The Conservation of Forest Genetic Resources

Case Histories from Canada, Mexico, and the United States

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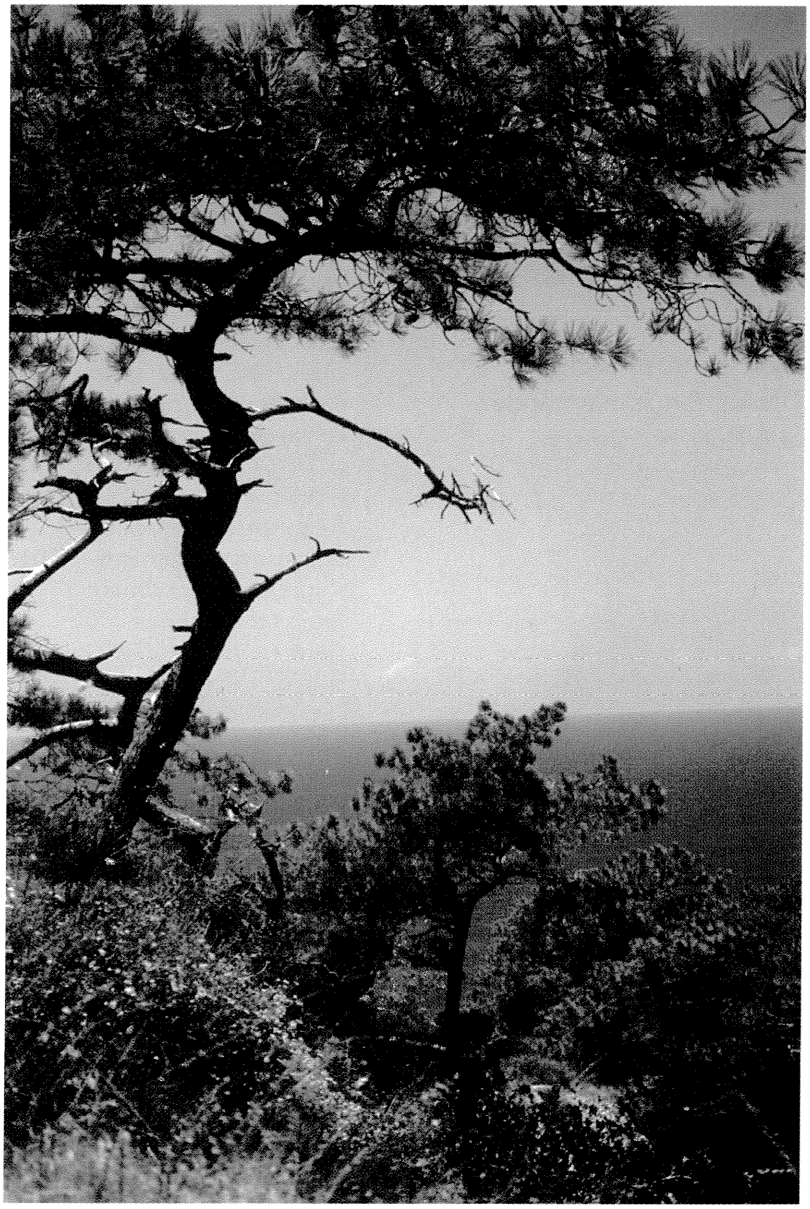
By F. Thomas Ledig,
J. Jesús Vargas-Hernández,
and Kurt H. Johnsen

Prepared as a task of the Forest Genetic Resources Study Group/North American Forestry Commission/Food and Agriculture Organization of the United Nations.



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The genetic codes of living organisms are natural resources no less than soil, air, and water. Genetic resources—from nucleotide sequences in DNA to selected genotypes, populations, and species—are the raw material in forestry: for breeders, for the forest manager who produces an economic crop, for society that reaps the environmental benefits provided by forests, and for the continued evolution of the species itself.

Breeding, of course, requires genetic variation. Continued improvement in medicines, agricultural crops, and forest crops depends on breeders' access to genetic resources.

In terms of human economy, we rely on the finely tuned match of organisms to their environment to maintain productivity of our forests. If populations are lost or diversity is reduced, site productivity can decline (e.g., Ledig 1991). The ultimate loss of genetic resources is the economic loss of commercial species, such as American chestnut *(Castanea dentata)* and St. Helena redwood *(Trochetiopsis erythroxylon)*. The loss of genetic resources can also mean a reduction in commercial value: the poorly formed coastal populations of Calabrian pine *(Pinus brutia)* in the eastern Mediterranean result from exploitation in antiquity (Palmberg 1975), and the stunted examples of mahogany *(Swietenia mahagoni)* in the most accessible areas of the Caribbean result from recent exploitation (Styles 1972).

In a broader sense, the health of society depends on forest genetic resources for the ecological services that are often taken for granted: release of oxygen and storage of carbon, amelioration of climate, protection of watersheds, and others. Should genetic resources be lost, ecosystem function may also be damaged, usually expressed as a loss of primary productivity, the rate at which a plant community stores energy and produces organic matter (e.g., Fetcher and Shaver 1990). Losses in primary productivity result in changes in nutrient and gas cycling in ecosystems (Bormann and Likens 1979).

The loss of a plant population is a secret extinction, eliminating valuable but often cryptic sources of diversity.

Genetic diversity is the most basic element of biological diversity and provides the raw materials by which species evolve and adapt to changing conditions (Keystone Center 1991). In long-lived forest trees, genetic diversity may be necessary to buffer against environmental variation as well as provide for change on the evolutionary time scale.

