In situ genetic conservation of Monterey pine (*Pinus radiata* D. Don): Information and recommendations

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Cover photograph: Monterey pine in the Del Monte Forest, Monterey Peninsula, California.
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Foreword

Monterey pine occupies a special niche in California. It is valued in its native forests for the scenic character it gives those environments. It is less well recognized for the ecosystem services it provides in those forest ecosystems. As an agroforestry crop in California, it is found in the Christmas tree trade and used in landscaping. Dwarfing this relatively small commercial value in California, however, is the value of Monterey pine as a plantation tree elsewhere in the world, especially in the southern hemisphere. Because most of the native Monterey pine forests are found in California, this means that, for better or worse, these California forests are the primary remaining reservoir for the native genetic diversity of the species upon which the long-term success of the commercial plantation enterprises may ultimately depend.

This situation is in striking contrast with the status of most California plant commodities and the sources of their genetic diversity. Of California's approximately 300 commercial plant commodities, only a very few derive from the native flora of the State or even from the rest of the nation's flora. California is gene-resource poor for the commodities that make it the number one state in agricultural production in the USA. Thus, Monterey pine is exceptional in that the genetic resources to sustain this species as a global commodity exist only in California and on two Mexican islands off the west coast of the Baja California peninsula.

Is California doing a good job with its stewardship of its native Monterey pine genetic resources? Unfortunately, the answer is negative because there are many factors which make California's stewardship very challenging. The entities that own and manage native Monterey pine forests are diverse—state, county, regional, and city governments; land trusts; universities; nonprofit organizations; companies; and private owners. This diversity complicates planning and management processes and has contributed to controversies concerning the status of the species.

To date there is no unified plan or process to sustain the conservation of Monterey pine in California. This report is a substantial contribution in support of Monterey pine stewardship which can lead to a plan for action. Included are details about the issues of Monterey pine forest and species management, biological aspects of growth and reproduction, and descriptions of the genetic and social issues which make the long-term survival of this species vulnerable. The recommendations pertinent for the *in situ* conservation of this species comprise a framework for action by the several institutions, organizations, and commercial and private interests that have a role in managing and conserving Monterey pine in California. At the forefront of the report are the genetic issues that provide the rationale for conserving the native genetic diversity and underlie the offered recommendations. It is critical that scientific considerations and evidence drive the debate and guide the actions impacting the forests at every level, whether under private or public ownership.

This document is an example of the UC Genetic Resources Conservation Program's efforts to fulfill its mission of facilitating the conservation of genetic resources of California commodities and native species. Many persons have participated and were consulted during the preparation of the report and participated in its review. We sincerely hope that the appropriate agencies, organizations, companies, and individuals will advance the cause of science-based conservation of Monterey pine, one of California's important and interesting species.

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Preface

Monterey pine (*Pinus radiata* D. Don) is native to a narrow range and currently restricted to three populations along the central coast of California and one on each of two Mexican islands off Baja California. Seed collections from mainly two of these populations have formed the basis of breeding programs in Australia, Chile, New Zealand, Spain, South Africa, and other countries. The domesticated and commercially improved progeny from these programs are now of significant economic value, growing in plantations worldwide on over 4 million ha. In California, Monterey pine has commercial value as a Christmas tree and horticultural species. However, its greater value in California is best measured with other currencies—adding æsthetic value to coastal landscapes, defining a forest ecosystem with a diverse array of understory species, and harboring a gene pool that constitutes the species' evolutionary potential and traits possibly of future economic interest.

With the majority of its extant natural range in an increasingly populated and urbanized area, Monterey pine has lost considerable habitat and its genetic integrity may be compromised. Figures describing its loss of habitat vary, but most estimates converge on 50%. This loss, together with habitat fragmentation, continues with new housing and recreational developments. The majority of stands in the California populations occur on private property. Other concerns include genetic contamination from widely planted nonlocal Monterey pine throughout the natural California range of the species. Pitch canker disease, caused by the introduced fungus *Fusarium circinatum*, has been causing heavy mortality of Monterey pine in California within the last decade. Fire suppression throughout the California range of the species has likely affected natural regeneration and contributed to shifts towards oak-dominated forests in some areas. These threats to genetic diversity and integrity are cumulative, and exacerbated by the additional selective pressures of climate change. The Guadalupe Island population is on a trajectory towards extinction, suffering from lack of regeneration due to grazing by introduced goats. The second island population—on Cedros Island—may have fewer threats, but comprehensive genetic information on this population is not available. It is within this context of both domestic and international values, and serious concerns for the long-term viability of the species in its native habitat, that this report is undertaken.

Genetic diversity underlies all biological diversity. It allows local populations of a species to adapt to a variety of niches. It provides evolutionary flexibility for the species to adjust in the long term in response to changing climates and other conditions. Thus, both spatially and temporally, genetic diversity provides a species with the potential to adjust to environmental changes.

The overall objective of *in situ* genetic conservation for Monterey pine is to provide the best opportunity, given current information and understanding of the species' biology, to maintain adaptive potential and patterns and levels of genetic diversity that are within the historical range for the species. Genetic conservation plans must be firmly based on the available scientific information if they are to be the basis of effective policies and practices.

Given the diverse ownership of Monterey pine forests, the array of influences and their relative significances across the five populations, and the dearth of basic planning tools such as accurate current descriptions of the remaining forests, this report is meant to provide support for *in situ* genetic conservation. This report summarizes the available science—primarily evolutionary, genetic, and ecological information—that relates to genetic conservation of Monterey pine; presents available information about the native populations, their genetic threats, and their *ex situ* reserves; and provides specific conservation principles and recommendations towards genetic conservation of the species.

The primary audience for whom this report has been prepared includes forest owners, managers, and educators: those in a position to directly practice or influence *in situ* genetic conservation. In a broader sense, it can provide support to those who value, manage, study, or administer the native forests of Monterey pine. It is also potentially of use to scientists, administrators, policy-makers, and regulators.

Acknowledgements

This report reflects the generous contributions and stellar expertise of many individuals. The commitment, interest, and resources of many agencies and organizations have been offered, through the involvement of reviewers, in presenting this information in the most comprehensive and transparent form possible. I am very grateful for the dedicated interest of several individuals, in particular, who offered their scholarly insights and wealth of experience in review of the entire report. Kenneth G. Eldridge reviewed the report in its entirety at several stages, providing much additional information and thoughtful, provocative challenges to its subjective elements. Rowland D. Burdon reviewed and commented on the entire report, providing the depth of insight and scope of knowledge that derives from career-long study of Monterey pine. Michael G. Barbour directed his wealth of experience with California flora towards a thoughtful review of the report, adding a broader ecological perspective and encouraging more clarity. F. Thomas Ledig provided a scholarly review of a substantial portion of the report, improving the focus and tightening the genetic description of Monterey pine, in particular.

The report was also reviewed and improved, in part or in its entirety, by Sonia Martin Albertos, William S. Dvorak, Karen K. Ferlito, Susan J. Frankel, Edward O. Guerrant, Jr., Susan P. Harrison, Richard H. Hawley, Kimberly A. Hayes, Deborah S. Hillyard, William J. Libby, Laurie A. Lippitt, Mary Ann Matthews, Patrick E. McGuire, Constance I. Millar, Nicole E. Nedeff, Regena M. Orr, Donald R. Owen, Calvin O. Qualset, Linda L. Smith, Jesús Vargas-Hernández, Detlev R. Vogler, and B. Diane West-Bourke.

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Participants in an April 25–26, 2000 workshop near Big Sur, California, contributed to the development of the genetic conservation recommendations. Some of the recommendations reflect outcomes from discussions among the 25 participants (Appendix A). However, many recommendations were refined or developed after the workshop, and none are necessarily consensus statements. Participants in an October 10, 2001 workshop at Pebble Beach, California, contributed to the development of a list of invasive, exotic plant species in native Monterey pine forests in California.

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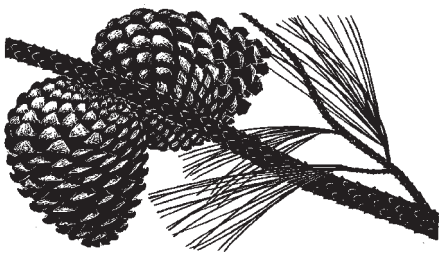
The illustration of Monterey pine needles and cones that graces the first page of each chapter is by Paul Landacre from *A Natural History of Western Trees* by Donald Culross Peattie, copyright 1953, renewed 1981 by Paul Landacre. It is reprinted here by permission of the publisher Houghton Mifflin Company; all rights reserved.



Executive summary

Monterey pine (*Pinus radiata* D. Don) is a species with a very small native range and immense international commercial importance. The extant native forests of Monterey pine currently occupy three disjunct locations on the central coast of California and on two Mexican islands—Guadalupe and Cedros—off Baja California. Internationally, and primarily in the southern hemisphere, Monterey pine grows in plantations that cover over 4 million ha; contributes significantly to the wood supply and GDP of New Zealand, Chile, and Australia, in particular; and, therefore, supports the conservation of native forest tree species in those countries because of its high productivity. In contrast to the broad range and extent of exotic plantations of Monterey pine worldwide, its natural range is restricted and has been reduced considerably by human activity. In California, the native Monterey pine forests have little commercial value, but add æsthetic value to coastal communities and provide source material for landscaping and Christmas tree businesses. Internationally, the native California and Mexican forests of Monterey pine are valued as the original source of seeds for their plantation enterprises, and as an important continuing reservoir of genetic diversity for the improvement of the plantation crop.

The ownership and management of native Monterey pine forests is diverse—including state, county, and city governments; landtrusts, universities, and other nongovernmental organizations; and private owners. This diversity of ownership complicates planning and management processes and has contributed to controversies concerning the status of the species. No species-wide plan or coordination for *in situ* conservation currently exists. Genetic diversity is critical to the long-term survival of Monterey pine in its native habitat. The overall objective of *in situ* genetic conservation of Monterey pine is to provide the best opportunity, given current information and understanding of the species' biology, to maintain the species' adaptive potential and the patterns and levels of genetic diversity that are within the normal range for the species. This report has been prepared to document current knowledge of the genetic structure and diversity of the species, describe its genetic status in relation to current and historical influences, and provide recommendations for genetic conservation. Emphasis is on native populations and *in situ* conservation, although some of the *ex situ* reserves and their essential role in conserving genetic resources also are described. It is expected that this report will assist those in the regulatory, management, education, advocacy, and research communities to make decisions that are better informed by science and more likely to contribute to genetic conservation of this species.

Monterey pine's evolutionary history suggests a dynamic relationship with climate. Historically, the species occupied a wider geographic range than today. The range, size, and continuity of Monterey pine populations have fluctuated over the last several million years apparently in response to climate changes. Genetic diversity within the species is modest compared to other western North American conifers, but high relative to other California closed-cone pines. The five native populations are rather strongly genetically differentiated. The within-population genetic structure is less well known.

Given the genetic differentiation among populations and the different ecological and sociopolitical context for each, *in situ* genetic conservation for Monterey pine is most effectively approached at the population level. Currently, there are no *in situ* genetic reserves for Monterey pine. Forest areas that currently have some protection have not been selected with genetic criteria in mind and are not necessarily being managed to conserve genetic diversity. To have genetic reserves—perhaps including some lands adjacent to existing forests where possible—is particularly critical for the species because of the historically dynamic relationship between Monterey pine and climate. With climate change and other

influences, Monterey pine populations are being severely challenged while having their historic suite of responses—including migration by dispersal—reduced.

