

The Western Bark Beetle Research Group: A Unique Collaboration With Forest Health Protection

Proceedings of a Symposium at the 2007
Society of American Foresters Conference

October 23–28, 2007, Portland, Oregon

J.L. Hayes and J.E. Lundquist, compilers



U.S. Department of Agriculture, Forest Service
Pacific Northwest Research Station
Portland, Oregon
General Technical Report PNW-GTR-784
April 2009

What Risks Do Invasive Bark Beetles and Woodborers Pose to Forests of the Western United States? A Case Study of the Mediterranean Pine Engraver, *Orthotomicus erosus*¹

Steven J. Seybold and Marla Downing²

Abstract

Recently reported, and likely to threaten the health of standing trees in the urban and peri-urban forests of the West, are at least five new subcortical insect/pathogen complexes [*Agrilus coxalis* Waterhouse (Buprestidae) and four species of Scolytidae: *Orthotomicus (Ips) erosus* (Wollaston), *Hylurgus lignipruderda* F., *Scolytus schevyrewi* Semenov, and *Pityophthorus juglandis* Blackman, which vectors the invasive fungus, *Geosmithia* sp.]. Through the Forest Insect and Disease Leaflet and Pest Alert series and other extension-type publications, personnel from USDA Forest Service Research and Development (R&D) have worked closely with USDA Forest Service Forest Health Protection (FHP) specialists in the western regions to disseminate information to the public on the distribution, identification, biology, and potential impact of these new pests to western U.S. forests. Because the Mediterranean pine engraver, *O. erosus*, has the most potential to have a strong impact on conifers in western U.S. forests and elsewhere in North America, we focus on this species as a case study for the development of a species-specific national risk map (=Potential Susceptibility map) to illustrate how USDA Forest Service R&D and USDA Forest Service FHP [in this case the Forest Health Technology Enterprise Team (FHTET)], can work cooperatively to address an issue of pressing national concern.

Keywords: Aleppo pine, bark beetles, invasive insect species, Italian stone pine, risk-mapping.

¹ This manuscript was prepared at the request of the compilers to address the WBBRG priority area: Develop methods and strategies for detecting, monitoring, and eradicating or mitigating invasive bark beetles and woodboring insects, which was not included in the 2007 SAF Symposium because of time constraints.

² **Steven J. Seybold** is a Research Entomologist, USDA Forest Service, Pacific Southwest Research Station, Chemical Ecology of Forest Insects, 720 Olive Drive, Suite D, Davis, CA 95616; email: sjseybold@gmail.com. **Marla Downing** is a Biological Scientist, USDA Forest Service, Forest Health Technology Enterprise Team, 2150 Centre Ave., Bldg. A, Suite 331, Fort Collins, CO 80526-1891; email: mdowning@fs.fed.us.

Introduction

Native bark and ambrosia beetles (Coleoptera: Scolytidae, *sensu* Wood, 2007 and Platypodidae) and woodborers (broadly defined as Coleoptera: Anobiidae, Bostrichidae, Buprestidae, Cerambycidae, Curculionidae, Lyctidae, Oedemeridae; Hymenoptera: Siricidae; and Lepidoptera: Cossidae and Sesiidae) have historically represented a major threat to forests and wood products of the western U.S. (Furniss and Carolin 1977, Solomon 1995). Because these insect guilds feed on the most vital tissues of trees (phloem, cambium, and sapwood of the main stem, root, and root crown), they are considered to have the highest impact on host growth and reproduction, and thus, have been ranked as the most damaging among all forest insects (Mattson 1988). The impact of these endophytic insects is magnified further by their interactions with fungi (Goheen and Hansen 1993, Paine et al. 1997). With the evolution of multiple native complexes of tree-killing bark beetles (e.g., *Dendroctonus*, *Ips*, and *Scolytus* spp.) and, in rare cases, woodborers (e.g., *Melanophila californica* Van Dyke), these feeding groups of insects have reached the pinnacle of their impact in the drought- (Koch et al. 2007), fire- (Parker et al. 2006), and wind-challenged (Gandhi et al. 2007) coniferous forests of the western U.S.

Throughout much of the development of forest entomology in the West, these coniferous forests have been largely unchallenged by invasive insect species in these guilds. In western U.S. forests, Furniss and Carolin (1977) listed only two bark beetles [*Scolytus multistriatus* (Marsham) and *S. rugulosus* (Müller)], one curculionid stem borer [*Cryptorhynchus lapathi* (L.)], and one cerambycid stemborer (*Saperda populnea* L.) as introductions from other continents. None of these insects feeds on conifers, and *C. lapathi* is now considered to be a native holarctic species (D.W. Langor, Canadian Forestry Service, personal communication). However, since the monograph by Furniss and Carolin, increasing numbers of invasive bark beetles and woodborers have been detected and have established populations in urban and wildland forests of the West (Haack 2006; Langor et al. 2008; Lee et al. 2005, 2006, 2007; Liu et al. 2007; Mattson et al. 1992; Moser et al. 2005) (Table 1). Notably, some of these additions to our subcortical forest insect fauna are well-documented pests of conifers on other continents (Table 2).

In this paper we briefly discuss the concept of new invasive subcortical insects in western U.S. forests from the perspectives of: (1) the resources threatened and (2) the risks posed by the invaders. We use the Mediterranean pine engraver, *Orthotomicus (Ips) erosus* (Wollaston), as a case study for the development of a species-specific national risk map to illustrate how USDA Forest Service Research and Development (R&D) and USDA Forest Service Forest Health Protection (FHP) [in this case the Forest Health Technology Enterprise Team (FHTET)] can work cooperatively to address an issue of pressing national concern.

Table 1—Invasive bark and woodboring beetles first detected in the western U.S. between 1984 and 2008¹

Species	Family	State where initially detected
<i>Heterobostrychus brunneus</i> (Murray)	Bostrichidae	California
<i>Sinoxylon ceratoniae</i> (L.)	Bostrichidae	California
<i>Agrilus coxalis</i> Waterhouse	Buprestidae	California
<i>Agrilus prionurus</i> Chevrolat	Buprestidae	Texas
<i>Phoracantha recurva</i> Newman	Cerambycidae	California
<i>Phoracantha semipunctata</i> (F.)	Cerambycidae	California
<i>Dendroctonus mexicanus</i> Hopkins	Scolytidae	Arizona
<i>Hylurgus ligniperda</i> F.	Scolytidae	California
<i>Orthotomicus erosus</i> (Wollaston)	Scolytidae	California
<i>Phloeosinus armatus</i> Reitter	Scolytidae	California
<i>Scolytus schevyrewi</i> Semenov	Scolytidae	Colorado
<i>Trypodendron domesticum</i> (L.)	Scolytidae	Washington
<i>Xyleborinus alni</i> (Niisima)	Scolytidae	Washington
<i>Xyleborus similis</i> Ferrari	Scolytidae	Texas

¹We consider Texas to be part of the continental western U.S.; these introductions were documented in Haack (2006), except for *P. semipunctata*, which was reported in Scriven et al. (1986); *D. mexicanus* (Moser et al. 2005); *H. ligniperda* (Liu et al. 2007); *A. coxalis* (Coleman and Seybold in press); and *T. domesticum* (R. Rabaglia, USDA Forest Service, Washington, D.C., personal correspondence).