Although the value of genetic resources is generally not contested, methods of conserving it are. Discussion has centered on whether genetic resources should be conserved in the native habitat *(in situ)* or in special collections *(ex situ)*. Genetic resource collections maintained in seed banks and field gene banks (such as clone banks and seedling plantations) are examples of *ex situ* conservation. For agronomic crops, conservation in huge seed banks is the rule. The US National Seed Storage Laboratory in Fort Collins, Colorado, maintains more than 46,000 separate lots of wheat alone (Chang 1989). But for forest trees, conservation in the natural habitat has long been considered the better alternative

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(Rogers and Ledig 1996). Conservation *in situ* generally is less expensive than collecting and managing genetic resources in seed banks and allows natural processes of evolution to continue. Also, *in situ* reserves can serve multiple purposes—providing forest products, recreation, and ecological benefits (e.g., Ledig 1986; Wilson 1990; Millar and Westfall 1996).

Genetic resources *in situ*, however, are subject to loss through human activities or through fire, flood, wind, introduced pests and pathogens, and climate change. Donald Falk (1992), when he was director of the Center for Plant Conservation, argued that *ex situ* conservation should therefore be an integral component of conservation strategies. Yet no country in North America has a comprehensive strategy for conserving forest genetic resources or any program for long-term *ex situ* conservation. The Canadian Forest Service is just beginning to develop systematic and comprehensive collections of Canada's native tree species (D. Simpson, pers. commun., 1997), and only a few of North America's major commercial species are adequately maintained, generally by university-industry tree improvement cooperatives.

The case studies below are compelling arguments for national programs of *ex situ* conservation (e.g., as outlined in Ledig 1992) as insurance against the loss of forest genetic resources in their natural habitat. These three examples illustrate the breadth, severity, and international nature of the genetic conservation issue. We could have chosen numerous examples; many other species are similarly at risk of dramatic reductions in genetic diversity. However, the cases we chose are not merely examples of endangered resources, they are, in some respects, success stories in conservation. As members of the Forest Genetic Resources Study Group, North American Forestry Commission, Food and Agriculture Organization of the United Nations, we present these cases to draw attention to the need for conservation strategies that integrate *in situ* and *ex situ* methods.

Ottawa Valley White Spruce

The white spruce of the Ottawa Valley, Ontario, represent a unique gene pool that is rapidly disappearing from nature. Ex situ *conservation may be the best hope for maintaining this genetic resource for future generations.*

White spruce *(Picea glauca)* is one of the most widely distributed tree species in North America. Its range is transcontinental, extending over most of Canada and into the northern United States. It is the most-planted tree species in Canada (Kuhnke 1989) and is included in several commercial and provincial tree improvement programs.

Seed source tests (also called common garden tests and provenance tests) of white spruce were established in the 1950s to quantify and analyze genetic variation for breeding programs. In many tests across eastern Canada and the northeastern United States, white spruce seed lots that originated in the Upper Ottawa Valley in Ontario grew as fast as or faster than the local seed sources (e.g., Nienstaedt and Teich 1972). Best known as Beachburg, superior sources appear to extend from the vicinity of Pembroke, Douglas, Renfrew, and Beachburg to the Upper Ottawa Valley, an area of 1,719 km^2 (Teich et al. 1975). Although shown to be genetically distinct, Ottawa Valley white spruce are not taxonomically distinguished from other white spruce.

Demography. Ottawa Valley white spruce has been reduced in extent and is threatened with further reduction. From the mid-1880s to the mid-1900s, native forests were cut extensively. Until this century, the forest resource was exploited with little or no concern for regeneration. After logging, much of the area was converted to farm and pasture, and natural occurrence of the commercial tree species in the valley was greatly reduced. The losses continue.

Genetic variation. Several tests of 91 white spruce seed sources were established in Ontario, and at 13 to 20 years the trees from the Beachburg-Cobourg corridor averaged 21 percent taller than the local seed source (Teich et al. 1975). Similar results were observed in tests in the Canadian Maritime Region and the northeastern and north central United States (Fowler and Coles 1977; Genys and Nienstaedt 1979). In British Columbia, Upper Ottawa Valley white spruce not only grow very well, they are also resistant to weevil attack (Kiss et al. 1994). The value of these genetic resources is recognized by breeders throughout Canada and the northern United States. Breeders from as far away as the Canadian Maritimes and British Columbia have incorporated Upper Ottawa Valley white spruce in their local breeding programs (Fowler and Coles 1977; B. Jaquish, pers. commun., 1997).

Conservation. Recognizing the genetic superiority of the Upper Ottawa Valley white spruce seed source as well as the continued erosion of natural populations, forest geneticists from the Canadian Forest Service and the Ontario Ministry of Natural Resources sought to increase seed availability (Winston et al. 1981). Their goals were to establish and maintain the following:

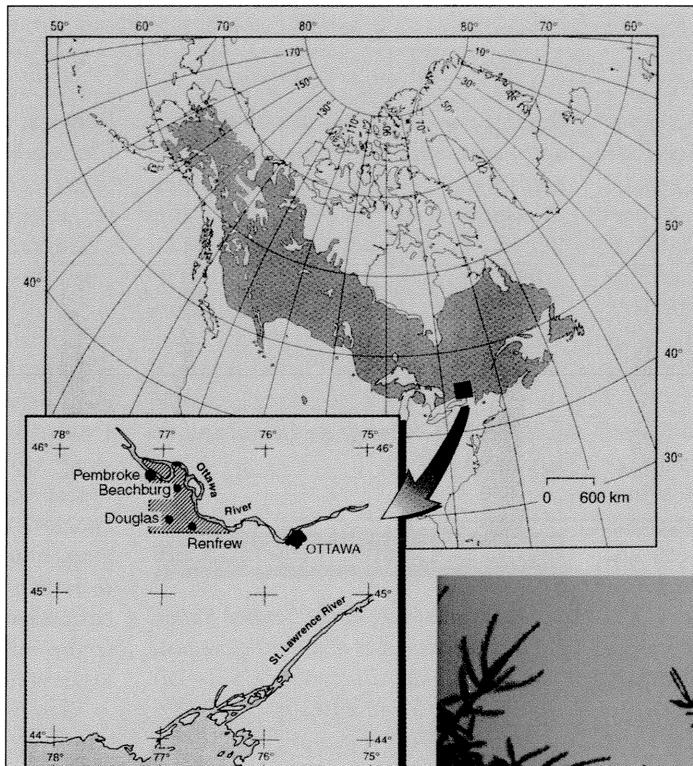
1. A seed production area (that is, selected natural stands thinned to the best trees to encourage abundant seed crops and facilitate cone collection) to meet seed requirements in the short term and conserve the gene pool in the long term.
2. A production seed orchard (that is, plantations established for producing seed) of Upper Ottawa Valley white spruce of superior genetic quality.
3. Experiments to reduce the time to produce seed and increase seed yield and quality.
4. A clone bank for conservation of selected Upper Ottawa Valley white spruce genetic resources.

The seed production area was never established, and the production seed orchards and the experimental units were not completed because of funding cuts. However, the clone bank—the activity most directly related to the genetic conservation of Upper Ottawa Valley white spruce—was completed in 1988.

The first step in establishing the clone bank was a land and aerial survey of existing white spruce stands in the region (vanBorrendam 1984). The survey identified all stands with more than 20 white spruce trees. Stands were small, up to 200 trees, often mixed with other species. Those finally chosen were all on private land. With the approval of the owners, a total of 310 trees from 35 stands were sampled. The "best" trees were selected from each stand on the basis of appearance (phenotype). Nevertheless, the often-used term "plus tree" may be inappropriate because budworms and timber harvest had left populations in a depleted and degraded state. The selected trees were probably similar to, and of the same cohort as, those sampled for the seed source tests that identified the genetic superiority of the Ottawa Valley white spruce.

Sampling took place from winter 1982–83 through winter 1987–88. Successful grafts were made with scions from 252 of the original 310 selections, representing 34 stands, and the grafted trees are growing in two clonal archives at the Petawawa National Forestry Institute, Chalk River, Ontario. Two to eight grafts per selection are archived.

Was this clonal population necessary to conserve the genetic resource? The 16 responses to a 1993 survey of the 34 landowners revealed that 12 stands remained largely as they were in 1983, one stand was cut for road and home construction, one was approximately half its former size because of blowdown and fire, and in the remaining two stands, populations had been reduced by approximately a third by logging and home construction. We speculate that the nonresponses signify a situation at least as dire. Thus, loss and erosion of the natural populations continue. If Upper Ottawa Valley white spruce were a named taxon, it would qualify as endangered under the guidelines of the International Union for the Conservation of Nature and Natural Resources because it is so reduced in numbers.



White spruce has an extensive range, but one of its most valuable populations is confined to the Upper Ottawa Valley (inset), where continued development threatens the stands. The genetic resource is conserved in local clonal archives.

Because the clonal archive was implemented to conserve genetic resources valuable to tree breeders, sampling within stands was not random; only the largest, best-formed trees were chosen for the clonal archive. From nine of the 34 stands, Cheliak et al. (1988) surveyed 82 of the selected trees and 447 randomly sampled trees for genic variation in 12 enzyme systems. Gene frequency and genic diversity (measured by a statistic called expected heterozygosity) were not significantly different between the two groups, but the selected trees did have a reduced genic richness by one measure: 25 percent of the genes in the random sample were missing from the sample preserved in the clonal archive. All common genes but only two of 12 rare genes (frequency of 0.01 to 0.02) were found in the archive, which might be a result of chance because the sample size was only 82 trees. In any case, the failure to capture all rare genes in the archive is probably not a serious loss: most conservation geneticists and breeders feel it is not necessary to conserve rare alleles (e.g., Marshall and Brown 1975; Holsinger and Gottlieb 1991).

For Ottawa Valley white spruce, *in situ* conservation is an unlikely option because the widely separated stands are all on private land, and in fact, the *in situ* resource continues to decline. In only five to 10 years, white spruce declined or was lost entirely in four of 16 stands that were revisited. If loss of the natural populations continues, the clone bank and seed source tests (that is, the tests reported by Nienstaedt and Teich 1972; Fowler and Coles 1977; Genys and Nienstaedt 1979) will be the only sources of the genes and genotypes of "superior" Ottawa Valley white spruce available to future breeders.

Guadalupe Island Pine

The Guadalupe variant of Monterey pine grows on dozens of sites in Australia. These plantations can be a source of materials for reintroduction should pine disappear from Guadalupe Island.

Guadalupe Island pine is a variety of Monterey pine *(Pinus radiata),* one of the most valuable genetic resources on earth. In fact, Monterey pine is the most widely planted exotic conifer species in the world, covering 4 million hectares in commercial timber and pulpwood plantations in New Zealand, Australia, Africa, and South America (Rogers and Ledig 1996). Monterey pine has been introduced to many other countries as well, as an economic crop and for soil protection (Scott 1960).

