. comm.). Host specificity studies with the flower bud weevil A. tenebrosus have been initiated in U.S. quarantine (Medal and Cuda, 2001).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

As of March 2002, no arthropod natural enemies have been released for classical biological control of tropical soda apple in the United States. However, the TAG recommended the release of *G. boliviana* from quarantine in April 2002.

Suppression of Target Weed

A combination of mowing and herbicide application is currently recommended for controlling tropical soda apple in pastures (Mullahey and Colvin, 1993; Mislevy *et al.*, 1996). Hence, a post-mowing application of *R. solanacearum* or mowing with a simultaneous application of *R. solanacearum* were considered rational methods for field application of this bacterium.

Initial trials were done on 187-day-old plants by clipping the main stem 3 cm above the soil and swabbing the cut surface with a 1-day-old bacterial suspension of *R. solanacearum* Race 1, Biovar 1. The inoculum was applied at two rates, 0.74 and 1.74 A at 600 nm. After 12 weeks post treatment, 100% of the plants subjected to the high inoculum level were killed and the shoot biomass was reduced in the low inoculum level treatment.

As a novel method of application, the Burch Wet BladeTMmower system (BWB) also was used to deliver the bacterial pathogen *R. solanacearum* (Fig. 13).



Figure 13a.



Figure 13b.



Figure 13c.

Figure 13. (a) Burch Wet Blade Mower[™] used for applying the bacterial pathogen *Ralstonia solanacearum* (E. F. Smith) Yabuuchi to tropical soda apple, *Solanum viarum* Dunal; (b) wilted tropical soda apple plant exhibiting disease symptoms; (c) field plots in Immokalee, Florida, United States, showing control of tropical soda apple two months post-treatment in 1998. The bacterial pathogen *R. solanacearum* was applied using the Burch Wet Blade Mower[™] to plots visible on left side that were previously infested with tropical soda apple. (Photographs courtesy of R. Charudattan.) The BWB is commonly used to deliver chemical herbicides to target weeds during mowing, but it had not been tested to deliver a biological control agent. The bacterium *R. solanacearum* Race 1, Biovar 1 was suspended in sterile water and applied to tropical soda apple growing in a pasture located in Hendry County, Florida, with the BWB. The bacterium applied with the BWB reduced the ground cover of tropical soda apple to approximately 1% after 67 days (Fig. 13). Thus, *R. solanacearum* applied during mowing or as a post-cut treatment is an effective way to integrate biological with mechanical control of tropical soda apple under field conditions (DeValerio and Charudattan, 1999; DeValerio *et al.*, 2000).

Recovery of Native Plant Communities

In field trials, pasture grass regrowth after treatment of tropical soda apple with *R. solanacearum* applied with the BWB mower system was comparable to surrounding areas where the weed did not occur. Furthermore, symptoms of bacterial wilt were not observed on any of the pastures grasses exposed to the bacterium.

RECOMMENDATIONS FOR FUTURE WORK

Because the leaf beetle *L. texana* accepted turkey berry as a host plant in laboratory tests (Cuda *et al.*, 2002), a request should be submitted to state regulatory officials to obtain approval to introduce the insect from Texas into Florida for biological control of turkey berry. However, additional species of the genus *Solanum* that are endemic to Florida would have to be tested prior to release to determine whether native species are at risk for non-target damage by *L. texana*. For example, the native potato tree that is considered a threatened species in Florida would not be attacked by *L. texana* because the beetle failed to complete its development on this critical test plant in no choice laboratory tests (J. P. Cuda, 2002).

Additional screening tests with the tropical soda apple leaf beetle *M. elatior* were completed in the Florida quarantine laboratory as recommended by the TAG, and a petition for field release was resubmitted in December 1999. The supplemental petition requesting release of *M. elatior* from quarantine was denied until open field experiments and surveys are undertaken in South America to resolve the discrepancies observed in development of the insect on eggplant, potato, and tomato in the laboratory larval feeding tests (Hill and Hulley, 1996; Gandolfo, 1997; Medal *et al.*, 1999a).

Five additional natural enemies of tropical soda apple have been identified in South America (Medal and Cuda, 2000; Medal *et al.*, 2000b). Specificity tests with another leaf beetle *Platyphora* sp. (Coleoptera: Chrysomelidae), a leafroller (Lepidoptera: Pyralidae), a leaf-tier (Lepidoptera: Oecophoridae), and a stemmining fly (Diptera: Agromyzidae) should be initiated.

Wetland nightshade is an ideal target for classical biological control. This species tends to form extensive impenetrable thickets in remote, periodically flooded areas. The extreme conditions that characterize this habitat make controlling the plant by conventional means a difficult task. Field surveys in Florida and in the native range would need to be conducted to discover potential biological control candidates for wetland nightshade.

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24 BRAZILIAN PEPPERTREE

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PEST STATUS OF WEED

Schinus terebinthifolius Raddi, commonly called Brazilian peppertree in North America, is an introduced perennial plant that has become well established and invasive throughout central and southern Florida (Ferriter, 1997; Medal et al., 1999). This species is native to Argentina, Brazil, and Paraguay (Barkley, 1944, 1957) and was brought to Florida as an ornamental in the 1840s (Ferriter, 1997; Mack, 1991). The plant is a dioecious, evergreen shrub-to-tree that has compound, shiny leaves. Flowers of both male and female trees are white and the female plant is a prolific producer of bright red fruits (Fig. 1). Although the plant is still grown as an ornamental in California, Texas, and Arizona, S. terebinthifolius is classified as a state noxious weed in Florida and Hawaii (Ferriter, 1997; Habeck et al., 1994; Morton, 1978).



Figure 1. Fruit clusters on plant of *Schinus terebinthifolius*. (Photograph by S. Hight)

Nature of Damage

Economic damage. As a member of the Anacardiaceae, *S. terebinthifolius* has allergen-causing properties, as do other members of the family. While not affecting as many people as poison ivy (*Toxicodendron radicans* [L.] Kuntze), poison oak (*T. toxicarium* [Salisb.] Gillis), or poison sumac

(T. vernix [L.] Kuntze), all of which are in the Anacardiaceae, the sap of Brazilian peppertree can cause dermatitis and edema in sensitive people (Morton, 1978). Resin in the bark, leaves, and fruits is sometimes toxic to humans, mammals, and birds (Ferriter, 1997; Morton 1978). Even the odors of the flowers of S. terebinthifolius can induce allergic reactions (Morton, 1978). Abundant growth of this poisonous plant may damage the multi-billion dollar tourist industry in Florida. The value of wildlife-related recreational activities in Florida has been estimated at \$5.5 billion (UF-IFAS, 1999). Visitors sensitive to S. terebinthifolius who would otherwise come to Florida for such activities may decide to vacation elsewhere rather than risk exposure to this toxic weed. Wood of Brazilian peppertree is of little value due to its low quality, multiple, low-growing stems, and poisonous resin (Morton, 1978).

Ecological damage. In Florida, S. terebinthifolius is an aggressive, rapidly spreading weed that displaces native vegetation by forming dense monocultures (Fig. 2). These thickets reduce the biological diversity of native plants and animals (Bennett et al., 1990; Medal et al., 1999). As early as 1969, S. terebinthifolius was recognized as an important invader in Everglades National Park (Morton, 1978). The Florida Department of Agriculture and Consumer Services recognizes the plant as a noxious weed (Morton, 1978) and in 1990 the sale of S. terebinthifolius was prohibited by the Florida Department of Environmental Protection (Langeland, 1998). Conservation organizations consider S. terebinthifolius a high priority target because it is already widespread and has great potential to increase its range even further (Randall, 1993). The U.S. Fish and Wildlife Service (1998) identified S. terebinthifolius as one of the most significant non-indigenous species currently threatening federally-listed threatened and endangered native plants throughout the Hawaiian islands. In Florida S. terebinthifolius is considered one of the worst invasive species by the Florida Exotic Pest Plant Council, and is recognized as the most widespread exotic plant in the state; infesting nearly 300,000 ha and found in all the terrestrial ecosystems of central and southern Florida (Habeck, 1995; Ferriter, 1997).



Figure 2. Dense stand of *Schinus terebinthifolius* trees in Evergaldes National Park. (Photograph by J. Cuda and J. Medal.)

In southern and central Florida, S. terebinthifolius colonizes disturbed sites such as highways, canals, powerline rights-of-ways, fallow fields, and drained wetlands. It also is able to establish in many undisturbed natural environments (Woodall, 1982), including pine flatwoods, tropical hardwood hammocks, and mangrove forests (Loope and Dunevitz, 1981; Ewel et al., 1982; Woodall, 1982). The invasion of this aggressive, woody plant poses a serious threat to biodiversity in many of Florida's native ecosystems, and is eliminating many indigenous food sources for wildlife (Morton, 1978). Attributes of the plant that contribute to its invasiveness include a large number of fruits produced per female plant, an effective mechanism of dispersal by birds (Panetta and McKee, 1997), and tolerance to shade (Ewel, 1978), fire (Doren et al., 1991), and drought (Nilsen and Muller, 1980).

Extent of losses. Direct losses have not been quantified due to lack of long-term monitoring programs and data collection and analysis.

Geographical Distribution

Schinus terebinthifolius is native to Argentina, Brazil, and Paraguay (Barkley, 1944, 1957). The plant was spread around the world as an ornamental, beginning in the mid to late 1800s (Barkley, 1944; Mack, 1991). Naturalization of *S. terebinthifolius* has

occurred in more than 20 countries worldwide throughout subtropical areas (15 to 30° N or S latitudes) (Ewel *et al.*, 1982). In the United States, the plant occurs in Hawaii, California, Arizona, Texas, and Florida (Habeck *et al.*, 1994; Ferriter, 1997). In Hawaii, the plant is commonly called Christmasberry due to its attractive green foliage and red fruits present in December. The plant is sensitive to cold temperatures (Langeland, 1998). Its distribution in eastern North America is limited to central and southern Florida, although along the Florida coast, plants can be found as far north as Levy and St. Johns Counties (ca. 29° N).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The order Sapindales, one of the eighteen orders within the subclass Rosidae, contains fifteen families and about 5,400 species. More than half of the species belong to only two families, the Sapindaceae and Rutaceae, each with nearly 1,500 species. The Anacardiaceae is a small but well known family, consisting of 60 to 80 genera and about 600 species (Cronquist, 1981). The family is primarily pantropical, but some species occur in temperate regions. Species of Anacardiaceae, which may be trees, shrubs, or woody vines, are characterized by well developed resin ducts or latex channels throughout most plant parts. Leaves of these plants are typically alternate and either pinnately compound or trifoliolate. Flowers are usually unisexual, with parts in groups of five. Nectary disks are five-lobed and fruits are typically drupes (Cronquist, 1981). The genus Schinus has 28 species and its center of distribution is northern Argentina (Barkley, 1944, 1957). Schinus species are native to Argentina, southern Brazil, Uruguay, Paraguay, Chile, Bolivia, and Peru (Barkley, 1944, 1957). Barkley (1944) recognized five varieties of S. terebinthifolius. Differences between the varieties are based on leaf length, leaflet number and shape, and the form of leaflet margins (Barkley, 1944). Two varieties of S. terebinthifolius have been introduced into Florida, but the most abundant is S. terebinthifolius var. radianus (M. Vitorino, pers. comm.).

Biology

The main flowering period of S. terebinthifolius in Florida is September through October, with a muchreduced bloom from March to May. Small, white flowers occur in dense axillary panicles near the end of branches. The flowers are insect pollinated and successful fertilization leads to the production of prolific numbers of bright red fruits from November to February. A small fruit set occurs from June to August. Fruits are eaten and dispersed by birds and mammals. In fact, fruits have a near-obligate requirement for ingestion before seeds can germinate, as seeds within fruits that have not passed through the digestive tract have little chance of germinating before they loose viability (Panetta and McKee, 1997). Seeds remain viable in soil for six or nine months, in Florida and Australia, respectively (Ewel et al., 1982; Panetta and McKee, 1997). Removal of the seed from the fruit by ingestion and excretion or mechanical means promotes seed germination, and germination rates do not differ between bird-ingested seeds or mechanically cleaned seeds (Panetta and McKee, 1997). Water extracts of S. terebinthifolius fruits inhibit germination of *S. terebinthifolius* seed as well as other plant species, presumably due to the presence of phenolic acid compounds (Nilsen and Muller, 1980).

Leaves are present on *S. terebinthifolius* plants throughout the year. However, vegetative growth ceases in winter (October to December), corresponding to the flowering period. Growth and extension of the shoot tips occurs more or less continuously throughout the rest of the year (Tomlinson, 1980; Ewel *et al.*, 1982).

Similar to many hardwood species, *S. terebinthifolius* is capable of resprouting from aboveground stems and crowns after damage from cutting, fire, or herbicide treatment. In addition, root sprouts form from trees with or without evidence of damage and can develop into new individuals. Resprouting and suckering is often profuse and the growth rates of the sprouts are high, leading to the formation of dense clumps (Ferriter, 1997; Woodall, 1979).

Analysis of Related Native Plants in the Eastern United States

The order Sapindales includes fifteen families, of which ten (Staphyleaceae, Sapindaceae, Hippocastanaceae, Aceraceae, Burseraceae, Anacardiaceae, Simaroubaceae, Meliaceae, Rutaceae, and Zygophyllaceae) have native members in eastern North America. Nine of these ten families have native species within the range of S. terebinthifolius in Florida. The tenth family, Staphyleaceae, has a species that occurs in northern Florida. The Rutaceae includes important fruit crops grown in subtropical Florida (Citrus spp.). Four genera of Anacardiaceae are indigenous to eastern North America: Rhus, Toxicodendron, Metopium, and Cotinus (Brizicky, 1962; Gleason and Cronquist, 1963). Except for Cotinus, the above genera are each represented by several species in Florida that overlap in range with S. terebinthifolius (Ferriter, 1997). A number of additional species of Anacardiaceae have been introduced and are currently cultivated in Florida for their edible fruits or seeds, including Mangifera indica L. (mango), Pistacia spp. (pistachio), and Spondias spp. (purple mombin).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The center of distribution of the genus Schinus is northern Argentina, and its natural distribution is in South America (Argentina, southern Brazil, Uruguay, Paraguay, Chile, Bolivia, and Perú) (Barkley, 1944, 1957). Only the species Schinus molle L. historically extended north into Mexico (Barkley, 1944, 1957). However, Barkley (1957) believed that even S. molle was originally from warm temperate regions of South America and has been introduced throughout Central America where it became readily established. Barkley (1944, 1957) lists the South American distribution of the five varieties of Brazilian peppertree as follows: S. terebinthifolius var. terebinthifolius Raddi -from Venezuela to Argentina; S. terebinthifolius var. acutifolius Engl. - southern Brazil and Paraguay to Missiones, Argentina; S. terebinthifolius var. pohlianus Engl. (the most common variety of the species) southern Brazil, Paraguay, and northern Argentina; S. terebinthifolius var. raddianus Engl. - south-central Brazil; and S. terebinthifolius var. rhoifolius (Mart.) Engl. – south-central Brazil.

Areas Surveyed for Natural Enemies

Natural enemies associated with S. terebinthifolius have been evaluated in Florida (Cassani, 1986) and Hawaii (Hight, unpub.). During a 14-month survey in Florida, 115 arthropods were recorded. Even though 40% of the arthropods were phytophagous on S. terebinthifolius, they did not cause significant damage to the plant (Cassani, 1986). Collections that occurred over approximately one year in Hawaii revealed only 34 insect species feeding inconsequentially on introduced S. terebinthifolius. Occasional outbreaks of an introduced polyphagous noctuid caterpillar, Achaea janata L., have occurred in Hawaii. Although the caterpillars may defoliate large stands of S. terebinthifolius, outbreaks tend to last only one generation and occur sporadically at various locations on the island of Hawaii, having no effect on populations of S. terebinthifolius (Yoshioka and Markin, 1994; Hight, unpub.).

Surveys were conducted in South America (primarily Brazil) for potential biological control agents by researchers from Hawaii in the 1950s (Krauss, 1962, 1963) and by Florida researchers in the late 1980s to 1990s (Bennett *et al.*, 1990; Bennett and Habeck, 1991; Medal *et al.*, 1999). Krauss (1963) provided an annotated list of 33 insect species that he collected from *Schinus* species, many of which were undescribed. Exploratory surveys in southern Brazil conducted by Floridian researchers identified at least 200 species of arthropods associated with *S. terebinthifolius* (Bennett *et al.*, 1990; Bennett and Habeck, 1991).

Natural Enemies Found

Surveys of *S. terebinthifolius* in both Hawaii and Florida revealed only one species that was potentially damaging to this plant. The seed-feeding wasp *Megastigmus transvaalensis* (Hussey) (Hymenoptera: Torymidae), originally from South Africa, was accidentally introduced into both Hawaii (Beardsley, 1971) and Florida (Habeck *et al.*, 1989; Cuda et al., 2002). The original host plants of this insect were four South African *Rhus* species (Grissell and Hobbs, 2000). In Florida and Hawaii, this wasp has been found only in *S. terebinthifolius* fruits (Wheeler *et al.*, 2001; Hight, unpub.). Overall mortality of *S. terebinthifolius* seeds caused by this wasp was reported to be as high as 76% in Florida (Wheeler *et al.*, 2001) and 80% in Hawaii (Hight, unpub.). Given

that seedling survival is low (Ewel, 1986), wasp damage may contribute significantly to reducing the spread of this weed species.

Based on the Hawaiian surveys for natural enemies in South America, three insect species native to Brazil were released into Hawaii: a seed-feeding beetle, *Lithraeus (=Bruchus) atronotatus* Pic (Coleoptera: Bruchidae), in 1960 (Davis, 1961; Krauss, 1963); a leaf-rolling moth, *Episimus utilis* Zimmerman (Lepidoptera: Tortricidae), in 1954 to 1956 (Beardsley, 1959; Davis, 1959; Krauss, 1963); and a stem-galling moth, *Crasimorpha infuscata* Hodges (Lepidoptera: Gelechiidae), in 1961 and 1962 (Davis and Krauss, 1962; Krauss, 1963). The first two species became established but cause only minor damage (Clausen, 1978; Yoshioka and Markin, 1991).

Based on surveys in Brazil by Florida scientists, two insect species were selected as initial biological control agents to undergo host specificity studies – the sawfly *Heteroperreyia hubrichi* Malaise (Hymenoptera: Pergidae) and the thrips *Pseudophilothrips ichini* Hood (Thysanoptera: Phlaeothripidae). The sawfly was introduced into the Gainesville quarantine facility in 1994 and underwent host specificity tests from March 1995 to June 1998 (Medal *et al.*, 1999). An additional plant species (*Rhus michauxii* Sargent) was tested at the request of the U.S. Fish and Wildlife Service in 1999 (Cuda and Medal, unpub.). Host specificity testing of the thrips began in the Gainesville quarantine in 1995, and was completed in 2002 (Cuda, unpub.).

Host Range Tests and Results

No-choice, larval development tests were conducted with the sawfly *H. hubrichi* on 34 plant species in 14 families at the Gainesville quarantine facility and 12 species in seven families in Brazil (Table 1) (Medal *et al.*, 1999). None of these plants were used successfully as hosts by this insect. Hight *et al.* (2003) conducted no-choice, host specificity tests in Hawaiian quarantine on 20 plant species in 10 families. The Hawaiian analysis included both larval development tests and female oviposition tests. While only three of the Hawaiian test plants had been evaluated in Florida, 17 plant species were tested for the first time (Table 1).

A petition to release the schinus sawfly into the Florida environment was submitted to the Technical Advisory Group (TAG), USDA, APHIS in 1996. TAG reviewed the petition and considered the sawfly

Faxon	Plant Species	Hawaii	Florida	Brazil
MAGNOLIOPHYTA				
Rosidae				
Sapindales				
Anacardiaceae	Schinus terebinthifolius Raddi	Х	Х	Х
	Schinus molle L.		Х	Х
	Rhus copallina L.		Х	
	Rhus michauxii Sargent		Х	
	Rhus sandwicensis A. Gray	Х		
	Mangifera indica L.	Х	Х	Х
	Anacardium occidentale L.		Х	
	Cotinus coggygria Scop.		Х	
	Toxicodendron radicans (L.) Kuntze		Х	
	Toxicodendron toxicarium (Salisb.) Gillis		Х	
	Toxicodendron vernix (L.) Kuntze		Х	
	Metopium toxiferum (L.) Krug & Urb.		Х	
	Spondias dulcis Parkinson		Х	
	Spondias purpurea L.		Х	
	Pistacia chinensis Bunge		Х	
Sapindaceae	Dodonaea viscosa Jacq.	Х		
	Sapindus saponaria L.	Х		
	Litchi chinensis Sonn.	Х		
	Euphoria longan Lam.	Х		
	Alectryon subcinereum Gaertn.	Х		
	Nephelium mutabile L.	Х		
Rutaceae	Melicope hawaiensis (Wawra) T. Hartley & B. Stone	Х		
	Citrus sinensis (L.) Osbeck	Х	Х	Х
Aceraceae	Acer rubrum L.		Х	
Apiales				
Araliaceae	Reynoldsia sandwicensis A. Gray	Х		
Apiaceae	Daucus carota L.		Х	
Myrtales				
Myrtaceae	Metrosideros polymorpha Gaud.	Х		
	<i>Eucalyptus grandis</i> Hill ex Maiden			Х
	Eucalyptus uniflora L.			Х
Fabales				
Fabaceae	Acacia koa A. Gray	Х		
	Sophora chrysophylla (Salisb.) Seem.	Х		
	Arachis hypogaea L.		Х	
	Phaseolus vulgaris L.		Х	
	<i>Vigna unguiculata</i> (L.) Walp.		Х	
Capparales				
Caricaceae	Carica papaya L.		Х	

TABLE 1. Plants Used in Host Specificity Tests at Various Locations with *Heteroperreyia hubrichi* for Biological
Control of *Schinus terebinthifolius*¹.