Estimates of current and historical areas of native Monterey pine forest vary, but losses in habitat are probably 50% or greater. Habitat has been lost because of intentional conversion to residential, recreational, and other land uses. All populations, the island populations in particular, have been influenced by invasive exotic animal, plant, and fungal species. The Guadalupe Island population has only about 200 trees remaining and no recruitment from regeneration because of grazing by introduced goats. Exotic invasive plant species are pervasive and negatively affecting natural regeneration in the coastal California populations. The mainland California populations are also negatively impacted by other influences. An introduced fungal disease (pitch canker), caused by *Fusarium circinatum*, has caused significant mortality. In addition to other types of forest loss, some pine-dominated areas may be shifting toward oak dominance due, in part, to fire-suppression policies. Forests have been fragmented with transportation corridors and residential developments, with probable although unstudied impacts on genetic diversity. Monterey pines are undoubtedly influenced by genetic contamination from planted nonlocal trees. The mainland populations, particularly the southern two, are highly constrained in range by the ocean to the west and by urbanization or alternative land uses in other directions.

A series of recommendations has been provided to contribute towards *in situ* genetic conservation of Monterey pine (see below). These 18 recommendations are organized into four categories: planning, *in situ* management, outreach needs, and research. Some of the threats to the genetic diversity and integrity of Monterey pine populations are severe, transparent, and can be addressed directly. Examples include the removal of goats on Guadalupe Island and control of exotic invasive plant species in the California mainland populations. Other threats are multifaceted and require long-term planning and coordination. Included in this category are the establishment of *in situ* genetic reserves, protection of existing populations from further fragmentation, and conservation of areas adjacent to some populations that could become future habitat for Monterey pine. Finally, some threats are probable but not clearly defined, and require more research. For example, the extent and significance of genetic contamination in the mainland populations requires study, as does the fire ecology of the species.

With more attention, financial support, and the development of appropriate policies, there is still much potential to conserve the genetic diversity of the native populations of Monterey pine. In addition, the international interest in the native gene pools of Monterey pine can continue to play a valuable role in genetic research and conservation of the native populations.

Recommendations for *in situ* genetic conservation of Monterey pine

1. Biologically significant losses of genetic diversity within the species overall and within each of the five native populations of Monterey pine should be avoided.

2. Native Monterey pine populations should not be allowed to become further domesticated, meaning uncoupled from natural processes and thus requiring constant input and management to ensure standard biological functions such as growth and reproduction.

3. *In situ* genetic reserves should be designated for each of the five native populations, guided by within-population genetic structure. They are critical to genetic conservation and research objectives. A management plan to guide the protection of genetic values and a framework for genetic monitoring should also be established for these reserves.

4. 'Outliers' (trees at edges of populations) should be conserved because some may contain genetic diversity important for adaptation to new environmental conditions and may represent opportunities to expand the natural range or allow the populations some movement.

5. The establishment of *in situ* genetic reserves should be guided by theory such as desirable effective population size. However, given that theory might suggest reserves larger than areas available, efforts should be made to extend the boundaries of genetic reserves through appropriate genetic management of surrounding urban or recreation areas.

6. Additional seed collections should be undertaken in the five native populations using genetic sampling criteria.

7. Protocols for any extant *ex situ* genetic reserves should:

   i. Determine the maintenance strategy for that collection, including risk management by subdividing the collection among several locations;

   ii. Recommend and preferably secure a long-term or perpetual sponsor or steward for the collection(s);

   iii. Establish priorities for the most appropriate uses of the collection (i.e., decision-making criteria for seed distribution for uses such as research, commerce, restoration, or mitigation); and

   iv. Recommend a pricing structure for returning support to the collections based on their use.

In addition to these considerations, plans for any future genetic collections should include an assessment of the effect of the collection on the genetic diversity of the natural population (e.g., risk assessment).

8. Management history, for the mainland populations in particular, should be well documented to allow appropriate site choices and data interpretations for scientific research and for support in forest management.

9. Further fragmentation of remaining Monterey pine forests should be avoided.

10. The genetic and associated demographic risks from planted Monterey pines (e.g., roadside plantings, landscape trees, residential trees, and Christmas trees) within the current reproductive range of native Monterey pine populations should be evaluated. This evaluation should

include an examination of geographic scope, timeframe over which trees have been planted, and genetic source of material.

11. For any planting of Monterey pine within an area where mixing with the native gene pool is possible, the planting stock should be locally adapted and contribute to maintenance of natural genetic diversity of the native pine forests. Seeds should be preferred to seedlings. Clonal material should not be used except in limited scope in situations where this is the only feasible or well-reasoned alternative. For large planting projects, the source for propagules should be chosen so as to create a large effective population size.

12. Any breeding and delivery program aimed at providing disease-resistant trees for use within the genetic sphere of influence for native Monterey pine populations should be well informed about the genetic basis of resistance for that disease, the inheritance of the desired trait, its interaction with the environment, and the overall impact of artificially selected genotypes on the genetic diversity and population viability of Monterey pine and should not unnecessarily screen out potentially valuable genetic diversity.

13. The nature and extent of exotic invasive plants in the range of Monterey pine forests should be determined and an effective approach devised towards the control or elimination of those exotic species considered harmful.

14. The international concern and interest for the Guadalupe Island and Cedros Island populations of Monterey pine should be used by Mexican authorities and scientists to provide support for conservation policies and practices.

15. The Guadalupe Island population of Monterey pine requires immediate attention including removal or control of the goats, an assessment of the impacts of the introduced flora and development of a plan to manage these effects, and a genetic assessment of the remaining pines to determine if direct restoration activities are required.

16. An educational forum on Monterey pine should be organized that provides ongoing opportunities for exchange of ideas, presentation of scientific information, and discussion of applications among managers, scientists, and conservationists.

17. Public outreach, particularly on the importance of maintaining local adaptations in native Monterey pine forests, is critical to enabling an appropriate suite of options for genetic conservation of Monterey pine and should be aggressively pursued.

18. Research, surveys, or reviews that should be undertaken for Monterey pine are:

- A comprehensive vegetation survey of native Monterey pine forests, including associated plant species and extending to the geographic limits of the species.
- Mycorrhizal studies that will illuminate the relationship between forest ecosystem health and mycorrhizal dynamics, and the specificity of this relationship—if any—among the five populations.
- Soil/vegetation/ecological surveys for all populations, acknowledging that much of this has been done for the ecological staircase area of the Monterey population.
- Examination of relationship between microclimate or 'distance from ocean' effect and genetic diversity within the Monterey population.
- Determination of whether the 'outliers' near the Año Nuevo population are planted or naturally occurring.
- Investigation of genetic differences between the main Cambria population and the Pico Creek stand.
- Investigation of phenological differences within and between Monterey pine populations *in situ*.
- Determination of the effects on genetic diversity and structure from various enhanced or artificial regeneration techniques (e.g., mechanical creation of gaps).
- Investigation of the viability of seeds *in situ* over their temporal and spatial range, including persistence and viability in the 'canopy seedbank' over time and the effects on seed viability of site conditions and microclimate.
- Determination of optimum species-specific seed storage conditions that maintain viability and genetic integrity for long-term conservation.
- Research on the amount of genetic diversity in the Guadalupe Island population, losses of genetic diversity since goat introduction, and current level of inbreeding.
- Research on the relationship between fire and function of the Monterey pine forest ecosystem, including the effects of fire on nutrient cycling, litter removal, soil sterilization, seed release and germination, seedling recruitment, age structure, and genetic composition.
- Identification of an array of private or semi-private DNA marker alleles for the three mainland populations to enable identification and quantification of genetic contamination.
- Research on population dynamics including the role of adaptation in genetic structure, the genetic interactions of extant populations, and dispersal rates and efficacy.

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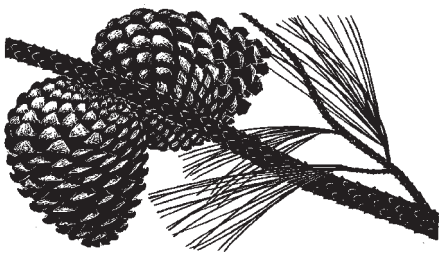


Introduction

At a 1998 workshop in Canberra, Australia to focus on *ex situ* conservation of Monterey pine (*Pinus radiata* D. Don), participants raised the question of whether the appropriate authorities in the USA would consider the *in situ* conservation of Monterey pine a responsibility (Spencer et al. 1998). Californians are the custodians of the genetic resources of a major world crop plant (K.G. Eldridge, pers. comm.). This responsibility—to protect the genetic resources upon which the wealth of other nations may depend—has been acknowledged previously (e.g., Ledig 1988), but not planned or supported adequately.

Monterey pine, native only to five small areas in California and Baja California (Figure 1), is nevertheless of great value to the international community. Internationally, it is more commonly known as radiata pine, but will be referred to as Monterey pine in this report given the focus on native populations and *in situ* conservation. Domesticated populations, varieties, and clones of this species are grown in plantations amounting to over 4 million ha worldwide. Over recent decades, domestication processes have been applied to this species in various programs worldwide to shape a more desirable tree type. These processes are similar to those used historically with food crops, and can be framed as having four elements: the original genetic variability, selection of the desired trees or genes, packaging of those genes in trees to be used, and benefit capture—converting those gene packages into growing trees that are harvested as a renewable resource (Libby 1973). Monterey pine's success as a plantation species is largely attributable to its capacity to respond to both genetic improvement and management. The planted-forest technology for Monterey pine is probably the most advanced of any tree species (Sutton 1999). The tremendous commercial value of this species is illustrated by its status in Chile, New Zealand, and Australia, in particular. In Australia, for example, Monterey pine plantations account for 75% of the total pine plantations currently established. Current value of the sawn timber produced from the total pine plantations is over $1 billion AUD per year. Furthermore, research investments have paid off handsomely, with first-generation breeding efforts for Monterey pine recently evaluated as representing a benefit/cost ratio of approximately 15 (CSIRO 1999). In New Zealand, this benefit/cost ratio has been reported to be much higher (R.D. Burdon, pers. comm.). This return on genetic research investment emphasizes the extent of genetic diversity that was inherent in the species and its value.

Indirect conservation value can be achieved through domestication of some species. For example, highly productive and concentrated forest plantations can make it possible to allocate native forests to parks and reserves, and at the same time generate positive environmental effects as plantations replace degraded marginal agricultural lands (e.g., Gladstone and Ledig 1990; Sedjo 1999). A case in point is New Zealand where forest plantations now provide 98% of that country's annual wood harvest, more than 90% of which is Monterey pine. Over half of this harvest is exported. A century ago, almost all of the wood used in New Zealand came from native forests (Sutton 1999). This shift towards plantation production has allowed New Zealand to protect most of the remaining native forests (Sutton 1995). The high productivity of Monterey pine plantations provides conservation leverage (Libby 1995).

Monterey pine is valued in California mainly for its æsthetic value and ecological roles within the restricted ecosystems that it dominates. These values, however, are frequently dwarfed by the value of this habitat for other land uses. Consequently, a considerable fraction of the Monterey pine forest has been lost to development. And valuing the ambience of the Monterey pine forest often works to the detriment of the underlying ecosystem. As more homes and recreational structures and corridors are built in the forest,

Figure 1. Locations of current natural populations of Monterey pine: Año Nuevo, Monterey, and Cambria in California and Guadalupe Island and Cedros Island in Mexico. (Figure modified from Ledig et al. 1998, p. 36 with permission of the publisher, Society of American Foresters, 5400 Grosvenor Lane, Bethesda MD 20814-2198.)

the landscape is further fragmented and natural ecosystem processes are interrupted.