Although Monterey pine plantations now cover extensive areas, natural populations of this species are restricted to five isolated locations. The Cambria, Monterey, and Año Nuevo populations are along the coast in mainland California between 35° and 37° north latitude. Two other populations grow on Guadalupe and Cedros Islands, off the coast of Baja California, Mexico. The island populations are about 7° south of the mainland populations.

Despite Monterey pine's limited native range, it has been adapted to many sites around the world and its productivity improved by selection (Burdon and Bannister 1973; Hood and Libby 1980; Guinon et al. 1982). Most of the plantings that provided base populations for the genetic improvement of Monterey pine were established with seeds of unknown or uncertain origin, from one or more of the mainland stands. There is, therefore, a desire to broaden the genetic base by including Guadalupe Island pines. Furthermore, Guadalupe Island pines carry resistance to important diseases of Monterey pine (Cobb and Libby 1968; Old et al. 1986).

Guadalupe Island is about 30 km long, 11 km wide, and approximately 250 km off the coast of Mexico. Pines are restricted to the northern tip of the island on Mount August, at elevations of 300 to 1,100 m. Dry to arid conditions prevail, particularly at lower elevations, which receive less than 250 mm of rain annually (Rico 1983; Perry 1991). Nevertheless, because of winds, ocean currents, and topography, heavy fogs and mist are common throughout the year on Mount August.

Access to the island is by small plane or boat—and difficult either way. The airstrip is not maintained, and there are no piers. A permit is required to visit; the island is officially under control of the Ministry of the Interior and is guarded by the navy. The only inhabitants are the staff at a small meteorological station and naval post.

Taxonomy. Taxonomic relationships of the pines from Guadalupe and Cedros Islands have been problematic since their discovery in the late 19th century. Initially, the Guadalupe trees were classified as a variety of Monterey pine (*Pinus radiata* var. *binata*), whereas the Cedros trees were described as a variety of bishop pine (*P. muricata* var. *cedrosensis*; Newcomb 1959). Currently, both island populations are considered a single variety of Monterey pine, *P. radiata* var. *binata* (Perry 1991). Recent studies have shown that the island populations retain characteristics of an ancestral pine from which *P. radiata* var. *radiata* of Alta California descended (Axelrod 1980; Millar et al. 1988). Thus, both island populations can be regarded as relictual variants of Monterey pine. Both are interfertile with the mainland populations (A.G. Brown and R.D. Burdon, pers. commun., 1997).

Demography. On Cedros Island, pines grow in two major stands, covering about 50 and 100 hectares on the central and northern parts of the island, respectively. The population consists of at least 30,000 mature trees, with very dense patches of reproduction (Libby et al. 1968). Although fire scars and some damage from grazing animals are evident, the pines are not in any apparent peril.

The genetically distinct Guadalupe Island pines, however, are found in only one small population. The trees are scattered in small groves along the northern ridges (Libby et al. 1968), the southernmost of which has only 15 trees and is now 2.5 km from the rest of the population (Rico 1994). The number of mature trees on Guadalupe Island dropped from 383 in 1964 (Libby et al. 1968) to 368 in 1978 (Eldridge 1978) and to about 150 in 1987 (Rico 1994). Recently, only about 100 trees were seen (Mandujano 1992), most with some degree of crown damage from lightning, old fires, or wind. The decline of Guadalupe Island pine is the result of browsing by feral goats.

Goats, introduced in the 19th century, soon reached the island's carrying capacity and since then have prevented natural regeneration of the pines. From Howell's (1941) visit to the island in 1931 to the present, no seedlings or saplings have been found, except on some inaccessible cliffs (Libby et al. 1968; Mandujano 1992). The goats have already helped cause the extinction of several other plant species endemic to the island (Ravest 1983). Mice, also introduced, have been a factor as well (Libby et al. 1968; Ravest 1983).

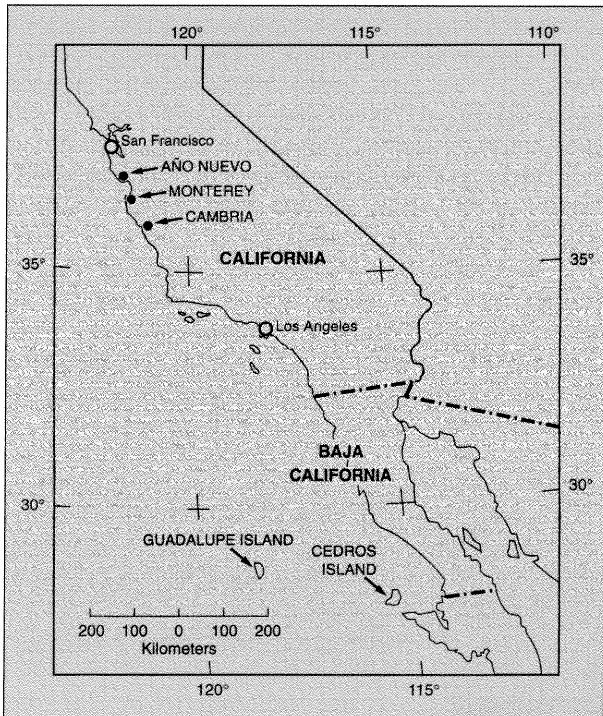
In the past, the goat population was periodically reduced by commercial hunters. During the 1980s, the government tried to control the herd through massive killings, but only after the population had become too large. One visitor to the island in 1994 reported that about 7,000 goats had been eliminated two years earlier, reducing the population to about 5,000, but in the two intervening years the population had again risen above 10,000.