Taxon	Plant Species	Hawaii	Florida	Brazil
MAGNOLIOPHYTA				
Magnoliopsida				
Asteridae				
Scrophulariales				
Myoporaceae	Myoporum sandwicense A. Gray	Х		
Proteales				
Proteaceae	Macadamia integrifolia Maiden & Betche	Х		
Rubiales				
Rubiaceae	Coffea arabica L.	х		
Solanales				
Convolvulaceae	<i>Ipomoea batatas</i> (L.) Lam.		Х	х
	<i>Ipomoea indica</i> (J. Burm.) Merr.	Х		
Solanaceae	Capsicum annuum L.		Х	Х
	Solanum tuberosum L.		Х	Х
	Lycopersicon esculentum Mill.		Х	Х
Capparales				
Brassicaceae	Brassica oleracea L. (broccoli)		Х	
	Brassica oleracea L. (cauliflower)		Х	
Malvales				
Malvaceae	Gossypium hirsutum L.		Х	
	Abelmoschus esculentus (L.) Moench		Х	
Laurales				
Lauraceae	Persea americana Mill.		Х	Х
Fagales				
Fagaceae	Quercus virginiana Mill.		Х	
Juglandales				
Juglandaceae	Carya glabra (Mill.) Sweet		Х	
Cyperales				
Poaceae	Zea mays L.		Х	
	Oryza sativa L.		Х	
	Saccharum officinarum L.		Х	Х
PTERODOPHYTA				
Dicksoniaceae	Cibotium glaucum (Sm.) Hook. & Arnott	Х		

TABLE 1. Plants Used in Host Specificity Tests at Various Locations with Heteroperreyia hubrichi for Biological Control of *Schinus terebinthifolius*¹ (continued).

¹ List of plant species are arranged in phylogenetic order with regards to their degree of relationship to the target weed; i.e., plants at the beginning of the list are more closely related to S. terebinthifolius than plants at the end of the list.

sufficiently host-specific for introduction into Florida. An Environmental Assessment (EA) was prepared by APHIS and submitted for public comment. The U.S. Fish and Wildlife Service requested host specificity tests be conducted on R. michauxii, a federally-listed endangered species that was not on the original test plant list. Tests indicated that R. 316

michauxii was not an acceptable host plant of the sawfly (Cuda, unpub.), and the information was sent to APHIS. Field observations in Brazil and laboratory feeding trials indicated H. hubrichi to be highly host specific to S. terebinthifolius. This insect was able to feed, develop, and become a reproductively mature adult only on S. terebinthifolius (Medal et al., 1999).

The potential host range in Hawaii appears to be slightly broader than that identified in Florida and Brazil. Tests in Florida evaluated two North American species of sumac (Rhus copallina L. and R. michauxii) and found them unsuitable for H. hubrichi oviposition and incapable of supporting larval development (Medal et al., 1999). Hawaiian tests indicated that the Hawaiian sumac (*Rhus sandwicensis* A. Gray) did support larval development and was highly attractive to the female for oviposition. Chemicals still present in ancestral, continental species that deter herbivorous insects may have been lost over time in the Hawaiian sumac. Of the five varieties of S. terebinthifolius recognized in South America (Barkley, 1944), H. hubrichi prefers the most pubescent varieties (S. t. rhoifolius and S. t. pohlianus) (M. Vitorino, pers. comm.). The dense pubescent nature of R. sandwicensis may stimulate female oviposition regardless of the quality of the plant for larval development. Both S. terebinthifolius and R. sandwicensis were comparable in their acceptability to ovipositing females as measured by the proportion of females that oviposited on the test plant and the number of eggs that a female laid. But R. sandwicensis was a dramatically poor host for H. hubrichi larvae in both performance characteristics of larval survival (1%) and development time (30% longer) (Hight et al., 2003).

Field surveys of plants in Brazil indicated that *P. ichini* is probably host specific to *S. terebinthifolius* (Garcia, 1977). Larval feeding and adult oviposition tests for *P. ichini* were completed and a petition for field release in Florida was submitted to the TAG in October 2002. The test plant list was the same as that approved by TAG for *H. hubrichi* with the addition of the native plant *R. michauxii*. The results of field surveys in Brazil and host specificity tests indicated that *P. ichini* can reproduce only on *S. terebinthifolius* and *S. molle* (Cuda, unpub.).

Releases Made

To date, no biological control agents have been purposefully introduced in Florida against *S. terebinthifolius.* A decision to release the sawfly in Florida has been delayed pending a finding of no significant impact of the vertebrate toxins lophyrotomin and pergidin discovered in the larvae of *H. hubrichi* (Cuda, unpub.; see also p. 125).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Heteroperreyia hubrichi Malaise (Hymenoptera: Pergidae)

Adults of the leaf-feeding sawfly are generally black in color with yellow legs (Fig. 3). The life cycle begins when females emerge from pupal cases in soil near the base of S. terebinthifolius trees and search for well-developed, non-woody young stems in which to oviposit. A female and male H. hubrichi mate on the surface of the soil or on plants, although females do not need to mate for oviposition to occur. Each female inserts a single egg mass shallowly into non-woody stems. Eggs are arranged in rows and the female "guards" her eggs until she dies, just before the eggs hatch (Fig. 3). Eggs hatch in 14 days. Neonate larvae feed gregariously on both surfaces of young leaflets at the tip of shoots (Fig. 4). As they grow they move as a group onto new leaflets and larger leaves until the third to fourth instar when they disperse throughout the plant and feed individually. Larvae are green with red spots and black legs. After reaching the seventh instar, larvae move into soil and pupate. Insects reared on S. terebinthifolius took 26 to 42 days from egg hatch to pupation. The pupal stage lasts from 2 to 7 months (Medal et al., 1999; Hight et al., , 2003).



Figure 3. Adult female *Heteroperreyia hubrichi* guarding her eggs. (Photograph by S. Hight.)



Figure 4. Gregarious larvae of *Heteroperreyia hubrichi* feeding on leaf of *Schinus terebinthifolius*. (Photograph by S. Hight.)

Pseudophilothrips ichini Hood (Thysanoptera: Phlaeothripidae)

Adult and larval meristem-sucking thrips are generally red and black in color (Figs. 5 and 6). Adults are usually found on new unfolding leaves of *S. terebinthifolius* while immatures occur on stems of young shoots (Cuda *et al.*, 1999). Both immature and adult stages consume plant juices with their raspingsucking mouthparts, often killing new shoots. Eggs are laid singly or in small groups at the base of leaves or within terminal shoots and hatch in seven to eight days. Eggs from unmated females produce male offspring whereas eggs from mated females give rise to female offspring. The nymphal stage lasts about 25 days and females need a five to 15 day period before they begin oviposition. A new generation of *P. ichini* can occur every 38 days (Cuda *et al.*, 1999).



Figure 5. Adult *Pseudophilothrips ichini* on leaflet of *Schinus terebinthifolius*. (Photograph by J. Cuda and J. Medal.)



Figure 6. Larval *Pseudophilothrips ichini* on young shoot of *Schinus terebinthifolius.* (Photograph by J. Cuda and J. Medal.)

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

No classical biological control agents have yet been purposefully introduced into Florida against S. terebinthifolius. However, plans are being developed to evaluate the establishment and spread of H. hubrichi in Florida once the insect has been approved for field release (Cuda, unpub.). At least three study sites will be established in Florida throughout the geographical range of S. terebinthifolius. Releases of H. hubrichi will be made in cages. A series of annual photographs from fixed locations will be taken at each release site to document vegetation changes. Solar powered remote weather stations will be placed at each release site to monitor and identify environmental conditions that may lead to H. hubrichi establishment. Weather data also will be used to separate effects of H. hubrichi on S. terebinthifolius from annual variations in plant growth due to abrupt differences in weather patterns. Effects of this insect on S. terebinthifolius and non-target plants will be evaluated in release cages. Annual productivity of S. terebinthifolius and dominant native vegetation will be compared between cages with and without

H. hubrichi. To monitor changes and effects on vegetation over a landscape scale, a remote sensing project is being developed that will allow automated computer recognition of various vegetation components and monitor changes in vegetation over time. Finally, conventional vegetation analysis techniques will be used to evaluate the effect of *H. hubrichi* on the target and non-target plants.

RECOMMENDATIONS FOR FUTURE WORK

Additional surveys for phytophagous insects of S. terebinthifolius need to be conducted in northern Argentina, the most likely center of origin of this species (Barkley, 1944). Virtually all previous South American explorations by workers from Hawaii (Krauss, 1962, 1963) or Florida (Bennett et al., 1990; Bennett and Habeck, 1991) have taken place in southern Brazil. Although this work has identified several promising biological control candidates, surveys might be more successful in Argentina. For example, on a 10-day survey in January 2000 of S. terebinthifolius natural enemies in the state of Missiones, Argentina, two species of stem-boring cerambycids and a bark-girdling buprestid were collected (Hight, unpub.). Identifications of these insect species are pending. No stem-boring or bark-girdling insects were identified from Brazilian surveys.

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SECTION V: WEEDS OF FORESTS

Kudzu Mile-a-Minute Weed Skunk Vine Cogon Grass Garlic Mustard

25 KUDZU

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PEST STATUS OF WEED

Nature of Damage

Kudzu (Pueraria montana [Lour.] Merr. var. lobata [Willd.] Maesen and Almeida) was originally introduced into the United States as an ornamental vine at the Philadelphia Centennial Exposition of 1876. David Fairchild observed extensive use of kudzu as pasturage in Japan. In 1902, he planted seedlings around his Washington, D.C. home to explore their potential in the United States. By 1938, he became disenchanted with kudzu because it "grew all over the bushes and climbed the pines, smothering them with a mass of vegetation which bent them to the ground and became a tangled nuisance. I spent two hundred dollars in the years which followed trying to get rid of it, but when we sold the place there was still some kudzu behind the house " (Fairchild, 1938). In 1907, kudzu hay was exhibited at Jamestown, Virginia. Mr. C. E. Pleas, a farmer in Chipley, Florida, was thrilled to accidentally discover the growth potential of kudzu, and that many animals on his farm liked to eat it. He became an enthusiastic promoter of kudzu, grew 35 acres to sell as a fodder crop, and sold rooted cuttings through the mail (Shurtleff and Aoyagi, 1985). In the 1930s and 1940s, kudzu was propagated and promoted by the Soil Conservation Service as a means of holding soil on the swiftly eroding gullies of the deforested southern landscape, especially in the Piedmont regions of Alabama, Georgia, and Mississippi. Farmers were paid \$8.00 per acre by the Soil Erosion Service to plant kudzu, and more than 1.2 million acres were planted under this subsidized program. Kudzu seedling nurseries produced and distributed more than 73 million seedlings between 1935 and 1941 (Tabor and Susott, 1941). In his 1949 book, Front Porch Farmer, Channing Cope presents kudzu as the panacea that will allow farmers to adopt a life of leisure and relaxation, as this new crop "works while you sleep." Kudzu was widely promoted as a drought-resistant, high-nitrogen forage crop. Research in the 1930s examined optimum planting density, fertilization (Ahlgren, 1956), and the optimum time of mowing to maximize yield without depleting the kudzu root starch so much as to prevent regrowth each spring (Sturkie and Grimes, 1939). However, it proved difficult to bale. Direct grazing was used to some extent, but the vines are damaged by trampling, and this practice fell into disuse. In the 1950s, kudzu was recognized as a weed, and removed from the list of species acceptable for use under the Agricultural Conservation Program. In 1998, kudzu was listed by the U.S. Congress as a Federal Noxious Weed. Ornamental use accounts for the predominance of kudzu around many old, collapsed southern homesteads (Fig. 1). Erosion control plantings explain the extensive colonization of ravines in fields that once grew cotton or native forests, but have since been abandoned or turned into pasture. Although most spread is slow (apparently through local movement of infested soil), where kudzu exists it completely covers all other vegetation (Fig. 2). Estimates of kudzu infestation in the southeast vary greatly, from as low as two million (Corley et al., 1997) to as high as seven million acres (Everest et al., 1991).

Economic damage. Kudzu completely replaces existing vegetation. No information has been published on the resulting economic damage, and the following estimates rely upon the personal experience of Dr. Coleman Dangerfield (University of Georgia, forest economist). "Losses vary with the potential use of the land in an uninfested state. Where productive forest land has been overtaken, lost productivity is estimated at \$48 per acre per year. The present net value of an average stand of pines grown on cutover land for 25 years in the southeast is



Figure 1. Landscape uses probably account for kudzu patches surrounding crumbling homesteads throughout the South. (Photograph by Kerry Britton.)



Figure 2. Kudzu kills trees by shading them and spreads inexorably, mostly through soil movement and vegetative growth. (Photograph by Kerry Britton.)

approximately \$650 per acre. Kudzu control costs exceed \$200 per acre per year for five years. Thus, kudzu control for forest production is not economically feasible." Dr. James Miller (USDA Forest Service plant ecologist, Auburn, Alabama), who has researched herbicides for kudzu control for the last 20 years, estimates control costs by power companies alone at \$1.5 million per year.

Ecological damage. Few plants can survive once smothered by kudzu. It does not strangle competition, but simply blankets trees with a dense canopy, through which little light can penetrate. Kudzu's competitive edge has been attributed to its resource allocation strategy (i.e., its very high ratio of leaf surface area to structural tissues) (Wechsler, 1974); a high rate of net photosynthesis; and diurnal leaf movements that maximize exposure of lower canopy leaves and reduce overheating of upper canopy leaves (Forseth and Teramura, 1987). There is little spread by seed, so expansion of kudzu patches occurs mainly by rooting of runners at nodes. Adventitious rooting gives rise to large storage tubers that can survive repeated herbicide treatments over many years (Miller, 1985; Moorhead and Johnson, 1996).

Geographical Distribution

Van der Maesen (1985) considered China, Indo-China, Japan, Malaysia, Oceania, and the Indian subcontinent the native range of the genus *Pueraria*. Despite repeated introductions, *P. montana* var. *lobata* was not known to have established in Africa. This variety was successfully introduced to South America and Switzerland, as well as Queensland and New South Wales, Australia. Only in the southeastern United States is kudzu considered a serious pest.

Kudzu rarely occurs in the northeastern United States (Frankel, 1989), but is occasionally found from Connecticut to Illinois. In Illinois, more than 90 infestations have been documented (Wiedenmann, 2001). Kudzu is distributed south as far as Florida, and as far west as eastern Oklahoma and Texas. The most severe infestations occur in the piedmont regions of Mississippi, Alabama, and Georgia.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Kudzu is a perennial, semi-woody, climbing leguminous vine, of the tribe Phaseoleae Benth., subtribe Glycininae Benth. (Maesen, 1985). The kudzu species present in the United States is currently considered Pueraria montana (Lour.) Merr. var. lobata (Willd.) Maesen and Almeida (Ward, 1998). The most common synonyms are Pueraria lobata (Willd.) Ohwi, P. thunbergiana (Sieb. and Zucc.) Benth, and P. hirsuta (Thunb.) Matsumura non Kurz (Maesen, 1985). Characteristics that had been used previously to differentiate P. montana from P. lobata and Pueraria thomsoni (Benth.) are lobed leaflets, and the size of wing and keel petals, all of which can be quite variable. Maesen, therefore, treated these as varieties of one species, now called P. montana (Maesen and Almeida, 1988).

Hairy, sprawling vines emerge from a root crown and produce alternate, pinnately trifoliate leaves 7 to 25 cm long with three leaflets that may or may not exhibit shallow lobes. The vines grow up to 18m/yr in Georgia (Weschler, 1977). In late July to early September, plants in full sun produce flower clusters on upright, climbing vines, but rarely on horizontal vines. The flowers are borne in panicles, pea-like and purple, with a pronounced grape-like odor. Clusters of 20 to 30 hairy, bean-shaped pods are produced that contain tiny kidney-bean-shaped seeds. Seed pods are often empty, but may contain 10 to 12 seeds per pod (Tabor, 1942).

Biology

Seed production by kudzu in the United States varies from 0 to 1,800 seeds per m² soil surface, with higher values occurring where vines are climbing on structures (Thornton, 2001). The extremely low viability of these seeds has been assumed to be due to a lack of pollinators. However, Thornton demonstrated that there are a variety of both native and naturalized pollinators, the most important of which are native Hymenoptera. An exclusion cage study conducted in 1998 and 1999 revealed that low levels of kudzu seed viability were the result of arthropod damage. A concurrent inclusion cage study demonstrated that most of this damage was due to feeding by native Hemiptera (Thornton, 2001). Feeding by a naturalized Asian bruchid (Borowiecius ademptus Sharp) resulted in a small amount of damage in both years (Thornton, 2001).

Seedlings develop a woody root crown, with multiple runners and extensive tuberous roots. These roots contain carbohydrate reserves that permit the plant to survive repeated mowing and/or herbicide applications.

Analysis of Related Native Plants in the Eastern United States

No congeners of kudzu exist in the continental United States, but there are many important economic relatives (Pemberton, 1996). Kudzu's nearest relative in the United States is the soybean, *Glycine max* (L.) Merr., which also is of Asian origin. Native American members of the subtribe Glysininae are *Amphicarpaea bracteatea* (L.) Elliott ex. Nutall (American hog peanut), and four *Cologania* species: *C. angustifolia* Kunth, *C. lemmonii* Grey, *C. pallida* Rose, and *C. pulchella* Kunth. Native American genera in the tribe Phaseolinae that contain plants of ecological and/or economic importance include: Phaseolus (P. vulgaris L., P. lunatus L., P. coccineus L., and P. acutifolius Gray), Strophostyles (S. helvola [L.] Ell. and S. umbellata [Muhl. ex Willd.] Britton), and Vigna (V. radiata [L.] Wilczek, V. unguiculata [L.] Walp. and V. subterranea [L.] Verdc.).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The genus *Pueraria* contains seventeen species, distributed from Japan to northeastern India, south to eastern Australia, and east throughout Micronesia. Maesen's (1985) extensive examination of herbarium specimens led him to conclude that the kudzu in Japan, Korea, China north of Shanghai, and throughout the Phillipines, Malaysia, and Indonesia, was P. montana var. lobata. This is the variety that has been introduced to the United States, and South America. The range of this variety overlaps with that of P. montana var. montana in China south of the Yangtze River to Hong Kong. The distribution of *P. montana* var. montana also includes Vietnam, Burma, Laos, and Thailand. In these countries, and in southern China, P. montana var. montana shares its distribution with P. montana var. thomsoni. Specimens from northeast India were identified as P. montana var. thomsoni (Maesen, 1985).

Areas Surveyed for Natural Enemies

Pemberton (1988) reported an abundance of natural enemies of kudzu in China and Korea. Other researchers who visited China (DeLoach, Markin, and Schiff, pers. comm.) agreed and encouraged the initiation of a biological control research program. A climatic matching study showed that Anhui Province was the area of China most similar in climate to Atlanta, Georgia. Three systematic survey sites were therefore established in Anhui Province in 1999, in a program funded by the USDA Forest Service. Because of intensive agricultural land use, most of the kudzu that exists in China occurs in mountain regions, which could be cooler than indicated by current weather records. A fourth survey site was therefore established in Guangdong Province. In 2000, a site in Shaanxi Province was added to this survey.

Natural Enemies Found

A systematic survey for kudzu biocontrol agents was initiated in May 1999. At each of the four survey sites, five vines were chosen for sampling. Insect feeding, mating, and egg laying behavior was observed at 10-day intervals from May through November. Representative insects, and herbarium specimens of their feeding damage were collected and preserved. Defoliation was visually estimated in five 1 ft² areas on each vine. The main vine and branches were monitored for feeding damage and gall formation.

The insects that fed on kudzu are still being identified. So far, seven out of 25 species (Deporaus sp., Alcidodes trifidus [Pasco], Sagra femorata [Drury], Aristobia hispida [Saunders], Paraleprodera diophthalma [Pascoe], Anomala corpulenta [Motschulsky], and Epicauta chinensis [Castelnau]) are known to feed on other crops (often beans), and therefore, have been dropped from consideration. Leaf-feeding beetles and sawflies that have no other known hosts have been identified. Two kinds of weevils were found to attack the succulent stems, and eight kinds of large beetles (Cerambycidae, Buprestidae, Scarabidae) lay eggs and develop as larvae in the main vines or roots (Fig. 3).



Figure 3. Borers destroy roots and stems directly, and also may introduce decay fungi. (Photograph by Yang, Zhong-qi.)

Six fungal pathogens have been identified by collaborators at South China Agricultural University (Jiang *et al.*, 2000). One Phycomycete (*Synchytrium puerariae* P. Henning) Miyabe (Chytridiaceae) may hold some potential as a biological control agent. This pathogen has been reported on several *Pueraria* species from Japan, New Guinea, Java, the Phillipines, India, China, and California (specimen at National Fungus Collection, Beltsville, Marlyand (Karling, 1964), but further investigations are necessary to confirm its host specificity.

Host Range Tests and Results

Preliminary host range testing with soybean and peanut were begun in the summer of 2000. As far as possible, initial host testing will be conducted in China, where quarantine facilities are not required for these native insects. In the later screening stages, extensive testing of American plants and crops will be conducted in U.S. quarantine facilities to ensure host specificity before any insect can be released.

Biological Control Using Pathogens Native to the United States

Pseudomonas syringae pv. *phaseolicola*. This bacterium is the causal agent of "halo blight" of bean and kudzu, causing a small necrotic leafspot surrounded by a bright halo of chlorotic tissue. Zidak and Backman (1996) reported that the bacterium could kill eight- to ten-week-old kudzu seedlings, but produced few, if any, secondary infections under fairly dry conditions in the field.

Myrothecium verrucaria (Albertini and Schwein.) Ditmar: Fr. (Moniliales). This fungus has a fairly broad host range. Yang and Jong (1995) reported good control of leafy spurge, and eight other Euphorbia species using isolates of this fungus. Walker and Tilley found that an isolate from sicklepod (Senna obtusifolia [L.] Irwin and Barneby) affected a number of important crops, ornamentals, and weeds, representing six different families. Sprays directed to soybean stems and lower leaves did not reduce soybean dry weight (Walker and Tilley, 1997). It was patented for sicklepod biocontrol, and, although originally isolated from sicklepod, it is even more effective against kudzu. Two years of testing in Mississippi demonstrated that the fungus attacks leaves and stems, with greater activity at 25 to 40°C than at 10 to 20°C. Field tests demonstrated that 95 to 100% control could be achieved within 14 days of inoculation by girdling runner stems with this fungus, which produces asexual spores in a sporodochium, with a matrix suggesting dispersal by splashing rain. In inoculation studies, a surfactant was needed for good infection (Boyette, 2000). A patent for kudzu control has been applied for.