Its æsthetic value in horticultural use may also have worked to the detriment of the species—both in ecosystem health and public sentiment. Symmetrical when young, dramatic when mature, often with vigorous, dense, deep green foliage, this species has much horticultural potential. However, it has been overplanted and inappropriately matched to site in many cases, undermining its reputation and underrepresenting its potential value (Sigg 1987).

Pitch canker, an introduced disease caused by the fungus *Fusarium circinatum*, which was first noted in Monterey pines in California in 1986, has spread to 18 counties throughout coastal and near-coastal California and may potentially cause high mortality in native Monterey pine populations (Owen and Adams 1999). This disease has heightened interest in conserving remaining native gene pools as they are the context within which disease-resistant trees may emerge for regenerating the native areas. Concern was sufficient to produce California State Senate Bill 1712 for disease mitigation. Disease-influenced mortality—together with habitat losses from urban development; possible genetic contamination from planted, nonlocal trees; habitat fragmentation; changes in natural disturbance regimes and age structure; and other pressures—prompted the organization of a 1996 conference entitled 'Monterey pine forest: A forest at risk' (Smith and Ferlito 1997). Continuing and mounting conservation concerns prompted the 1999 submission of a petition by the California Native Plant Society to list the species as threatened under the California Endangered Species Act (CNPS 1999).

Role of genetic diversity

Maintaining the natural levels and structure of Monterey pine's genetic diversity is important because of the potential consequences for both the species and its associated ecosystems. At the population level, genetic diversity may provide opportunities for adaptation to local conditions. This is increasingly important in situations where environmental conditions manifest considerable change over time and where there is little potential for direct migration. The adaptational system may be thought of as having two types of environmental conditions: those conditions that cause modifications of the individual (e.g., leaf shedding) and those that cause selection and hence adaptation. Given the limited ability to control these environments and the lack of understanding about their interconnections, maintenance of genetic diversity and evolutionary flexibility are very important. For example, detrimental effects of human activities on the stability of forest ecosystems could be due to the disruption of existing natural connections between these two (modifying and adaptive) environments (Gregorius and Kleinschmit 1999).

At the ecosystem level, disturbances to genetic diversity or structure of a population can have cascading effects throughout the system. Any genetic changes that alter a given species' ecological properties are likely to be felt and magnified in the community, as much as if the species were removed or a new species were added (Endler et al. 2000).

Need for *in situ* genetic conservation

An international workshop on conservation of forest genetic resources of the North American temperate zone was held in Berkeley, California in 1995. At least three of the workshop's 12 consensus recommendations are directly related to this endeavor (Rogers and Ledig 1996). Workshop participants recommended:

1. The development of national programs to address issues in the conservation of forest genetic resources.
2. That conservation of forest genetic resources should be addressed by multiple approaches and that, whenever possible, they should include ecosystem reserves.
3. Recognizing that many North American temperate forest tree species are important plantation species on this and other continents, and that it may be necessary to draw upon these forest genetic resources in the future, Canada, Mexico, and the United States should conserve these resources *in situ*.

In situ genetic conservation activities for Monterey pine are called for because genetic integrity is at risk, genetic information in its entirety is not being considered by other present actions and planning efforts, genetic values affect

and are affected by current and possible management activities, and only a dedicated focus on genetic conservation will provide an effective and comprehensive framework for considering genetic information in relation to the broader ecology of the species and related conservation options. In 1981, the Guadalupe Island population of Monterey pine was declared 'endangered' by the FAO Panel of Experts on Forest Gene Resources due largely to grazing pressure from introduced goats (FAO 1986). Concurrently, the panel found the genetic integrity of the Monterey and Cambria populations endangered due to the highly urbanized environment in which much of the remaining forest occurs and the genetic contamination from planted trees. A report by this expert committee in 1993 again identified Monterey pine as a species with high global, regional, and national priority for genetic conservation (FAO 1994). The species is on the World List of Threatened Trees and the five populations have been classified according to the International Union of Conservation of Nature and Natural Resources' (IUCN) Red List Categories. In the IUCN system, the Guadalupe and Cedros Island populations are listed as endangered and the three mainland populations as conservation-dependent (i.e., in which the cessation of conservation activities would result in the populations qualifying for one of the IUCN threatened categories within a period of five years) (Hilton-Taylor 2000).

The IUCN categories of threat are widely used and have become an important tool in conservation activities at international levels and at national and lower scales. However, their utility and comparability could be improved with more objectivity in the assignment of threat categories. One reassessment of this system suggests, for example, that an assignment of *vulnerable* status might be appropriate for species estimated to have at least a 10% probability of extinction within 100 years (Mace and Lande 1991).

There is theoretical as well as empirical evidence that genetic conservation attention is necessary for Monterey pine. Generally, the species that need special attention (and hence, here, a species-based plan) are those with the largest area requirements, specialized habitat needs, functional importance in the community, or greatest sensitivity to human activities (Noss et al. 1997). This concept encompasses both areas that are naturally fragile because of large, natural and internal successional changes and those that change as a result of external disturbances (Nilsson and Grelsson 1995). Sensitivity to climate change and the loss of natural fire regimes may be particular areas of vulnerability for Monterey pine.

In fact, the genetic integrity and long-term viability of native Monterey pine populations were at sufficient risk even in the early 1980s to inspire the drafting of a conservation proposal that focused on their *in situ* and *ex situ* genetic resources (Kafton 1985). That proposal highlighted such issues as genetic contamination in the native stands and poor storage conditions and lack of funding for the seed collections that resided within the State. It is apparent that the proposal was not implemented.

Report attributes

My procedure in compiling relevant information and developing recommendations for genetic conservation for this species:

- was based on scientific information;
- included all five populations although my emphasis was on the USA mainland populations;
- employed expert opinion in the absence of complete information;
- considered both *in situ* and *ex situ* genetic resources, with an emphasis on *in situ* conservation; and
- was embedded within the broader goal of conservation of ecosystem function and processes.

This report is an information document, not an implementation instrument. It therefore lacks authority for direct implementation but serves to inform management decisions. The information provided should be considered within the context of broader values, economic considerations, and public will. The advice of Noss et al. (1997)—that conservation plans should be "biologically conservative, scientifically defensible, politically realistic, and able to provide a high probability of meeting widely accepted conservation goals"—is well applied here.

Genetic conservation efforts are ideally conducted in a proactive manner, before the genetic resource is so depleted as to leave few options for recovery and before it has lost significant current and potential adaptations. It is difficult to sense the urgency of such action, however, because the loss of locally adapted gene complexes is cryptic, hence called 'secret extinctions' (Ledig 1991). In some cases, the loss of genetic diversity may be apparent—as may happen if there are rapid and extreme losses in the number of trees (e.g., on Guadalupe Island). In other cases, the genetic resource may be severely degraded without an immediate loss in census number. For example, mahogany *(Swietenia mahogani*) has been so seriously exploited in the Caribbean that it is no longer found in its tree form (Ledig 1991), but has been reduced to a multi-stemmed shrub (Styles 1972). The alleles specifying the tree form in this species have certainly been reduced in frequency and may have been lost, even though the species itself is still widespread (Ledig 1991).

This report is rather unusual—in the domain of conservation plans—in its focus on genetic attributes and processes, its inclusion of the entire range of a species, its consideration of both *in situ* and *ex situ* genetic resources, and its proactive nature (i.e., as compared with a species recovery plan). No perfect models for such a report are known. Perhaps the most germane is the conservation plan for black poplar (*Populus nigra*) (Heinz et al. 2001), a dicœcious European forest tree species with riparian habitat. Black poplar is not endangered in the sense of few remaining individuals. Rather, concern is based on the facts that the number of poplar populations is decreasing, that remaining populations are more and more fragmented, that natural regeneration has been impacted by floodplain alteration and regulation,

and that there is a potential threat of introgression from cultivated poplar clones that have been planted extensively across continental Europe (de Vries and Turok 2001; Heinze and Lefèvre 2001).

Although there are yet more complex challenges in crossing the political border to include the two Mexican populations, this inclusion is considered essential to assess appropriately the genetic resources and the most effective conservation activities. These island populations have some genetic attributes that not only deserve conservation in their own right, but may have broader significance. For example, the Guadalupe Island Monterey pines have shown some resistance to red band needle blight (caused by *Scirrhia pini*) and western gall rust (caused by *Endocronartium harknessii*)—diseases that could be of great concern to countries where Monterey pine is grown as a commercial plantation species (Cobb and Libby 1968; Old et al. 1986; Ledig 1991). Trees from both island populations have shown significantly greater resistance to wind-induced toppling than those from the mainland populations (Burdon et al. 1992a). More generally, Mexico is a major center of diversity for the genus *Pinus*, and home to almost half of all pine species known worldwide (Styles 1993).

Objectives

Effective conservation strategies demand clear definition of objectives, adequate knowledge, and appropriate conservation methods (Eriksson et al. 1993). The overall objective of *in situ* genetic conservation of Monterey pine is *to provide the best opportunity, given current information and understanding of the species biology, to maintain adaptive potential and patterns and levels of genetic diversity that are within the normal range for the species*. Under ideal conditions and for a species with numerous populations, the normal sequence of activities in genetic conservation of forest tree species is as follows (Graudal et al. 1997):

1. Assessment of genetic variation (i.e., amount and pattern) within the species;
2. Assessment of the conservation status of the species;
3. Identification of populations to be conserved; and
4. Identification of possible conservation measures.

Due to time constraints imposed by a sense of urgency and because there are only five populations to consider, these sequential steps can be somewhat condensed for Monterey pine. No new research was performed specifically for this report during its preparation. Specific objectives of this report—containing both relevant information and recommendations for *in situ* genetic conservation entire planning—were to:

- Determine the status of the genetic resources of Monterey pine;
- Identify key genetic issues;
- Recommend actions related to genetic conservation for various management contexts, including management of the species in parks, reserves, and at the interface with development or situations in which there may be genetic impacts such as roadside or median strip planting;
- Identify needs associated with increasing public appreciation for long-term genetic conservation;
- Determine and discuss theoretical and empirical issues related to establishing *in situ* genetic reserves to conserve adaptive potential, appropriate levels of genetic diversity, and meaningful aspects of genetic structure;
- Inform discussions about other conservation plans for Monterey pine;
- Identify missing information on the genetic diversity, genetic structure, and related natural processes of Monterey pine in its native habitat;
- Address both the more immediate (e.g., genetic contamination, reduction in gene pool due to tree removal and disease) and longer-term (e.g., genetic bottleneck, inbreeding effects, regeneration success) genetic issues; and
- Formulate tentative functional genetic relationships among the natural populations of Monterey pine and the *ex situ* reserves of seeds and trees in California and worldwide.

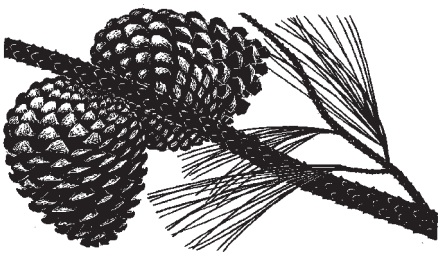
Riggs (1990) suggests that, in view of our incomplete knowledge about genetic materials, environmental relationships, and our own future needs, we should strive to achieve three goals in the pursuit of genetic conservation:

- Improve access to existing knowledge;
- Maintain genetic continuity and integrity wherever possible; and
- Integrate and coordinate a diversity of conservation activities to the best possible effect.

This report clearly attempts to satisfy the first goal and contributes to the other two.