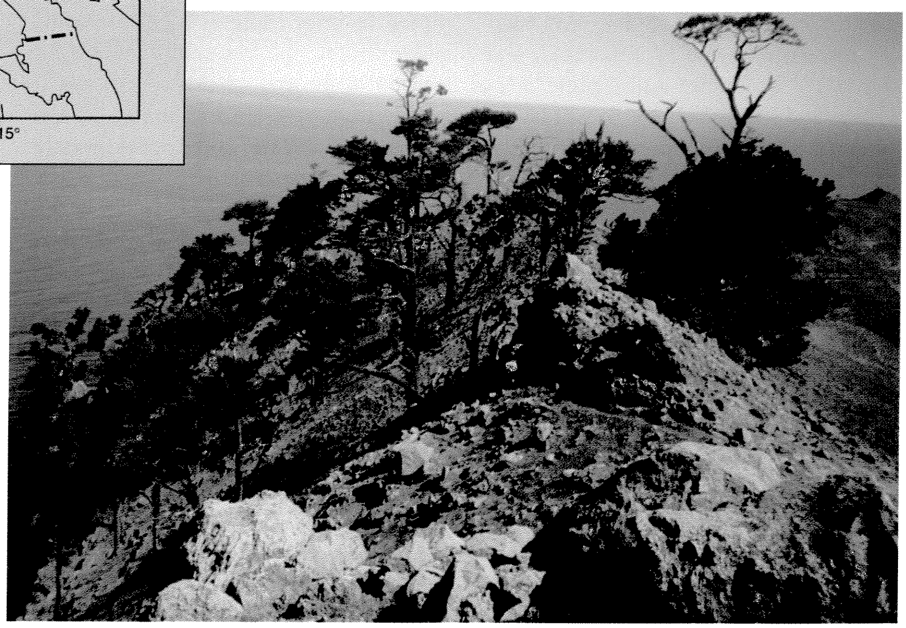
Fencing and other control measures—including plans to move the goats out or use biological agents (myxomatosis virus)—have been proposed but never implemented. Lack of coordination among government agencies compounds the problem. Another difficulty is economic: goat hides and meat are valuable to the few people living on or visiting the island. Finally, the goats have themselves become the object of conservation. In the 100-plus years since they were introduced, a landrace has evolved. They are described as "cimarron," black and white goats with long hair (Ravest 1983).

Genetic variation. Despite the small size of the pine population on Guadalupe Island, substantial variation exists among trees for morphological traits (Rico 1994). Based on analysis of numerous genes that control enzymes, both the Guadalupe and the Cedros Island pines maintain amounts of genic variability similar to that of mainland Monterey pine but differ substantially from each other (Millar et al. 1988; Moran et al. 1988).

The island populations also differ from the mainland populations in several characteristics that are adaptive or economically important. Island progenies have thinner bark and higher wood density (Nicholls and Eldridge 1980) and show less frost damage (Alazard and Destremau 1982) than mainland progenies when grown together in common garden tests. Seedlings from Guadalupe Island are also less susceptible to western gall rust *(Endocronartium harknessii)* and to red-band needle blight *(Scirrhia pini)*, at least in California (Cobb and Libby 1968; Old et al. 1986). Since diseases pose a serious threat to young Monterey pine plantations, the high tolerance of the island populations could be a boon to growers.

Conservation. Attempts to increase the recruitment of pine seedlings on Guadalupe Island have failed because of the goats. In 1980 a small temporary nursery was fenced to raise seedlings, but none were planted among the mature pines because of lack of funding. Fourteen years later, only six young trees were still alive





Ernesto L. Mandujano-Ocampo

Monterey pine occurs in three isolated populations at Año Nuevo, Monterey, and Cambria in California; its single variety is native to the Cedros and Guadalupe Islands of Mexico. The 100 or so remaining pines on Mount August, Guadalupe Island, cannot regenerate because of browsing by feral goats.

on the abandoned nursery site, protected by the fence (Jose Rico, pers. commun., 1994). Goats aside, natural recruitment of seedlings would be infrequent because of the harsh environmental conditions, the rocky volcanic substrate, and the small number of seed trees. *In situ* conservation of Guadalupe Island pine is thus very difficult.

Ex situ conservation has more promise. In this century, at least 10 seed collections of the Guadalupe Island pines have been made, several of which have been established as plantings in California, New Zealand, Australia, and other countries (Rico 1994). Although complete records are not available for plantings established before 1963, it is known that all trees of Guadalupe Island pine planted before that year came from seed collections that sampled only a few trees (Libby et al. 1968).

The first extensive seed collection was made in 1958, when separate cone samples were selected from 50 trees over most of the main population. Six years later an even more comprehensive seed collection took cones from 77 trees, covering all the groves on the island and complementing the 1958 collection. Some of the exceptional trees (best-formed, tallest, and largest-diameter) found on the island were included in the sample (Libby et al. 1968).

At least four plantings were established from the 1964 seeds. In 1965 about 1,100 Guadalupe Island pines were outplanted in randomized experimental designs at the Kaingaroa State Forest in New Zealand. Three other plantings with seedlings from 76 trees were established as progeny tests and seed orchards in California. Plantings from earlier seed collections were summarized by Libby et al. (1968).

Seeds from collections made in 1978, 1985, 1987, and 1992 have been sent to New Zealand, Australia, Chile, and Spain to establish conservation plantations in those countries (Jose Rico, pers. commun., 1994). Other seeds were sown at the nurseries of the Forestry Division of the Universidad Autonoma Chapingo and the Centro de Genética Forestal, A.C. in Mexico, but the germination percentage was low and the resulting seedlings were never outplanted because of limited funding. A few seed samples remain in storage at both Mexican institutions.