Colletotrichum gloeosporiodes (Penz.) Penz. and Sacc. in Penz. (Sphaeriales). A strain of this widely-distributed pathogen was isolated from kudzu in Houston County, Georgia, and its virulence was increased by repeated selection for growth on Czapek Dox medium amended with kudzu extract. Field inoculations showed a synergistic effect was achieved by inoculations of spores together with 20% of the recommended rate of dicamba. The fungus attacks both leaves and vines, and produces asexual spores in a pycnidium (Farris and Reilly, 2000).

RECOMMENDATIONS FOR FUTURE WORK

For biological control agents from China, no-choice host testing on bean, peanut, and soybean are being initiated in China. Rearing systems need to be developed. In 2001, a wider range of plants common to the United States and China will be tested in China, and a host test list will be submitted to the Technical Advisory Group before United States quarantine tests are planned.

For native fungal pathogens, testing to develop stable formulations and demonstrate efficacy in field situations are recommended.

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26 MILE-A-MINUTE WEED

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PEST STATUS OF WEED

Nature of Damage

Mile-a-minute weed, *Polygonum perfoliatum* L., is an annual or perennial vine of Asian origin that infests nurseries, orchards, openings in forested areas, road-sides, and drainage ditches in the eastern United States. In natural areas, the plant displaces native vegetation.

Economic damage. This weed is a particular threat to forest regeneration (Stanosz and Jackson, 1991). In commercial forest areas where mile-aminute weed has affected regeneration, costs ranging from about \$60 to 500/ha are incurred for site preparation, weed management (e.g., herbicides, burning), and labor to replant seedlings (Charles Brown, pers. comm.). Unfortunately, in both commercial and natural regeneration areas, this weed is difficult to control with a single herbicide application due to prolonged persistence of seeds in the soil. Seeds are able to survive in the soil and germinate after as long as four years (Johnson, 1996; McCormic, pers. comm.). Also, seeds can germinate over a wide temperature range (4.4 to 20°C) after at least nine weeks of cold-wet stratification at 2°C (McCormick and Johnson, 1997). Plants growing along forest edges near regeneration areas are potential sources of seed (McCormick and Johnson, 1997). Mile-a-minute weed can invade apple orchards (Moul, 1948) and Christmas tree plantations (Lehtonen, 1994).

Disturbed areas such as railroad and utility rights-of-way, roadsides, and stream banks are ideal habitats for mile-a-minute weed. For example, along a power line right-of-way in Mineral County, West Virginia, mile-a-minute weed covered all other vegetation to a height of approximately 2 m (Fig. 1). The routine use of herbicides along power lines (treated



Figure 1. Mile-a-minute weed covering a power line right-of-way. (Photograph by Yun Wu.)

every four years) creates open spaces and ideal conditions for this early successional species.

Mile-a-minute weed also infests recreational and residential areas, such as Rock Creek Park near Washington, D.C. (Fleming and Kanal, 1992), Frick Park and Schenley Park in Pittsburgh, Pennsylvania (*The Dominion Post* [Morgantown, West Virginia] 14 September 1999), and Valley Forge National Park in Valley Forge, Pennsylvania (Hartwig, 1995). The dense, prickly thickets formed by this weed are especially bothersome to tourists and their pets.

In eastern Asia where it originated, mile-aminute weed is considered a harmful weed of agriculture (Kasahara, 1954; Barbora, 1972; Anon., 1978), a beneficial plant used as an herbal medicine (He *et al.*, 1984; Zhu, 1989; Sook and Myung, 1992; Yang and Kim, 1993; Hoque *et al.*, 1989), or an edible wild fruit (Bajracharya, 1980). Mile-a-minute weed is considered a harmful weed throughout Japan (Kasahara, 1954). In China, mile-a-minute weed is widely distributed but not considered to be a serious weed (Wang, 1990), but it may be a problem in less-intensively managed agricultural areas (Chen and Lin, 1989). Mile-a-minute weed is found at fewer sites in northern China than in southern China. It invades tea plantations and grows along cornfields in Henan Province in central China, where agricultural fields are intensively managed. It is distributed widely in southern China (e.g., Zhejiang, Fujian, Sichuan, and Guangxi provinces), where it grows along rivers and invades orchards.

Ecological damage. In the eastern United States mile-a-minute weed germinates in full sun in early spring. It grows rapidly and out competes native species (Moul, 1948; Hill et al., 1981; The New York Times, 16 August 1994; Oliver, 1994). It also grows rapidly in areas where other weeds are killed by herbicides, for example in kudzu eradication areas in cities such as Washington, D.C. (The New York Times, 16 August 1994; Sue Salmons, pers. comm.). Gerlach-Okay (1997) investigated the changes in plant diversity on sites with and without mile-a-minute weed in Virginia. Plant diversity was reduced in the first year in plots with mile-a-minute weed, compared to controls. Loss of native plant species diversity from milea-minute weed affects wildlife species by reducing or eliminating their food plants and habitats (Oliver, 1994).

Geographical Distribution

In North America, the first recorded specimen was found near Portland, Oregon, in the 1890s, although establishment did not occur (Hickman and Hickman, 1977). In the late 1930s, mile-a-minute weed was found in Pennsylvania and Maryland. In 1954, a plant specimen was collected in British Columbia, although there was no report of establishment (Hill et al., 1981; Park, 1986). By 1989, mile-a-minute weed infestations were reported in only three states - Pennsylvania, Maryland, and West Virginia (Mountain, 1989). By 1994, this plant was reported in eight states (Pennsylvania, Maryland, Ohio, West Virginia, Virginia, Delaware, New Jersey, and New York) and the District of Columbia (Lehtonen, 1994). Recently, the state of Connecticut was added to the list (Donna Ellis, pers. comm.) and the infestations are larger and expanding in all of the eight states and District of Columbia (Fig. 2). Fifteen additional states, all within Plant Hardiness Zones 6 and 7, have climates favorable for the propagation of mile-a-minute weed (Okay, 1997).

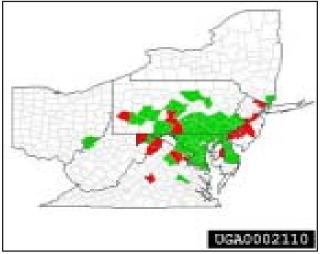


Figure 2. Current distribution of mile-a-minute weed by county in the eastern United States (green – before 1995, [Mountain, 1995]; red – after 1995). (Data prepared by Yun Wu; map by Gino Luzader.)

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Synonyms of Polygonum perfoliatum L. include Fagoparum perfoliatum (L.) Rafine., Chylocalyx perfoliatus (L.) Hassk., Echinocaulos perfoliatus (L.) Meisn., Echinocaulon perfoliatum (L.) Hassk., Tracaulon perfoliatum (L.) Greene, Persicaria perfoliata (L.) H., Ampelygonum perfoliatum (L.) Roberty and Vautier, and Truellum perfoliatum (L.) Sojak (Steward, 1930; Park, 1986). Common names include mile-a-minute weed, devil's tearthumb, Giant climbing tearthumb, Asiatic tearthumb (Walker, 1976), and devil's tail tearthumb (Hartwig, 1995).

Mile-a-minute weed is in the family Polygonaceae (Cronquist, 1993), subfamily Polygonoideae (Vánky and Oberwinkler, 1994), tribe Polygoneae (Steward, 1930), subtribe Polygoninae (Vánky and Oberwinkler, 1994), genus *Polygonum* (Steward, 1930), and section Echinocaulon (Steward, 1930).

Biology

Plant height varies depending on where it grows. In open areas mile-a-minute weed forms a dense, tangled mat that covers everything including small trees and shrubs. Along forest edges, plants climb on trees and can reach 8 m in height.

The almost perfectly triangular-shaped leaves have long petioles and thin blades and grow alternately on the stem. They are bright green, 4 to 7 cm long and 5 to 9 cm wide, and the main veins and petioles are armed with recurved prickles. A pale green, saucer shaped sheath of 1 to 2 cm of diameter encircles the node (Fig. 3). Stems are green when young, red when aged and are armed with recurved prickles; stems become woody at the base. Inflorescences are spike-like clusters of 10 to 15 tiny flowers that are terminal in position or in the axils of the upper leaves. Inflorescences are up to 2 cm long and flowers are 1.5 mm across. Seeds consist of spherical, shiny-black achenes, covered by a white or pink perianth, which becomes blue and fleshy when mature. They form blueberry-like "fruits," each 5 mm in diameter, arranged in clusters. Annual plants have fibrous and shallow roots.



Figure 3. Mile-a-minute weed, Polygonum perfoliatum L. (Photograph by Yun Wu.)

The life cycle of mile-a-minute weed is varied, sometimes listed as an annual (Kasahara, 1954; He *et al.*, 1984), other times as a perennial (Riefner, 1982; Zhu, 1989). It behaves like an annual in North America (Mountain, 1989; Cusick and Ortt, 1987; McCormick and Johnson, 1997). Mile-a-minute weed specimens have been collected from areas that are tropical (e.g., Hainan Province in China, Java in Indonesia, and Luzon in the Philippines) (Park, 1986), but it is not as abundant (Zi-de Jiang, pers. comm.). In the southern subtropical area of Yunnan Province in China, where frost does not occur and mild weather presents all year, mile-a-minute weed was observed to grow throughout the year. New roots grow from nodes on climbing stems and develop into new plants producing flowers and fruits. The main stems on these old plants were observed as thick as 1 cm in diameter, and were supported by a taproot. In the subtropical area of Guangzhou, China, mile-a-minute weed plants will die when the first frost appears in December, and seeds will start to germinate in late January or early February in the following year (Yun Wu and Zi-de Jiang, unpub.). Mile-a-minute weed is generally considered an annual plant that needs coldwet stratification of seeds to break dormancy in temperate regions (Gerlach-Okay, 1997; Will Mountain, pers. comm.). In the northeastern United States, milea-minute weed will die during the first frost around late October or early November in Pennsylvania and West Virginia, and start to germinate in early to mid-March to April, although some plants may germinate late in the season (Mountain, 1989; McCormick and Johnson, 1997; Moul, 1948; Wu, unpub.). Flowering begins in June or early July and continues throughout the rest of the growing season (Reifner, 1982; McCormick and Johnson, 1997). Fruits are produced between early August and the first frost (Mountain, 1989). Seeds are dispersed by water, birds, and small mammals (Mountain, 1989; Gerlach-Okay, 1997), and by human activities.

Analysis of Related Native Plants in the Eastern United States

There are about 40 genera and 800 species of Polygonaceae (Buckwheat family) in the United States and Canada (Bailey and Bailey, 1976). They include 14 economically important plant species including those grown as human and animal food, such as Fagopyrum spp. (buckwheat) and Rheum spp. (rhubarb), and a few grown as ornamental plants such as Coccoloba diversifolia Jacq. (pigeon-plum), C. uvifera (L.) L. (sea grape), Eriogonum crocatum Davidson (saffron-buckwheat), Eriogonum fasciculatum Benth. (wild buckwheat), Oxyria digyna (L.) Hill (mountain sorrel), and Polygonum amphibium L. (water smartweed) (Table 1). The rest of the species are weeds and are a potential source of seed contamination (Germplasm Resource Information Network, 2001). There are 20 species designated as rare and endangered plants (Table 1) in six genera although most of them are in Chorizanthe, Eriogonum, and Polygonella (Germplasm Resource Information Network, 2001).

Table 1. Native or Economic Important Plants Related to Polygonum perfoliatum in Polygonaceae in the United	b
States	

Scientific Name (Common Name)	Economic Species	Endangered Species (USFWS)	Rare Plants (Center for Plant Conservation)	Native Species	Found in Easterr U.S.
Chorizanthe howellii Goodman (Mendocino spineflower)		х		х	
Chorizanthe orcuttiana Parry (Orcutt's spineflower)		Х		х	
Chorizanthe pungens Benth. var. hartwegiana Reveal & Hardham (Hartweg's spineflower)		Х		x	
Chorizanthe pungens Benth. var. pungens (Monterey spineflower)		х		х	
Chorizanthe robusta Perry (rubust spineflower)		х		х	
Chorizanthe valida S. Watson (Sonoma spineflower)		х		х	
C <i>occoloba diversifolia</i> Jacq. (pigeon-plum)	ornamental			х	
<i>Coccoloba uvifera</i> (L.) L. (sea-grape)	erosion control/ornamental/ fruit			Х	
Dodecahema leptoceras (A. Gray) Reveal & Hardham (slenderhorn spinyherb)		Х		х	
Eriogorum apricum J. T. Howell (incl. rar. prostratum) lone buckwheat)		Х		х	
Eriogonum argophyllum Reveal			х	х	
E <i>riogonum crocatum</i> Davidson saffron-buckwheat)	ornamental			х	
E <i>riogonum fasciculatum</i> Benth. (wild buckwheat)	ornamental			х	
Eriogonum gypsophilum Wooton and Standl. (Seven River Hills buckwheat)		х		х	
Eriogorum kennedyi Porter ex. S. Wats. var. <i>austromontanum</i> Munz. & Johnston (Kennedy's buckwheat)		Х		х	
Eriogorum longifolium Nutt. var. gnaphalifoliumGandog. (longleaf buckwheat)		Х		х	
<i>Eriogorum ovalifolium</i> Nutt. var. vineum (Small) Nelson. (cushion buckwheat)		Х		х	
Eriogorum ovalifoliumNutt. var. villiamsiae Reveal Williams' buckwheat)		Х	х	х	
Eriogorum pelinophilum Reveal clayloving buckwheat)		Х	х	х	
Fagopyrum esculentum Moench Japanese buckwheat)	bee plants/human or animal food			Intro.	х

Table 1. Native or Economic Important Plants Related to *Polygonum perfoliatum* in Polygonaceae in the United States (continued)

Scientific Name (Common Name)	Economic Species	Endangered Species (USFWS)	Rare Plants (Center for Plant Conservation)	Native Species	Found in Eastern U.S.
Fagopyrum tataricum (L.) Gaertn. (tartary buckwheat)	human food/ animal food/weed			Intro.	х
<i>Oxyria digyna</i> (L.) Hill (mountain sorrel)	ornamental			х	х
Ox <i>ytheca parishi</i> i Parry var. <i>goodmaniana</i> Ertter (Goodman's puncturebra)		х		х	
<i>Polygonella basiramia</i> (Small) Nesom & Bates (Florida jointweed)		х	х	x	
Polygonella macrophylla Small Polygonella myriophylla (Small) Horton (Small's jointweed)		Х	X X	x x	
Polygonum amphibium L. (water smartweed)	ornamental weed			х	х
Polygonum arifolium L. (halberd-leaf tearthumb)				х	х
<i>Polygonum carey</i> i Olney (Carey's smartweed)		Х		х	x
Polygonum cespitosum Blume (oriental ladysthumb)				х	х
Polygonum erectum L. (erect knotweed)	weed			х	х
Polygonum hirsutumWalt. (hairy smartweed)				Х	х
Polygonum hydropiperoidesMichx. (mild water-pepper)	weed			х	х
Polygonum lapathifoliumL. (curlytop knotweed)				х	х
Polygonum pensylvanicumL. (Pennsylvania smartweed)	weed			х	х
Polygonum punctatumElliott (dotted smartweed)	weed			х	х
Polygonum sagittatum L. (arrow-leaf tearthumb)	weed			х	х
Rheum rhabarbarum L. (garden rhubarb)	human food			Intro.	х
<i>Rumex altissimus</i> Wood (pale dock)	weed			х	х
Rumex hymenosepalus Torr. (canaigre)	tannin, dyestuff			х	
Rumex orthoneurus Rech. f.			Х	х	
<i>Rumex venosus</i> Pursh (wild begonia)	weed			х	

All information except the three introduced species from the Germplasm Resources Information Network (GRIN) (http://www.ars-grin.gov/npgs/tax/index.html) and the Plant List of Accepted Nomenclature, Taxonomy, and Symbols (PLANTS) (USDA, NRCS) (http://plants.usda.gov/plants/qurymenu.html).

Plants in the genus Polygonum are annual or perennial herbs, shrubs, or vines of moist habitats, and often grow as weeds in disturbed areas (Park, 1986). There are about 150 species in the genus Polygonum in the United States and Canada (Bailey and Bailey, 1976). The species in Polygonum are grouped into eight subgenera (called sections) (Steward, 1930). Polygonum perfoliatum belongs to the section Echinocaulon Meisn., which consists of 21 species. Of these, 15 are found in Asia (Park, 1986). Native species in the United States in this section include Polygonum sagittatum L. and Polygonum arifolium L. (Park, 1986). Other Polygonum species native to the United States that belong to a closely related section, Persicaria L., include Polygonum pensylvanicum L., Polygonum amphibium L., Polygonum lapathifolium L., Polygonum punctatum Elliot, Polygonum hydropiperoides Michx., Polygonum careyi Olney, Polygonum hirsutum Walt., Polygonum persicaria L., and Polygonum cespitosum Blume. Another native species, Polygonum erectum L., belongs to section Avicularia Meisn. (Bailey and Bailey, 1976).

The North American species *P. sagittatum* and *P. arifolium* are chemically distinct from *P. perfoliatum*. In contrast, *Polygonum senticosum* (Meisn.) Fr. et Sav., a species distributed in eastern Asia, has morphological and chemical characteristics that are very similar to those of *P. perfoliatum*, including the complete absence of flavones (Park, 1986).

In contrast to *P. perfoliatum*, which mainly grows in moist, temperate woodlands, *P. pensylvanicum* mainly grows in nonforested areas within temperate deciduous forests, and *P. arifolium* and *P. punctatum* are aquatic plants (Baskin and Baskin, 1998), although, in the eastern United States, the four species were found to coexist on the same sites (Gerlach-Okay, 1997).

Plants of economic or ecological importance (including threatened and endangered species) in North America in the same family as mile-a-minute weed are listed in Table 1. Some widely distributed weeds (*Polygonum persicaria* L., *Polygonum convolvulus* L., *Polygonum hydopiper* L., *Polygonum aviculare* L., *Polygonum coccineum* Muhl. ex Willd., *Rumex acetosella* L., and *Rumex crispus* L.) are not listed because they are introduced species. *Polygonum orientale* L. is another introduced species that occurs in the eastern and midwestern portions of the United States.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of the Weed

Mile-a-minute weed is a widely distributed species of east Asia, including Japan, China, Korea, India, Indonesia, Bangladesh, Siberia, the Philippines, the Malay Peninsula, the Indochina Peninsula, Nepal, and Turkey (Steward, 1930; Fernald, 1950; Ohwi, 1965; and Guener, 1984).

Introduced into the United States from Japan in the late 1930s (Moul, 1948), mile-a-minute weed was found growing in a nursery in Stewartstown, York County, Pennsylvania. It was also introduced to the Glenn Dale Introduction Garden, Prince Georges County, Maryland from Nanjing, China at a similar time. It was eradicated from the introduction Garden (Moul, 1948), while the population in York, Pennsylvania became established and spread from the site.

Areas Surveyed for Natural Enemies

In 1996, the U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team (FHTET) initiated a project to determine the feasibility of using natural enemies to control mile-aminute weed. Natural enemy surveys were conducted in the eastern United States and in China from 1997 through 2000. The survey areas in the eastern United States included Pennsylvania, Maryland, Delaware, West Virginia, and Virginia.

The survey areas in China included 18 provinces (Heilongjiang, Jilin, Liaoning, Inner-Mongolia, Hebei, Beijing, Tianjin, Henan, Shandong, Hubei, Hunan, Sichuan, Guangxi, Guangdong, Zhejiang, Fujian, Yunnan, and Guizhou) (Fig. 4).

Natural Enemies Found

Arthropods – eastern United States. One of the earliest surveys for natural enemies of mile-a-minute weed in the eastern United States was by Wheeler and Mengel (1984) who surveyed in southcentral Pennsylvania from 1981 through 1983. They recovered 34 species (five orders, 15 families) that developed on the weed and 12 species that fed on mile-aminute weed only as adults. None of them appeared to cause significant damage to the weed. In 1998, Jim



Figure 4. The distribution of mile-a-minute weed and natural enemy survey areas by province in China (brown – surveyed areas; gray – areas with weed, not yet surveyed). (Map by Ding Jian-qing.)

Fredericks (University of Delaware) surveyed selected sites in Pennsylvania and Delaware. The most abundantly recovered insect causing damage to milea-minute weed was adult Japanese beetles, Popillia japonica Newman, which caused significant defoliation. Other recovered insects appeared to cause no significant damage to the weed (Fredericks, 2001). The FHTET sponsored surveys at several sites in five states provided collections of natural enemies across a broad range of habitats. By the end of the 2000 field season, more than 1,500 arthropods were recovered from mile-a-minute weed representing 100 insect species in 50 families and seven orders although many have not been identified beyond the family level. Insects that attack the seeds or roots have not been recovered.

Arthropods – China. One hundred insect species in 32 families and seven orders were found associated with mile-a-minute weed (Jian-qing Ding, pers. comm.). Most of the insects collected in China fed on leaves, but stem borers, gall makers, and flowerand fruit-feeders also were recovered. No insects that attack the roots have been recovered. Of the 100 insect species recovered, several species appear to have potential for use as biological control agents, based on their distribution, host range, population density, and potential to damage the plant. These species are two geometrid moths, *Timandra griseata* Petersen (Fig. 5), and *Timandra convectaria* Walker (Lep.: Geometridae); a bug, *Cletus schmidti* Kiritschenko (Hem.: Coreidae); a weevil, *Homorosoma chinensis* (Col.: Curculionidae) (Fig. 6); and a sawfly, *Allantus nigrocaeruleus* (Smith) (Hym.: Tenthredinidae).

In addition to the above species, several others damaged mile-a-minute weed, but appear to have relatively broad host ranges based on the literature and would require detailed study to confirm their actual level of host specificity. These apparently polyphagous species were the stem borers *Pleuroptya ruialis* (Scopoli) and *Ostrinia scapulalis* (Walker) (Lep.: Pyralidae); the defoliators, *Smaragdina nigrifrons* (Hope) (Col.: Eumolpidae), *Gallerucida bifasciata* Motschulsky, and *Gallerucella* sp. (Joannis) (Col.: Chrysomelidae); and the noctuids *Trachae atriplicis* L. and *Agrogramma agnata* Staudinger (Lep.: Noctuidae).