2

Selected biological features of Monterey pine and its forests



Taxonomy

There are some 100 species of pine worldwide. Monterey pine is classified in genus *Pinus*, subgenus *Pinus*, section *Pinus*. Within this section, there is less uniformity among taxonomists about its classification. There have been at least seven different taxonomic treatments of Monterey pine, placing it alternatively in the subsections *Pinaster*, *Oocarpæ*, *Attenuatæ*, or *Patula* (Millar 1999a). Recent classifications have split Little and Critchfield's (1969) *Oocarpæ* into two subsections, but these newer arrangements vary in species composition (Dvorak et al. 2000; Table 1). There remains considerable confusion and disagreement about phylogenetic relationships of the Mexican/Central American and southeastern USA pine species classified within and among subsections *Oocarpæ* and *Australes* (following the classification of Little and Critchfield 1969). Regardless of the accepted taxonomic placement, Monterey pine is commonly grouped with two other pines (among others) that occur in California and Baja California (Table 1). These three, *P. radiata*, *P. attenuata* (knobcone), and *P. muricata* (bishop) are closely related closed-cone pines which hybridize with each other to some extent (Critchfield 1967).

Within Monterey pine, there has been dispute concerning the taxonomic relationship of the Guadalupe and Cedros Islands populations to mainland populations. It is now generally accepted that they belong in the same species, although as recently as the early 1960s the Cedros Island pines were referred to as a variety of bishop pine (Fielding 1961). The Cedros Island population has been given the varietal name of *P. radiata* var. *cedrosensis* (Howell) Axelrod and the Guadalupe Island population, *P. radiata* var. *binata* (Engelm.) Lemmon (Axelrod 1980; Millar 1986). However, these names are not universally accepted (e.g., Farjon and Style 1997; W.S. Dvorak, pers. comm.). These populations are considered relictual variants of Monterey pine (Axelrod 1980; Millar 1986).

Evolution

The evolution of the genus *Pinus* has received differing interpretations. It is generally accepted that the genus evolved more than 100 million years ago, radiating out from centers of origin in eastern North America and western Europe. More specifically, the oldest pine fossils are dated at approximately 130 million years BP (Millar and Kinloch 1991). Changing global climatic patterns and tectonics scattered the early pines to refugia, later to re-emerge from secondary centers of origin in the southern latitudes and polar regions in the early Tertiary (Axelrod 1986; Millar 1993). One of these secondary centers of origin—in Mexico and Central America—gave rise to the species of subsection *Oocarpæ* (following Little and Critchfield 1969) with the California closed-cone pines (bishop, Monterey, and knobcone) having evolved, it is believed, approximately 15 to 25 million years ago. That the California closed-cone pines are closely related to one another, originated in Mexico/Latin America, and are more distantly and inconsistently related as a group to other Latin American taxa of *Oocarpæ* are supported with genetic, phenetic, tectonic, floristic, and fossil evidence (Millar 1999a). Recent genetic data suggest that knobcone and Monterey pines have a common ancestor, and thus a more recent evolutionary connection than either with bishop pine (Wu et al. 1999).

The more recent history of Monterey pine—that occurring during the Quaternary or last four to five million years and responsible for the current distribution of the five disjunct populations—has been the subject of recent studies and interpretations. A long-held view is that the distribution has become increasingly restricted and coastal over the last five million years in response to changes in the California and Baja California climates towards drier and more Mediterranean conditions. Accompanying these changes in distribution are also adaptations reflected in characteristics such as cone morphology (e.g., Axelrod 1980, 1981).

Largely based on fossil evidence, this view holds that Monterey pine was historically more widespread along the California coast throughout the Ice Age. Climatic warming in the early- to mid-Holocene is presumed to have initiated contraction in the distribution, resulting in the present 'refugia' populations, with the island populations (which have the smallest and most symmetric cones of the extant populations) being the most ancestral. This evidence suggested a dynamic history of Monterey pine, with widespread and variable populations in the past, local extinctions, and population shifts that could account for the absence of a geographic cline in some characteristics of present-day populations (Axelrod 1980).

More recently, this interpretation of a dynamic past has been amplified and refined, suggesting that the current distribution is not a result of gradual contraction, but that Monterey pine has experienced various local extinctions and colonizations associated with climatic changes and eustatic changes in sea level since the late Tertiary (Burdon et al. 1992a). Taking advantage of the new and more detailed data available in the past two decades from new fossil discoveries and improved diagnostic techniques, there is now a better opportunity for understanding the relationship between pine evolution and climate (Millar 1998a). These data support the long-held view that Monterey pine has always had a dynamic spatial structure and further suggest that its evolutionary history is best described as consisting of a varying number and distribution of local populations that colonize, coalesce, and disappear repeatedly over time. Specifically, the species is thought to increase its representation during transitional climates (i.e., the end of glacial periods) and other cool—but not full glacial—periods (Millar 1999a).

Both the traditional and revised views hold that Monterey pine historically has occupied a range that extends beyond the current latitudinal and longitudinal distribution. Macrofossil remains, mostly cones identified with certainty as Monterey pine, have been found in abundance from many sites along coastal California, extending from Tomales Bay (near Point Reyes) south to the Mexico–USA border (Figure 2; Millar 1999a). Both views identify climate as the major force in determining population range. The major difference between these two views is in the interpretation of historic climate and the dynamics of recent evolution. Specific issues at question include: the period (or frequency) of climatic cycles over the last two million years; the identity of locations along the California coast that were simultaneously (versus sequentially) occupied by Monterey pine populations; and the specific climatic triggers for changes in distribution.

Inferences from many types of genetic data—including RAPD markers, isozyme markers, and morphological characteristics—are consistent with respect to the relationships of present-day populations. Generally, mainland populations are more closely related to each other than to island populations, and the latter are inferred to be most ancestral (Axelrod 1980; Millar et al. 1988; Wu et al. 1999). Of the mainland populations, Monterey is hypothesized to be the most ancestral and Cambria the most recent (Axelrod 1982).

Table 1. Some recent treatments of Monterey pine taxonomy. Species of *Pinus* classified in subsection *Oocarpæ* by Little and Critchfield (1969) have been variously grouped in two subsections by more recent treatments. Note: all treatments keep *P. radiata* and the closely related *P. attenuata* and *P. muricata* together in the same subsection. Table is adapted from Dvorak et al. 2000†; used here by permission from the senior author and Kluwer Academic Publishers.

Little and Critchfield 1969	**Perry 1991**	**Farjon and Styles 1997**	**Price et al. 1998**
Oocarpæ	*Oocarpa*	*Oocarpæ*	*Oocarpæ*
P. oocarpa	*P. oocarpa* vars.	*P. oocarpa* vars.	*Oocarpa* group
P. pringlei	*oocarpa*	*oocarpa*	*P. greggii*
P. patula	*trifoliata*	*trifoliata*	*P. jaliscana*
P. greggii	*microphylla*	*P. prætermissa*	*P. oocarpa* vars.
P. radiata	*ochoternai*	*P. tecunumanii*	*oocarpa*
P. attenuata	*P. tecunumanii*	*P. jaliscana*	*trifoliata*
P. muricata	*P. jaliscana*	*P. patula* var.	*P. patula vars.*
	P. pringlei	*patula*	*patula*
		longipedunculata	*longipedunculata*
		P. pringlei (?)	*P. prætermissa*
		P. durangensis (?)	*P. pringlei*
		P. lawsonii (?)	*P. tecunumanii*
		P. teocote (?)	
			Teocote group
			P. herreræ
			P. lawsonii
			P. teocote
	Patula	*Attenuatæ*	*Attenuatæ*
	***P. radiata* vars.**	***P. radiata* vars.**	***P. radiata* vars.**
	radiata	***radiata***	***binata***
	binata	***binata***	***cedrosensis***
	P. attenuata	***P. attenuata***	***radiata***
	P. muricata	***P. muricata***	***P. attenuata***
	P. greggii	*P. greggii*	***P. muricata***
	P. patula vars.	*P. coulteri* (?)	
	patula		
	longipedunculata		

†Species with (?) were provisionally included in the subsection by Farjon and Styles (1997).

Reproductive biology

As with other western USA pines thus far studied, Monterey pine has

maternal inheritance of mitochondrial DNA and paternal inheritance of chloroplast DNA (Neale and Sederoff 1989; Cato and Richardson 1996). Beccause nuclear DNA has biparental inheritance, this pattern of transmission genetics allows elegant opportunities to study the gene flow and genetic patterns of pines.

Recombination rates in pines are expected to be high because of the fairly large number of chromosomes ($2n$ = 24) and their large size, favoring crossing-over events. The karyotype of pine species is highly conserved throughout the genus: most pine species, including Monterey pine, have a karyotype of 11 long, metacentric to submetacentric chromosomes and one short, heterobrachial chromosome (Pederick 1970; Ledig 1998). Also, there is little variation in the length of chromosomes in *Pinus* and those of Monterey pine are the most uniform of a wide sample of congeneric species (Pederick 1967).

A generalized sequence of reproductive events for Monterey pine is shown in Figure 3. This figure is presented from a California seasonal perspective. The sequence of events and approximate duration of each is reliable, but the exact timing may vary from year to year, from population to population, and even from tree to tree—depending on environmental conditions (e.g., Sweet and Bollman 1976). For example, wet weather could adversely affect pollination in any year if it occurred early in the pollination period and stimulated closure of the seed cones before much pollen had been trapped (Lill and Sweet 1977). Much of the research on the reproductive biology of the species has been conducted in the southern hemisphere, complicating the translation of information to the natural populations. Seed cones may be produced on trees as young as 5 to 10 years—typical of about one-half the pines for which data are available—but substantial reproductive maturity is not normally reached until trees are 15 to 20 years old (Krugman and Jenkinson 1974). Pollen shedding may occur at earlier ages than seed cone production. Pollen is shed in late winter or early spring, typically in April, and seed cones are most receptive within a few weeks after first opening (Roy 1966). Fertilization doesn't occur until 15 months after pollination and morphological maturation of the embryo is five months later (Lill 1976). Thus, seeds mature the second autumn after pollination, continuing to ripen into the winter, and seeds are released under suitable environmental conditions—possibly years later. The time from pollination to morphological embryo maturity (20 months) is longer in Monterey pine than in other pine species that have been examined (Lill 1976). If the reproductive cycle is defined as beginning with seed cone development and ending with seed maturity, the entire cycle is close to 2.5 years—six months longer than that frequently described for other pine species (Sweet and Bollmann 1976).

Most pine species naturally produce abundant seed, which is important for long-term survival. Generally, this high reproductive output allows a large number of 'attempts'

Figure 2. Localities where fossil Monterey pine cones have been recovered (adapted from Millar 1999a with permission from the New Zealand Journal of Forestry Science). *Key:* 1 Tomales; 2 Drakes Bay; 3 Mussel Rock; 4 Spring Valley Lakes; 5 Little Sur; 6 Point Sal; 7 Veronica Springs; 8 Carpinteria; 9 Seacliff; 10 Potrero Canyon; 11 Rancho La Brea; 12 Mount Eden; 13 Laguna Niguel; 14 San Clemente; 15 Chula Vista; 16 San Miguel Island; 17 Drill site, Hole 893, Santa Barbara Basin.