Ex situ conservation is not without problems. Seed banks and field gene banks are at least as ephemeral as *in situ* reserves. Of 67 seed source tests with Guadalupe Island pine planted in Australia between 1933 and 1994, seven were destroyed by fire or harvested and several are difficult to relocate because of inadequate records; all of the early collections inadequately sampled the resource (K.G. Eldridge, pers. commun., 1996). Libby (1990) has described the loss of field gene banks in California due to lack of institutional support.

Nevertheless, long-term seed storage and plantations appear to be the best hope for conserving this genetic resource. Many more trees of Guadalupe Island pine now grow on other continents than exist on the island. These living gene banks are being used to increase the genetic base for breeding new generations of Monterey pine plantations by genetic recombination and selection. They could also be used to restore the native Guadalupe Island population if the goats were controlled (Eldridge 1996).

Mainland Torrey Pine

A genetically depauperate population of Torrey pine, vulnerable to environmental challenges, was nearly destroyed by an infestation of ips beetles. But the Torrey Pines State Reserve was able to restore the groves from a seed bank.

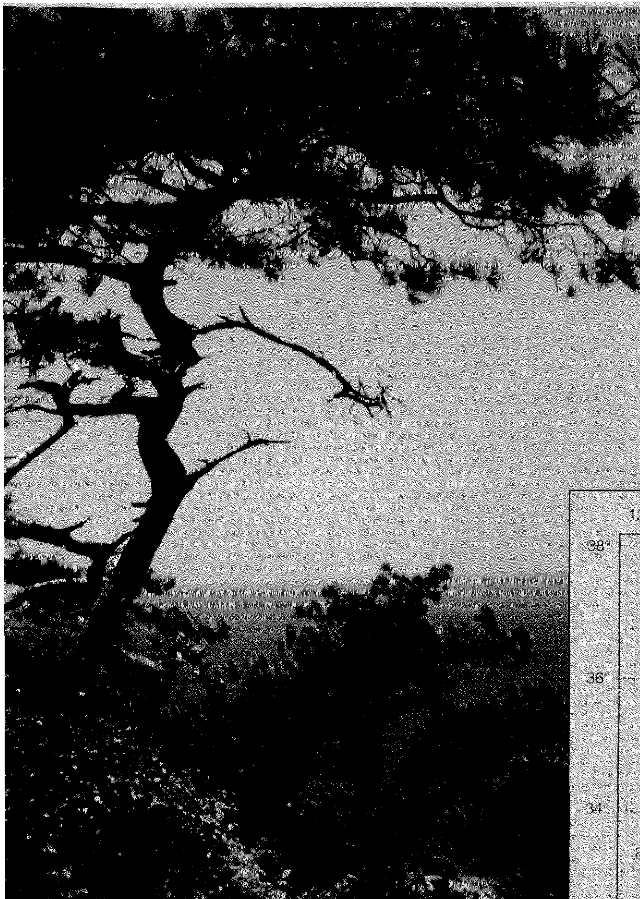
Torrey pine *(Pinus torreyana)*, among the rarest of pines, is valuable for its aesthetic appeal. Growing on sandstone bluffs above the Pacific Ocean at the Torrey Pines State Reserve, California, these picturesque trees attract 1.25 million visitors a year.

The species is found only on the La Jolla–Del Mar area of coastal San Diego County and on Santa Rosa Island in Santa Barbara County. The two populations are separated by 280 km. The mainland trees are protected within the 445-hectare Torrey Pines State Reserve, which has been called a wilderness island in the urban sea of San Diego and its suburbs (California Department of Parks and Recreation 1975). The Santa Rosa Island population is within the Channel Islands National Park.

Taxonomy. Torrey pine is related to Coulter pine *(Pinus coulteri)* and grey pine *(Pinus sabiniana)*. The three form the big-cone pine *sabinianae* subsection of the subgenus *Pinus*. Controlled crosses of Torrey pine with grey pine succeed only with difficulty, however, and no hybrids with Coulter pine have been produced despite several attempts (Critchfield 1966). Furthermore, Torrey pine is allopatric with both Coulter and grey pines, so gene exchange with them is extremely unlikely.

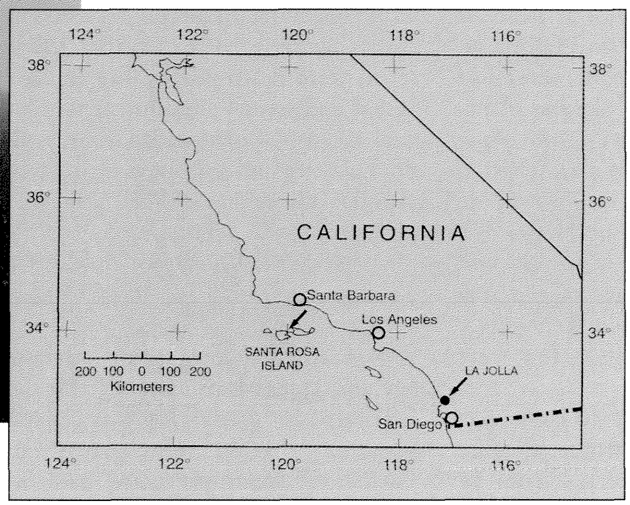
The two populations of Torrey pine differ genetically in a number of characteristics, as established by common garden tests: branch elongation, needle length, cone width-length ratio, and new branches per year (Haller 1986). The difference in elongation shows up as a difference in height and form of the trees as they mature, and needle color of island trees seems to be bluer (F.T. Ledig, pers. observ.). Terpene composition of the oleoresin also differs (Zavarin et al. 1967). Although the morphological and terpene differences are not great, the lack of intermediates and the uniformity within populations led Haller (1986) to name the island population as a subspecies, *Pinus torreyana* subsp. *insularis*.