Figure 5. *Timandra griseata* moth. (Photograph by Ding Jian-qing.)



Figure 6. Homorosoma chinensis adult. (Photograph by Ding Jian-qing.)

Specimens of all the species being considered as potential natural enemies for importation into quarantine facilities in the United States have been submitted to the USDA, ARS Systematic Entomology Laboratory for taxonomic confirmation.

Pathogens - United States and China. Fungal isolates were isolated from symptomatic mile-aminute weed plants collected in the eastern United States and China. Symptoms associated with these agents included wilting or spotting of leaves and stems. Pathogenicity screening tests of these fungal isolates using various inoculation methods (a detached-leaf assay, a toothpick-insertion test [Fig. 7], or seedling-root dipping) have been conducted at the USDA, ARS, Foreign Disease-Weed Sciences Research Unit containment greenhouse facility in Frederick, Maryland. About 20 isolates caused symptoms in the detached-leaf assay, and two caused systemic symptoms or whole plant mortality when evaluated using the toothpick-insertion test (Wu et al., 1999). Additional tests are planned as well as the continued development of procedures to identify isolates.



Figure 7. Toothpick-insertion test for pathogenicity of a fungal isolate on mile-a-minute weed plants and a control. (Photograph by Yun Wu.)

Host Range Tests and Results

Numerous preliminary host range tests for several natural enemies, including *T. griseata, H. chinensis*, and *Gallerucella* sp., were conducted in China on selected plant species within and outside of Polygonaceae. Additional host range tests were conducted in the United States for *T. griseata* and *H. chinensis* on several crop species within Polygonaceae.

In China, choice and no-choice tests were conducted on nearly 50 plant species for T. griseata. The results showed that larvae of this moth prefer milea-minute weed and did not attack other plants in choice tests. In no-choice tests, T. griseata larvae fed on Polygonum thumbergii Sieb. et Zucc., P. lapathifolium, Polygonum bistorta L., Polygonum bungenum Turcz., P. hydropiper, Polygonum alpinum All., Rumex japonicus Houtt., and Fagopyrum dibotry (D. Don) Itara. Additional host range testing conducted in the United States showed that larvae completely defoliated P. perfoliatum and two buckwheat species (Fagopyrum esculentum Moench. and Fagopyrum tartaricum [L.] Gaertn) in no-choice tests and were able to complete their life cycle to adults on all three host species. In choice tests, larval preferences for F. esculentum, F. tartaricum, and P. perfoliatum were equal (Price, 2001).

Choice and no-choice tests also were conducted in China on larvae and adults of the weevil H. chinensis. Forty plant species in 14 families were tested, of which 18 species were in the Polygonaceae. In both choice and no-choice tests, H. chinensis did not feed on the 22 species from 13 families outside of the Polygonaceae. In choice tests, using species within the Polygonaceae, the weevil did not attack any of 17 non-target test species. In no-choice tests, adult weevils did feed on Rumex japonicus, P. lapathifolium, and P. lapathifolium var. lanatum. Both adults and larvae fed on Rheum altanicum A. Los. and P. bistorta L.; but weevils did not oviposit or complete their life cycle on these plants. Weevils feeding on these species lived for 14 to 25 days as adults, and for 24 to 36 hours as larvae. Comparably, weevils feeding on milea-minute weed lived for 69 days as adults and for 216 hours as larvae, and completed their life cycle on milea-minute weed. In the United States, adult female H. chinensis did not lay eggs on *F. esculentum* or *R. rhabarbarum* in no-choice tests but did on mile-aminute weed. *H. chinensis* adults fed on *F. esculentum* and *R. rhabarbarum* in choice tests (Price, 2001).

BIOLOGY AND ECOLOGY OF NATURAL ENEMIES

Timandra griseata Petersen (Lepidoptera: Geometridae)

This insect is also known as *Calothysanis amata* (L.), Calothysanis amataria (L.), and Timandra amataria (L.) (Skou, 1986). It has two generations per year in Europe, with a flight period from mid-May until mid-September. In northern Europe, there is only one generation, with a flight period from late June to late July. In Europe, larvae feed on plants in the Polygonaceae (e.g., Rumex [dock, sorrel], Polygonum [knotgrass]) and the Chenopodiaceae (e.g., Atriplex). Pupation takes place in loosely woven cocoons between leaves, often on the host plants. The species is capable of overwintering either as a larva or pupa. This moth is widely distributed in Europe, Asia, and North Africa (Skou, 1986; West, 1986; Skinner, 1998). In China, larvae feed on leaves, young buds, and fruits of P. perfoliatum. When populations are high, larvae nearly destroy all the young leaves and buds on the plant.

Homorosoma chinensis (Wagner) (Coleoptera: Curculionidae)

No literature was found on this species, which has been recovered in Henan, Hunan, Hubei, and Heilongjiang provinces in China. Adults feed on flowers, buds, and young leaves of *P. perfoliatum*. Larvae attack buds and bore into stems prior to pupation (Fig. 8).

Cletus schmidti Kiritschenko (Hemiptera: Coreidae)

This bug is widely distributed in China. Both adults and larvae feed on the skin of the fruit, exposing the immature seeds, and adversely affecting reproduction of the weed. Preliminary host range testing results indicated that mile-a-minute weed is the major host of *C. schmidti*.



Figure 8. Homorosoma chinensis larva and its damage on a stem of milea-minute weed. (Photograph by Ding Jian-qing.)

RECOMMENDATIONS FOR FUTURE WORK

Surveys for natural enemies of mile-a-minute weed in China need to be completed for arthropods in Jiangsu, Jiangxi, and Anhui provinces, where mile-aminute weed is widely distributed, and in southern China for plant pathogens.

Screening tests of exotic and native fungi isolated from mile-a-minute weed plants need to be completed. Fungi need to be identified and their host ranges estimated. Additional host range testing of *T.* griseata and *T. convectaria*, *H. chinensis*, *C. schmidti*, *Galerucella grisescens (Joannis)*, and *A. nigrocaeruleus* need to be conducted in China and in the United States.

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27 SKUNK VINE

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PEST STATUS OF WEED

Skunk vine, *Paederia foetida* L. (Fig. 1), is a recently recognized weedy vine of natural areas in Florida that is spreading into other parts of the southern United States. The weed, which is native to Asia, appears to have the potential to spread well beyond the South to the northeastern states. Control of the plant by chemical or mechanical means damages valued vegetation supporting the vine. Skunk vine is a Category I Florida Exotic Pest Plant Council weed (Langeland and Craddock Burks, 1998), a listing that groups the plant with the most invasive weed species in Florida.



Figure 1. Skunk vine (*Paederdia foetida*), showing its leaves and flowers. (Photograph by K. A. Langeland, University of Florida, Gainesville.)

Nature of Damage

Economic damage. Although *P. foetida* is primarily a weed of natural ecosystems, economic damage does occur in agricultural and urban environments. In Florida, the weed can invade citrus groves located near unmanaged lands (Possley and Brazis, 1998), although the weed is not currently a significant problem in commercial citrus. Skunk vine also invades pasturelands, where cattle have been observed grazing on the weed. Effects on growth and reproduction of livestock, however, are unknown (Gann and Gordon, 1998). In urban landscapes, this vine entwines branches of woody ornamental plants and also spreads horizontally through lawns, rooting at the nodes (Martin, 1995). In westcentral Florida, *P. foetida* is considered the most troublesome weed along roadside right-of-ways (W. Moriaty, pers. comm.), and it also entangles power lines and associated structures (Martin, 1995).

On the island of Hawaii, *P. foetida* is a very serious weed in nurseries producing ornamental foliage plants (Pemberton, pers. obs.). The weed infests field plantings used for propagation. Control of the weed is very difficult because stock plants are easily injured if herbicides are applied. At times, growers have had to abandon or destroy stock plants that have become overgrown by skunk vine. Florida's large ornamental foliage industry also could be affected by skunk vine, as would the container plant industries in other states should the weed spread.

A cursory estimate of economic losses may be determined as the cost of removing or treating the weed. Stocker and Brazis (1999) estimated the cost of manually removing *P. foetida* from a moderately infested area at \$1,622/ha. Estimates for herbicidal treatments of light (5.1 vines per m²) and moderate (33.6 vines per m²) infestation levels were \$430/ha and \$645/ha, respectively (B. Nelson, pers. comm.). Complete control was not achieved with a single treatment, regardless of the method.

Ecological damage. While little is known concerning the optimal growing conditions for this weed, it is apparent that skunk vine can tolerate a broad range of climatic, hydrological, and edaphic conditions (Gann and Gordon, 1998). This tolerance is exemplified by the diverse habitats that *P. foetida* has invaded in the southeastern United States, which include xeric uplands (sandhill), rockland hammocks, mesic uplands (hardwood, mixed, and pine forests), and floodplain wetlands (floodplain forest and marsh) (Dehring, 1998; Gann and Gordon, 1998; Wunderlin, 1998; Pratt and Pemberton, 2001). These habitats are characterized as climax systems that harbor many threatened and endangered species (Anon., 1990).

Ecological damage is widely recognized as a result of invasion by P. foetida; specifically the displacement of the native flora (Schmitz et al., 1997; Gann and Gordon, 1998; Langeland and Craddock Burks, 1998). Skunk vine is charged with displacing one of the few remaining populations of the native, federally endangered Cooley's water willow, Justicia cooleyi Monach. and Leonard (Langeland and Craddock Burks, 1998). Skunk vine can create dense canopies leading to damage or death of native vegetation (Gann and Gordon, 1998). Prostrate growth can develop into a dense layer of overlapping vines across the soil surface, smothering understory plants (Fig. 2). Climbing vines can scale and cover midlevel and overstory vegetation, eventually resulting in the collapse of trees or their branches. Direct damage to overstory plants increases the probability of gap formation and may alter the impact of fire, which occurs in many of the invaded communities (Gann and Gordon, 1998). Community level impacts have not been assessed.



Figure 2. Infestation of skunk vine growing over native forest in central Florida. (Photograph by K. A. Langeland, University of Florida, Gainesville.)

Extent of losses. The extent of losses from *P. foetida* is difficult to ascertain, in part, to a lack of monitoring of impacts of the plant on native communities and unclear valuation of the natural systems it invades.

Geographic Distribution

The geographic distribution of *P. foetida* is currently restricted to the southeastern United States (Fig. 3)

and Hawaii. On the mainland, herbaria records show a concentration of *P. foetida* in central and northern Florida, as well as widely separated occurrences in Texas, Louisiana, Georgia, North Carolina, and South Carolina (Brown, 1992; Gann and Gordon, 1998; Diamond, 1999). The probability that skunk vine also has invaded Mississippi and Alabama is high, although no herbaria samples have been collected, and no surveys have been made. Recent discoveries of the weed in North Carolina and in the more tropical regions of southern Florida demonstrate the weed's continued expansion north and south (Diamond, 1999; Pratt and Pemberton, 2001). It is unknown if and how skunk vine spreads over long distances.

While it seems clear that skunk vine can invade much of the southeastern United States, it is difficult to predict the exact area at risk of invasion. It is likely that the northern range limits of this plant in the United States have yet to be realized. In Japan, the northern limit of the plant's range is the Tohoku region, an area with minimum temperatures of -10 to -20°C (Maekawa and Shidei, 1974; Muller, 1982). This distribution suggests that skunk vine can tolerate similar temperatures to those found in the United States Department of Agriculture Plant Hardiness Zone 6 (Cathey, 1990). Using Zone 6 as a northerly limit, the weed can potentially spread to 40° latitude, north of Delaware, Maryland, and the Virginias.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

Paederia foetida is one of 30 species in the genus *Paederia* in the family Rubiaceae (Mabberley, 1997). *Paederia* is a genus of subtropical vines and shrubs occurring mainly in southeast Asia (16 spp.) and Africa-Madagascar (12 spp.); two species live in tropical America (Puff, 1991a). Skunk vine is one of two *Paederia* species that have become naturalized in Florida. *Paederia foetida* is naturalized primarily in central Florida, whereas *Paederia cruddasiana* Prain, commonly called sewer vine, is naturalized only in Dade County.

Wunderlin (1998) separates the genus *Paederia* from other members of the Rubiaceae that are either native to or naturalized in Florida by the following suite of characteristics. The plants are woody vines, have flowers and fruits in open solitary inflorescences,

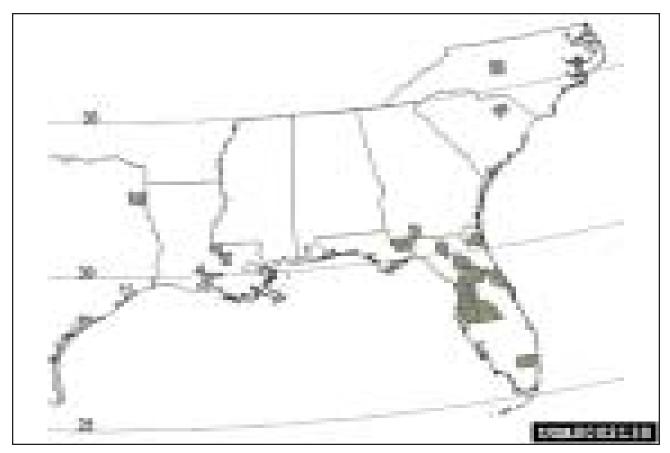


Figure 3. Known distribution of skunk vine by county in the eastern United States.

lack thorns, have similarly sized flowers within the inflorescence, have flowers and fruits with stalks, have corollas that are pale lilac in color with pubescent outer surfaces, and bear yellow-orange fruits. Skunk vine and sewer vine are easily separated from one another by their fruits. Skunk vine has spherical fruits and the seed (diaspores) lack wings, whereas sewer vine has fruits that are laterally compressed and seeds that are conspicuously winged. The leaves of sewer vine are typically larger than those of skunk vine. The common English names of these plants relates to the odor of the leaves, which is due to the presence of sulfur compounds (Mabberley, 1997). The odor is another helpful character to identify these vines and separate them from other plants.

Recent work (Puff, 1991a) has confirmed skunk vine and sewer vine from Florida as *P. foetida* and *P. cruddasina*. The large native range in both temperate and tropical Asia and considerable variation in leaf morphology, pubescence, and floral tube length resulted in taxonomic confusion. The most common but invalid names of skunk vine are *Paederia scandens* (Lour.) Merrill, *P. chinensis* Hance, *P. tomentosa* Blume, and *P. crudassiana*.

Biology

The biology of skunk vine is virtually unstudied. Paederia foetida is evergreen in southern Florida and deciduous from central Florida north, probably because frost is rare in southern Florida but usual from central Florida north. The weed occurs in a great diversity of habitats in its native range. The following habitats were recorded on herbarium specimens of skunk vine or observed for the plant in Japan and Taiwan: grassy hillsides, secondary forests, open places in primary forests, forest shade, river banks, canal banks, waste ground, hedges and thickets, roadsides, and fences, even in large cities. The large native range and the diversity of climatic zones and habitats occupied indicate that skunk vine has exceptionally broad environmental tolerances. It appears not only to be the most widespread Paederia species but also the most common Paederia species in most of its range.

Analysis of Related Plants in the Eastern United States (Florida)

Native species. The Rubiaceae, to which skunk vine belongs, is a large, mostly tropical family with more than 10,000 described species in 630 genera (Mabberley, 1997). Florida has 44 native species belonging to 20 genera (Wunderlin, 1998). These native plants are diverse in life form, and include herbs, woody vines, shrubs, and trees. Thirty-two native plants, in 10 genera, belong to the same subfamily (Rubioideae) as *Paederia* (Robbrecht, 1988; Wunderlin, 1998).

Five native species in four genera in the Rubiaceae are rare in Florida and are legally protected endangered or threatened plants (Coile, 1996). Three are endangered (Catesbaea parviflora Sw., Ernodea cokeri Britton ex Coker, and Strumpfia maritima Jacq.), and two are threatened (Ernodea littoralis Sw. and Pinckneya bracteata [W. Bartram] Raf.). Two of these rare species are *Ernodea* species that belong to the same subfamily Rubioideae as skunk vine. One of the others, the small shrub S. maritima, has uncertain affinities within the Rubiaceae, and so its relative relatedness to skunk vine is unknown. Although there are many native species in the Rubiaceae in Florida, none are very closely related to skunk vine because none are in either the genus Paederia or tribe Paederieae to which skunk vine belongs. The tribe Paederieae has no native members in the continental United States.

Economically important species. The checklist of the woody cultivated plants of Florida (Burch et al., 1994) lists 24 genera of plants in the family Rubiaceae. Eight of these (Catesbaea, Cepahalanthus, Chiococca, Genipa, Hamelia, Mitchella, Pinckneya, and *Psychotria*) are native groups dealt with above. Most of the other genera (12 of 16) could be placed with available literature, and only one genus (Serissa) belongs to the same subfamily and tribe as skunk vine (Burch et al., 1994; Robbrecht, 1988). The genus Serissa has one cultivated species (S. foetida Lam.), a tiny shrub commonly used in planters and edge plantings in Florida (Watkins and Sheehan, 1975). There are important Rubiaceous cultivated shrubs that are distantly related to skunk vine (they belong to other subfamilies). For instance, Gardenia species (particularly Gardenia jasminoides Ellis = Gardenia augusta [L.] Merr.) are grown as fragrance plants and produced commercially for use as cut flowers. Ixora species (Ixora coccinea L. and others) are grown for their showy red, orange, and yellow flowers, and are one of the most common hedge plants in South Florida. *Mussaenda* species are shrubs that increasingly are being cultivated because of their colorful flower-like bracts. Coffee (*Coffea arabica* L.) is grown at times as an ornamental curiosity.

Only a few herbaceous members of the Rubiaceae are cultivated in Florida. *Pentas lanceolata* (Forssk.) Deflers, a subfamily Rubioideae member, is very commonly cultivated for its showy flowers, which attract butterflies. For more detailed analysis of economic and native members of the Rubiaceae and their subfamilial and tribal placements in Florida, see Pemberton and Pratt (1999).

Natural Enemy Host Specificity Level Needed

Herbivores suitable for use as natural enemies of skunk vine would be those whose feeding and development are restricted to the tribe Paederieae. If skunk vine natural enemies are limited to Rubiaceous plant species belonging to the genus Paederia or, more broadly, to the tribe Paederieae, no native plants would be used as hosts because none of Florida's native plants belong to this tribe. However, the introduced ornamental plant S. foetida might be used by such an agent (with tribe level specificity), because this plant also belongs to the Paederieae. This cultivated plant should be included in host range tests, and its horticultural worth more carefully evaluated if it appears to be an acceptable host of any candidate biological control agents. No other rubiaceous plants cultivated in Florida would be hosts of natural enemies with this tribe level specificity. We expect that many insects with this tribe or genus level of host specificity should be associated with P. foetida and other Paederia species in their native ranges.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of the Weed

The native range of skunk vine was determined by Puff (1991b) and by Pemberton, who examined ca. 400 skunk vine specimens in the herbaria of the National Museum of France (Paris), the Royal Botanical Garden at Kew (UK), the British Museum of Natural History (London), and the Makino Herbarium at Tokyo Metropolitan University (Japan). The plant reaches north as far as 42° at the tip of the island of Honshu in Japan. Its southern limits are Christmas Island (south of Java) and Timor in Indonesia – both at about 10° S. To the east the plant reaches Honshu and Japan's Bonin Islands at about 143° E, to the west skunk vine reaches Nepal at about 85° E.

Paederia foetida was reportedly introduced as a potential fiber plant to an unknown location in Florida by the U.S. Department of Agriculture prior to 1867 (Morton, 1976). The geographic origin of the introduced material is unknown. This plant was identified as a problematic weed as early as 1916, when it was found to have entangled ornamental plants near the city of Brooksville (Hernando County) in central western Florida (USDA, 1918).

Early references to skunk vine in the region, coupled with its current geographic distribution (Fig. 2), suggest the site of original introduction and epicenter for subsequent dispersal was westcentral Florida (USDA, 1918; Small, 1933; Morton, 1976). Subsequent introductions from Darjeeling, India were made to the USDA Miami Plant Introduction Station in 1932 but the fate of these plants is unknown, as is the rationale for the introduction.

In addition to the United States, skunk vine has naturalized in Mauritius, Reunion, Sri Lanka (probably), New Guinea (probably), and Hawaii (Puff, 1991b). In Hawaii, the plant is known from the islands of Hawaii, Oahu and Kauai (Puff, 1991b), and also Maui (D. O'Dowd, pers. comm.).