Recently Introduced Subcortical Insect/Pathogen Complexes in Western U.S. Forests

For a variety of historical, biological, and societal reasons, it appears that the conifer-dominated forests of the western U.S. have accumulated a relatively depauperate fauna of invasive subcortical insects. The situation is similar in Canada where a recent survey of all non-native terrestrial arthropods associated with woody plants revealed that only 12% of these invasive species were bark- and wood-feeders (and this guild was liberally defined to include external feeders on roots and gall makers on twigs) (Langor et al. 2008). Among all of the families of subcortical insects noted above, only one invasive cerambycid, nine invasive scolytids, and one invasive sesiid were listed for western Canada (provinces west of Manitoba). Factors such as species composition, abundance, and locations of native and adventive stands of trees and shrubs; diversity and abundance of competing native species of subcortical insects; historical patterns of trade and land use; historical working locations of collectors and survey entomologists; and locations of urban centers relative to forest lands may all have played a role in the relatively low number of subcortical insects recorded from western North American forests. Forests of the western U.S. have high levels of native biodiversity of conifers as well as bark beetles and woodborers (Bright and Stark 1973, Furniss and Johnson 2002, Little 1971, Wood 1982). Thus, although invading species have had a range of potential hosts at their disposal, they may also have faced greater competition for various niches by native subcortical species. Historically, the contraposition of these factors, and the societal factors listed above, may have made western U.S. forests less vulnerable to invasion by subcortical insects.

Cataloging invasive species is a dynamic process, and the lists developed in the literature are ephemeral (Langor et al. 2008). Nonetheless, of 25 bark and woodboring Buprestidae, Cerambycidae, and Scolytidae first reported to be established in the continental U.S. between 1985 and 2005, seven species were in the western U.S. (Haack 2006). Two other invasive species of woodboring Coleoptera (Bostrichidae), traditionally more associated with wood products, have also been reported from California (Table 1). Established populations of eucalyptus longhorned borer, *Phoracantha semipunctata* (F.) (Cerambycidae), were first discovered in southern California in 1984 (Scriven et al. 1986), but this species was not included in the survey by Haack (2006). In total, established western U.S. populations of at least 14 subcortical insect taxa have been reported in the literature since 1984 from Arizona, California, Colorado, Texas, and Washington (Table 1). Not all of these bark and woodboring taxa are likely to assume pest status in U.S. forests.

However, some of the more recently reported subcortical insect/pathogen complexes are likely to threaten the health of standing trees in the urban, peri-urban, and wildland forests of the West (Table 2).

Table 2—Emerging threats posed by recently detected invasive bark beetles, woodborers, and/or pathogens in the western U.S

Species	Hosts	Fungal associates in U.S. population	Observed levels of tree mortality in the western U.S.	References
<i>Agrilus coxalis</i> ¹	<i>Quercus</i> spp.	Unknown	Locally extensive, wildland urban interface (S. CA)	Coleman and Seybold, 2008a,b
<i>Dendroctonus mexicanus</i>	<i>Pinus</i> spp.	Unknown ²	Locally extensive in a species complex of other <i>Dendroctonus</i> (S. Az)	Moser et al. 2005
<i>Hylurgus ligniperda</i>	<i>Pinus</i> spp.	<i>Ophiostoma ips</i> , <i>O. galeiforme</i> , and ten other ophiostomoid fungi	None	Lee et al. 2007, Liu et al. 2007, 2008, S. Kim and T.C. Harrington personal communication
<i>Orthotomicus erosus</i>	<i>Pinus</i> spp.	<i>Ophiostoma ips</i>	Minor levels, urban forests (CA)	Lee et al. 2005, 2007, 2008, T.C. Harrington personal communication
<i>Pityophthorus juglandis</i>	<i>Juglans</i> spp.	<i>Geosmithia</i> sp.	Westwide, urban forests, rural landscapes (CA, CO, UT)	N.A. Tisserat, personal communication
<i>Scolytus schevyrewi</i>	<i>Ulmus</i> spp.	<i>Ophiostoma novo-ulmi</i>	Locally extensive, urban forests (WY, CO)	Negrón et al. 2005; Jacobi et al. 2007; Johnson et al. 2008 ; Lee et al. 2006, 2007, In press

¹(Coleoptera: Buprestidae); all other species in this table are (Coleoptera: Scolytidae).

²Fungal isolations from the U.S. population of *D. mexicanus* were in progress as of Nov. 2008 (K.D. Klepzig, USDA Forest Service, Asheville, NC, and D.L. Six, University of Montana, Missoula, MT, personal communication).

Two of these complexes are on pines in California [*O. erosus* and the redhaired pine bark beetle, *Hylurgus lignipruderda* F. (both Scolytidae)]; one is on pines in Arizona [the Mexican pine beetle, *Dendroctonus mexicanus* Hopkins (Scolytidae)]; one is on oaks in California [the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Buprestidae)], and two are on other hardwoods across the West [the banded elm bark beetle, *Scolytus schevyrewi* Semenov, and the walnut twig beetle/thousand cankers complex, *Pityophthorus juglandis* Blackman (Scolytidae) and *Geosmithia* sp.]. *Agrilus coxalis*, *D. mexicanus*, and *P. juglandis* are not invasive insects from other continents, but the recent discoveries of *A. coxalis* and *D. mexicanus* in the U.S. appear to be range expansions or regional introductions (Coleman and Seybold 2008a, Moser et al. 2005); *P. juglandis* appears to be damaging native and adventive stands of walnut trees through an association with an invasive fungal pathogen (N.A. Tisserat, Colorado State University, personal communication). The occurrences of regional introductions or range expansions leading to “indigenous exotic species” may reflect either more lax intracontinental and interstate commercial regulatory enforcement (Dodds et al. 2004) or effects of climate change (Hicke et al. 2006) on native subcortical insect distributions. These subtly continuous or discrete geographical shifts in subcortical forest insect populations may be a challenging wave of the future in invasive species management.

Through the Forest Insect and Disease Leaflet and Pest Alert series and other extension-type publications, personnel from USDA Forest Service R&D have worked closely with specialists from the western regions of USDA Forest Service FHP in conjunction with University of California at Davis entomologists to disseminate information to the public on the distributions, identification, biology, and potential impacts of the new subcortical insect pests to western U.S. forests (Coleman and Seybold 2008; Lee et al. 2005–2007; Liu et al. 2007; Negrón et al. 2005). It appears that most of the invasive species in this ensemble of subcortical insects successfully colonize trees under some form of stress. However, based on the damage that it has caused to stressed pines in other continents, *O. erosus* has perhaps the most potential to have a strong impact on conifers in western U.S. forests and elsewhere in North America.

Orthotomicus erosus: Introduction, Establishment, Biology, and Behavior

In May 2004, a new exotic bark beetle for North America was discovered in baited flight traps in Fresno, California, during an annual bark beetle and woodborer survey led by Richard L. Penrose of the California Department of Food and Agriculture. This bark beetle was identified as *Orthotomicus erosus* (Wollaston), the Mediterranean pine engraver, a well-documented pest of pines in its native range, which includes the Mediterranean region, the Middle East, Central Asia, and China (Eglitis 2000, Mendel and Halperin 1982, Yin et al. 1984). In July 2007, the widespread occurrence and host range of the pest in China was confirmed by one of us (SJS), through an examination of the holdings of the Chinese Academy of Sciences insect collection in Beijing. How the beetle entered the U.S. is unknown, but it may have arrived with solid wood packing material associated with imported goods. In a survey of records from the USDA APHIS Port Information Network (1985–2001) (Haack 2001), *O. erosus* was the second most frequently intercepted bark beetle species at U.S. ports with a total of 385 interceptions.