Demography. Little is known of the prehistoric status of Torrey pine. No fossil record exists, which may suggest that the species has always been rare and restricted. Parry recalled seeing only about 100 individuals at the mainland site when he "discovered" the species in 1850 (Lemmon 1888). Lemmon (1888) enumerated 83 trees north of the San Dieguito River and "not above a few hundred individuals" south of the river, in the heart of the present Torrey Pines State Reserve. Although natural recruitment over the past 20 years appears to be relatively low, especially in the Torrey Pines State



F. Thomas Ledig

The picturesque Torrey pine occurs on the mainland of California at La Jolla, and its insular subspecies is found on Santa Rosa Island. Each population is genetically homogenous and therefore vulnerable to insect or disease attack.



Reserve (McMaster et al. n.d.), both populations are larger now than they were a century ago. Ellen Browning Scripps preserved the mainland site, and planting of Torrey pines under her direction may have helped increase the population: a 1973 census in the reserve counted 3,401 mature trees (California Department of Parks and Recreation 1975), and the total population may have reached 6,000 by 1989.

The Santa Rosa Island population was first reported in 1888 and estimated at 100 trees (Lemmon 1888); the National Park staff now estimates 1,000.

Gene diversity. A survey of genic variation in enzymes of Torrey pine revealed that every tree sampled at the Torrey Pines State Reserve was genetically identical to every other at 59 gene loci, as though a single clone were present (Ledig and Conkle 1983). No other tree species appears to be as uniform, although red pine *(Pinus resinosa)* is nearly so. Every Torrey pine on Santa Rosa Island seemed to be identical to every other one on the island. However, the two populations differed at two of the 59 gene loci (a malic dehydrogenase gene and a shikimate dehydrogenase gene). With certain assumptions, this corresponds to an estimated 8 percent of their genes. Thus, in Torrey pine all the detected variation is *between* populations, which is far from the case for any other tree species. Conserving only one population of Torrey pine would result in the loss of all the known genetic diversity in the species.

Genetic uniformity leaves a species vulnerable to pests and environmental change. If an insect or disease finds one tree attractive and susceptible to attack, it will find all trees equally susceptible. Or if the environment becomes unsuitable for one tree, it will be unsuitable for all. Crop plants illustrate how rapidly genetically uniform populations can crash: the Irish potato famine, for example, was the result of using a single potato clone throughout Ireland (US Committee on Genetic Vulnerability of Major Crops 1972).

Conservation. To preserve Torrey pine, the USDA Forest Service Institute of Forest Genetics collected cones from 149 trees at the Torrey Pines State Reserve in 1986. The total inventory was 29,512 seeds, which were dried and stored in freezers. Cold, dry seeds of many pine species should retain viability for decades (Krugman and Jenkinson 1974), perhaps even a century. The seeds were collected none too soon: five years later the sources—trees at Parry Grove, Guy Fleming Grove, and Razor Point—were gone, killed by bark beetles.

California five-spined ips *(Ips paraconfusus)* had killed an occasional tree in Torrey Pines State Reserve before 1989. In late summer of 1989, however, the staff noted an unusual amount of mortality, a problem undoubtedly exacerbated by the prolonged drought of 1987–93. By early May 1991, more than 840 trees had been killed by ips and another 38 were infested (Shea and Neustein 1995)—more than 25 percent of the mature trees counted in the 1973 census, or at least 14 percent of the estimated 6,000 total. The infestation began near the coastal bluffs and moved inland. The line between the dead and the living was clear. Virtually every tree between the Pacific Ocean and the line of green trees was killed: no trees appeared resistant to the insect. This episode appeared to confirm predictions a decade earlier that genetic uniformity made Torrey pine extremely vulnerable (Ledig and Conkle 1983).

To slow or stop the beetles' advance, P.J. Shea of the Forest Service Pacific Southwest Research Station placed a line of Lindgren funnel traps within the zone of dead trees parallel to the line of green, healthy trees (Shea and Neustein 1995). The aggregation pheromone of the California five-spined ips was placed in each trap. Then antiaggregation pheromones were placed within the boundary of the living, green trees, paralleling the line of funnel traps. The aggregation pheromones pulled the beetles into the dead zone, and the antiaggregation pheromones pushed them away from the green, uninfested trees. During the first nine weeks, 131,000 ips were trapped. Traps were redeployed in 1992 and 1993. The number of ips trapped declined drastically, and no additional mortality or infestation of Torrey pine was seen after August 1992.

With the ips under control, attention turned to restoring the aesthetic value of the Torrey Pines State Reserve and improving the species' chances for survival. The Institute of Forest Genetics drew upon the conservation collection to provide seed and seedlings for planting. The trees killed by the ips were well represented in the seed inventory, and thus the California Department of Parks and Recreation was able to plant the dead groves with the appropriate seeds and seedlings.

Seeds were sown directly in the groves in 1993, protected by screenwire. Germination was very low, however: less than 2 percent. The fault probably lay with the seed storage facilities, which needed upgrading, and not necessarily with any peculiarity of Torrey pine seeds.

In late 1992, seeds were sown in the nursery at the Institute of Forest Genetics and seedlings raised for outplanting. In February 1994, 513 seedlings were delivered to the Torrey Pines State Reserve. Each seedling was planted near a beetle-killed tree and protected from animals with plastic sleeves. Survival was excellent, better than 98 percent, as of May 1994.

In Conclusion

The primary lesson from the case studies is that catastrophes overtake populations of many species. These are the secret extinctions—not immediate loss of species, but loss of genetic resources.