Table 1. Natural Enemy Types Observed in a Preliminary Survey of Skunk Vine (*Paederia foetida*) in CentralJapan and at One Site in Taiwan during October, 1997

Natural enemy (Order: Family)	Type Feeder/feeding	Type Feeder/feeding Places Recorded	
<i>Acyrthosiphon nipponicu</i> s (Essig et Kuwana) (Homoptera: Aphididae)	aphid	Mie Pref., Japan	at several sites, probably a specialist
Hornworm larvae either <i>Macroglossu</i> m spp. or <i>Asplendon himachal</i> a (Lepidoptera: Sphingidae)	leaf-feeding hawk moths (1 or 2 spp.)	Tokyo and Mie Pref., Japan	specificity unknown
Serpentine leafminer (Lepidoptera: unidentified family)	leaf-mining moth	Tokyo and Mie Pref., Japan	common, may be a specialist
Blotch leafminer (Lepidoptera: unidentified family)	leaf-mining moth	Tokyo and Mie Pref., Japan	at several sites, probably a specialist
<i>Nokona pernix</i> (Leech) (Lepidoptera: Sesiidae)	stem-galling moth	Nagoya, Japan	specialist
Fruit-boring moth (Lepidoptera: unidentified family)	feeds within fruit	Tokyo and Mie Pref., Japan	interesting because of damage, unknown specificity
Web-making moth (Lepidoptera: unidentified family)	feeds on and within fruit from a web	Mie Pref., Japan	interesting because of damage, unknown specificity
Spider mite (Acari: Tetranychidae)	distorted leaves	Tokyo, Japan	unknown specificity, probably a generalist
Blotch leaf disease (Cercosporia-like)	fungus? causing dead leaf blotches	N. of Taipei, Taiwan	not very damaging, could be a specialist

Natural Enemy (Order: Family)	Type of Feeder	Country	Estimated Specificity	Reference
<i>Acyrthosiphon nipponicu</i> s (Essig et Kuwana) (Homoptera: Aphidae)	aphid	Japan	high	Moritsu, 1983
<i>Lygaeus fimbriatus</i> Dallus (Hemiptera: Miridae)	plant feeding true bug	Japan	high	Tomokuni, 1993
<i>Dulinius conchatu</i> s Distant (Hemiptera: Tingidae)	lace bug leaf feeder	Japan	high	Tomokiuni and Saito, 1998
<i>Phygasia fulvipennis</i> (Baly) (Coleoptera: Chrysomelidae)	leaf beetle	China, Japan	low-multifamily	Chujo and Kimono, 1961
<i>Trachyaphthona sordid</i> a (Baly) (Coleoptera: Chrysomelidae)	leaf beetle	Japan	high	Chujo and Kimono, 1961
<i>Asphondylia</i> sp. (Diptera: Cecidomyidae)	flower-galling fly	Japan	very high	Yukawa and Masuda, 1996
Asphondylini tribe member-new species (Diptera: Cecidomyidae)	flower-galling fly	Japan	very high	Yukawa and Masuda, 1996
<i>Nokona chrysoidea</i> (Zukowsky) (Lepidoptera: Sesiidae)	stem-galling moth	Taiwan	very high	Kallies and Arita, pers. com.
<i>Nokona pernix</i> (Leech) (Lepidoptera: Sesiidae)	stem-galling moth	China, Japan	very high	Arita, 1994
<i>Nokona rubra</i> Tosevski and Arita (Lepidoptera: Sesiidae)	stem-galling moth	Ryukyu ls. (Japan)	very high	Arita, 1994
<i>Goniorhynchus exemplaris</i> Hampson (Lepidoptera: Geometridae)	moth	Japan, Korea	unknown	Ko, 1969
Asplendon himachala Butler (Lepidoptera: Sphingidae)	moth	China, Japan, Korea, Taiwan	unknown	Sugi, 1987; Ko, 1969
<i>Macroglossum pyrrhostica</i> Butler (Lepidoptera: Sphingidae)	moth	China, Japan, Korea, Taiwan, India,	high?	Ko, 1969; Miyata, 1983; Sugi,1987
<i>Macroglossum bombylans</i> Boisduva (Lepidoptera: Sphingidae)	moth	Japan	medium-other family	Miyata, 1983
<i>Macroglossum stellatarum</i> L. (Lepidoptera: Sphingidae)	moth	Africa, China, Europe, Japan, Korea	medium-other family	Ko, 1969
<i>Trichohysetis rufoterminalis</i> (Christoph.) (Lepidoptera: Pyralidae)	moth	Japan	unknown	Miyata, 1983

Areas Surveyed for Natural Enemies

Paederia foetida has not yet been a formal target of a biological control program. A feasibility study to determine the plant's suitability for biological control was conducted by the authors. Part of this study was to gather information to indicate whether promising natural enemies appear to be associated with the plant in its native range.

Searches of English language literature revealed few insects or diseases associated with skunk vine. A preliminary survey to obtain an indication of the occurrence of natural enemies associated with skunk vine was made in Japan and Taiwan during October 1997 by R. Pemberton. In addition, the published literature, particularly from Japan, was examined to identify the natural enemies that have been recorded on the plant.

Natural Enemies Found

Nine natural enemies – seven insects, one mite, and one fungal pathogen – were encountered during field surveys (Table 1). Most were unidentified Lepidoptera, including foliage feeders, leafminers, and fruit feeders. The leafminers and stem gallers are probably specialist herbivores of the plant. The fungal disease found in Taiwan may be *Pseudocercospora paederiae* (Swada ex.) Goh and Hsieh recorded recently in Florida (Walker *et al.*, 2001). It does not appear to cause significant harm to skunk vine in either Japan or Florida.

The 16 insect natural enemies recorded in the literature that attack skunk vine (Table 2) include an aphid and a mirid bug that bear the red-and-yellow warning coloration often seen in specialist herbivores. An Indian lace bug has recently invaded the Osaka area of Japan, where is causes considerable damage to skunk vine (Tomokiuni and Saito, 1998). Two gall flies in the genus Asphondylia have been recorded to gall the flowers of the plant and may reduce the reproductive potential. Three sesiid moths gall the stems of skunk vine in different parts of Asia. The impact of these galls on the plant is unknown. Two chrysomelid beetles have been recorded to use skunk vine as host and one of these, Trachyaphthona sordida (Baly), is believed to be a specialist on the plant (Chujo and Kimono, 1961). Because chrysomelid beetles have successfully controlled many weeds including alligator weed, leafy spurge, tansy ragwort, and purple loosestrife (Julien and Griffiths, 1998), T. sordida will be of special interest. The remaining six insects are Lepidoptera, four of which are leaf feeding sphingid moths with broad or unknown host ranges. The remaining two Lepidoptera include two little known pyralid and geometrid moths. These herbivores occupy diverse niches on the plant. Nine of these 16 insects are thought to have high degrees of host specificity suggesting biological control of skunk vine using insects has considerable promise.

RECOMMENDATIONS FOR FUTURE WORK

An essential first step in forming a biological control project against skunk vine will be to obtain funding for the work. The feasibility study of Pemberton and Pratt (2000) on the suitability for biological control of skunk vine provides a solid basis for a project. Potential conflicts with native and economic plants are well defined and some promising natural enemies are known. During the first phases of the project we recommend the actions listed below.

(1) Conduct surveys for natural enemies in the native region of the plant. Because skunk vine's distribution is in subtropical to warm temperate areas of Florida and the southern United States, surveys should focus on northeast Asia and parts of the Himalayan Mountains. Surveys in northeast Asia should include the parts of Japan, South Korea, and China that are climatically similar to the infested regions in the United States and that are known to have promising natural enemies. The chrysomelid, T. sordida, is of particular interest, as are the flowergalling flies. The plant is common in northeast Asia and easily surveyed. The second area that should be investigated is the western end of the plant's native distribution, in northern India and Nepal. Although the source of the skunk vine introduction(s) that became a problem in Florida is unknown, USDA introductions from northern India in 1932 suggest that the region might also have been the original source of the weed. Northern India and Nepal also have areas with climatic similarity to the infested areas in Florida. This region is home to many Paederia species, which may have co-evolved specialist herbivores. Because there are no native plants in the same genus or tribe as skunk vine in Florida, natural enemies of other species in the genus Paederia also could be safely employed against the weed. Surveys should include searches for plant pathogens of skunk vine.

(2) Design host specificity testing schemes based on the analysis of economic and native Rubiaceae in Florida and the American South. Acquisition of test plants will be aided by the fact that many Florida members of the Rubiaceae are in cultivation.

(3) Conduct surveys of existing natural enemies of skunk vine in Florida and other southern states. One specialized pathogen, *Pseudocercospora paederiae* [Swada ex.] Goh and Hsieh, native to Asia, has been found in Florida. Other natural enemies of *Paederia* spp. may have been introduced to Florida as well. Pathogens occurring in Florida, that might have moved to skunk vine from native members of the Rubiaceae, could have promise as mycoherbicides.

(4) Study the ecology of skunk vine in problem areas in the United States. Because almost nothing is

known about the ecology of the weed, studies to identify the susceptible stages of the plant (adult, juvenile, and seed bank), as well as the phenology and population dynamics, should assist in natural enemy selection.

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28 COGON GRASS

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PEST STATUS OF WEED

Cogon grass, Imperata cylindrica (L.) Beauv., has been ranked as one of the ten worst weeds of the world (Holm et al., 1977) (Fig. 1). In tropical and subtropical regions around the globe, this aggressive, rhizomatous perennial is generally considered a pernicious pest plant due to its ability to successfully disperse, colonize, spread, and subsequently compete with and displace desirable vegetation and disrupt ecosystems over a wide range of environmental conditions (Holm et al., 1977; Brook, 1989; Bryson and Carter, 1993; Dozier et al., 1998). These characteristics and consequences of cogon grass infestations are similarly evident even within the native or endemic range in the Eastern Hemisphere, as it has long been considered one of Southeast Asia's most noxious weeds (Brook, 1989).



Figure 1. Cogon grass, *Imperata cylindrica*, (a) a partial plant showing stems, leaves, roots and elongating rhizomes; (b) a stem with leaves; (c) plume-like inflorescence of many paired flowers. (Modified from Coile and Shilling, 1993.)

Nature of Damage

Economic damage. In areas other than closed-canopy forests or plantations, where cogon grass survives poorly due to shading, and heavily cultivated lands, where it is kept in check mechanically, infestations are treated by relatively costly, laborious, and repetitive control measures. Currently the most effective management strategies in the United States have involved integrating mechanical (e.g., discing, mowing), cultural (e.g., burning), chemical (e.g., herbicide applications of glyphosate and imazapyr), and revegetation methods (Shilling and Gaffney, 1995; Dozier et al., 1998). However, a single herbicide application can cost as much as \$400/ha. Impacts on non-target species from herbicide application are often severe, creating disturbances that allow for the re-invasion by cogon grass or secondary invasion by other weedy species (Gaffney and Shilling, 1996). For both economical and environmental reasons, the currently recommended control strategies often are unacceptable, necessitating consideration of some form of classical biological control (Shilling and Gaffney, 1995; Dozier et al., 1998). There are only a few localized benefits of cogon grass. These include use for thatch, forage, erosion control, paper making, and bedding material for livestock. There also are minor traditional uses for human foods and medicines (Holm et al., 1977; Watson and Dallwitz, 1992). Silica bodies in the leaves, razor-like leaf margins, relatively low yields, and very low nutritive and energy values make cogon grass a poor forage (Coile and Shilling, 1993; Colvin et al., 1993).

Outside of the United States, cogon grass has been reported as a problem in more than 35 annual and perennial crops, including rubber, coconut, oil palm, coffee, date, tea, citrus, forests, field crops (rice), and row crops (corn) (Holm et al., 1977; Brook, 1989; Waterhouse, 1999). Problems with cogon grass often have arisen on lands cleared of natural forest, which are then quickly colonized by cogon grass before cultivation, during plantation establishment and growth, or soon after the abandonment of land used for short-duration shifting agriculture (Brook, 1989). Left unchecked, colonized areas become densely infested with cogon grass, are difficult to convert to other vegetation, and are fire-prone climax communities (Seth, 1970). Cogon grass infestations damage crops through competition, causing suppressed growth, reduced yields, and delayed harvests. In addition to being highly competitive, the rhizomes of cogon grass may physically injure other plants and appear to be allelopathic in certain situations (Brook, 1989; Bryson and Carter, 1993).

Since the introduction of cogon grass into Alabama around 1912, and Mississippi and Florida in the early 1920s, infestations in the southeastern United States have created pest problems in lawns, pastures, golf courses, roadways, railways and other right-ofways, mine reclamation areas, plantations, forests (Fig. 2), and recreational and natural areas (Bryson and Carter, 1993; Dozier *et al.*, 1998; Willard *et al.*, 1990).



Figure 2. A severe infestation of *Imperata cylindrica* in a longleaf pine upland in central Florida.

Ecological damage. Cogon grass' tendency to form dense, persistent and expanding stands allows it to displace other vegetation. Its abundant biomass prevents recruitment of other plants and changes the properties of the litter and upper soil layers (Lippincott, 1997). In Florida sandhill communities, cogon grass stands can destroy the habitat of rare species such as gopher tortoises (*Gopherus*) polyphemus [Holbrook]) and indigo snakes (Drymarchon corais couperi [Daudin]) (Shilling et al., 1995; Lippincott, 1997). Cogon grass also is flammable and increases fine-fuel loads. Resultant fires tend to be hotter and taller, and potentially more frequent, even in communities adapted to frequent fire (e.g., longleaf pine [Pinus palustris Mill.] and wiregrass [Aristida beyrichiana Trin. and Rupr.] cover type). Extensive rhizome reserves of cogon grass enable it to quickly regrow. Also, fires induce flowering and seeding, reduce competition from other plants, and create openings for seedling establishment (Bryson and Carter, 1993; Dozier et al., 1998; Shilling et al., 1995).

Extent of losses. More than 500 million ha of cogon grass have been estimated to occur worldwide (Holm *et al.*, 1977). In Asia, where an estimated 200 million ha are dominated by cogon grass, infested areas are increasing at a rate of 150,000 ha annually (Soerjani, 1970). At least 100,000 ha. are estimated to be infested in Alabama, Florida, and Mississippi (Dickens, 1974; Schmitz and Brown, 1994).

Geographical Distribution

Cogon grass has been reported as a weed in 73 countries and on all six continents. It is widely distributed in Africa, Australia, southern Asia, and the Pacific Islands, and less extensively distributed, or a less serious problem, in southern Europe, the Mediterranean, the Middle East, Argentina, Chile, Colombia, the Caribbean, and the southeastern United States (Fig. 3). It has been found at latitudes from 45°N (Japan) to 45°S (New Zealand), and from sea level to over 2,000 m elevation (Holm *et al.*, 1977).



Figure 3. The general distribution of *Imperata cylindrica* throughout the world, depicted by areas of white. (Based on information from Holm *et al.*, 1997.)

In the United States, cogon grass occurs in Florida, Georgia, Alabama, Mississippi, Louisiana, South Carolina, and Texas (Fig. 4). It is distributed throughout Florida (Langeland and Burks, 1998) and is widely distributed in Mississippi (Patterson and McWhorter, 1983; C. Bryson, pers. comm.), and southern Alabama (Dickens, 1974). It is established at some locations in Louisiana, South Carolina (Allen *et al.*, 1991; Bryson and Carter, 1993), southern Georgia (Byrd and Bryson, 1999; Coile, pers. comm.), and in Tyler County, Texas (USGS, 1999).



Figure 4. The general distribution of *Imperata cylindrica* in the United States, depicted by area in red.

A red-tipped ornamental cultivar, *Imperata cylindrica* 'Rubra,' is extensively promoted as Red Baron, or Japanese Blood Grass, in many other states (Hall, 1998; C. Bryson, pers. comm.). This red-colored ornamental cultivar can revert to the green form, which is the invasive variety (Greenlee, 1992; Dozier *et al.*, 1998; Hall, 1998; C. Bryson, pers. comm.). Plants propagated by tissue culture, rather than division, seem particularly prone to revert to the aggressively spreading green form (Greenlee, 1992).

Imperata cylindrica 'Rubra' is very cold tolerant (Shilling et al., 1997), and has persisted in Michigan for several years in an ornamental garden (C. Bryson, pers. comm.). Should this cold-tolerant cultivar be introduced into the southeast and hybridize with *I. cylindrica* var. *major*, hybrids might exhibit both invasiveness and cold tolerance, allowing for significant range extension to the north and west (Shilling et al., 1997).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The descriptions of the genus (*Imperata* Cirillo. Pl. Rar. Neap. 2:26 1792) and species (*Imperata cylindrica* [L.] Beauv., Ess. Nouv. Agrost. 7. 1812) occurred in 1792 and 1812, respectively. Gabel (1982) identified 29 synonyms for *I. cylindrica*.

The genus *Imperata*, family Poaceae, subfamily Panicoideae, supertribe Andropogonodae, tribe Andropogoneae (Gabel, 1982; Watson and Dallwitz, 1992), subtribe Saccharinae (Clayton, 1972; Campbell, 1985), includes nine species worldwide (Gabel, 1982). Hubbard *et al.* (1944) recognized five varieties of *I. cylindrica* worldwide: *major, africana, europaea, latifolia*, and *condensata*, with the most widely distributed variety, *major*, occurring in the United States.

The global cultural impact and importance of *I. cylindrica* is suggested by the nearly 100 common names given to it (Holm *et al.*, 1977). Some of the most widely recognized of these are blady grass, alang-alang, lalang, cogon grass, and speargrass.

Biology

Cogon grass is an erect, perennial grass, with linear to lanceolate, mostly basal leaf blades up to 1.5 m tall and to 2 cm wide (Gabel, 1982; Lippincott, 1997; Langeland and Burks, 1998). Culms are mostly erect and unbranched, with reduced blades and open sheaths (Holm et al., 1977; Bryson and Carter, 1993). Pubescent at their base, leaf blades have a noticeably off-center whitish midvein and scabrous margins (Fig. 5). Varying in form, from loose to compact tufts, cogon grass is strongly rhizomatous with extensive, sharply pointed, creeping scaly rhizomes (Holm et al., 1977; Langeland and Burks, 1998). Panicles (6 to 22 cm long by 3.5 cm wide) are plume-like, cylindrical, dense, and silvery (Holm et al., 1977; Lippincott, 1997; Langeland and Burks, 1998). Spikelets are 3 to 6 cm long, crowded and paired on unequal stalks, with each spikelet surrounded by white hairs up to 1.8 mm in length (Bryson and Carter, 1993; Langeland and Burks, 1998)



Figure 5. Portion of leaf blade showing offcenter midrib and scabrous leaf margins. (From Coile and Shilling, 1993.)

Cogon grass is a C₄ grass found mainly in tropical and subtropical areas with 75 to 500 cm of annual rainfall (Bryson, 1999). Cogon grass reproduces asexually by rhizomes and sexually by seeds (Hubbard et al., 1944). Imperata cylindrica is the most morphologically variable species in the genus Imperata (Gabel, 1982). Rhizomes are very resistant to heat and breakage, and may penetrate soil up to 1.2 m deep, but generally occur in the top 0.15 m in heavy clay soils, and 0.4 m of sandy soils (Holm et al., 1977; Bryson and Carter, 1993). Rhizome biomass can reach 40 tons of fresh weight per hectare (Terry et al., 1997; English, 1998), and regrowth potential of roots is a critical issue in development of control methodologies, including biological control. Regeneration from rhizome segments as small as 2 mm has been observed. Success of segment regeneration is determined by the original location of the segment on the rhizome, including proximity to, or inclusion of, axillary and apical buds, as well as environmental conditions (Holm et al., 1977; Wilcut et al., 1988a; Gaffney, 1996; English, 1998). Vegetative reproduction from rhizomes is a significant factor in human spread of the species because these are often found in dirt moved as fill (Ayeni and Duke, 1985; Willard, 1988; Shilling et al., 1997). Cogon grass rhizomes exhibit apical dominance (English, 1998), which may be an important factor both in limiting the local spread of cogon grass via rhizomes (Wilcut et al., 1988a), and reducing the efficacy of herbicidal control due to sub-lethal herbicide sink activity in dormant axillary buds (Shilling et al., 1997; English, 1998).

Incapable of self-pollination (Gabel, 1982), *I. cylindrica* produces viable seed only when cross-pollinated (McDonald *et al.*, 1996), and the success rate

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of outcrossing is low (Shilling et al., 1997). Cogon grass produces as many as 3,000 seeds per plant (Holm et al., 1977). Having no dormancy, seeds are highly germinable (90% or higher), but often with low spikelet fill (less than 40%) in natural populations. Seed viability is highest for seeds less than three months old (Shilling et al., 1997). Sexually produced seeds are capable of long distance dispersal, ranging from an average of 15 m (Holm et al., 1977) to 100 m (Shilling et al., 1997). Flowering is variable between individual plants and stands, but generally occurs in spring or fall, and often in response to a range of disturbances (e.g., burning, mowing, soil disturbance) throughout the year. Flowering has been observed throughout the year in most of Florida. (Holm et al., 1977; Willard, 1988). Cogon grass seedling survivorship is low with less than 20% of emergent seedlings surviving to one year.

Cogon grass has invaded a variety of habitats, from highly xeric uplands to fully shaded mesic sites. Sandhills, flatwoods, hardwood hammocks, sand dunes, grasslands, river margins, swamps, scrub, and wet pine savanna communities all are invaded by cogon grass. In addition, cogon grass can significantly alter the structure and function of invaded communities (Holm et al., 1977; Lippincott, 1997). While cogon grass is tolerant of wide variations in soil fertility, organic matter, and moisture, it grows best in relatively acidic soils (pH 4.7) (Hubbard et al., 1944; Wilcut et al., 1988a). Moosavi-nia and Dore (1979) found that increasing shade levels of more than 50% reduces shoot dry weight and both rhizome length and dry weight; causing an increase in the shoot/rhizome ratio. Temperature markedly affects shoot and rhizome growth, with increased growth occurring at 29°/23°C (day/night), compared to lower temperatures (Patterson et al., 1980). In general, rhizomes do not exhibit extreme cold hardiness, but stands of cogon grass have survived temperatures as low as -14°C (Wilcut et al., 1988b). In greenhouse studies, King and Grace (2000a) found cogon grass to be most sensitive to soil saturation during early establishment (following seed germination). Cogon grass invasion by seed may therefore be limited by excessive moisture in the spring, during early seedling development. Once established, cogon grass becomes increasingly tolerant of flooding. Cogon grass seed germination rates and survival rates of newly germinated seedlings were not significantly affected by gap size or disturbance type (King and Grace, 2000b). Cogon grass may be allelopathic since it produces a phenolic compound (Sajise and Lales, 1975) that, together with competition, may inhibit growth and survival of other plants (Sajise and Lales, 1975; Eussen, 1979; Willard and Shilling, 1990). However, Lippincott (1997) suggests that other explanations may exist for the competitive success of cogon grass and that the existence of allelopathy is not certain.

Analysis of Related Native Plants in the Eastern United States

The genus Imperata belongs to the tribe Andropogoneae, in the subtribe Saccharinae Griseb. (Clayton, 1972). Of the nine species of Imperata worldwide, two occur in the eastern United States -I. cylindrica and Imperata brasiliensis Trin. A third species, Imperata brevifolia Vasey, occurs in the western United States (Gabel, 1982). Though considered by Gabel (1982) to be native to Florida, South America, Central America, southern Mexico, and Cuba, I. brasiliensis is listed as an introduced Federal Noxious Weed in the United States, as well as a statelevel noxious weed in Florida and North Carolina (USDA, 1999). Imperata cylindrica has been distinguished from *I. brasiliensis* based on number of stamens. Imperata cylindrica has two stamens and I. brasiliensis has one stamen (Gabel, 1982). However, overlapping variability often occurs in this character, and Hall (1998) has suggested the possibility that the two species may be the same. Imperata brasiliensis and I. cylindrica have undergone human-disturbanceassociated range extension (Brook, 1989; Hall, 1998). Evidence of frequent hybridization between the two species has been observed (Gabel, 1982), and all seed produced by crossing the two species in a study by McDonald germinated (Shilling et al., 1997).