Beetles were most frequently associated with imports from the following countries in descending order: Spain, Italy, China, Turkey, and Portugal. Based on remnants of old galleries observed in dead standing trees and in weathered cut pine logs, this beetle was likely present in California for at least three years before its detection in 2004. The distances between the observation points of some of these remnant galleries, the widespread occurrence of *O. erosus* in the state (see below), and its marked abundance, all suggest that this is a minimum estimate of the initial introduction of the species to California.

Since the initial detection, this species has been found in flight traps or has been collected in host material in ten counties in California, primarily in the southern Central Valley (R.L. Penrose, CDFA, unpublished data). Furthermore, in Fresno, Tulare, and Kern Counties, abundant overwintering populations of larvae, pupae, and adults have been found in cut logs of Aleppo, *Pinus halepensis*, Canary Island, *Pinus canariensis*, and Italian stone pine, *Pinus pinea*. These exotic trees are a frequent and esthetically important component of the urban forests of the southern Central Valley and the Los Angeles Basin (Seybold et al. 2006b). They are also widely planted along highway corridors and as shelterbelts in rural regions of California. The Mediterranean pine engraver has so far been detected in urban and peri-urban locations, particularly parks, golf courses, and green waste recycling facilities. The highest population density appears to be in the southeastern Central Valley along the somewhat industrialized State Highway 99 corridor.

Orthotomicus erosus adults generally behave as secondary pests. They are most likely to infest recently fallen trees, standing trees that are under stress, logging debris, and broken branches with rough bark that are at least 5 cm in diameter. Healthy trees have rarely been attacked. In Israel, beetles are often found on the main stem and larger branches of stressed trees that are over 5 yr old (Halperin et al. 1983). In California, this species, or evidence of its past activity, has been found in cut logs from 15 to 90 cm in diameter, on stumps from 10 to 90 cm in diameter, on declining branches of live standing trees, and on the main stem of moribund or dead standing trees. This species has two or more generations per year in its native range. In California, it has three to four generations per year and adults are active year round with the exception of a short period between mid-December and late-January (Lee et al. 2007, In press; R.L. Penrose, CDFA, unpublished data).

Males are the initial sex to colonize cut logs or fallen or standing trees. They construct a nuptial chamber, in which they are typically joined by two females (Mendel and Halperin 1982). Males produce an aggregation pheromone consisting of 2-methyl-3-buten-2-ol and (+)-ipsdienol, whose attraction is enhanced by the host monoterpene α -pinene (Lee et al. In prep., Seybold et al. 2006a). The monoterpene co-attractant is important to the activity of this pheromone in contrast to related beetles in the genus *Ips* where monoterpenes play a relatively minor role (Seybold et al. 2006a). Once in the nuptial chamber, each *O. erosus* female mates and constructs an egg gallery in opposite directions and in longitudinal orientation with the grain of the wood. In the relatively rare (approx. 4%) instances when a third female joins the familial gallery, she excavates her

egg gallery parallel to one already established (Mendel and Halperin 1982). Each female lays 26 to 75 eggs and may leave the gallery to lay eggs in a second gallery (Mendel and Halperin 1982). The eggs hatch and larvae develop through three instars expanding the tunnels as they feed. As the tunnels expand, they may overlap with one another. When larvae are ready to pupate, they tunnel towards the bark, especially in cases where the phloem is thick such as *P. canariensis* and *P. pinea*. Observations in the Central Valley of California indicate that this species overwinters as larvae, pupae, and adults beneath the bark surface. Overwintered adult beetles start flying in January and February and establish brood galleries by mid-March. Subsequent broods are initiated in early June, late July, and over an extended period between early September and late November (R.L. Penrose, CDFA, unpublished data). Flight of parent and new adults continues until November and even early December (Lee et al. In press). In Israel, adults start brood production in early March and require a period of feeding before reaching sexual maturation (Mendel 1983). When beetles complete their development, the adults emerge, leaving a small round exit hole in the outer bark, approx. 1.5 mm in diameter. During the warmer parts of the season, there is a bimodal, diurnal pattern of adult flight dispersal with peaks in the morning and evening (Mendel et al. 1991). This has been noted in California as well (D.-G. Liu, SJS, personal observations). New adults may re-infest the same host material that they emerged from or may attack new material.

Laboratory studies in Israel have provided data on the lower temperature thresholds for various aspects of the life history of *O. erosus* (Mendel and Halperin 1982). Females oviposited between 18 and 42°C, but eggs exposed to lower temperatures did not hatch below 16–17°C. Larvae exposed to lower temperatures did not complete development below 18°C (they fed and developed, albeit not completely, for a short period at 14°C). Prepupal development was delayed at temperatures below 16 to 17°C, but individuals did continue to develop at 14°C and became adults after 30 d. In the field in Israel, *O. erosus* developed in areas where winter temperatures ranged from 7.8 to 14°C. As long as the adults initiated the life cycle during periods of warmer temperatures, the immature stages developed through the winter, likely during periods when daily temperatures exceeded 18 to 20°C. The cold temperature tolerances of *O. erosus* have not been studied in the field in California, but lower lethal temperatures and supercooling points of the California population are being investigated in laboratory studies in the Minnesota Department of Agriculture-University of Minnesota BL2 Quarantine Facility in St. Paul, Minnesota (Venette et al. 2009).

In addition to its native range and the recent introduction in California, *O. erosus* has also been introduced into Chile, South Africa, and Swaziland. In all of these locations, the beetle reproduces in a variety of pines, including some that occur in native stands or ornamental plantings in the U.S. (Eglitis 2000). Outside the U.S., *O. erosus* has also been found in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, spruce, *Picea* sp., fir, *Abies* sp., cypress, *Cupressus* sp., and cedar, *Cedrus* sp., but these non-pine hosts were thought to be used mainly for maturation feeding or overwintering sites for adults (Eglitis 2000). Recently, in laboratory no-choice host range tests of 22 conifers, Lee et al. (2008) reported that *O. erosus* reproduced on four pines from its native Eurasian

range—Aleppo, Canary Island, Italian stone, and Scots pines; 11 native North American pines—eastern white, grey, jack, Jeffrey, loblolly, Monterey, ponderosa, red, Sierra lodgepole, singleleaf pinyon, and sugar pines; and four native non-pines—Douglas-fir, black and white spruce, and tamarack. Among non-pines, fewer progeny developed and were of smaller size on Douglas-fir and tamarack, *Larix laricina* (Du Roi) K. Koch, and the number of progeny did not replace the number of founder adults in tamarack. Beetles did not develop on white fir, incense cedar, or coast redwood.

Although *O. erosus* is not a tree-killing bark beetle under normal circumstances, it has demonstrated the capacity to kill trees following disturbances. These have included forest thinning followed by drought in Israel (Halperin et al. 1983; Mendel and Halperin 1982); forest thinning alone in Israel (Mendel et al. 1992); and fire in South Africa (Baylis et al. 1986). Bevan (1984) also provides anecdotal evidence of the reaction of populations of *O. erosus* to various pre-disposing factors in Swaziland; Zwolinski et al. (1995) suggest that in South Africa, *O. erosus* has a higher rate of infestation in pines that were previously wounded by hail and infected with fungi through the wounds. In one instance where *O. erosus* has killed trees in the apparent absence of any pre-disposing conditions, Jiang et al. (1992) reported that *O. erosus* colonized healthy *P. massoniana* and caused a 20% loss of standing pines in the Zhejiang University Forest in China. Seybold and colleagues have observed about 10 cases where *O. erosus* has colonized the main stem of standing ornamental or windbreak pines in the Central Valley of California, but in each instance it was not clear whether the trees were first declining due to some other factor perhaps related to moisture or root pathogens.