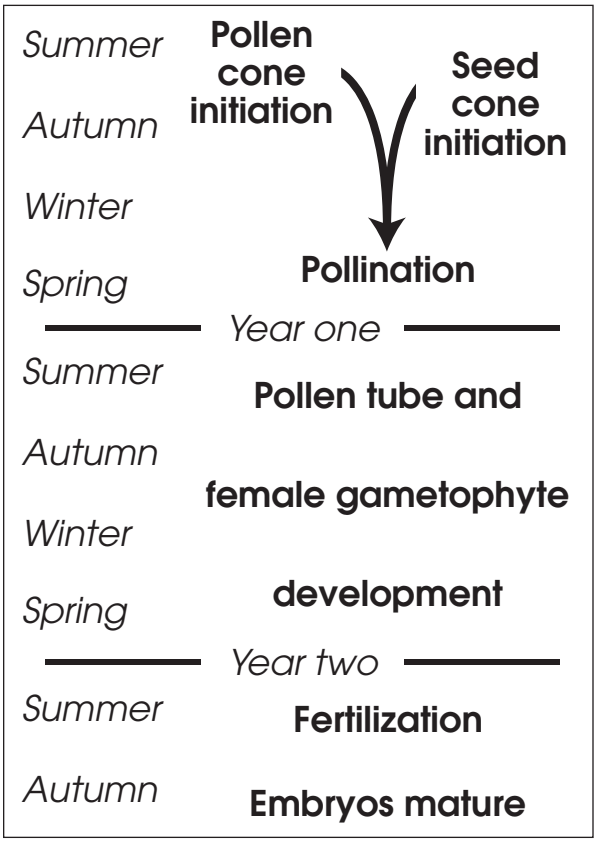


Figure 3. Sequence of reproductive events for Monterey pine.

to match changing environmental conditions, increasing the chance that at least some will be well adapted (Lanner 1998; Ledig 1998). In the native stands of Monterey pine, cones may remain on the tree for several years after maturity and are usually closed. Heavy seed crops occur almost annually (Vidaković 1991). Monterey pine is not strictly fire-dependent for cone opening and seed release, unlike the other closed-cone pines, bishop and knobcone pine. However, even in a more strictly serotinous species like knobcone pine, the persistence of this closed-cone habit varies among different populations (Newcomb 1962; Vogl 1973). Although fire produces optimal conditions for Monterey pine seed release, cones can open during hot, dry weather. Because the weather over much of the year in native Monterey pine habitats is cool, humid, or both, cones may open infrequently and re-close. Thus, seeds from a single reproductive cycle may be shed over several years (McDonald and Laacke 1990).

Pine pollen is well adapted to wind dispersal, having two air bladders that develop as part of the pollen grain. A number of generalizations prevail regarding pollen dispersal, but are well tempered with exceptions. For example, while most pine pollen probably does settle within a short distance of the source tree, given the large amount of pollen produced there is a good likelihood that at least a small proportion may travel large distances, thus leading to possible long-distance gene flow. Similarly, this does not mean that trees are most likely to be pollinated predominantly by their nearest neighbor (Ledig 1998). One explanation is the often huge number of overlapping pollen clouds from various trees. For example, measurements in a Monterey pine plantation showed that less than 2% of the pollen received by a given tree would come from any other single neighbor (Bannister 1965a).

The winged seeds are released fully in the event of fire or gradually in response to hot, dry weather (Roy 1966). Seed weight (approximately 23 000 to 35 000 seeds kg^{-1}; Vidaković 1991) is in the low- to mid-range for the genus whose seed weights can vary by a factor of 270 among species (Krugman and Jenkinson 1974). Seed weight also differs among the populations (K.G. Eldridge, pers. comm.; Burdon 2001b). Although normally and mostly wind-dispersed, some seeds may also be dispersed by animals, particularly those that cache seeds, such as Steller's jay (*Cyanositta stelleri*), scrub jay (*Aphelocoma cœrulescens* ssp. *californica*), deer mouse (*Peromyscus maniculatus*), and dusky-footed woodrat (*Neotoma fuscipes*) (Roy 1966). When wind dispersed, dispersal distance will depend on a constellation of factors including height of tree, weight of seed, area of seed wings (generally, the greater the wing area:seed weight ratio, the greater the potential travel distance), wind strength and direction, and topography of release site (reviewed in Lanner 1998). With wind-dispersed pine species, it is generally concluded that seeds are dispersed along a negative exponential curve whose peak frequency is at or just downwind from the forest edge, and the tail descends to a value close to zero within a few tens of meters (Lanner 1998). Animals may move some seeds farther in caching events. In addition, there are long-distance seed dispersal events which, although relatively rare, may have significant genetic impacts such as founding new populations or decreasing genetic differentiation among populations (e.g., Hamrick 1987). A study of Monterey pine in New Zealand revealed that new colonies of the species had been established in some cases over 3 km from the seed source (Bannister 1965a).

Concepts and description of population structure

It is typical of many western USA conifers (e.g., coast redwood (*Sequoia sempervirens*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*P. lambertiana*)) to have fairly large and contiguous geographic ranges. Associated with such large and overlapping population structure is the expectation of much gene flow and relatively little genetic differentiation among populations. In contrast, the physical population structure of the three California closed-cone pine species is that of fairly small and disjunct populations, with Monterey pine having the fewest and most disjunct populations of the three. This physical population structure has consequences for the genetic structure (described in Chapter 3). There is considerable evidence that this pattern is not only recent but that Monterey pine's evolutionary history has been marked by variable and shifting populations, including local extinctions (e.g., Axelrod 1980; Burdon et al. 1992a; Millar 1999a). One compelling observation towards this conclusion is that current populations do not represent a cline in some characteristics (Axelrod 1980).

More recently, it has been suggested that this dynamic and patchy structure might be described as a metapopulation (Millar 1999a). In general terms, this means that while some populations of the species go extinct, others recolonize over time, as opposed to a more static population structure. Whether Monterey pine populations represent a metapopulation structure in the classical sense has not been determined. The term was loosely applied to Monterey pine largely on the basis of paleohistorical data: the classic metapopulation model is based on genetic dynamics—the latter of which is not readily discernible from paleohistorical data. Indeed, a strictly metapopulation model was not meant to be implied for Monterey pine: only a loose characterization as such, and mainly referring to the fragmentation among populations, with local colonizations and extinctions, and a dynamic situation with varying levels of gene flow among populations (C.I. Millar, pers. comm.). We need more information on the genetic dynamics of Monterey pine to determine whether it has more defining attributes of metapopulation structure and whether any aspects of metapopulation theory can be reasonably applied to the conservation of *in situ* populations of Monterey pine (Box 1).

Fire ecology

Parsing fire into its components—fuel, weather, topography, and ignition—hints at the relationship between fire regimes and patterns of vegetation (Pyne 1982). Fire has played a

Box 1. The concept of metapopulations and its relevance to Monterey pine.

The general concept of metapopulations was introduced by Levins (1969). In the classical metapopulation model, all populations are equally prone to extinction and the metapopulation persists through recolonization. This classical model may not be common in nature (Hastings and Harrison 1994). More common models of metapopulation structure include: a) local populations that may be unequal in size or longevity, creating a 'mainland-island' dynamic; b) local populations that may be so strongly interconnected by dispersal that local extinctions seldom occur, producing a single patchy population; and c) local populations that may be so weakly connected by dispersal that local extinction is not balanced by recolonization and the entire metapopulation is on its way to extinction (Harrison and Hastings 1996).

There are different consequences for genetic variation and adaptive evolution for the various models of metapopulations. However, metapopulation structure is generally associated with low levels of among-population genetic variation, a situation that does not provide much potential for adaptive evolution by selection among populations (Harrison and Hastings 1996). Monterey pine, however, exhibits considerable genetic differentiation among populations. The difference between observed and expected (under a metapopulation model) genetic differentiation could be: a) a consequence of subjective differences in what constitutes high or low differentiation values; b) an exception to the generalization; or c) the modern history of Monterey pine distorting its normal trajectory with habitat losses that may have increased apparent diversity among populations and land conversions that have prohibited expansion or recolonization of populations.

Examples of metapopulation structure in nature have been difficult to find (e.g., Harrison 1994). Nevertheless, even if we assume a metapopulation structure for Monterey pine, it is important to interpret properly the interrelationship between random population extinctions and nonrandom habitat destruction. Lande (1987) suggested that some species cannot persist if the proportion of suitable habitat falls below a certain level. A metapopulation suffering persistent habitat destruction will have a lower equilibrium value of occupied patches than a metapopulation suffering only random extinctions because the former suffers both the loss of suitable habitat and the additional local extinctions caused by the destruction of occupied patches (Hess 1996).

It is not known whether Monterey pine actually and functionally exhibits a classical metapopulation structure. Harrison (1991) points out that there are many ways for a population to appear to have metapopulation structure but depart significantly from the assumptions and the dynamics of the classic metapopulation model. She gives three such examples:

1. The 'source-sink' situation where one or more populations are large relative to the others and thus there is considerable imbalance among populations in terms of which ones go extinct.
2. The 'patchy population' scenario in which dispersal events are too frequent to allow extinction. In that case, the sink population is maintained largely by recruitment from the source population directly and the system is effectively a single population.
3. The 'nonequilibrium' situation in which extinctions take place in the context of a regionwide decline of a species rather than a colonization-extinction equilibrium.

Thus, the dynamics of a situation are critical to determining whether a certain species fits the classic metapopulation model and, hence, its assumptions and applications. Metapopulations are difficult to test in practice (Doak and Mills 1994). For example, detailed long-term data on population sizes, dispersal distances, and reproductive success and spatial and temporal correlations between populations are necessary to understand a metapopulation's structure (Doak and Mills 1994). However, some of the genetic attributes expected under such models can be measured and some informed sense of direction taken from these measures. For example, the suggestion that genetic drift may play a larger and adaptation a smaller role in Monterey pine populations under a metapopulation structure assumption (Millar 1999a) can be tested. An appropriate role of the metapopulation theory may be, in this case, suggesting a series of hypotheses to be tested. Indeed, the renewed interest in research concerning dispersal capabilities and the correlation between extinction risks and dispersal probabilities may be one of the most positive effects of metapopulation models to date (Doak and Mills 1994).

Furthermore, genetic characterizations must always be placed within an appropriate spatial and temporal context to be reasonably interpreted. For example, low among-population differentiation could be due to recent colonization, high contemporary gene flow among populations, little local adaptation, or other life history or breeding system characteristics (S.P. Harrison, pers. comm.). Similarly, the total amount of genetic variation within the species could be low due to ongoing extinction and recolonization (as in a metapopulation situation), genetic bottlenecks, strong and consistent selection pressures, or other factors. Thus, all information—genetic parameters, spatial structure, breeding system, and evolutionary history—must be considered together and appropriate reference groups used in describing genetic diversity and genetic structure. For example, in the presence of nonadditive genetic effects, measurements of additive genetic variance in natural populations must be taken at the proper spatial scale with respect to natural selection or they will provide an inaccurate description of evolutionary potential both within local populations and within the species as a whole (Whitlock et al. 1993).

Given that the term 'metapopulation' has only been applied to Monterey pine tentatively, based on paleohistorical data, and in the broadest sense of dynamic population ranges, it is premature and likely inappropriate to draw conservation conclusions from classic metapopulation theory. More appropriately, the species' genetic patterns and processes should be studied as completely as possible, compared with various models of historic population dynamics, and the most probable model used to inform conservation decisions.

significant role in shaping vegetation patterns in California, including the coastal fogbelt area (e.g., Wells 1962; Vogl 1973; Greenlee and Langenheim 1990). The role of fire in shaping Monterey pine forests over evolutionary time has been well studied (e.g., Axelrod 1980; Millar 1999a). The more recent and human-influenced fire history and its relationship to the forests are less studied and less certain.