Campbell (1985) agrees with Clayton (1972, 1981), placing *Imperata* Cirillo in the subtribe Saccharinae Griseb. Other genera in *Saccharinae* include *Erianthus* Michx. and *Microstegium* Nees. Dahlgren *et al.* (1985) placed *Imperata* in the *Saccharum* Group, including *Saccharum* L., *Imperata*, and *Eulaliopsis* Honda. Hitchcock and Chase (1951) consider *Miscanthus* Andersson, *Saccharum*, *Erianthus*, and *Microstegium* Nees closely related to *Imperata*.

Outside the genus *Imperata*, the species most closely related to *I. cylindrica* that are native to the eastern United States are five species in the genus *Erianthus* (Hitchcock and Chase, 1951; Clayton, 1972; Campbell, 1985). They are *Erianthus strictus* Baldwin (narrow plumegrass), *Erianthus contortus* Baldwin ex Elliot (bent-awn plumegrass), *Erianthus alopecuroides* (L.) Elliot (silver plumegrass), *Erianthus coarctatus* Fernald, and *Erianthus giganteus* (Walt.) Muhl. (sugarcane plumegrass). All five species occur in soil types and habitats that overlap with those of cogon grass.

While comparatively few native species are closely related to I. cylindrica, several notable nonnative species should mentioned. be Mangoendihardjo and Soerjani (1978) felt that the biological control potential of cogon grass in Indonesia was limited by its close relationship to many graminaceous food plants. In the United States, the closeness of this relationship is of greatest concern with sugarcane (Saccharum spp.), with approximately 88% of domestic cane sugar production in the United States occurring in Florida, Louisiana, and Texas (Haley, 2000). Fertile, intergeneric hybrids have been procured by crossing species of *Imperata* with those of Saccharum (Gabel, 1982; Watson and Dallwitz, 1992).

Additionally, several species of the genera *Miscanthus* and *Microstegium* have been introduced into the eastern United States. *Miscanthus sinensis* (Andersson) has been identified as invading clearings in wooded areas throughout the eastern United States (Randall and Marinelli, 1996). *Microstegium vimineum* (Trin.) A. Camus, Japanese stilt grass, is an invasive, exotic grass currently established in sixteen eastern states (Swearington, 1997).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The exact center of origin of *I. cylindrica* is in doubt, but is believed to be East Africa (Evans, 1987, 1991). *Imperata cylindrica* var. *major* originated in Southeast Asia and occurs throughout the tropical and warmer regions of the world, from Japan to southern China, through the Pacific islands, Australia, India, East Africa, and the southeastern United States (Holm *et al.*, 1977). Differences in the areas of origin of the various introductions of *I. cylindrica* var. *major* in the United States are a likely source of genetic variation in the growth potential and range of different populations and ecotypes present in the United States (Patterson *et al.*, 1980; Gabel, 1982).

Areas Surveyed for Natural Enemies

Despite the importance of the problems caused by cogon grass throughout the tropical areas of the world, biological control efforts have been few and rather piecemeal (Caunter, 1996). This weak effort can be explained, in large part, by the historical emphasis in weed biological control projects on insects as biological control agents and lack of host specific insects associated with weedy grasses (Evans, 1991; Julien and Griffiths, 1998). This has resulted in a general absence of attempted, and thus of successful, biological control projects against grasses (Waterhouse, 1999). Other complicating factors include existence of closely related grasses of economic or ecologic value (Holm et al., 1977) and potential conflict of interest with groups that value cogon grass (Evans, 1991). Similarly, little information exists on the pathogens of cogon grass and their potential as biological control agents (Evans, 1991), even though pathogens often exhibit specific host associations (McFadyen, 1998). It is likely that fungi associated with cogon grass are more diverse and abundant than indicated by herbarium records (Evans, 1991; Charudattan, 1997; Minno and Minno, 2000).

Considerable scope exists for additional field surveys, given that *I. cylindrica* is distributed worldwide, has five major geographical varieties, and an undetermined center of origin. Locations of potential interest would include Southeast Asia, from which the common form *major* is believed to have come; East Africa, believed to be the center of origin; and the Mediterranean, where the plant is not a serious weed problem.

Ravenell (1985) lists twelve pathogenic fungi identified on cogon grass in Alabama. From 1994 to 1997, field surveys looking for diseased cogon grass or related grasses in Florida collected 70 fungal isolates. Recently, Minno and Minno (1999, 2000) surveyed cogon grass in Florida, Mississippi, and Alabama, looking for native or naturalized enemies.

Limited surveys also have been made in East Africa and Southeast Asia. Surveys of *I. cylindrica* in East Africa did not locate any suitably monophagous insects (Evans, 1991). In Egypt (Giza), Tawfik *et al.* (1976), and Ammar *et al.* (1977) periodically surveyed *I. cylindrica*, and respectively found one Hemiptera species, and three planthopper species.

A review of the literature on insects associated with *I. cylindica* in southeast Asia concluded that none of the recorded species were promising biological control agents (Syed, 1970). However, field surveys in Java from 1973 to 1976 identified 15 species of insects associated with *I. cylindrica* (Mangoendihardjo, 1980). Apart from the United States, field surveys for pathogens of *I. cylindica* have been made only in Malaysia (Caunter, 1996).

Natural Enemies Found

Literature records and on-line databases suggest an extensive number of potential natural enemies, including pathogens, arthropods, and other invertebrates found within and outside of North America. Outside the United States, 66 pathogens (primarily fungi), 42 insects, two nematodes, and one mite have been found on *I. cylindrica*. Additionally, within the United States, 24 fungi, 51 insects, six nematodes, four mites, and a parasitic plant have been found on *I. cylindrica*, primarily by Minno and Minno (1999, 2000).

Of the arthropods recorded on cogon grass worldwide, only one is repeatedly reported to be host specific to *I. cylindrica* – the gall midge *Orseolia javanica* Kieffer and van Leeuwen-Reijnvaan (syn. = *Orseoliellia javanica*). Introduction of this midge to infested areas outside of southeast Asia was recommended as early as 1975 (Mangoendihardjo, 1975), but no introductions were ever made. Other invertebrates from outside of the United States that may be host specific and damaging to cogon grass include the nematode *Heterodera sinensis* Chen, Zheng, and Peng (Chen *et al.*, 1996), the mite *Aceria imperata* (Zaher and Abou-Awad) (Zaher and Abou-Awad, 1978), and two unidentified dipteran stem borers (Mangoendihardjo, 1980).

Evans (1987, 1991) suggested that some of the known pathogens of cogon grass should be considered for introduction to the United States as classical biological control agents. Promising species include the fungi *Colletotrichum caudatum* (Sacc.) Peck (Caunter, 1996), which recently was found on cogon grass in Florida (Minno and Minno, 2000); *Puccinia fragosoana* Beltrán (USDA, ARS, 2001); *Puccinia imperatae* Poirault (Evans, 1987); and *Sphacelotheca schweinfurthiana* (Thümen) Saccardo (Evans, 1987). Other fungi known as cogon grass pathogens pose greater difficulties because of conflicting or confusing taxonomy or insufficient information. Interestingly, the smut *S. schweinfurthiana* is common in the Mediterranean region where *I. cylindrica* is not a serious problem (Evans, 1991). This smut has recently been found on *I. cylindrica* in Florida (Minno and Minno, 1999).

Of the pathogens detected in the United States, at least 11 fungal isolates collected from cogon and other grassy weeds in Florida have been tested for their pathogenicity to I. cylindrica in greenhouse trials. Of these, six (three Bipolaris spp., a Drechslera sp., and two Exserohilum spp.) merit further evaluation as potential bioherbicides (Charudattan, 1997). More recently Yandoc et al. (1999) have conducted greenhouse and miniplot trials with isolates of Bipolaris sacchari (E. Butler) Shoemaker and Drechslera gigantea (Heald and F. A. Wolf) Kaz. Ito. Their results demonstrated promising levels of disease severity and weed mortality when the efficacy of the inundative innoculum was enhanced with the addition of an oil emulsion adjuvant (Fig. 6). Further development of these two fungi as bioherbicides is continuing, but neither fungus is host specific.



Figure 6. High levels of disease and damage severity on an *Imperata cylindrica* mini-plot following treatment with a potential mycoherbicide consisting of a formulation of *Bipolaris sacchari* fungal spores, in an oil and water emulsion. (C. Yandoc, Department of Plant Pathology, University of Florida.)

Host Range Tests and Results

The only insect enemy of *I. cylindrica* that has been subjected to host range testing is the gall midge *O. javanica*. *O. javanica* was studied on corn, sorghum, five species of rice, and two other grasses, and found to be specific to *I. cylindrica* (Mangoendihardjo, 1980). Further host range testing is necessary. The fungus, *C. caudatum* proved to be host specific to *I. cylindrica* in limited host range tests in Malaysia (Caunter and Wong, 1988), which led to an examination of its potential as a bioherbicide in Malaysia (Caunter, 1996). Applications of spore suspensions of this fungus failed to kill whole plants, but it may be possible to enhance disease severity with the addition of yeast or other amendments. Because the two fungi currently being investigated in the United States as potential bioherbicides (i.e., *B. sacchari* and *D. gigantea*) are not specific to *I. cylindrica*, host range testing of the bioherbicidal mixtures are planned (R. Charudattan, pers. comm.).

Releases Made

No releases have been made of any natural enemies.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The alang-alang gall midge, *O. javanica*, (Fig. 7) has been considered the most important insect pest of *I. cylindrica* due to its host specificity (Mangoendihardjo, 1980; Soenarjo, 1986). No species in the genus *Orseolia* have been identified in North America (Gagné, 1989).

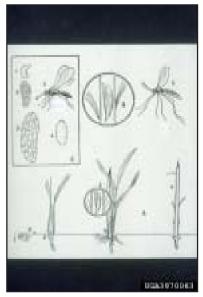


Figure 7. Orseolia javonica in Imperata cylindrica, (a) (1) eggs, (2) larva, (3) elongated gall, and (4) section of the gall following adult release, (5) adult; (b) section of gall showing the pupa; (c) life stages of chalcid wasp parasite of *O. javanica*. (From Soerjani, 1970.) The life cycle of *O. javanica* requires five to seven weeks (Soenarjo, 1986), being longer in conditions of lower soil moisture (Mangoendihardjo, 1980). Mangoendihardjo (1980) found *O. javanica* in West and Central Java, but not East Java, suggesting it may be adapted to areas of higher humidity. In Indonesia, the highest degree of gall-midge infestation on *I. cylindrica* was observed from 250 to 300 m above sea level (Mangoendihardjo, 1980), although infestations occur up to an elevation of 800 m (Soenarjo, 1986). Densities of *O. javanica* were significantly higher in areas where *I. cylindrica* was regularly cut or slashed (Soerjani, 1970; Soenarjo, 1986). However, parasitism of *O. javanica* larvae by a chalcid wasp also increased in slashed areas (Mangoendihardjo, 1980).

Females can produce from 200 to 560 eggs, which hatch two to three days after being laid and have a 98% viability rate (Soerjani, 1970; Mangoendihardjo, 1975). After hatching, less than 2% of the larvae successfully enter the plant, primarily due to predation by ants (Mangoendihardjo, 1980). Resultant infestation of *I. cylindrica* by the gall midge varies from 0 to 18% (Mangoendihardjo, 1975).

The larva enters *I. cylindrica* between the lower leaf sheaths to penetrate the shoot apical meristem, where it forms a cell in which it develops and pupates (Soerjani, 1970). In laboratory studies, only 1% of the total eggs produced survived to adulthood (approximately 50% of the larvae that entered the plant) (Mangoendihardjo, 1980).

The potential of O. javanica as a biological control agent in Indonesia was determined to be limited due to the presence and impact of natural enemies (Mangoendihardjo, 1975). Key natural enemies of O. javanica include a parasite (Hymenoptera: Platygasteridae, *Platygaster* sp.), which has been found to attack more than 20% of field-collected larvae; and predaceous ants, which attack gravid females, eggs, and larvae (Mangoendihardjo, 1975). Three other hymenopteran larval parasites of O. javanica are Obtusiclava sp. (Pteromalidae), Euplemes sp. (Eupelimidae), and Tetrastichus sp. (Eulophidae) (Mangoendihardjo, 1980). Pupae are parasitized by the wasp Platygaster oryzae (Cameron) (Soenarjo, 1986). In the southeastern United States, the red imported fire ant (Solenopsis invicta Buren) is one potential predator that may reduce the potential of O. javanica to suppress I. cylindrica.

Infestation by *O. javanica* is likely to reduce photosynthesis due to leaf blade reduction, leading to lower rhizome carbohydrate reserves. Infestation by *O. javanica* also may vector various pathogens. However, because *O. javanica* does not directly harm the plant's rhizomes, it is unlikely to control the plant by itself (Brook, 1989).

RECOMMENDATIONS FOR FUTURE WORK

The gall midge O. javanica needs to be evaluated for potential introduction into the United States. It is likely to be highly host specific and may cause more damage to infested plants than suggested by the amount of tissue consumed. Removed from its native parasites and predators, O. javanica may prove to be an effective biocontrol agent in the United States, as occurred with the Australian bud-galling wasp, Trichilogaster acaciaelongifoliae Froggatt, released in South Africa against Acacia longifolia (Andr.) Willd. (Center et al., 1995). However, gall midges are notoriously parasitized by generalist parasitoids after introduction, severely limiting their effectiveness (B. Blossey, pers. comm.).

Secondly, DNA fingerprinting (Amplified Fragment Length Polymorphisms) should be used to identify the native range of U.S. cogon grass varieties. This information could then be used to direct survey efforts to areas most likely to have the widest range of natural enemies (Evans, 1987).

Thirdly, intensive surveys of natural enemies of the native *I. brevifolia* in the southwestern United States might yield indigenous biological control agents able to attack *I. cylindrica* if introduced into the southeast. Interestingly, *I. brevifolia* is a minor component of the flora where it occurs in the southwest and has been difficult to cultivate, unlike cogon grass. However, preliminary, limited surveys of *I. brevifolia* in 2000 failed to identify any potentially useful natural enemies.

In addition to the above, work with existing and new pathogens is needed both in the area of developing effective bioherbicides and to explore the potential of possible introductions of host specific foreign pathogens.

Lastly, the most commonly practiced method of biological control of *I. cylindrica* in southeast Asia

is the use of competitive vegetation (Soerjani, 1970). To control cogon grass in the United States, an integrated program of biological control and revegetation with more desirable species will be needed (Shilling *et al.*, 1998).

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29 GARLIC MUSTARD

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PEST STATUS OF WEED

Garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara and Grande, (Fig. 1), a cool-season, shade-tolerant, obligate biennial herb, is currently one of the most serious invaders in forested areas of the northeastern and midwestern United States. *Alliaria petiolata* is one of the few non-indigenous herbaceous species able to invade and dominate the understory of North American forests. Garlic mustard is not known as a weed on other continents.



Figure 1. Garlic mustard plant. (Photo by V. Nuzzo.)

Nature of Damage

Economic Damage. Alliaria petiolata is a weed of natural areas and little direct economic damage has been described or documented. The invasion potential of *A. petiolata* and its ability to cause changes in forest productivity has not been assessed.

Ecological Damage. Little long-term research has been conducted to document the impact of garlic mustard on native ground layer vegetation. However, sites invaded by *A. petiolata* frequently have low native herbaceous richness (Fig. 2) and garlic mustard has been implicated as the cause of this low diversity (White *et al.*, 1993; Anderson *et al.*, 1996; McCarthy,

1997; Meekins and McCarthy, 1999). Garlic mustard invades sites independent of presence or cover of native species, and species-rich sites are more likely to be invaded than species-poor sites (Nuzzo, unpub. data). Once established, *A. petiolata* becomes a permanent member of the community, steadily increasing in presence but with large annual fluctuations in cover and density (Byers and Quinn, 1998; Nuzzo, 1999; Meekins, 2000). Long-term presence of garlic mustard was associated with a significant decline in cover of native perennial herbaceous species (Nuzzo, unpublished data). Phytotoxic chemicals produced by *A. petiolata* may interfere with growth of native species, potentially through inhibition of mycorrhizal activity (Vaughn and Berhow, 1999).



Figure 2. Dense garlic mustard. (Photo by V. Nuzzo.)

Presence of garlic mustard interferes with oviposition of the rare native butterflies *Pieris napi* oleraceae Harris and *Pieris virginiensis* W. H. Edwards (Lepidoptera: Pieridae). The native hosts of *P. napi* oleraceae and *P. virginiensis* are toothworts *Cardamine concatenata* [Dentaria laciniata] (Michx.) O. Schwarz and *Cardamine* [Dentaria] diphylla (Michx.) A. Wood, Brassicaceae. Eggs laid by females hatch but larvae are unable to complete development on garlic mustard (Chew, 1981; Porter, 1994; Huang et al., 1995; Haribal and Renwick, 1998).

Extent of Losses. Lack of long-term data makes quantification of direct losses impossible.

Geographical Distribution

By 2000, *A. petiolata* was most abundant in the northeastern and midwestern United States, ranging from southern Ontario, south to Georgia, Arkansas, and Kansas. Isolated occurrences are known from Utah and Colorado, and populations established in the Pacific Northwest appear to be spreading.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

In North American floras, *A. petiolata* was often referred to as *Alliaria officinalis* Andrz; other names found in older floras include *Alliaria alliaria* L. (Britton), *Sisymbrium alliaria* Scop., *Sisymbrium officinalis* D. C. (not *S. officinale*), and *Erysimum alliaria* L.

Biology

Basal leaves are dark-green and kidney-shaped with scalloped edges (6 to 10 cm diameter). Stem leaves (3 to 8 cm long and wide) are alternate, sharply toothed, triangular or deltoid, gradually reduced in size towards the top of the stem. All leaves have pubescent petioles 1 to 5 cm long. In spring, new leaves produce a distinct garlic odor when crushed, which fades as leaves age. Plants usually produce a single flower stalk, although up to 12 separate flowering stalks have been reported for robust plants. Flowers are produced in spring in terminal racemes. Some plants produce additional axillary racemes in mid-summer. Flowers are typical of the mustard family, consisting of four white petals that narrow abruptly at the base, and six stamens, two short and four long. Flowers average 6 to 7 mm in diameter, with petals 3 to 6 mm long. Fruits are linear siliques, 2.5 to 6 cm long and 2 mm wide, held erect on short (5 mm), stout, widely divergent pedicels. Individual plants produce an average of 22 siliques, arranged alternately on both sides of a papery sinus and containing up to 28 seeds. Seeds are black, cylindrical (3 by 1 mm) and transversely ridged, and range in weight from 1.62 to 2.84mg. Chromosome number of 2n=36 has been recorded for European, and 2n=24 for North American and European individuals (Cavers *et al.*, 1979).

Alliaria petiolata is an obligate biennial plant with a phenology typical of cool-season European plants. Alliaria petiolata grows rapidly in late fall and early spring when native species are dormant (Cavers et al., 1979; Anderson et al., 1996), and all individuals that overwinter successfully will flower and subsequently die (Cavers et al., 1979; Bloom et al., 1990; Byers and Quinn, 1998; Meekins, 2000). Flowers open as early as April and are insect pollinated, but plants can self-pollinate (Cruden et al., 1996). Seed production varies according to habitat conditions (Byers and Quinn, 1998; Nuzzo, 1999; Susko and Lovett-Doust, 2000), but can be as high as 7,900 seeds for robust plants (Nuzzo, 1993). Seeds require 50 to 105 days of cold stratification (1 to 10°C) (Byers, 1988; Baskin and Baskin, 1992; Meekins and McCarthy, 1999), resulting in a dormancy period of 8 months in southern, and 8 to 22 months in northern, locales (Cavers et al., 1979; Byers, 1988; Baskin and Baskin, 1992; Solis, 1998). Garlic mustard forms a short-lived seed bank (Roberts and Boddrell, 1983; Baskin and Baskin, 1992). Seeds germinate in early spring (Cavers et al., 1979; Baskin and Baskin, 1992) with seedling densities as high as 20,000/m² (Trimbur, 1973; Anderson et al., 1996). First year rosettes are sensitive to summer drought (MacKenzie, 1995; Byers and Quinn, 1998; Meekins, 2000) and 60 to 90% die by fall (Anderson et al., 1996; Byers and Quinn, 1998).

Analysis of Related Native Plants in the Eastern United States

Alliaria petiolata belongs to the Brassicaceae with 43 different genera represented in the northeastern United States alone (Gleason and Cronquist, 1991). Alliaria petiolata is the only species of the genus Alliaria in North America (Gleason and Cronquist, 1991). Many introduced species are of economic interest; mustards (Brassica) are the most important genus. Among native taxa, Cardamine [Dentaria] are particularly diverse and grow in the same habitats as A. petiolata. Other native genera include Cakile, Lepidium, Subularia, Draba, Lesquerella, Leavenworthia, Sibara, Arabis, Rorippa, Barbarea, Iodanthus, Erysimum, and Descurainia; all other 29 genera are introduced (Gleason and Cronquist, 1991).

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Research in North America and Europe began in 1998 with field surveys for potential control agents.

Establishment of Area of Origin of Weed

Alliaria petiolata is native to Europe, ranging from England to Sweden to the western regions of the former USSR (Turkestan, northwestern-Himalayas), India and Sri Lanka, and south to Italy and the Mediterranean basin (Tutin *et al.*, 1964; Cavers *et al.*, 1979; Hegi, 1986). The species has been introduced to New Zealand (Bangerter, 1985), Canada (Cavers *et al.*, 1979) and the United States (Gleason and Cronquist, 1991; Nuzzo, 1993). In North America, *A. petiolata* was first recorded on Long Island, New York in 1868 (Nuzzo, 1993).

Areas surveyed for Natural Enemies

Literature surveys for natural enemies of garlic mustard were conducted in Europe and North America. Field sites in Germany, Switzerland and Austria were investigated for their herbivore fauna associated with garlic mustard in 1998 and 1999 (Hinz and Gerber, 1999). Field sites in eastern North America were surveyed in spring and summer 2000.