Besides direct injury to pine trees, *O. erosus* can vector fungal pathogens. In South Africa, spores of *Ophiostoma ips* (Rumb.) Nannf., the causative agent of bluestain fungus, were found on 60% of 665 adult beetles or galleries on trap logs of *Pinus elliottii* Engelm. and *P. patula* Scheide & Deppe ex Schlecht. & Cham.; spores of *Leptographium lundbergii* Lagerb. & Melin were also found on a few samples (Zhou et al. 2001, 2002). Spores of *Graphium pseudormiticum* Mouton & Wingfield have been found with *O. erosus* on unspecified pine logs (Mouton et al. 1994). In Spain a small proportion of a sample population of *O. erosus* were reported to carry the pitch canker fungus, *Fusarium circinatum* Nirenberg and O'Donnell (Romon et al. 2007). In California, the mycoflora of *O. erosus* overwintering in *P. canariensis* and *P. halepensis* was heavily dominated by *Ophiostoma ips* (S. Kim et al. unpublished data, Iowa State University), which agrees with phytopathological studies of *O. erosus* in South Africa (see above) and North Africa (Ben Jamaa et al. 2007).

Given this background, *O. erosus* presents a relatively high risk to pines in North America. It has been included in the ExFor database (<http://spfnic.fs.fed.us/exfor>) as one of many species of concern to North American forests. Its establishment in much of the U.S. seems highly probable; subsequent spread is likely to cover a large geographic area; and economic damage is likely to be severe (Eglitis 2000). Plantation pines in the southeastern U.S. are particularly vulnerable because both climate and hosts are likely to be favorable. The National Plant Board recognized the threat that *O. erosus* poses for U.S. pines, and USDA APHIS considers the insect as “actionable” (J.F. Cavey, USDA

APHIS, personal correspondence). Out of this regulatory climate, in February 2007 the USDA Forest Service, FHTET with the support of the FHP Early Detection-Rapid Response National Program Coordinators formed an advisory committee chaired by one of us (MD) to develop a U.S. national risk map (Potential Susceptibility Map) for *O. erosus*. Input into the mapping process and research data on the behavior of the invasive population in California was sought from Forest Service R&D, so SJS and Research Biologist R.C. Venette (Northern Research Station) were invited to participate on the committee¹. What follows is a brief overview of the process, progress, and pitfalls encountered in the development of the *Orthotomicus erosus* Potential Susceptibility Map with an emphasis on the cooperative synergy achieved between R&D and FHP.

Development of the *Orthotomicus erosus* Potential Susceptibility Map

The *Orthotomicus erosus* Potential Susceptibility Map describes the relative potential for introduction and establishment of *O. erosus* at any given location in the conterminous U.S. (USDA FS 2008). The map was constructed by using techniques developed for the 2006 National Insect and Disease Risk Map (Krist et al. 2007), and for susceptibility maps for the invasive subcortical insects, *Ips typographus* (L.) (Coleoptera: Scolytidae) and *Sirex noctilio* F. (Hymenoptera: Siricidae), as well as the invasive pathogen, *Phytophthora alni* Brasier & S.A.Kirk (USDA FS 2008). The techniques rely on a compilation of both expert opinion and research findings, which are synthesized into a series of interacting layers with Geographic Information Systems (GIS) technology (i.e., ESRI 2008, Table 3). Location and level of risk are mapped in 1 km pixels.

The first major component of the map is the Potential Introduction model, which describes where the pest is most likely to enter and escape into the U.S. The model contains information about major ports, markets (=municipalities), and inland distribution centers (Table 3). A dispersal function (Table 4) is used to predict the movement of *O. erosus* from each of these potential points of introduction.

The second major component is the Potential Establishment model, which describes where the pest can survive and reproduce should it be introduced (Table 3). The model contains data related to the temperature tolerances and the host range of *O. erosus*, and a disturbance layer, which is the most data intensive portion of the effort. The factors that go into this layer include ozone, drought (= moisture deficit), fire, hurricane, tornado, avalanche, lightning, and extreme wind events.

¹Other committee members include: D. Borchert, F.H. Koch, F. Krist, F. Sapio, W.D. Smith, S. Smith, B. Tkacz, and M. Tuffly.

Table 3—Data layers included in the *Orthotomicus erosus* Potential Susceptibility Model

Data Layer	Purpose
Introduction: Marine Ports ¹	U.S. marine ports that handle commodities and solid wood packing materials shipped from countries with established populations of <i>O. erosus</i> . These are locations where <i>O. erosus</i> may be released.
Introduction: Markets	Possible destination locations where <i>O. erosus</i> may be released.
Introduction: Inland Distribution Centers	Possible destination locations where <i>O. erosus</i> may be released.
Establishment: Temperature Tolerance	A limiting maximum coupled with a minimum temperature range within which <i>O. erosus</i> can survive.
Establishment: Host Range	The distribution of tree species, which are used by <i>O. erosus</i> , for growth and reproduction.
Establishment: Disturbance	Depicts locations where natural or anthropogenic events occur and potentially affect tree health and vigor; <i>O. erosus</i> population densities increase in stressed trees.

¹The volume of imports into these ports was not considered in the analysis, but the types of imported goods (i.e., those with solid wood packing materials) were taken into consideration. Included in the analysis were all ports where previous USDA Animal and Plant Health Inspection Service interceptions of *O. erosus* had occurred.

Table 4—Distance-Decay (Dispersal) Function for the Probable Flight Range of *Orthotomicus erosus*

Distance (km)	GRID Value
0 (Source)	10
GE 1 and LT or EQ to 2	10
GT 2 and LT or EQ to 3	3
GT 3 and LT or EQ to 4	1
GT 4	0

Abbreviations include GE: greater than or equal to; LT: less than; EQ: equal to; and GT: greater than.

The final Susceptibility Model is a weighted overlay of the Introduction and Establishment components. For every pixel location (i), the values of each spatially coincident Introduction pixel (I_i) and Establishment pixel (E_i) are multiplied by assigned weights (x_i and x_E , respectively), then these values are multiplied, and the product is applied to the Susceptibility pixel (S_i).

$$S_i = I_i (x_i) \cdot E_i (x_E)$$

Without reason to do otherwise, the Susceptibility Map should be the result of an equally-weighted overlay of the Introduction and Establishment components (i.e., $x_i = x_E = 0.5$). Given sufficient reason though, it is possible to attribute more importance to one component by assigning different weights. For example, if the pest is not thought to already have been introduced and the dispersal distance of the pest is relatively limited, it may be more accurate to emphasize the Introduction component. Multiplying the Introduction pixel values by a greater weighting factor and the Establishment pixel values by the complementary factor (before multiplying the two products to create the Susceptibility Map) will prioritize areas where the pest is likely to first be released. On the other hand, if the pest is known to have already been introduced, prioritizing areas where the pest is most able to survive may be desired (i.e., $x_E > x_i$). In this case, the resulting Potential Susceptibility Map will allow pest specialists to focus detection efforts in areas where introduced populations of *O. erosus* may be expanding.