Understanding the role of fire in Monterey pine forests requires recognition that there may be differences in impact between naturally occurring fires in the evolutionary history of the species, and more recent fires—natural or human-caused—that occur in a context of other anthropogenic influences. Specifically, interpreting the role of fire in a healthy Monterey pine forest requires consideration of the time frame over which fires have an influence; the season, intensity, frequency, area, and burning pattern of fires; and the interaction of fire with other influences (e.g., grazing, logging, habitat loss, inbreeding, drought, and disease).

Over evolutionary time, the development of serotinous (or semi-serotinous) cones, now more commonly described as a closed-cone trait, suggests an adaptation of Monterey pine to fire (Linhart 1978). More specifically, cone morphology and scale thickness vary among pine populations in a manner that is consistent with selective influences from fire and squirrel predation. In areas where historically squirrels have been common and fires very hot, thick-scaled asymmetric cones may provide some protection from seed predation and mortality (Linhart 1978). Since about 20 000 years BP, intermediate climatic conditions (e.g., wet winters, moderate temperatures) and fire (which itself is weather related) show a cyclic pattern that is correlated with pine expansion. That is, over evolutionary time scales, fire has been important in stimulating expansion events in Monterey pine when coinciding with periods of climate change or favorable climates for expansion (C.I. Millar, pers. comm.)

However, fires intentionally set by native Americans and early settlers—for example, with the purpose of encouraging blackberry or grass production (Libby 1997) or increasing available habitat for domestic animals—may well have a different impact. There is compelling evidence that, prior to European contact, humans were using fires in California to cook, cremate the dead, burn fleas out of infested shelters, remove vegetation to make travel easier and to prevent surprise attack, flush wildlife, harass enemies, provide building material, encourage certain plants such as hazelnut (*Corylus cornuta* var. *californica*), and reduce the potential fire hazard around villages (Greenlee and Langenheim 1990).

The few fires experienced today—caused mostly by accident, arson, or lightning—undoubtedly differ in quality and impact. The intensity and frequency of these fires probably differ from historic fire cycles, and subsequent landuse changes influence seedling establishment and recruitment. In summary, the role of fire in the functioning of Monterey pine forests may change over time, depends on the nature of the fire, and is affected by interactions with climate and other environmental and anthropogenic factors.

Species range and population descriptions

The current natural range of Monterey pine is limited to five discrete populations (Figure 1). The three on the central coast of California are commonly named Año Nuevo or Swanton (the northernmost), Monterey, and Cambria. The two others are on islands off the coast of Baja California—Guadalupe and Cedros Islands. The reference to these areas as 'populations' does not imply the genetic definition of that term, but only that they occupy discrete geographic areas. Based on current understanding of climatic fluctuations and the relationship with Monterey pine distribution dynamics, Monterey pine should be expanding under current climate conditions, if there were no other constraints (Millar 1998b).

Distributions of the two other California closed-cone pine species are as follows. Knobcone pine extends from southern California to southwestern Oregon. Bishop pine occurs in disjunct locations along the coastal California mainland and on two islands off the southern California coast.

The general boundaries of the three mainland Monterey pine populations have been well known for over a hundred years. The precise natural limits, however, can no longer be determined (Griffin and Critchfield 1972). Estimates of the area of Monterey pine forest, particularly for the three mainland populations, vary considerably (Table 2). Given that the mainland populations exist within areas of rapid human population growth and considerable urbanization, it is not surprising to find contrasting estimates related to when and by which criteria the forests were assessed. Jones & Stokes associates, Inc. (1994a) review some of the reasons for the differences in reported Monterey pine forest area. Area of forest is only one measure of the species' pres-

Table 2. Estimates of the current area of native Monterey pine populations†.

	Source of estimate				
Population	Forde 1964b	Roy 1966	Burdon 1988	Huffman and Associates, Inc. 1994	Jones & Stokes Associates, Inc. 1994a
	(ha)				
Año Nuevo	< 400	< 400	400	600	
Monterey	4860	3200–4960	6000	2800	3800
Cambria	1210	~1215	1200	900	
Cedros Island			130		

†Guadalupe Island is not included here since it is more appropriate to measure that pine forest by number of trees rather than area occupied (see Table 3).

ence: number of trees, amount of contiguous forest, and demographic profile are also important measures.

The extent of Monterey pine forest can be classified both by natural features (e.g., type of understory or species dominance) and by land use (e.g., undeveloped, rural, or urban). It is not necessary to have one authoritative source for all forest land estimates for the purpose of this report. Rather, the most appropriate estimates will depend on the particular conservation question. For example, in planning *in situ* genetic reserves, only fairly large, contiguous, and undeveloped forest areas would normally be considered, while collections for *ex situ* conservation might still be made from other areas as long as genetic contamination was not suspected.

In California, Monterey pine forests are located within the coastal forest zone. This zone is influenced and characterized by a cool, foggy, maritime climate that contrasts sharply with the hot, arid environment to the east of the coastal mountains. General descriptions of the ecology and conditions of the California Monterey pine forests in the early- and mid-1900s, respectively, are found in Lindsay (1932) and Forde (1966).

These coastal California forests are perhaps more diverse than forests in any other region of California. They include ancient coast redwood and large Douglas-fir forests, pygmy forests on acidic soil, pine and cypress species, and woodlands and savannas of rare oak and walnut species on gently rolling hills and valleys (Barbour et al. 1993).

The mainland populations fall within a climatic region that is generally described as having mild winters, rarity of frost, prevalence of summer fog, moderate precipitation, absence of snow, and moderate summer temperatures. The mean temperature is above 10°C. Average annual rainfall is moderate (380 to 900 mm) and 70 to 75% of the rainfall occurs during the winter months of December to March. On average, there are no rainy days in July or August. The growing season begins in February or March, but the advent of warm weather is gradual. The mean temperature in the warmest month, usually August, is approximately 18°C. Little growth takes place after September, probably due to lack of rainfall. The most distinguishing feature of this region is the summer conditions of temperature and humidity. Humidity is high throughout the year but is higher in summer and winter than in spring and fall. Thus, humidity in summer months counterbalances the lack of rainfall and reduces evaporation (Lindsay 1932). Climate for the two island populations is described later under their subheadings.

Climatic requirements described for Monterey pine in plantations worldwide are not identical to the climate of the natural populations. A bioclimatic analysis of the major plantation areas of Monterey pine produced a description of its climatic requirements that included a mean annual rainfall of 650 to 1600 mm, among other criteria (Booth 1990). This is higher than that experienced, on average, in many of the native populations (Table 3). This discrepancy is probably due largely to the influence of summer fog in the native populations and its effect in reducing evapotranspiration stress. Also, climatic requirements for successful plantation culture are not necessarily the same as those for species survival within its native range.

Summer fog is a common climatic feature for all five populations. The significance of summer fog precipitation beneath coastal California forests may well be considerable, not only adding moisture and reducing evapotranspiration stress during warm months, but contributing nutrients to the soil as the fog percolates through the canopy (Azevedo and Morgan 1974).

Despite a restricted geographic natural range, Monterey pine grows on soils that are derived from a variety of parent materials, from shales to granite to limestones to sandstones to volcanic rock types on Guadalupe Island. On the mainland, the pines are often found on sandy loams with a clay layer at 50 to 85 cm depth. Soil pH underlying the pines is acidic to extremely acidic. Ectomycorrhizal associates are the norm (McDonald and Laacke 1990).

Ecologically, the Monterey pine forests support unique biotic assemblages including numerous species that are endangered, threatened, or 'of concern' at federal or state levels (e.g., CNPS 1999). The mainland populations harbor a remarkable number of rare and endemic species including Eastwood's golden fleece (*Ericameria fasciculata*), Monterey manzanita (*Arctostaphylos hookeri*), sandmat manzanita (*A. pumila*), Yadon's rein orchid (*Piperia yadonii*), Hickman's cinquefoil (*Potentilla hickmanii*), Pacific Grove clover (*Trifolium polyodon*), and others (Matthews and Nedeff 1995). One high-profile ecological function of these forests is as overwintering sites for Monarch butterfly (*Danaus plexippus*) populations that breed east of the Rocky Mountains

Table 3. Location and attributes of the five native populations of Monterey pine.

Population	Latitude†	Longitude†	Tree count‡	Elevation range§	Annual rainfall§
	(°N)	(°W)		(m)	(mm)
Año Nuevo	37.0	122.5	1 200 000	10–33	800
Monterey	36.5	122.0	3 000 000	10–440	400
Cambria	35.5	121.0	1 300 000	10–200	500
Guadalupe Island	29.0	118.3	220	400–1200	150
Cedros Island	28.3	115.3	80 000	380–640	150

†Latitude and longitude are derived directly from map locations and represent approximate center points of the islands or mainland pine populations.

‡From Moran et al. (1988), with the exception of number of trees for Guadalupe Island, which is from the May 2001 expedition to Guadalupe Island (Rogers et al. 2002).

§From Eldridge (1978b). Annual rainfall figures are approximate and average. In areas where there is a significant elevation gradient, precipitation can vary (e.g., Forde 1966; Burdon 2001b). Also, fog presence influences the relationship between effective moisture status and precipitation.

and migrate to the mountains of central Mexico. Aggregation sites for this species are known within Monterey pine stands where the necessary and very specific protective and supportive qualities, including appropriate microclimate, are found (Calvert and Brower 1982; Lane 1985; Sakai et al. 1989; Leong 1990; Weiss et al. 1991).

Año Nuevo

This northernmost of the three mainland populations begins approximately 75 km to the north of Monterey (Figure 4; Table 3). Figures reported for the extent of the current forest here range from 400 to 600 ha (Table 2). It is likely that much of this discrepancy is based on the methods and definitions used, rather than reflecting any real and dramatic changes in forest size over the 60 years spanned by these reports. For example, in some areas the Monterey pine forest intergrades into forests dominated by Douglas-fir and knobcone pine, leading to much ambiguity about the Monterey pine forest perimeter. There appears to be general agreement that the current forest range is approximately that of historical conditions (pre-European arrival). There is some documentation of planted trees—or seedlings from planted trees—extending the southern part of the forest at Año Nuevo (Forde 1966; McDonald and Laacke 1990), but this planted area is not considered part of a natural forest and is not included here.

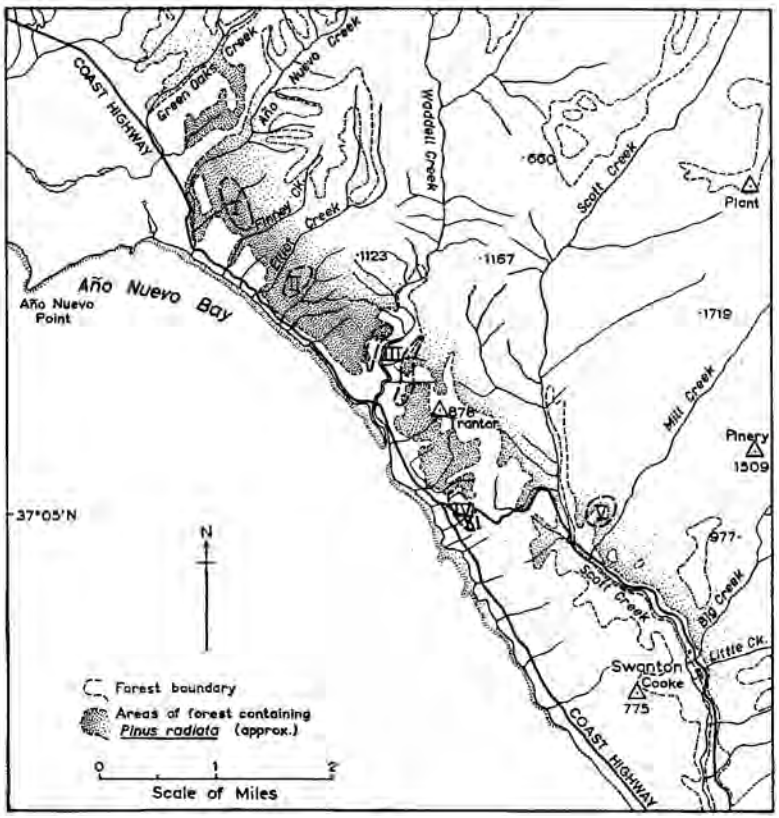


Figure 4. Map of the Año Nuevo Point area with approximate areas of forest containing Monterey pine (shaded) (reprinted from Forde 1964a with permission from SIR Publishing for and on behalf of the Royal Society of New Zealand, publishers of the New Zealand Journal of Botany; areas designated with Roman numerals were Forde's sample areas).