Natural Enemies Found

A literature survey followed by field investigation in western Europe revealed that 69 insect herbivores and seven fungi are associated with garlic mustard in Europe (Hinz and Gerber, 1998). The most important groups of natural enemies associated with garlic mustard were weevils (Curculionidae), particularly the genus *Ceutorhynchus*, leaf beetles (Chrysomelidae) and butterflies and moths (Lepidoptera). Most of these species are not considered sufficiently host-specific for introduction to North America.

Two stem-mining weevils, a stem-mining fly, a leaf-mining fly, a scale insect, two fungi, and aphids (taxonomic identification for all species is pending) were found attacking garlic mustard in North America. However, their attack was of little consequence to plant performance or reproduction of garlic mustard (Blossey and Nuzzo, unpub. data).

Host Range Tests and Results

Preliminary investigations of the host range of several potential control agents were conducted in 1999 (Hinz and Gerber, 2000) and continued in 2000. Among several non-target species tested, *Rorippa* spp. were identified as potential hosts for a flea beetle. Particular emphasis during host specificity screening will be on native forest understory species associated with garlic mustard in North America. Host range tests will continue through 2003 at CABI Bioscience Centre in Switzerland.

Releases Made

No releases of agents have yet been made against garlic mustard.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Based on information on their restricted host range and their damage, five weevils and one flea beetle were selected as potential biological control agents for garlic mustard (Blossey *et al.*, 2001). Descriptions of their life history and ecology are based on Hinz and Gerber (2000).

Ceutorhynchus alliariae Brisout and *Ceutorhynchus roberti* Gyllenhal (Coleoptera: Curculionidae)

The two weevil species *Ceutorhynchus alliariae* Brisout and *Ceutorhynchus roberti* Gyllenhal (Fig. 3) share similar life history features and occupy the same niche on their host plant. Adults feed on leaves;



Figure 3. *Ceutorhynchus alliariae.* (Photograph by H. Hinz and E. Gerber.)

larvae develop in stems and leaf petioles of garlic mustard. Both species are univoltine. Adults can be distinguished morphologically using coloration of their tarsi, but no reliable features distinguish immature stages (Hoffmann, 1954; Dieckmann, 1972; Hinz and Gerber, 2000). Both species show widely overlapping distributions in Europe (Hinz and Gerber, 2000) although *C. roberti* is the only species reported from Italy (Abazzi and Osella, 1992).

Adults of both species overwinter in soil and leaf litter, and become active simultaneously in early spring. In Europe, oviposition begins around mid March and continues until mid to late May. Eggs are laid individually (*C. alliariae*) or in clusters of up to nine eggs (*C. roberti*) into elongating stems and leaf petioles of garlic mustard. Larvae hatch after one to three weeks and feed internally on the host plant. Mature third instar larvae leave the host plant to pupate in the soil. Larval development from egg to mature larvae takes about seven weeks with new generation adults emerging in June and July.

Attack rates in Europe ranged from 48 to 100% of shoots at various field sites investigated during 1998 and 1999, with an average of 2 to 11 larvae/shoot (Hinz and Gerber, 2000). High attack rates appear to reduce seed production of *A. petiolata*; at densities of 20 to 30 larvae/shoot premature wilting and nearly complete prevention of seed production was observed.

Ceutorhynchus scrobicollis Nerensheimer and Wagner (Coleoptera: Curculionidae)

During recent surveys, Ceutorhynchus scrobicollis Nerensheimer and Wagner (Fig. 4), a univoltine root mining weevil, occurred only in eastern Germany and eastern Austria (Hinz and Gerber, 2000), but the species is also reported from eastern France and Italy (Colonnelli, 1987; Schott, 2000). Adults emerge in May and June, consume leaves for a brief period, followed by summer aestivation. In Europe, oviposition begins in mid September and continues through to spring. Eggs are laid mainly into leaf petioles and into the leaf surface of rosettes. Early instars mainly mine petioles but also growing points of rosettes. The majority of mature larvae feed in root crowns. Larvae overwinter and continue feeding on garlic mustard plants and leave the host plant in spring to pupate in the soil. Within the European distribution of C. scrobicollis, attack rates ranged from 50 to 100% of plants. On average 4 to 8 larvae complete development within a single plant, occasionaly many more. Attacked plants appear water stressed, have reduced seed production and at high infestations, dry up prematurely.



Figure 4. *Ceutorhynchus scrobicollis.* (Photograph by T. Haye.)

Ceutorhynchus constrictus (Marsham) (Coleoptera: Curculionidae)

Ceutorhynchus constrictus (Marsham) is a univoltine weevil. It is the most widespread of the *Ceutorhynchus* species associated with garlic mustard and is commonly found all over western and central Europe (Dieckmann, 1972). Adults feed on leaves and larvae feed on developing seeds (Fig. 5). Adults appear in April to feed and mate. Oviposition starts once



Figure 5. *Ceutorhynchus constrictus* and garlic mustard seed. (Photograph by H. Hinz and E. Gerber.)

A. petiolata begins to produce siliques (seed pods) in May and June. A single female may produce well over 150 eggs during a season. Larvae feed on developing seeds during June and July with each larva consuming 1 to 2 seeds before leaving the silique to pupate in the soil. Mature larvae form an earthen cocoon, pupate, and fully developed adults overwinter in the soil until the following spring. Although the species was found at all field sites in our surveys, attack rates were generally low with only 0.3 to 6.4% of seeds attacked in southern Germany and Switzerland.

Ceutorhynchus theonae Korotyaev (Coleoptera, Curculionidae)

This newly described species was collected in Daghestan, Russia in spring 2000 and shipments into quarantine at CABI, Switzerland were arranged. Preliminary investigations conducted in Switzerland confirm that the species is attacking seeds of garlic mustard. The biology of *C. theonae* appears similar to *C. constrictus*, however, feeding by *C. theonae* appears more damaging compared to *C. constrictus*. This new species will be included in the host specificity testing procedure if sufficient adults can be obtained and rearing methods be developed.

Phyllotreta ochripes (Curtis) (Coleoptera: Chrysomelidae)

The flea beetle Phyllotreta ochripes (Curtis) (Fig. 6) attacks leaves (adults) and roots (larvae) of bolting A. petiolata plants as well as of rosettes. The species has at least a partial second generation and is potentially multivoltine. Phyllotreta ochripes ranges widely over most of Europe and parts of northwestern Asia (Gruev and Döberl, 1997). During field surveys in Switzerland, Germany, and Austria, P. ochripes was commonly found at all field sites investigated. In Europe, adults overwinter in the leaf litter and were found feeding on garlic mustard rosettes as early as the beginning of March. Females lay an average of 280 eggs from the end of April until the beginning of August. Eggs are laid into the soil close to root crowns and larvae usually mine just below the epidermis of roots or root crowns of bolting plants and rosettes. Mature larvae pupate in the soil and adults emerge by the end of June. Emergence of adults continues until the end of September. Development from first instar to adult takes 30 to 65 days. At present, little is known about the impact of *P. ochripes* on plant performance.



Figure 6. *Phyllotreta ochripes.* (Photo by H. Hinz and E. Gerber.)

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

No introductions have occurred.

Suppression of Target Weed

Not applicable.

Recovery of Native Plant Communities

Not applicable.

Economic Benefits

Not applicable.

RECOMMENDATIONS FOR FUTURE WORK

The present focus in the garlic mustard biological control program is on evaluation of host specificity and impact of potential agents identified in Europe (Blossey *et al.*, 2001).

Description of Planned Work

The host specificity of all six insect species proposed as potential biological control agents for A. petiolata will be evaluated in Europe before any introductions are proposed. Host-specificity tests will follow the testing sequence suggested by Wapshere (1989). A sequence of different testing procedures will be used, involving about 50 different test plant species. Special attention will be given to native North American crucifers (especially Cardamine [Dentaria] and Rorippa spp.) cultivated crucifers (cabbages), and native plant species growing in the same habitats, particularly spring ephemerals. The five Ceutorhynchus species selected as potential biological control agents for garlic mustard are reported to be monophagous (Dieckmann, 1972) (C. theonae is assumed to be monophagous; B. Korotyaev, pers. comm.). Phyllotreta ochripes was reported to complete larval development on both A. petiolata and Rorippa amphibia (L.) Besser (Doguet, 1994). Host specificity investigations confirmed these results and successful larval development occurred on eight additional plants including Rorippa spp. and Brassica spp. (Hinz and Gerber, 2001). Several North American native Rorippa species occur through the North America distribution of A. petiolata, including Rorippa sinuata (Nutt.) A. S. Hitchc., Rorippa sessiliflora (Nutt.) A. S. Hitchc., Rorippa palustris fernaldiana (Butters and Abbe) Stuckey, Rorippa palustris hispida (Desv.) Rydb., Rorippa curvipes Greene, and Rorippa obtusa (Nutt.) Britt. (Fernald, 1970; Voss, 1985; Gleason and Cronquist, 1991). Many of these plant species will be incorporated into the host specificity testing to assess the potential of P. ochripes and of the Ceutorhynchus species to attack these North American plants.

Impact studies are planned to test the assumption of competition or of cumulative effects of herbivores attacking the same plant (Harris, 1991; Masters *et al.*, 1993; Denno *et al.*, 1995; McEvoy and Coombs, 1999). Results from these experiments will help determine, in combination with host specificity results, which species to propose for introduction to North America.

Management of garlic mustard or any other invasive plant aims to protect or restore native ecosystem properties. An important aspect of the biological control program is the collection of baseline data before any introduction of control agents occurs. The standardized protocol will incorporate measures of (1) garlic mustard abundance, (2) abundance and impact of biological control agents, and (3) changes in native plant communities and associated fauna. We anticipate a protocol sophisticated enough to allow rigorous statistical analysis, yet simple enough to allow widespread use by natural areas managers.

Anticipated Effects of Agents

At present little information on the impact of the potential control agents on garlic mustard performance is available. Attack by single or multiple herbivores is anticipated to reduce the competitive ability of garlic mustard in North America. We also anticipate that combinations of agents attacking different plant parts will be superior to the impact of a single species. We will use such predictions to develop a framework for cross-continental comparisons of plant and insect population dynamics.

Techniques to Be Used

Host specificity screening techniques are widely standardized and we will follow guidelines established in the literature and by USDA (Wapshere,1989; USDA, 1999).

Other Comments

Combining long-term monitoring, experimental research, and evaluation will provide a framework for improving management of invasive plants using biological control. In addition, such investigations will continue to improve the scientific basis and predictive ability of biological weed control.

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SECTION VI: CONCLUSION

30 SELECTION OF APPROPRIATE FUTURE TARGET WEEDS FOR BIOLOGICAL CONTROL

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The selection of appropriate target weeds is a serious consideration in classical biological control. It can take up to twenty scientist years (and actual years) for biological control of weeds projects to reach a successful conclusion (Harris, 1979; Peschken and McClay, 1995). Because not all programs are successful, the conclusion may be the completion of analyses associated with a project. During this time considerable investments, public or, private, will be devoted to a program. In addition, societal values may shift during this period, as has happened with the greater valuation of native species during the past 20 years. Currently, there is much debate about the safety of biological control (Louda et al., 1997; Strong and Pemberton, 2000; Follet and Duan, 2000; Wajnberg et al., 2001). Environmental considerations may restrict future biological control practice because of increased concerns about possible damage to nontarget native plants, but these same environmental concerns also may expand the use of biological control through greater use against invasive weeds that threaten natural communities and their functioning. Developing appropriate selection procedures for future target plants, ones that can be controlled in an efficient and predictable manner, will be a key step in future biological control practice.

NATIVE WEEDS VS. INTRODUCED WEEDS

All of the chapters in this book deal with biological control of introduced weeds, except for common reed (*Phragmites australis* [Cav.] Trin. ex. Steud. = *P. communis* [L.] H. Karst.), which is a mixture of native and introduced genotypes within a single species (see chapter on this species, this volume). Native weeds have occasionally been targets of classical biological

control, but it has proven difficult to release imported natural enemies against native plants because of the objections of conservationists and other biologists who feel that native species have unique ecological value. In addition, projects against exotic weeds have been favored because it has generally been believed that the chance of finding useful natural enemies is greater for exotic weeds. This is because introduced exotic weeds are usually attacked by generalist herbivores, whereas native weeds may have a saturated community of specialist insects occupying most of plants' niches. The absence of such suppressive specialized natural enemies is one of the primary reasons why populations of exotic weeds are thought to reach high pest densities.

Whether or not native weeds should be targeted for biological control has been the subject of disagreement and debate. Deloach (1980, 1985) argued for and conducted research programs on the use of biological control against native weeds of rangeland. Many of the most important weeds of rangelands in the southwestern United States are native species. Congeneric relatives of pest species of *Prosopis* and Gutierrezia in South America were found to be attacked by various herbivorous insects not found in the United States. These insects were considered as potential biological control agents of the U.S. plant species. The only insect released was an Argentine weevil (Heilipodus ventralis Kuschel), which was released against two native Gutierrezia spp. in New Mexico and Texas in 1988; establishment of the weevil was not confirmed (Julien, 1992). Pemberton (1985) argued against targeting native weeds for biological control because many of these plants are ecological dominants that have importance in natural communities. In addition, it is impossible to limit biological control agents only to situations where the target native weeds are problems. The introduced insects or pathogens would spread to parks and other natural areas, where plants are valued native species. Another concern is the wider host breadth needed for an agent introduced against a native weed. The agent's host specificity level would need to be broad enough for it to accept a novel host plant - the targeted native weed, which is usually a plant in the same genus as its original host(s). This increased host breadth could mean increased risks to closely related non-target plants. Native weeds are more likely to have closely related plants, particularly other members of the same genus, that could be harmed by biological control agents introduced against the targeted native weed. This is the situation with the introduction of Cactoblastis cactorum (Bergoth) to Nevis in the Caribbean in 1957 (Pemberton, 1995). The target Opuntia spp. were native weeds but other native Opuntia species that were adopted as hosts by the moth were not weeds (F. Bennett, pers. comm.). One of the targeted weeds (Opuntia stricta [Haw.] Haw. = O. dillenii [Ker Gawl.] L. D. Benson) is currently the principal non-target host of C. cactorum in Florida, where the moth either was accidentally introduced via commercial Opuntia importations (Pemberton, 1995) or spread on its own (Johnson and Stiling, 1996). Neither O. stricta nor the four other native Opuntia attacked by the moth in Florida are considered weedy, and one species is a federally-listed endangered species. If the moth spreads via O. stricta (which occurs along the Gulf of Mexico) to Texas and Mexico, many other Opuntia species, including rare species, will probably be harmed.

Although very few native weeds were ever targets of biological control, and the approach is now less acceptable than in the past, there remains some interest in the approach. A current list of candidate weeds for biological control in Texas contains some native weeds (J. DeLoach, pers. comm.). Projects against native weeds almost certainly would be a wasted effort. Alfred Cofrancesco, Chairman of the Technical Advisory Group (the multiagency federal committee that reviews release petitions for candidate biological control agents of weeds) has stated "It is highly unlikely that permission would be granted for the release of an exotic (imported) natural enemy for the control of a native weed in the United States" (A. Cofrancesco, pers. comm.).

SELECTING TARGETS TO MINIMIZE RISK TO NON-TARGET ORGANISMS

Avoidance of risks to economic plants that might be posed by introduced biological weed control agents has always been the most critical safety consideration of biological weed control. Biological control of weeds programs were, and still are, with few exceptions, the exclusive providence of federal and state departments of agriculture, and agricultural colleges in land grant universities. The regulation of biological control of weeds also has been the responsibility of federal and state agricultural institutions. Further, most of the target weeds have been agricultural problems. This agricultural orientation has worked exceptionally well to prevent non-target injury to economic plants but has worked less well to protect native plants. Native plants were not highly valued by society until about 30 years ago when the Endangered Species Act (1973) was passed. Adoption of native plants by introduced biological control agents then began to be reported in the scientific literature and the potential harm from such feeding debated, especially in the 1980s (Andres, 1985; Pemberton, 1985; Turner, 1985; Turner et al., 1987). Recent reports of damage by an introduced thistle weevil, Rhinocyllus conicus (Frölich), to native thistles (Louda et al., 1997), and the threat of C. cactorum to native American and Mexican native Opuntia cacti (Johnson and Stiling, 1997; Strong and Pemberton, 2000) have increased concern about the safety of biological weed control practices.

An analysis of the non-target use of native plants by introduced biological control agents has been recently published (Pemberton, 2000). Known field host plant use (complete development) of native plants by the 112 insects, three fungi and one mite established on 55 weeds in the Caribbean, the continental United States, and Hawaii from 1902 to 1993 was evaluated. Almost all (40 of 41) of the native plants used by the biological control agents were found to be very closely related (same genera or equivalent) to the target weeds for which the agents were introduced. About half (16 of 31) of the projects on target weeds with closely related native plants in the United States lead to some non-target native plant use. This compares to less than 5% (1/24) of the projects on target weeds without close relatives (no native congeners – members of the same genera). In all but one of these cases (which involved the adoption of an unrelated native plant as a host), nontarget usage was predictable process based on taxonomic affinities. The analysis also strongly indicates that the host ranges of herbivores introduced for biological control are very stable. Because almost all the risks to native plants by biological control agents is borne by close relatives of the target weed, harm to native plants can be avoided by targeting weeds with few or no close relatives in the country or broad region that the weed infests.

Projects on weeds with close native relatives will require agents with greater host specificity, which may or may not exist. It is likely that fewer candidate agents in such projects will be safe enough to employ than in projects against weeds without close native relatives. Projects against weeds with close native plant relatives may be able to find and employ safe agents, but these projects will probably require more extensive host specificity testing, resulting in higher costs and longer research periods before safe agents are identified. The probability of success and the effort required will depend on the number of close relatives, how closely related they are to the target weed, and the host ranges of candidate agents.

The biological control program against leafy spurge (Euphorbia esula L.), for example, was able to minimize the risk to native species even though there are 112 native Euphorbia species in North America (Pemberton, 1985). Of these species, 25 are in the subgenus *Esula*, and thus closely related to the target weed. Furthermore, only one species in this subgenus, Euphorbia robusta (Englem.) (Small), is both perennial in its life history and sympatric in distribution with leafy spurge in the western United States. About two thirds of the tested agents, various Aphthona flea beetles, were found to be specialists on the subgenus Esula or section Esula (part of the subgenus Esula) and to require perennial host plants. This meant that only one native species, E. robusta, might be attacked. This complex of Aphthona beetles has begun to control leafy spurge in much of its U.S. range (Nowierski and Pemberton, this volume), and thus far, *E. robusta* is not known to have been harmed. Modest levels of adult A. nigriscutis Foudras feeding have been observed in one E. robusta population in Wyoming, where the plant is increasing in abundance because of the beetle's control of leafy spurge. (L. Baker, pers. comm.). It is worthwhile pointing out,

however, that three fully evaluated candidate biological control agents were abandoned after years of study because of their ability to use *Euphorbia* species in other subgenera as developmental hosts.

The literature analysis of attack on non-target native plants and details of the leafy spurge biological control project both indicate that risk to native plants can be minimized. Host ranges of biological control agents are stable, and well designed host specificity research, based on taxonomic relationships between host plants and the flora where agents are to be released, can predict potential host range with confidence. Harm to non-target native plants has resulted from decisions about which weeds are targeted and which agents are released. Promising candidate biological control agents of exotic weeds are undergoing greater scrutiny and even ones posing only relatively modest risks to native plants may be rejected by the Technical Advisory Group (TAG) and the U.S. Fish and Wildlife Service.

Unlike conflicts with native plants, the resolution of conflicts between biological control agents and economic plants will depend largely on the dollar value of of the economic plants involved compared to the economic losses caused by the target weed. Potential harm to closely related crops may prevent projects from beginning, as has happened with potential projects against weedy grasses. Threats to horticultural plants may present less serious conflicts, depending on the value of the horticultural plants and the cultural attachments to the potentially affected species.

SELECTING TARGET WEEDS TO PROMOTE SUCCESS

McClay (1989) developed a system for ranking target weeds according to their suitability for classical biological control using the size of the infested area, environmental, and biological aspects as criteria. The method was revised by Peschken and McClay (1995). This interesting and thoughtful approach assigns specific numerical point values for each category within either economic or biological sections and then adds the points to obtain a suitability value. Up to 179 points are possible for weeds with no known biological control agents. In the section on economic losses, the target weed receives 30 points for "very severe," 20 points for "severe" and zero points for

"light" damage. Additional points can be added for elements related to size of the infested area, expected spread, toxicity, available means of control, and economic justification in the economic losses section. A beneficial aspects category may subtract 0, 15, or 30 points. In the biological aspects section, most points are assigned for the geographic origin and habitat stability elements. In the geographic origins category, 30 points are given for non-native weeds, 10 points for native to North America and other regions, and zero points for cosmopolitan or unknown area of origin. In the habitat stability category, 30 points are given for high habitat stability (rangeland and permanent pastures), 20 points for moderate habitat stability (perennial crops and extensive roadside infestations), and zero points for annual cropland. Possible conflicts with valued plants, other than the possible benefits of the weed itself, include elements for the number of economic and ornamental species in the same genus and tribe, and the number of native North American native species in the same genus and tribe. These elements subtract no points but add a few points for the absence of economic, ornamental, or native plants that are closely related to the weed. For instance, in the element "number of native North American plants in the same genus," zero native species adds two points, 1-20 native species adds one point, and more than 20 native species adds zero points. The points assigned for particular elements directly reflects their relative importance to these authors. In the McClay-Peschken system, the seriousness of the weed is by far the most important consideration, while potential conflicts with valued plants, aside from beneficial aspects of the weed, literally count for little in the ranking. This is a significant weakness in their system because potential risks to economic and native plants can prevent the release of potentially useful agents, as well as prevent the selection of a weed as a target for biological control. This system, however, reflects much of the traditional thinking with regard to target weed selection. This system is nevertheless valuable to assist in the evaluation and comparison of potential targets, if not to precisely select them. The seriousness of the current problems caused by a weed and the probable impact of a weed if left uncontrolled are obviously extremely important considerations, but the relative benefit of controlling the weed needs to be considered in light of the potential risk.