Contributions from Forest Service Research and Development (R&D) to the *Orthotomicus erosus* Potential Susceptibility Map

Research on *O. erosus* in California has provided data for the Introduction and Establishment components on the physiological host range and life history of the insect, the current distribution of the invasive population in California, and the innate flight capacity of adults. The latter is being studied through mark-recapture flight experiments in extremely level and open agricultural fields located in Kings and Tulare Co., California. There are no trees, and specifically no host trees, located within the immediate study areas. Although it is less than half the size of a grain of rice, *O. erosus* is a relatively strong flier that can move at least 10 km in a matter of 24-48 hr with prevailing winds (D.-G. Liu et al., unpublished data).

In addition, Forest Service R&D personnel provided additional locations for a series of inland commercial distribution centers identified during field research and population surveys conducted in the zone of infestation in California. These additional locations were provided to FHTET for incorporation into the Introduction component and as a consequence, similar distribution center data were collected on a national basis and included in the process. R&D personnel also guided the interpretation of the scientific literature for the incorporation of the impact of temperature on developmental thresholds for *O. erosus* into the Establishment component (Mendel 1983, Mendel and Halperin 1982, NAPPFAST 2008). A lower critical development threshold between 0 and 10°C was chosen for the analysis. R&D personnel have also provided advice on weighting various potential hosts and the urban vs. wildland habitats in the Establishment component.

No new data were available from California to aid in the development of the disturbance layer. Likely because it is early in the invasion phase, surveys to date by Forest Service R&D personnel and CDFA cooperators have revealed that populations of the beetle are confined to urban and rural agricultural areas and have not invaded the National Forest system or commercial forest lands in California. Thus, observations of the impact of disturbances such as fire, wind, thinning, etc. could not be recorded. Nevertheless, R&D encouraged strong consideration of the potential interactive power of thinning, drought, and ozone on the health of host pines (Grulke et al. 2002) in the development of this data layer. Through administrative access provided by the USDA FS Southern Research Station, the committee was able to include expertise on drought impacts (Koch et al. 2007) and ozone damage bioindicator data in the modeling procedure.

Finally, research data on the current distribution of *O. erosus* in California and the dispersal function (Table 4) have been combined to test the predictive power of the *O. erosus* Potential Susceptibility Map at locations where the beetle has been flight trapped or hand collected in host material in California.

Contributions from the Forest Health Technology Enterprise Team to the *Orthotomicus erosus* Potential Susceptibility Map

The role of FHTET is to develop technology that assists Forest Health Protection Staff and their cooperators in the management of North America's forests. The specific

purpose in developing invasive species tools such as the *O. erosus* Potential Susceptibility model and the resulting map is to provide geographic information for prioritizing detection efforts.

The construction of the *O. erosus* model has required extensive coordination and communication, which have been led by FHTET. Initially, FHTET identified individuals with expertise in risk assessment work, or who had particular knowledge and information about *O. erosus*. Once identified, the participating individuals were informed about the FHTET modeling methods and were invited to participate in the steering committee. Committee members and other experts were then regularly contacted for pertinent knowledge and information on both the biology and behavior of the pest as well as the pest hosts. The knowledge and information from the committee was collected from published research, unpublished documentation, or in the form of personal communication. These inputs were assimilated and essential parameters critical to developing the model were selected (see above).

Once the parameters were selected, an intensive data management effort was undertaken by the FHTET team (i.e., university cooperators and FHTET contractors). Datasets, which were not collected specifically for these purposes, had to be identified and investigated to determine whether they could be used to appropriately characterize the parameters necessary for the model. Often, myriad analyses were required to determine how a dataset can best be utilized to represent the input parameters. Once identified and acquired, representative datasets were processed and standardized and finally combined into Model Builder (ESRI 2008) for inclusion in the model by FHTET contractors.

The process frequently identified knowledge and data gaps, and to address these gaps, multiple versions of the model were provided to the committee. With each new iteration, new issues were discovered and resolved. Resolution of the issues sometimes required that weaknesses in the datasets had to be overcome. This is a difficult issue because it often required the expenditure of a large amount of FHTET resources to re-investigate, analyze, and process the existing data, or to find replacement data. Other issues elucidated the need to: 1) incorporate different and/or additional parameters; 2) set new and/or change parameter thresholds; and 3) make necessary assumptions.

In the development of the *O. erosus* Potential Susceptibility Map, FHTET was responsible for synthesis of information before, during, and after committee meetings; reporting outputs (e.g., loading products on web sites and maintaining web sites); coordination of expertise on the committee (driving the process forward); meeting deadlines; model construction; and hiring contracting and North Carolina State University personnel in order to obtain specific modeling expertise.

Limitations and Pitfalls of the *Orthotomicus erosus* Potential Susceptibility Map

The process of developing a susceptibility map involves a large number of assumptions, such as 1) assigning the magnitude of weights for various factors (see description of this above); 2) developing a course of action when no representative data are available;

3) anticipation of changes in the behavior of *O. erosus* in its new environment; and 4) addressing temporal issues. These assumptions along with all methods and “metadata” for *O. erosus* are disclosed in detail in the “metadata” found on the FHTET website (USDA FS 2008). Some examples of the assumptions follow.

The creation of the urban host layer involved an assumption made to address the lack of available representative data. No comprehensive information exists regarding the presence of host species and the proportion of those species within U.S. urban boundaries. However, it is widely understood that pines are cultivated in nearly all U.S. cities. Therefore, it was assumed that all U.S. cities contain *O. erosus* host type and an urban host layer was created to reflect that decision. In order to capture the maximum number of sample detection points, an expanded definition of urban forest was used that created two levels of risk: 1) the ESRI city (urban) polygons, which introduced a risk level of 7 into the Introduction component; and 2) an urban boundary that begins at the edge of the ESRI polygons and extends outward based on measurements of the lighting footprint created by urban areas (collected from remote sensing imagery), which introduced a risk level of 3-4. An analysis with a dataset assembled by R&D in cooperation with the California Department of Food and Agriculture on the collection locations of *O. erosus* in California revealed that approx. 50% of the detection sample points were in the city lighting areas (= white space).

A number of urban host areas were excluded from the Establishment component because they fell outside the *O. erosus* survival temperature thresholds set by the Committee. Because some of the excluded southwestern urban areas (e.g., Las Vegas, Phoenix, etc.) maintain large ornamental plantings of Mediterranean pines (e.g., *P. canariensis*, *P. eldarica*, *P. halepensis*, and *P. pinea*) susceptible to *O. erosus*, urban areas located within USDA Plant Hardiness Zones of 8b-10b (Cathey 1990) were included in the spatial scope of the model. The Committee concluded that these zones were indicative of the potential of typical Mediterranean pine hosts to grow in these urban areas and that this constituted indirect evidence for potential survival of *O. erosus* in suitable urban microhabitats.

Other assumptions were made to address temporal matters, such as deciding whether more predictive power could be attained with historical datasets (e.g., the preceding 100 yrs) or with contemporary datasets that may reflect present and future conditions (particularly in the context of climate change). Often, the datasets available to the committee were two or three years old because of lags between the time when the data were collected and when they were processed and made available for dissemination. In general though, where relatively current data (e.g., the previous 5 yrs) were available, the committee opted to use these more recent datasets.