In this general area, Monterey pines grow in nearly pure stands on some slopes, infrequently with California live oak (*Quercus agrifolia*) in the understory. In other areas, particularly those with deeper, moister soils, the pines grow in combination with Douglas-fir and coast redwood. In some restricted areas, generally ridgetops with shallow soils, they also grow together with knobcone pine towards the eastern (inland) extent of Monterey pine's natural range. Natural interspecific hybrids *(P. attenuata* × *P. radiata*) and advanced generations of these hybrids, have been observed in and close to this same area (B.D. West-Bourke, pers. comm., Griffin and Critchfield 1972).

The rainfall here is the highest experienced by any of the native Monterey pine populations (Table 3). Underlying rock formations in this area are shales and marine sandstones, intermixed with calcareous material from underlying rocks (Jensen 1939). Soils are often shallow and are generally of the type formed by the weathering of rock in place (Lindsay 1932).

Considerable morphological diversity in Monterey pine is noted in the Año Nuevo population, including prostrate forms in some coastal areas. Although the spatial pattern of genetic diversity within this population has not been well studied, the diversity and structure of environmental variables (including orientation of mountain ranges, soil type, elevation, rainfall, fogbelt coverage, and wind) provide a reasonable suggestion of some attendant genetic structure.

Almost all of the Monterey pine forests (approximately 85%) within this population are privately owned. Approximately 12 ha are contained within state parks and approximately 50 ha are owned and managed by California Polytechnic State University. Waddell Creek divides the population into two disjunct, although certainly not genetically isolated, segments. Most, if not all, of the Monterey pine forest here has had human impact in the form of logging in the 1800s, with some continuing today. The targeted commercial species have been coast redwood and Douglas-fir. Thus, impact on the Monterey pines may possibly be more indirect (e.g., damage to trees and seedlings from skidding of harvested trees) than direct (harvesting).

Based on poor growth (relative to other Año Nuevo subpopulations sampled) in some common-garden tests in New Zealand and Australia, it has been suggested that trees in the Swanton area (inland near the southern limit of the population, between Scott Creek and Mill Creek) may be suffering from inbreeding depression (Burdon et al. 1992a; Johnson et al. 1997). However, genotype × environment interactions may play a role here. For example, height growth after eight years of that Swanton-area collection is actually the highest of any of the four sampled subpopu-

lations on two specific sites in New South Wales, Australia (Johnson et al. 1997). The sites where the Swanton-area subpopulations were superior in height growth were also the sites where annual precipitation (750 to 800 mm) was similar to the Año Nuevo area. This suggests that specific adaptation, rather than inbreeding depression, may underlie the observations.

Monterey

The largest of the five populations, the effective area of the Monterey population is also perhaps the most difficult to interpret, with Monterey pine forests intermixed with other land uses including residential areas, recreational sites, urban parks, and transportation corridors. Reported estimates of the pine-forested area vary from 2800 to 6000 ha (Table 2; Figure 5). Estimates of both historical and extant forest at Monterey vary considerably but there is agreement that there has been a significant reduction in the native forest in recent decades. One estimate suggests a 40% reduction in forest area (Huffman and Associates, Inc. 1994) and another a 49% reduction (Jones & Stokes Associates, Inc. 1994a). Habitat loss and fragmentation continues in this area and this estimate continues to change. The lost forest habitat has been converted to agricultural, residential, commercial, or recreational uses. Approximately 60% of the current forest is in private ownership, and is thus subject to potential development (Huffman and Associates, Inc. 1994). Much of the forest in this area has been harvested at least once (e.g., McDonald 1959).

At least five Monterey pine forest types can be recognized, based on the associated canopy-level vegetation. In some areas, Monterey pine exclusively or almost completely occupies the canopy layer, although understory species may vary considerably. In many stands, Monterey pine shares the canopy with California live oak. Near the coast, Monterey cypress (*Cupressus macrocarpa*) is a frequent codominant species. Bishop pine and gowen cypress (*Cupressus goveniana* var. *goveniana*) grow with Monterey pine on the higher western slopes of Huckleberry Hill and near Gibson Creek. Coast redwood, white alder (*Alnus rhombifolia*), Scouler's willow (*Salix scouleriana*), and arroyo willow (*S. lasiolepis*) are often intermixed with the pines in riparian habitats (Jones & Stokes Associates, Inc. 1994b). Earlier reports also mention the coexistence of Monterey pine with foothill pine (*Pinus sabiniana*), tanoak (*Lithocarpus densiflorus*), blue oak (*Quercus douglasii*), interior live oak (*Quercus wislizenii*), broadleaf maple (*Acer macrophyllum*), and other woody species (McDonald 1959).

The underlying rock of the peninsula is primarily granite with overlying soils formed from marine deposits. East of the peninsula, the rocks are siliceous shales characterized by slow weathering. Soils have been formed over varying timeframes and varying conditions of rainfall and temperature

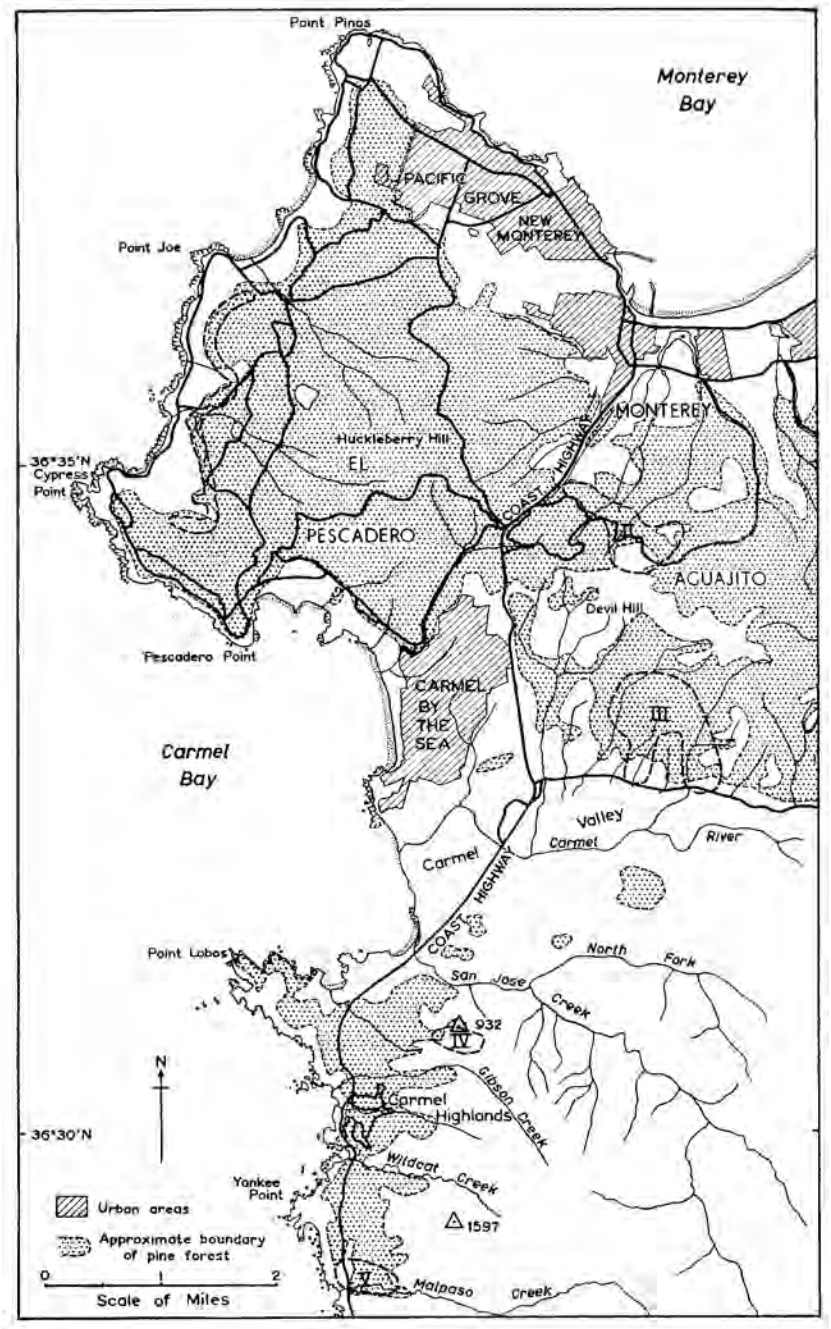


Figure 5. Map of the Monterey area with approximate areas of forest containing Monterey pine (shaded) (reprinted from Forde 1964a with permission from SIR Publishing for and on behalf of the Royal Society of New Zealand, publishers of the New Zealand Journal of Botany; areas designated with Roman numerals were Forde's sample areas).

that characterize this coastal area with an elevation range of over 400 m. Dune sands, sandy loams, and clay loams are common textures of some of the predominant soil types and series in this area (Lindsay 1932).

The successional stages of elevation, soils, and plant species present at the western edge of the Monterey Peninsula have been studied (e.g., McBride and Stone 1976; Jones & Stokes Associates, Inc. 1994b; Cylinder 1995). In one study, a successional sequence was described for the sand dunes of the Peninsula that has two different routes depending on the topographic position on the dunes. One route commences on the ridges and slopes and continues to an *Artemisia-Haplopappus* stage, then inland finally to a *Pinus-Quercus* or *Quercus* stage, and a *Quercus* climax stage. The second route begins in the sand swales, continues to a *Carex* stage, and eventually to a *Pinus*, *Pinus-Quercus*, and *Quercus* climax stage. These vegetational successional stages were correlated with the degree of soil development beneath them (McBride and Stone 1976). In a more recent study, significant soil-vegetation relationships have been described where Monterey pine is a primary species on a six-step marine terrace ecological staircase and soil chronosequence (Jones & Stokes Associates, Inc. 1994b; Figure 6).

The mean annual rainfall at Monterey is approximately 400 mm (Table 3). Within the forested areas and immediate borders there is constant fog drip throughout most of the summer, varying from a trace on most days in those areas farthest from the peninsula to approximately 15 mm per week on one of the higher elevations within the peninsula. There is some evidence to support the theory that Monterey pine will not persist in an area where there is no fog drip during the summer and where there is no other form of summer precipitation (McDonald 1959).