Pemberton (1996) drew on some known ecological patterns of plants and insects herbivores that predict herbivore species richness to help compare and judge potential target weeds. Larger numbers of herbivores are known to be associated with plants with larger geographic ranges (Southwood, 1960; Strong et al., 1984), increased commonness of a plant within its geographic range (Southwood, 1961; Strong, 1979), and the number of species of plants in a genus (Lawton and Schroeder, 1977). Plants with more complex architecture also are known to have more insect herbivores (Lawton and Schroeder, 1977). A greater abundance of insect species associated with particular plant characteristics can mean more potential biological control candidates, which in turn could relate to increased chance of control. Evaluating potential target weeds with and with out these plant characteristics may help identify weeds that will be more easily controlled.

PREDICTING SUCCESSFUL BIOLOGICAL CONTROL

Estimates of the rate of success for classical biological weed control vary widely, depending partly on whether success is defined in terms of control by specific agents or by whole programs (McFadyen, 1998), as well as differing methods of measuring or estimating success. It has been difficult to accurately predict the success in biological control of weeds, both with regard to the kinds of natural enemies that will be successful control agents and the types of weeds that can be controlled. Although it has not been possible to predict success, it is clear that biological control has been successfully used against a wide variety of weed types. Success has been achieved against weeds from a broad taxonomic spectrum, from primitive groups such as ferns (Salvinia molesta D. Mitch.) (Room et al., 1981) to members of advanced angiosperm families such as the Asteraceae (e.g., Senecio jacobaea L.) (Pemberton and Turner, 1990). Likewise, weeds of diverse life forms, from annual herbs to trees, have been controlled by the approach (Table 1). Also, weeds growing in a variety of habitats, from agricultural crops to natural areas, have been controlled (Table 2). Most targeted weeds have been problems of rangeland, aquatic habitats, or, increasingly, of natural areas. Programs have rarely been

Life Form	Weed Species	Region	Reference
Fern	Salvinia molesta D. Mitch.	Australia	Room et al.,1981
Annual herb	Ambrosia artemisifolia L.	Russia	Kovalev et al., 1983
Biennial herb	Carduus nutans L.	United States	Kok and Surles, 1975
Perennial herb	Hypericum perforatum L.	W. United States	Huffaker and Kennett, 1959
Shrub	Lantana camara L.	Hawaii	Knauss, 1962
Vine	Passiflora mollisima L.H. Bailey	Hawaii	E. Tujillo, pers. comm.
Tree	Acacia longifolia (Andrews) Willdenow	South Africa	Dennill and Donnelly, 1991

Table 1. Examples of Successful Biological Control Projects against Weeds of Different Life Forms

Table 2. Examples of Successful	l Biological Control of Weeds in Diverse Environments

Environment	Weed Species	Region	Reference
Annual row crop	Xanthium occidentale Bertol.	Australia	Morin et al., 1996
Perennial row crop	Solanum elaeagnifolium Cav.	South Africa	Hoffman et al., 1998
Range lands	Senecio jacobaea L.	W. United States	Pemberton and Turner,1990
Aquatic habitats	Alternanthera philoxeroides (Mart.) Griseb.	SE United States	Buckingham, 1994
Natural vegetation	Acacia spp.	South Africa	Dennill and Donnelly, 1991

attempted against weeds of row crop agriculture, but there have been a few successes (Table 2). Weeds infesting lands in both temperate and tropical areas and on both islands and continents also have been successfully suppressed. The diversity of weeds that have been controlled biologically is a clear indication of the great utility of the method and of the variety of situations in which it can be employed, even if it is not possible to predict the outcome of particular projects.

HOW TARGETS ARE SELECTED

Weeds are selected for biological control research in a number of ways. Individual scientists or laboratories often begin to develop projects on new weeds because they perceive the need for such a program because of their direct experience and cooperatorclient interest. Surveys of weed scientists, botanists, and land managers can be useful to determine and rank weeds for their importance. Because many biological control researchers are government scientists, administrators and program leaders may choose new targets for research in response to such perceived needs or political pressures. In some cases, legislative bodies mandate research on particular weeds. Regardless of the need for a project on a particular weed, little can be achieved or even attempted without specific funding for the project. Initial funding often is used for feasibility studies on prospective target weeds to clarify the problem, evaluate conflicts with valued plants, obtain preliminary information on the existence of potential control agents, and develop support for the program.

FUTURE TARGETS FOR BIOLOGICAL CONTROL OF WEEDS

Lists of weeds that are problems in agriculture and natural areas have been developed by various government agencies, private groups, and scientific organizations. I evaluated these lists to help identify and assess potential candidates for biological control. Increased interest in invasive, non-native weeds affecting natural areas has led to the creation of exotic pest plant councils in Florida, and more recently in Georgia, Tennessee, Kentucky, and New England . Each of these councils develops lists of weeds in categories related to the degree of invasiveness. To develop a compilation of the 26 most serious invasive species in the eastern United States (Table 3), I examined the unpublished lists of the Georgia, Kentucky, and Tennessee Exotic Plant Pest Councils, the Maryland Department of Natural Resources, the Virginia Department of Conservation and Recreation, the Morris Arboretum of the University of Pennsylvania, the Torrey Herbarium of the University of Connecticut, the South East Regional Association of Medical and Biological Organizations, The Nature Conservancy (Meyers-Rice and Randall, pers. comm.), and Randall and Marinelli (1996). The Florida Exotic Pest Council's list (Austin et al., 2001) and Langeland and Craddock Burks (1996) was used to create Table 4, which lists 26 highly invasive weeds found in Florida. Both tables exclude many of the most serious weeds because they are already targets of active biological control programs or preliminary biological control research, and are covered in other chapters of this book. Neither of these lists includes all of the serious invasive weeds. For instance, Florida's Category 1 list (the most invasive species) contains 71 weeds but I have selected 26 of the more severe of these. Three of the weeds, Ligustrum sinensis Lour., Lonicera japonica Thunb., and Sapium sebiferum (L.) Roxb., listed for the eastern United States (Table 3), are Catergory 1 weeds on the Florida Council's list. Likewise, Nandina domestica Thunb. and Lygodium japonicum (Thunb.) Sw., on the Florida list, are significant invasive weeds of the eastern United States. Table 5 lists important agronomic and nuisance weeds in the eastern United States and Florida. To help create this list, I drew upon an unpublished list of Texas weeds that are considered candidates for biological control (Tracy, unpub.).

Ideally, the relative benefits and risks associated with potential projects on particular weeds should be judged in order to choose the best targets. It is, however, beyond the scope of this analysis to obtain and compare data (should they even exist) on the damage and threats associated with all of the weeds under consideration. Also, because we are not able to predict success of biological control, it is difficult to meaningfully compare the benefits likely to be achieved. All of the listed invasive weeds are considered by many workers and organizations to be significant problems, so significant benefit from biological control can be assumed, if not easily compared. There is less certainty regarding the benefits to be achieved from controlling the listed agronomic weeds. The potential risk of introduced agents to valued plants based on the weed's taxonomic affinities to other plants is easier to judge and compare. For each weed, the tables list the number of native congeners in the United States, the eastern United States (and for Florida, for the relevant lists), as well as qualitative indications of the number of economic relatives and whether or not the weeds themselves are valued.

All of the weeds on these lists are introduced species and are therefore more appropriate targets for biological control than native weeds. Some important invasive weeds in both the eastern United States and Florida have many native relatives and others have none. Exotic honeysuckles (Lonicera japonica and the three other invasive Lonicera species) are among the most serious invaders in the eastern region, but unfortunately there are 18 Lonicera species in the U.S. flora, including 12 in the eastern United States. The invasive and native Lonicera species belong to many of same subgeneric groups (Krussmann, 1977), which may make it very difficult to avoid nontarget damage to native Lonicera from introduced biological control agents. Exotic privets (Ligustrum sinense and L. vulgare L.) also are serious weeds in the region and there are no native Ligustrum species in the New World. Ligustrum spp. would therefore be much better targets than Lonicera with regard to environmental safety. From an economic perspective, both the honeysuckles and privets have economic value themselves as ornamentals and both genera have many other ornamental species. Privets are among the most common hedge plants used in the region. Japanese honeysuckle (L. japonicum) has significant cultural value because its fragrant flowers are much loved and the plant is a symbol of the American South. Horticultural usage and cultural values related to invasive plants may be reshaped by scientific evidence and education. Weeds of row crop agriculture have been infrequent targets of classical biological control. In many crop situations the weeds are a complex of species and so the reduction of one weed may not contribute to significantly lower the level of weed infestation in these crops. Biological control of a particular species probably would not reduce herbicidal application in most row crops. However, there are some situations in which a large

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Weed	Common Name	Family	Area of Origin	Native Congeners US; E US	Economic Relatives	Valued Plant
Acer platanoides L.	Norway maple	Sapindaceae (Aceraceae)	Eurasia	9; 7	yes	yes
<i>Ailanthus altissima</i> (Miller) Swingle	tree of heaven	Simaroubaceae	China	none	OL	yes
Ampelopsis brevipedunculata (Maxim) Trautv.	porcelain berry	Vitaceae	NE Asia	2; 2	OL	some
Berberis thunbergii DC.	Japanese barberry	Berberidaceae	Japan	20; 6	yes	some
Celastrus orbiculatus Thunb.	oriental bittersweet	Celastraceae	NE Asia	1; 1	OL	some
Coronilla varia L.	crown vetch	Fabaceae	Eurasia, N. Africa	none	many	yes
Dioscorea oppositifolia Thunb.	Chinese yam	Dioscoreaceae	NE Asia	3; 3	yes	some
<i>Elaeganus umbellat</i> a Thunb.	autumn olive	Elaeagnaceae	temperate Asia	1; 1	OL	some
Euonymus alatus (Thunb.) Siebold	burning bush	Celastraceae	NE Asia	4; 3	yes	yes
Euonymus fortunei (Turcz) HandMazz.	winter creeper	Celastraceae	Asia	4; 3	yes	some
Ligustrum sinensis Lour.	privet	Oleaceae	Japan-Korea	none	yes	yes
Ligustrum vulgare L.	privet	Oleaceae	Europe	none	yes	yes
<i>Hedera helix</i> L.	English ivy	Apiaceae (Araliaceae)	Eurasia	none	OL	yes
Lonicera japonicum Thunb.	Japanese honeysuckle	Caprifoliaceae	E. Asia	18; 12	QL	yes
<i>L. maackii</i> Maxim.	Amur bush honeysuckle	Caprifoliaceae	NE Asia	18; 12	OL	some
L. morrowii Gray	Morrow's honeysuckle	Caprifoliaceae	Japan	18; 12	OL	some
L. tartarica L.	tartarian honeysuckle	Caprifoliaceae	Turkey, C. Asia	18; 12	OL	some
Meila azedarach L.	Chinaberry	Meliaceae	Asia	none	yes	some
Microstegium vimineum (Trin.) A. Camus	Japanese grass	Poaceae	Asia	none	many	OL
Miscanthus sinenis Andersson	miscanthus	Poaceae	NE Asia	none	many	yes
Rhamnus cartharticus L.	European buckthorn	Rhamnaceae	Eurasia	11; 3-4	ОП	some
<i>R.</i> (Frangula) <i>alnus</i> L.	smooth buckthorn	Rhamnaceae	Eurasia	11; 3-4	QL	some
Sapium sebiferum (L.) Roxb.	Chinese tallow	Euphorbiaceae	NE Asia	1; 0	ОЦ	yes
Wisteria sinensis (Sims) Sweet	Chinese wisteria	Fabaceae	China	3; 3	yes	yes

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Weed	Common Name	Family	Area of Origin	Native Congeners in US; E US; FL	Economic Relatives	ValuedPlants
Acacia auriculiformis A. Cunn. ex Benth.	earleaf acacia	Fabaceae	N. Australia	17; 8; 6	yes	yes
Ardisia crenata Sims	coral ardisia	Myrsinaceae	India to Japan	1; 1; 1	Ю	some
Ardisia elliptica Thumb.	shoebutton ardsia	Myrsinaceae	Indomalaysia	1; 1; 1	Ю	some
<i>Bishofia javanica</i> Blume	bishofia	Euhorbiaceae	Indomalaysia	none	none	some
Causurina equsetifolia L.	Australian pine	Causurinaceae	Australia-SE Asia	none	QL	yes
Colubrina asiatica (L.) Brongn.	latherleaf	Rhamnaceae	Old World tropics	6; 5; 3	ou	ou
Cupaniopsis anacardioides(A. Rich.) Redkf.	carrot wood	Sapindaceae	Australia	none	Ю	some
Dioscorea bulbifera L.	air potato	Dioscoreaceae	Old World tropics	3; 3; 3	yes	e E
<i>Ficus altissima</i> Blume.	lofty fig	Moraceae	SE Asia	2; 2; 2	yes	some
Ficus benghalensis L.	banyan fig	Moraceae	India-Pakistan	2; 2; 2	yes	yes
Ficus microcarpa L.F.	laurel fig	Moraceae	Indomalaysia	2; 2; 2	yes	some
Hygrophila polysperma (Roxb.) T. Anders.	green hygro	Acanthaceae	Indomalaysia	1; 1; 1	ои	ou
Hymenachne amplexicaulis (Rudge) Nees	West Indian marsh grass	Poaceae	tropical America	none	many	QL
Lygodium japonicum (Thunb.) Sw.	Japanese climbing fem	Lygodiaceae	E Asia	1; 1; 0	р	OL
Jasminum dichotomum Vahl	Gold Coast jasmine	Oleaceae	tropical W Africa	none	yes	some
Jasminum fluminense Vell.	Brazilian jasmine	Oleaceae	tropical W Africa	none	yes	some
Macfadyena unguis-cati (L.) A. Gentry	cat's claw vine	Bignoniaceae	tropical America	none	yes	some
Nandina domestica Thunb.	heavenly bamboo	Berberidaceae	India-NE Asia	none	Q	some
<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchc.	silk reed	Poaceae	SE Asia	none	many	OL
Panicum repens L.	torpedo grass	Poaceae	Old World	33; 23; 13	many	some
Pennisetum purpureum Schumach.	Napier grass	Poaceae	Africa	none	many	yes
Rodomyrtus tomentosa (Ait.) Hassk.	downy rose myrtle	Myrtaceae	tropical Asia	none	yes	some
Scaevola sericea Vahl	Beach naupaka	Goodeniaceae	Old World tropics	1; 1; 1	Ю	some
Schefflera actinophylla (Endl.) Harms	octopus tree	Apiaceae(Araliaceae)	Australia-Indonesia	none	Q	some
Solanum tampicense Dunal	wetland nightshade	Solanaceae	W Indies, Mexico	32; 24; 8	yes	СЦ
<i>Thespesia populnea</i> (L.) Sol. ex Correa	seaside mahoe	Malvaceae	Old World tropics	none	yes	OL

 Table 5. Agronomic Weeds of the Eastern United States (Excluding Weeds Covered in Other Capters)

Weed	Common Name	Family	Area of Origin	Native Congeners US; E. US	Economic Relatives	Valued Plant
Abutilon theophrasti Medic.	velvetleaf	Malvaceae	India	16; 3	yes	Q
Agrostemma githago L.	corn cockle	Caryophyllaceae	Europe	none	Q	Q
Capsella bursa-pastoris (L.) Medic.	shepherd's purse	Brassicaceae	Eurasia	none	yes	О
Chenopodium album L.	lambs quarter	Amaranthaceae (Chenopodiacea)	Eurasia	30; 17	СL L	some
Cyperus rotundus L.	purple nutsedge	Cyperaceae	Eurasia	82; 67	QL	Q
Digitaria sanguinalis (L.) Scop.	large crabgrass	Poaceae	Europe	20+; 15+	yes	ou
Lamium amplexicaule L.	henbit	Lamiaceae	Eurasia	none	yes	OL
Lamium purpurea L.	purple deadnettle	Lamiaceae	Europe	none	yes	Q
<i>Malva neglect</i> a Wallr.	common mallow	Malvaceae	Eurasia	none	yes	some
Plantago lanceolata L.	narrow leaf plantain	Plantaginaceae	Eurasia	23; 14	Q	Q
Plantago major L.	broad leaf plantain	Plantaginaceae	Eurasia	23; 14	Q	Q
Portulaca oleraceae L.	common purselane	Portulacaeae	Europe	8; 8	е	ou
Rumex crispus L.	curly dock	Polygonaceae	Eurasia	25; 13	yes	Q
Saponaria officinalis L.	bouncing bet	Caryophyllaceae	Eurasia	none	Q	Q
Sesbania punicea (Cav.) Benth.	rattlebush	Fabaceae	South America	5; 5	yes	Q
Sisymbrium altissimum L.	tansy mustard	Brassicaceae	Europe	1;0	yes	ou
Sisymbrium irio L.	London rocket	Brassicaceae	Mediterrean	1;0	yes	OL
Sonchus asper (L.) Hill	spiny sowthistle	Asterace	Europe	none	yes	Q
Sonchus oleraceus L.	annual sowthistle	Asterace	Eurasia	none	yes	ou
Sorghum halepense (L.) Pers.	Johnson grass	Poaceae	Mediterrean	none	yes	yes
S <i>tellaria media</i> (L.) Cyrillo	chickweed	Caryophyllaceae	Eurasia	28; 15	оц	ou
Verbascum thapsus L.	mullein	Scrophulariaceae	Eurasia	none	QL	Q

acreage crop is infested primarily by one weed, such as *Cirsium arvense* (L.) Scop. in wheat in western North America. In such cases, biological control of the key weed would be likely to significantly improve crop yield. Biological weed control has been most useful in controlling agricultural weeds that infest pastures and rangeland, and this may continue to be the best place for its use in agriculture.

The agricultural weeds listed in Table 5 are similar to invasive species infesting natural areas with respect to the numbers of these weeds that have closely related native species in the eastern United States. Of the listed weeds, only Johnson grass, Sorghum halepense (L) Pers., an important forage plant, has significant economic value. Johnson grass is the only listed weed that has a crop plant congener, Sorghum bicolor (L.) Moench. However, many of these agricultural weeds belong to families (Brassicaece, Lamiaceae, Malvaceae, Asteraceae, and Poaceae) that contain many crop plants. Targeting these weeds would likely entail host specificity testing against many crop plants and probably require longer and more expensive programs.

Grass weeds have rarely been targets of biological control, primarily because of the large number of crop grasses, but also because of the concern that grass insects may not have the same levels of specificity as insects feeding on other plant families. Lower levels of specificity in grasses may be incorrect (Pemberton, 1980), and recently, some projects on grass weeds have been initiated. Two grasses, Phragmites australis (Cav.) Trin. ex Steudel and cogongrass, Imperata cylindrica (L.) P. Beauv., are subjects of other chapters in this book. Another project involves a cordgrass, Spartina alterniflora Loisel, a native of eastern North America that has invaded salt marshes on the west coast of North America. A delphacid bug, Prokelisia marginata Van Duzee that is native to the eastern United States, was recently introduced into the state of Washington to try to control it (D. Strong, pers. comm.). Japanese stiltgrass, Microstegium vimineum (Trin.) A. Camus, one of the most aggressive weed invaders of forest understory, also appears to be good candidate for biological control. Japanese stiltgrass has no congeneric native or economic species in the United States.

In my opinion, the potential risk of biological weed control to native plants should be viewed as more important than any potential risks to nonnative ornamental plants. Native species are not re-

placeable, but alternatives exist for most ornamental species. Substitutes are available for both weeds that are valued as ornamentals and for the ornamental relatives of targeted weeds, given the array of commercially available horticultural plants. Plants having high cultural value, such as Japanese honeysuckle, might be difficult to replace. It is interesting to note that many of the invasive weeds in the eastern United States and Florida are woody species imported for horticultural use. Most of these weeds are still valued as ornamentals to some degree. Biological control of some weeds with ornamental value may be possible by adopting the more limited goal of slowing the spread of such plants, without killing existing plants in the horticultural landscape. The privets L. vulgare and L. sinense are valued primarily for their leafy stems that can be are planted and trimmed into hedges. Their small white flowers and fruits are of little horticultural importance, so introducing natural enemies attacking these reproductive structures, instead of the roots, stem, and leaves, may be a suitable approach and a reasonable social compromise. The lost seed of these kinds of plants would not limit the ability of nurseries to reproduce them because most are propagated vegetatively.

It is interesting to note that all the more serious invasive weeds of the temperate eastern United States (Table 3) are native to the north temperate zone, and most (18 out of 26) are native to northeast Asia. Invasive weeds in Florida (Table 4), with the exception of the warm temperate northern part of the state, are of diverse geographic origins from areas with warm climates. The agronomic weeds (Table 5), with the exception of Sesbania punicea (Cav.) Benth, are herbaceous plants from Europe or Eurasia, with some species extending to temperate Asia. The USDA, ARS currently has biological control laboratories in Argentina, Australia, and France. These laboratories focus on the discovery and development of biological control agents for both insect and weed pests that are problems in the United States. CABI (Commonwealth Agricultural Bureaux International) biological control laboratories in Switzerland and the United Kingdom also are important developers of biological control agents for North American pests. The Sino-American Biological Control Laboratory in Beijing is the result of a cooperative arrangement between USDA-ARS and the Chinese Academy of Agricultural Sciences, intended to facilitate biological control surveys by American biological control scientists in China. If invasive weeds in the temperate areas of the eastern United States are targeted more frequently, a greater presence of USDA-ARS or CABI biological control staff will be needed in temperate Asia to support these programs.

There are a great number of weeds in the eastern United States that could become targets of biological control. But limited resources make it possible to address only a portion of these weeds. Selecting targets with fewer conflicts with native and economic plant relatives should lead to shorter, less costly programs, and so may be the best use of these resources. Avoiding native weeds and choosing weeds with fewer native relatives also will evoke less criticism and conflict with conservationists and others concerned with protecting native plants. This will help preserve biological control, which is a critical tool for use against invasive species. It is certain that the pressure on the environment from invasive weeds will increase in the future. Many invasive weeds will become more damaging to the environment than they presently are. Some plants that have naturalized, but are not currently invasive, will invade in natural areas. Other plants presently used in horticulture will naturalize, and new weeds will be accidentally introduced. Large numbers of novel plants with invasive potential will continue to be purposely imported, unless the current laissez-faire policy toward plant importation is replaced by policies restricting importations of species likely to become invasive. Given the great momentum of economic globalization and the international horticultural trade, regulating and limiting horticultural imports may be difficult. The need for biological control of weeds will, therefore, without question, be more critical in the future.

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