The availability and the maintenance of various datasets was also an issue that the committee had to contend with. For example, in the process of developing the disturbance layer, the committee realized that thinning or harvesting was not included as a factor. Given that outbreak activity of this pest on other continents has been correlated with thinning events (Halperin et al. 1983, Mendel and Halperin 1982, Mendel

et al. 1992), the absence of this information in the model is a considerable limitation. Unfortunately, the committee ascertained that there was no available national database that consolidates information from National Forests, or state, municipal, private, or Native American lands regarding harvests or thinning operations, so we could not include these data in the map. The committee also found that other datasets in the disturbance layer, e.g., those that document occurrence of tornadoes and hurricanes, were not frequently updated. At the time of this writing (Nov. 2008), the disturbance impact of Hurricane Katrina, which occurred in Aug. 2005, had not been incorporated into the tornado/hurricane database.

The committee also found several instances where the interaction of datasets had to be reconciled. For example, it was accepted by the committee that ozone affects trees that are stressed by drought to a greater extent than trees not experiencing a moisture deficit (Grulke et al. 2002). Therefore, Environmental Protection Agency data on direct ozone concentrations were combined with USDA Forest Service Forest Inventory and Analysis (FIA) program plant damage data, as the latter were thought to better depict the locations where ozone would actually impact the health of pines. Thus, an indirect measure of ozone (i.e., ozone damage to plant bio-indicators) was incorporated into the disturbance layer. Unfortunately, all currently available ozone bioindicator maps had data gaps (i.e., states where bioindicator data were not collected). Although preliminary regional models that relate ozone injury to ambient ozone levels, moisture status, and other environmental variables were available, the committee decided to re-interpolate FIA bioindicator data to fill in the current gaps.

Future Application of the *Orthotomicus erosus* Potential Susceptibility Map

The *O. erosus* Potential Susceptibility Map was developed to understand where *O. erosus* may be entering the U.S. and where it is possible for *O. erosus* to sustain populations. The latter was accomplished by focusing on factors that affect distribution. It was intended that such predicted distributional information could be used by forest resource managers to better direct and pinpoint future monitoring and survey activities for *O. erosus*. In some instances, pest detection specialists may be more interested in using the Potential Introduction portion of the product (i.e., in those states that are far from the current area of infestation); in other instances (e.g., in California and neighboring states) resource managers may be more interested in using the Potential Establishment portion to guide their forest management decisions.

The models should be used with the knowledge that they are an approximation of the risk and the location of the risk posed by *O. erosus*. Local knowledge should always be considered when using these products. The relatively large knowledge and data gaps prevent these products from being completely precise. Indeed, they were constructed with data that was not entirely collected for these purposes and based on expert interpretation of incomplete knowledge about the invasive pest and its susceptible hosts. In addition, information as to where imports are coming from and ending up is not available. The applicability of the products is also limited in the scope of time; they describe risk in the short-term, and these risks may change with even the passage of a few years as environmental and societal conditions change.

Summary

The *O. erosus* mapping project demonstrates the interdependence of R&D and FHP staff and provides a clear example of how the two groups can work both cooperatively and synergistically to:

1. conduct timely research;
2. attain needed population and biological information;
3. immediately implement research findings to develop tools; and
4. create tools that are useful to forest management personnel for taking appropriate actions in the field.

The project has also illustrated the benefit to government agencies of retaining some agility in directing resources toward developing problems. When the Washington Office FHP staff identified the need for tools to better understand the potential impact of *O. erosus*, the Pacific Southwest and Northern Research Stations were also identifying the need to improve the state of the science for *O. erosus* in North America. Research funding was in limited supply, so FHTET provided seed funds to the research cooperators to attain the needed population and biological information as well as to characterize the behavior of *O. erosus* in North America. In so doing, personnel with the appropriate support mechanisms and skill-sets, were brought together to develop needed tools.

The *O. erosus* Potential Susceptibility Map will be completed in early 2009, and the final products will be posted on the FHTET web site (USDA FS 2008), where the current and future status can be monitored by users. Final products will include three maps (the Potential Introduction, the Potential Establishment, and the Potential Susceptibility); a recommended survey sampling design for the U.S. (survey sample areas); links to the biological attributes of *O. erosus* (via the ExFor site, <http://spfnic.fs.fed.us/exfor>); links to key pieces of scientific literature (e.g., Lee et al. 2005, 2008, In press); a list of forest species (hosts) at risk; the methods used in developing the Susceptibility Potential Map; the metadata; and the membership of the steering committee.

For the first time in the history of forest insect investigations in the western U.S., invasive subcortical pests from other continents have established populations that threaten conifers. The appearance of *O. erosus* and *H. ligniperda* in the urban forests of California will likely impact our future management of urban and peri-urban pines in this state and beyond if the populations expand. The capacity of the new invaders to compete with native populations of bark beetles in pines will be a research question of considerable interest (Amezaga and Rodríguez 1998). This new period of invasion of western U.S. forests by exotic subcortical insects has presented and continues to present an opportunity for USDA Forest Service R&D and FHP to pool their talents and resources to address a problem of pressing national concern.

Acknowledgments

We appreciate critical reviews of an earlier version of the manuscript by Robert A. Haack and Therese M. Poland (both USDA Forest Service, Northern Research Station, East Lansing, MI), John E. Lundquist (USDA Forest Service, Pacific Northwest Research Station, Anchorage, AK), and Robert C. Venette (USDA Forest Service, Northern Research Station, St. Paul, MN). We also thank Jana C. Lee, Deguang Liu, Mary Louise Flint (all UC-Davis, Dept. of Entomology), Frank H. Koch (North Carolina State University), Sujin Kim and Thomas C. Harrington (Department of Plant Pathology, Iowa State University), Whitney Cranshaw and Ned A. Tisserat (Colorado State University, Dept. of Bioagricultural Sciences and Pest Management), Richard L. Penrose (California Department of Food and Agriculture, Sacramento), Tom W. Coleman (USDA Forest Service, Forest Health Protection, San Bernardino, CA), John W. Coulston and William D. Smith (USDA Forest Service), and R.C. Venette for permission to cite or discuss unpublished data and for assistance with research on the invasion biology of *O. erosus* and other invasive species. Much of the information discussed in this paper was synthesized from several recent publications from Seybold's laboratory (Lee et al. 2005, 2007, 2008, In press; Liu et al. 2007, 2008) and we wish to acknowledge the numerous contributions of our co-authors and cooperators to them. Funding sources for these publications and associated research efforts came from USDA Forest Service Pacific Southwest Research Station; a University of California IPM Exotic/Invasive Pests and Diseases grant #05XU039 to SJS, M. L. Flint, and J. C. Lee; USDA NRI CSREES postdoctoral grant #2006-35302-16611 to J. C. Lee; USDA FS FHTET project "Dispersal potential of the Mediterranean pine engraver, *Orthotomicus erosus*, in support of risk mapping," to SJS, R.C. Venette, and M.L. Flint; and USDA Forest Service Special Technology Development Program grant "Improved early detection for the Mediterranean pine engraver, *Orthotomicus erosus*, an invasive bark beetle (R4-2008-01)," to SJS, A.S. Munson, R.C. Venette, and M.L. Flint.