One of the uses of case histories is to draw generalizations. The stories of Upper Ottawa Valley white spruce, Guadalupe Island pine, and mainland Torrey pine have some commonalties: the most important is that they all represent conservation of single, unique populations within species. The US Endangered Species Act of 1973 does not protect unique populations of endangered plants. Mainland Torrey pine might be eligible for listing because it is a named subspecies. As long as any populations of white spruce or Cedros Island pines are extant, however, Ottawa Valley white spruce and Guadalupe Island pine will not be listed. Of course, listing by the US Endangered Species Act carries little weight in other countries, but it is likely that Canadian and Mexican policy would follow the US example. Canada's Endangered Species Protection Act is in Parliament, and at the time of writing we cannot predict the final outcome.

In all three cases, *in situ* conservation threatened to break down or was difficult to accomplish:

- For Upper Ottawa Valley white spruce, *in situ* conservation was not a likely option because most of its habitat has been converted to agriculture and urban development, and the remaining stands occur only on private land, so they are likely to suffer the same fate.
- *In situ* conservation would seem theoretically possible for Guadalupe Island pine because the island is under government control and the pines retain a fair amount of genetic diversity. However, economic interests in the feral goats make control and *in situ* conservation highly unlikely.
- *In situ* conservation for mainland Torrey pine seemed assured when the state of California established the Torrey Pines State Reserve at La Jolla in 1959. Because Torrey pine lacks genetic variation, however, it proved especially vulnerable to pests and other stresses.

Differences among the case histories also are worth noting. Perhaps most important, the conservation objectives differed. Ottawa Valley white spruce was conserved largely because of its breeding potential. Mainland Torrey pine was conserved largely for research and for restoration. The case history of Guadalupe Island pine illustrates the potential for both uses—breeding and restoration. The field gene banks for Guadalupe Island pines were set up because of the species' breeding value but could be used to provide seed or rooted clones for restoration of Guadalupe Island if the goats were eliminated.

Although *ex situ* conservation figured prominently in all three cases, the type of material conserved differed:

- Ottawa Valley white spruces were preserved in a clone bank by vegetative propagation, which maintained the native gene combinations exactly as they stood in the forest. It was preserved near its origin in a climate to which it was, in all likelihood, adapted.
- Guadalupe Island pine was preserved as seedling offspring produced through sexual reproduction, which recombines genes and results in a variable progeny, many of which might normally be culled by natural selection. In nursery and plantation culture, however, most survive, changing the genetic base. Furthermore, selection in the exotic settings of Australia and California will likely modify the genetic resource (e.g., see Wilcox and Miller 1975 on the evolution of land-

The Reasons for *Ex Situ* Conservation

The major losses of forest genetic resources are the loss of unique populations, not the extinction of species per se. Pressures on natural habitat make it likely that in many species, active management will be needed to conserve genetic resources. The ideal approach to conservation uses multiple tactics, integrating native reserves and off-site, or *ex situ*, conservation methods. *Ex situ* conservation in seed banks, clone banks, and plantations functions as an insurance policy against the loss of natural populations. Such collections can be a resource for breeders and for ecological restorers; if native populations are lost, *ex situ* collections are indispensable sources of genes for breeding and of seeds or cuttings for restoring habitat. National and international efforts are needed to develop systematic core collections of forest genetic resources.

races in New Zealand).

• Mainland Torrey pine was preserved as seeds in cold storage.

All three cases illustrate the frustration of inadequate conservation efforts. *Ex situ* collections, like *in situ* reserves, are ephemeral and vulnerable to loss. Lack of a modern seed bank operation caused the Torrey pine collections to deteriorate after only a few years, when pine seeds should be capable of storage for at least half a century. Some of the plantations of Guadalupe Island pine were abandoned because of inadequate institutional commitment (Libby 1990). Likewise, the government-backed program for Upper Ottawa Valley white spruce failed to carry out all its objectives because of reduced funding. Even in more richly funded agricultural programs, such as the US National Plant Germplasm System, lack of adequate maintenance and technological failure are expected to result in loss of half the germplasm (Christensen 1987). Libby (1990) therefore argued that endowment funding was necessary for long-term conservation.

Any conservation program should include both natural habitat and *ex situ* populations. The case studies presented here illustrate the threats faced by natural populations and demonstrate the utility of seed banks and field gene banks as insurance against the loss of genetic diversity. Effective programs for *ex situ* conservation must provide for replacement, or renewal, of the seed banks or field gene banks.

Huge seed banks like those maintained for agricultural crop plants are not required, however. In many cases, forest geneticists can choose representative and unique samples for a core collection. Core collections are collections that represent as much genetic diversity as possible while limiting the number of samples (Brown 1989). In forest trees, the geographic patterns of variation are largely clinal, with gradual, continuous changes along environmental gradients. It is therefore relatively simple to choose representative samples. When genetic variation is not continuous, it is usually associated with gaps in the range or with other easily recognizable features, such as the interface between soil types. In some cases, mostly noncommercial species, forest geneticists may have to begin afresh to evaluate patterns of variation before choosing seed or clones for conservation banks. Molecular markers can rapidly evaluate differences among stands and guide the choice of what to conserve.

An international group of foresters and geneticists reached several consensus recommendations at a workshop on temperate North American forest genetic resources held in Berkeley, California, June 12–14, 1995 (Rogers and Ledig 1996). Their first recommendation urged "the development of national programs to address issues in the conservation of forest genetic resources." The second advised that "conservation of forest genetic resources be addressed by multiple approaches." We could not agree more.

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