Literature Cited

- Amezaga, I.; Rodríguez, M.Á. 1998.** Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species. *Forest Ecology and Management*. 109: 127–135.
- Baylis, N.T.; de Ronde, C.; James, D.B. 1986.** Observations of damage of a secondary nature following a wild fire at the Otterford State Forest. *South African Forestry Journal*. 137: 36–37.
- Ben Jamaa, M.L.; Lieutier, F.; Yart, A.; Jerraya, A.; Khouja, M.L. 2007.** The virulence of phytopathogenic fungi associated with the bark beetles *Tomicus piniperda* and *Orthotomicus erosus* in Tunisia. *Forest Pathology*. 37: 51–63.
- Bevan, D. 1984.** *Orthotomicus erosus* (Wollaston) in Usutu pine plantations, Swaziland. Forest Research Report Number 64. Usutu Pulp Company Limited. 34 p.

- Bright, D.E., Jr.; Stark, R.W. 1973.** The bark and ambrosia beetles of California, Coleoptera: Scolytidae and Platypodidae. Bulletin of the California Insect Survey, Vol 16. Berkeley, CA: University of California Press. 169 p.
- Cathey, H.M. 1990.** Plant hardiness zone Map. Miscellaneous Publication No. 1475. Washington, DC: US Department of Agriculture, U.S. National Arboretum, Agricultural Research Service. <http://www.usna.usda.gov/Hardzone/ushzmap.html> (12 January 2009).
- Coleman, T.W.; Seybold, S.J. [In press].** Previously unrecorded damage to oak, *Quercus* spp., in southern California by the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae). The Pan-Pacific Entomologist.
- Coleman, T.W.; Seybold, S.J. 2008.** New pest in California: The goldspotted oak borer, *Agrilus coxalis* Waterhouse. Pest Alert, R5-RP-22. Vallejo, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, State and Private Forestry. 4 p.
- Dodds, K.J.; Gilmore, D.W.; Seybold, S.J. 2004.** Ecological risk assessments for insect species emerged from western larch imported to northern Minnesota. Department of Forest Resources Staff Paper Series Number 174. St. Paul, MN: University of Minnesota. 57 p.
- Eglitis, A.E. 2000.** Mediterranean pine engraver beetle. In: Pest risk assessment for importation of solid wood packing materials into the United States. Washington, DC: U.S. Department of Agriculture, Animal and Plant Health Inspection Service and Forest Service: 190–193.
- Environmental Systems Research Institute (ESRI). 2008.** ArcGIS® Model Builder® Spatial Analyst®. 380 New York Street, Redlands, CA.
- Furniss, M.M.; Johnson, J.B. 2002.** Field guide to the bark beetles of Idaho and adjacent regions. Moscow, ID: University of Idaho, Idaho Forest, Wildlife, and Range Experiment Station. 125 p.
- Furniss, R.L.; Carolin, V.M. 1977.** Western forest insects. Misc. Pub. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.
- Gandhi, K.J.K.; Gilmore, D.W.; Katovich, S.A.; Mattson, W.J.; Spence, J.R.; Seybold, S.J. 2007.** Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews. 15: 113–152.
- Goheen, D.J.; Hansen, E.M. 1993.** Effects of pathogens and bark beetles on forests. In: Showalter, T.D.; Filip, G.M., eds. Beetle-Pathogen Interactions in Conifer Forests. London: Academic Press: 175–196.

- Grulke, N.E.; Preisler, H.K.; Rose, C.; Kirsch, J.; Balduman, L. 2002.** O₃ uptake and drought stress effects on carbon acquisition of ponderosa pine in natural stands. *New Phytologist*. 154: 621–631.
- Haack, R.A. 2001.** Intercepted Scolytidae (Coleoptera) at U.S. ports of entry: 1985–2000. *Integrated Pest Management Reviews*. 6: 253–282.
- Haack, R.A. 2006.** Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research*. 36: 269–288.
- Halperin, J.; Mendel, Z; Golan, Y. 1983.** On the damage caused by bark beetles to pine plantations: Preliminary report. *La-Yaavan* 33: 46.
- Hicke, J.A.; Logan, J.A.; Powell, J.; Ojima, D.S. 2006.** Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research*. 111: [Not paged] G02019, doi:10.1029/2005JG000101.
- Jacobi, W.R.; Koski, R.D.; Harrington, T.C.; Witcosky, J.J. 2007.** Association of *Ophiostoma novo-ulmi* with *Scolytus schevyrewi* (Scolytidae) in Colorado. *Plant Disease*. 91: 245–247.
- Jiang, Y.-P.; Huang, Z.-Y.; Huang, X.-C. 1992.** Studies on *Orthotomicus erosus*. *Journal of Zhejiang Normal University (Natural Science)* 15: 79–81 In Chinese.
- Johnson, P.L.; Hayes, J.L.; Rinehart, R.E.; Sheppard, W.S.; Smith, S.E. 2008.** Characterization of two non-native invasive bark beetles, *Scolytus schevyrewi* and *Scolytus multistriatus* (Coleoptera: Curculionidae: Scolytinae). *The Canadian Entomologist*. 140: 527–538.
- Koch, F.; Smith, B.; Coulston, J. 2007.** Mapping drought conditions using multi-year windows. 10 p. Unpublished report. On file with: U.S. Department of Agriculture, Forest Service, Forest Health Monitoring Program, Forest Sciences Laboratory, 3041 Cornwallis Road, Research Triangle Park, NC 27709.
- Krist, F.J.; Sapio, F.J.; Tkacz, B. 2007.** Mapping risk from forest insects and diseases. FHTET 2007–06. Washington, DC: US Department of Agriculture, Forest Service, Forest Health Protection Forest Health Technology Enterprise Team. 115 p.
- Langor, D.W.; DeHass, L.J.; Footit, R.G. 2009.** Diversity of non-native terrestrial arthropods on woody plants in Canada. *Biological Invasions*. 11: 5–19.

- Lee, J.C.; Aguayo, I.; Aslin, R.; Durham, G.; Hamud, S.M.; Moltzan, B.D.; Munson, A.S.; Negrón, J.F.; Peterson, T.; Ragenovich, I.R.; Witcosky, J.J.; Seybold, S.J. [In press].** Co-occurrence of two invasive species: The banded and European elm bark beetles (Coleoptera: Scolytidae). *Annals of the Entomological Society of America*.
- Lee, J.C.; Flint, M.L.; Seybold, S.J. 2008.** Suitability of pines and other conifers as hosts for the invasive Mediterranean pine engraver (Coleoptera: Scolytidae) in North America. *Journal of Economic Entomology*. 101: 829–837.
- Lee, J.C.; Haack, R.A.; Negrón, J.F.; Witcosky, J.J.; Seybold, S.J. 2007.** Invasive bark beetles. Forest Insect & Disease Leaflet 176. U.S. Department of Agriculture, Forest Service. 12 p.
- Lee, J.C.; Jiroš, P.; Liu, D.; Hamud, S.M.; Flint, M.L.; Seybold, S.J. [in prep].** Pheromone production and flight response to semiochemicals by the Mediterranean pine engraver (Coleoptera: Scolytidae), a recently invasive bark beetle in California. *Journal of Chemical Ecology*.
- Lee, J.C.; Negrón, J.F.; McElwey, S.J.; Witcosky, J.J.; Seybold, S.J. 2006.** Banded elm bark beetle - *Scolytus schevyrewi*. Pest Alert, R2-PR-01-06. Golden, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Forest Health Protection. 2 p.
- Lee, J.C.; Smith, S.L.; Seybold, S.J. 2005.** The Mediterranean pine engraver, *Orthotomicus erosus*. Pest Alert, R5-PR-016. Vallejo, CA: U.S. Department of Agriculture, Forest Service, State and Private Forestry, Pacific Southwest Region. 4 p.
- Little, E.L., Jr. 1971.** Atlas of United States trees, Volume 1, Conifers and important hardwoods. Miscellaneous Publication 1146. Washington, DC: U.S. Department of Agriculture. 400 p.
- Liu, D.-G.; Bohne, M.J.; Lee, J.C.; Flint, M.L.; Penrose, R.L.; Seybold, S.J. 2007.** New introduction in California: The redhaired pine bark beetle, *Hylurgus ligniperda* Fabricius. Pest Alert, R5-PR-07. Vallejo, CA: US Department of Agriculture Forest Service, State and Private Forestry, Pacific Southwest Region. 3 p. <http://www.fs.fed.us/r5/spf/publications/pestalerts/HylurgusPertAlert.pdf>.
- Liu, D.-G.; Flint, M.L.; Seybold, S.J. 2008.** A secondary sexual character in the redhaired pine bark beetle, *Hylurgus ligniperda* Fabricius (Coleoptera: Scolytidae). *The Pan-Pacific Entomologist*. 84: 26–28.

- Mattson, W.J.; Lawrence, R.K.; Haack, R.A.; Herms, D.A.; Charles, P.-J. 1988.** Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of association with insects. In: Mattson, W.J.; Leveux, J.; Bernard-Dagan, C., eds. Mechanisms of woody plant defenses against insects: search for patterns. New York: Springer Verlag: 3–38.
- Mattson, W.J.; Niemela, P.; Millers, I.; Inguanzo, Y. 1992.** Immigrant phytophagous insects on woody plants in the United States and Canada: an annotated list. Gen. Tech. Rep. NC-GTR-169. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 27 p.
- Mendel, Z. 1983.** Seasonal history of *Orthotomicus erosus* (Coleoptera: Scolytidae) in Israel. *Phytoparasitica*. 11: 13–24.
- Mendel, Z.; Halperin, J. 1982.** The biology and behavior of *Orthotomicus erosus* in Israel. *Phytoparasitica*. 10: 169–181.
- Mendel, Z.; Boneh, O.; Riov, J. 1992.** Some foundations for the application of aggregation pheromone to control pine bark beetles in Israel. *Journal of Applied Entomology*. 114: 217–227.
- Mendel, Z.; Boneh, O.; Shenhar, Y.; Riov, J. 1991.** Diurnal flight patterns of *Orthotomicus erosus* and *Pityogenes calcaratus* in Israel. *Phytoparasitica*. 19: 23–31.
- Moser, J.C.; Fitzgibbon, B.A.; Klepzig, K.D. 2005.** The Mexican pine beetle, *Dendroctonus mexicanus*: first record in the United States and co-occurrence with the southern pine beetle—*Dendroctonus frontalis* (Coleoptera: Scolytidae or Curculionidae: Scolytinae). *Entomological News*. 116: 235–243.
- Mouton, M.; Wingfield, M. J.; Van Wyk, P. S.; Van Wyk, P. W. J. 1994.** *Graphium pseudormiticum* sp. nov.: A new hyphomycete with unusual conidiogenesis. *Mycological Research*. 98: 1272–1276.
- NAPPFast. 2008.** North Carolina State University-Animal Plant Health Inspection Service: Weather based plant pest prediction system. <http://www.nappfast.org/> (12 January 2009).
- Negrón, J.F.; Witcosky, J.J.; Cain, R.J.; LaBonte, J.R.; Duerr, D.A., II; McElwey, S.J.; Lee, J.C.; Seybold, S.J. 2005.** The banded elm bark beetle: a new threat to elms in North America. *American Entomologist*. 51: 84–94.
- Paine, T.D.; Raffa, K.F.; Harrington, T.C. 1997.** Interactions among scolytid bark beetles, their associated fungi, and host conifers. *Annual Review of Entomology*. 42: 179–206.

- Parker, T.J.; Clancy, K.M.; Mathiasen, R.L. 2006.** Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology*. 8: 167–189.
- Romón, P., Iturrondobeitia, J.C.; Gibson, K.; Lindgren, B.S.; Goldarazena, A. 2007.** Quantitative association of bark beetles with pitch canker fungus and effects of verbenone on their semiochemical communication in Monterey pine forests in northern Spain. *Environmental Entomology*. 36: 743–750.
- Scriven, G.T.; Reeves, E.L.; Luck, R.F. 1986.** Beetle from Australia threatens eucalyptus. *California Agriculture*. 40(7/8): 4–6.
- Seybold, S.J.; Huber, D.P.W.; Lee, J.C.; Graves, A.D.; Bohlmann, J. 2006a.** Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochemistry Reviews*. 5: 143–178.
- Seybold, S.J.; Lee, J.C.; Luxová, A.; Hamud, S.M.; Jiroš, P.; Penrose, R.L. 2006b.** Chemical ecology of bark beetles in California's urban forests. In: Hoddle, M.S.; Johnson, M.W., eds. *Proceedings of the 5th Annual Meeting of the California Conference on Biological Control*, Riverside, California, July 27–28, 2006. [Publisher unknown]: 87–94.
- Solomon, J.D. 1995.** Guide to insect borers in North American broadleaf trees and shrubs. *Agric. Handbook 706*. Washington, DC: U.S. Department of Agriculture, Forest Service. 735 p.
- U.S. Department of Agriculture, Forest Service. 2008.** Forest Health Technology Enterprise Team. Invasive species information program; invasive species risk maps. http://www.fs.fed.us/foresthealth/technology/invasive_species.shtml (12 January 2009).
- Venette, R.C.; Walter, A.J.; Seybold, S.J. 2009.** Comparing risks from native and exotic bark beetles to the health of Great Lakes forests. In: *Proceedings Society of American Foresters 2008 Annual Meeting*. Reno, NV. CD-ROM. Society of American Foresters, Bethesda, MD.
- Wood, S.L. 1982.** The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Provo, UT: Great Basin Naturalist Memoirs 6. 1359 p.
- Wood, S.L. 2007.** Bark and ambrosia beetles of South America (Coleoptera, Scolytidae). Brigham Young University, Provo, UT: M.L. Bean Life Science Museum. 900 p.
- Yin, H.-F.; Huang, F.-S.; Li, Z.-L. 1984.** Economic Insect Fauna of China, Fascicle 29, Coleoptera: Scolytidae. Beijing, China: Science Press: 138–139. In Chinese.

- Zhou, X.-D.; Burgess, T.; de Beer, Z.W.; Wingfield, B.D.; Wingfield, M.J. 2002.** Development of polymorphic microsatellite markers for the tree pathogen and sapstain agent, *Ophiostoma ips*. *Molecular Ecology Notes*. 2: 309–312.
- Zhou, X.-D.; de Beer, Z.W.; Wingfield, B.D.; Wingfield, M.J. 2001.** Ophiostomatoid fungi associated with three pine-infesting bark beetles in South Africa. *Sydowia*. 53: 290–300.
- Zwolinski, J.B.; Swart, W.J.; Wingfield, M.J. 1995.** Association of *Sphaeropsis sapinea* with insect infestation following hail damage of *Pinus radiata*. *Forest Ecology and Management*. 72: 293–298.