Although genetic diversity has not been studied comprehensively in relation to the ecological staircase and other environmental variation here and elsewhere within the Monterey population, there may be genetic differentiation due to selection, especially as a result of the extreme differences in soil conditions (Jones & Stokes Associates, Inc. 1994b). Morphological variation in the pines, providing a suggestion but not proof of underlying genetic differences, has been noted in this population. For example, extreme prostrate growth forms in the pines were noted near the coast of Carmel more than 75 years ago (Gray 1925; Box 2). This habitat and most of the associated prostrate forms are now gone (L.L. Smith, pers. comm.).

Cambria

This southernmost of the three mainland populations begins approximately 100 km south of the Monterey population (Figure 7). Estimates for the extent of the Cambria pine forest range from 900 to 1200 ha (Table 2). One of the more recent estimates suggests that the former forest was approximately 1400 ha and was reduced by over one-third

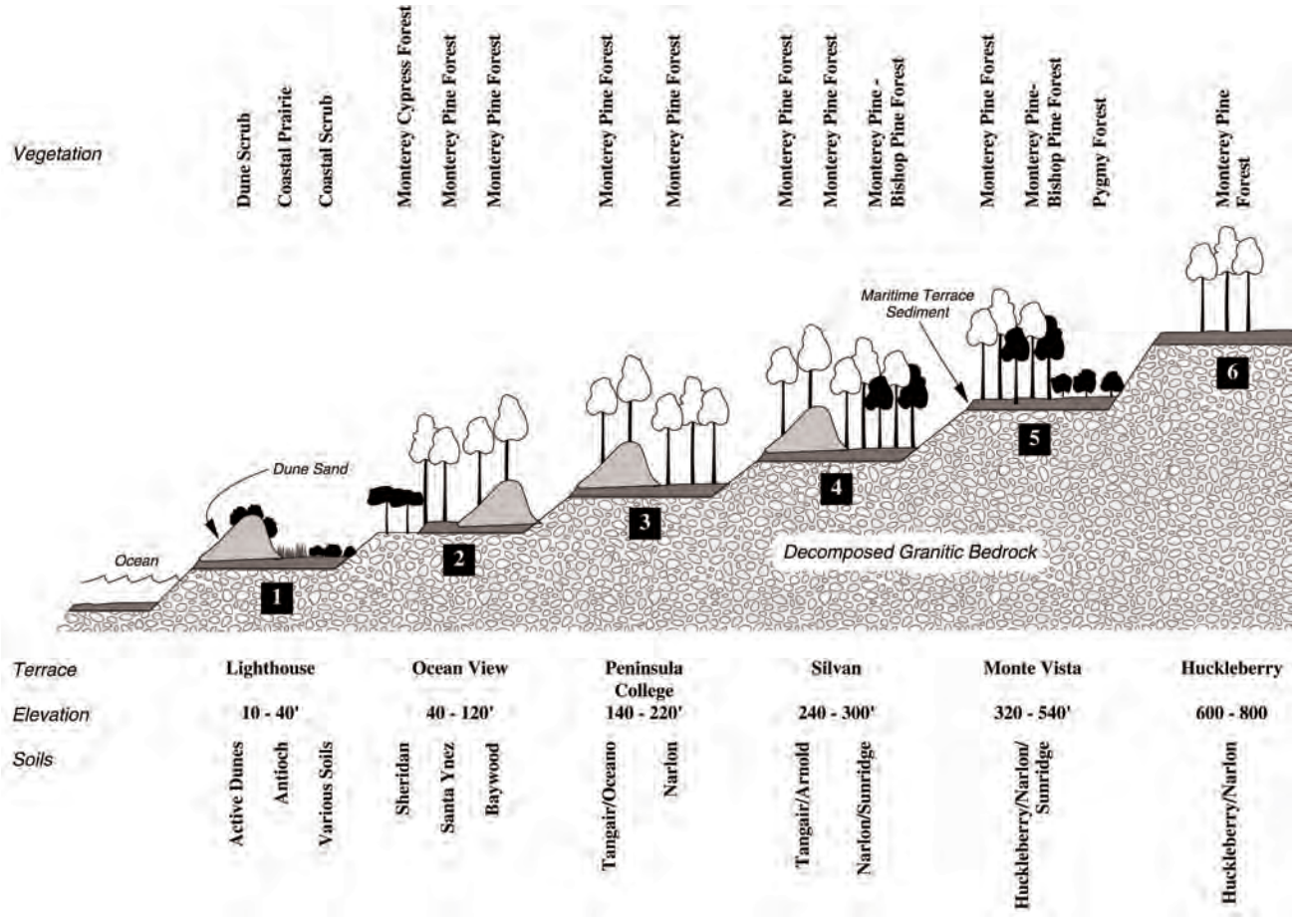


Figure 6. A cross-section of the Monterey ecological staircase (from Jones & Stokes Associates, Inc. 1994b).

to approximately 900 ha by the early 1990s, primarily as a result of housing development (Huffman and Associates, Inc. 1994). Until recently, only approximately 35 ha within this Monterey pine population had some kind of protected status. Currently, approximately 430 ha (48% or less of the total forest area, depending on which estimate for total forest area is used) have some form of protection. The majority of the pine forest here is privately owned.

The annual precipitation (approximately 500 mm) is intermediate to that of the other two mainland populations (Table 3). Soils are generally derived from slates, sandstones, and limestones (Carpenter and Storie 1933).

The Cambria population is the only mainland population that does not have an admixture of other coniferous species. The common overstory associate is California live oak. Monterey pine is more common on the north-facing (more mesic) than south-facing (more xeric) slopes. Although a detailed fire history of this area has not been prepared, one survey of the entire San Luis Obispo County shows that there has been only one large (>40 ha) fire since 1930, occurring in 1960 and covering approximately 30 000 ha (Orr 1998). One of the larger protected areas of Monterey pine—approximately 30 ha in San Simeon State Park—is very mature, apparently having not burned for close to 100 years (D.S. Hillyard, pers. comm.).

A disjunct Monterey pine area spanning Pico Creek, north of the main Monterey pine area, is apparently not a natural forest. This area was planted and probably not with local genetic material (H.W. Elliott, pers. comm.).

Much of the remaining forest of the Cambria population is in fragmented areas and 'boutique forests'—residential areas where homes are intermixed with trees. Major threats are the continued loss of pines and pine habitat due to residential development—currently an annual rate of increase of 2.3% in number of homes started—particularly within and adjacent to the town of Cambria (R.H. Hawley, pers. comm.)

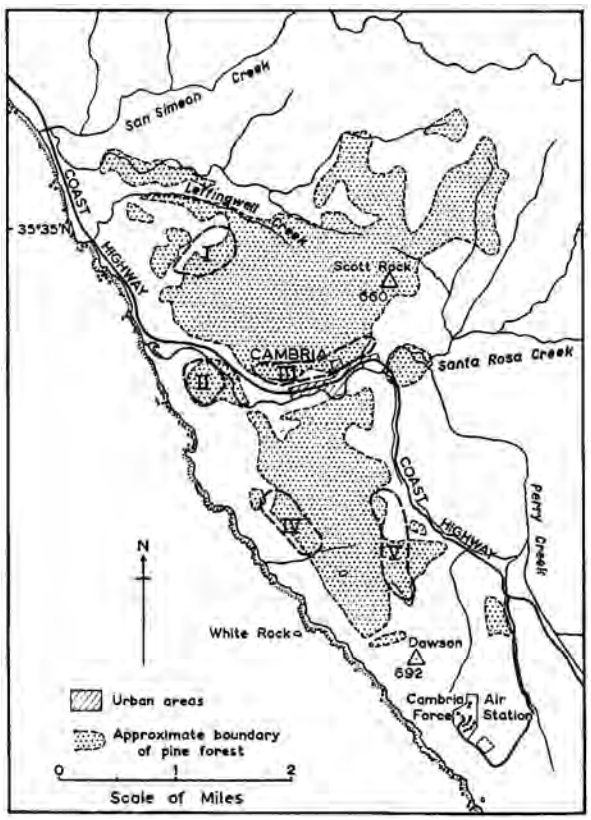


Figure 7. Map of the Cambria area with approximate areas of forest containing Monterey pine (shaded) (reprinted from Forde 1964a with permission from SIR Publishing for and on behalf of the Royal Society of New Zealand, publishers of the New Zealand Journal of Botany; areas designated with Roman numerals were Forde's sample areas). The Pico Creek stand, of uncertain origin, lies about 3 km north of San Simeon Creek.

Guadalupe Island

Located approximately 250 km off the Pacific coast of Baja California, Guadalupe Island is approximately 35 km long and 12 km wide (Rico C. 1997c). The island is part of an archipelago of volcanic origin, approximately seven million years old. At the northern end of the island, Mount Augusta (elevation 1298 m) represents the crest of a volcanic mountain that slopes 3660 m into the floor of the eastern Pacific (Bostic 1975; Figure 8). Dry to arid conditions prevail. Annual rainfall (approximately 150 mm) is based on records from the south end of the island; the north end, for which we have no records, apparently has a higher level of rainfall. Various expeditions to the island have reported varying numbers

Box 2. Description of the Monterey pine landscape near the Carmel coastline in 1925.

"The present business section of [Carmel] was once clad with a vigorous growth of mature pines which came to a symmetrical height in natural aisles. At the ends of these one caught glimpses of the bay, azure and shining, in contrast to the soft deep green of the pine plumes. Toward the sea, the tree form was influenced by the wind and drifting sand. There still remain groups of these crouching, flat-topped pines, which make an interesting study for the naturalist as well as the painter.

"The writer has on her property two pines of this remarkable self-protective type. Their lower limbs lie close to the ground on a horizontal line from twenty to twenty-six feet in length. At this distance from the trunk they make an abrupt turn toward the sunshine and upper air. They ascend thirty feet or more, and branch out into well-shaped, separate young trees in appearance. It is only by following their trunks down to the turn, and in several cases under matted pine needles, that one finds the connection between them and the parent tree. The upper limbs of these trees also run out at great length, and the interlaced tops of the two form a flattened mass which tilts toward the southeast and shows the force of the north and west winds before there were buildings or natural growth to break it. The vaulted space beneath these trees, whose huge trunks stand within three feet of each other, is circular and fully forty feet in diameter." (Gray 1925).

of extant, endemic, and introduced species (Moran 1996; Rico C. 1997b). A comprehensive assessment of the Guadalupe Island flora by Moran (1996) indicates that there is a total known flora of 216 species, but not all of them occurring at the same time. He estimates that 45 are relative newcomers (weeds), leaving 171 species that are possibly native. Over 30 species have probably gone extinct. No doubt, the accurate assessment of biodiversity here is complicated by the rare occurrence of some species and new information that affects endemic status, species extinctions, and recognition of introduced species. In particular, the definition of what is 'native' on a volcanic island, is somewhat subjective.

The island is owned by the federal government of Mexico. As a result of a federally sponsored 1921 expedition to the island in collaboration with the California Academy of Sciences and other scientific institutions from the USA, an agreement was reached on October 19, 1922 in recognition of its natural biodiversity (Rico C. 1997a). Today, the island is considered a protected area by SEMARNAT (Mexican Secretaria de Medio Ambiente y Recursos Naturales, Secretariat of Environment and Natural Resources), mainly because of the marine life, and as an important area for bird conservation by CONABIO (La Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, National Commission for the Knowledge and Use of Biological Diversity). Together, CONABIO (created in 1992) and SEMARNAT (created in 1994 as SEMARNAP, re-organized in 2001 as SEMARNAT), have raised the political profile of environmental conservation, enabled funding for protected areas and biodiversity research, and provided structures by which biodiversity conservation can be approached in a more scientific and well-informed manner (Ezcurra 2002).

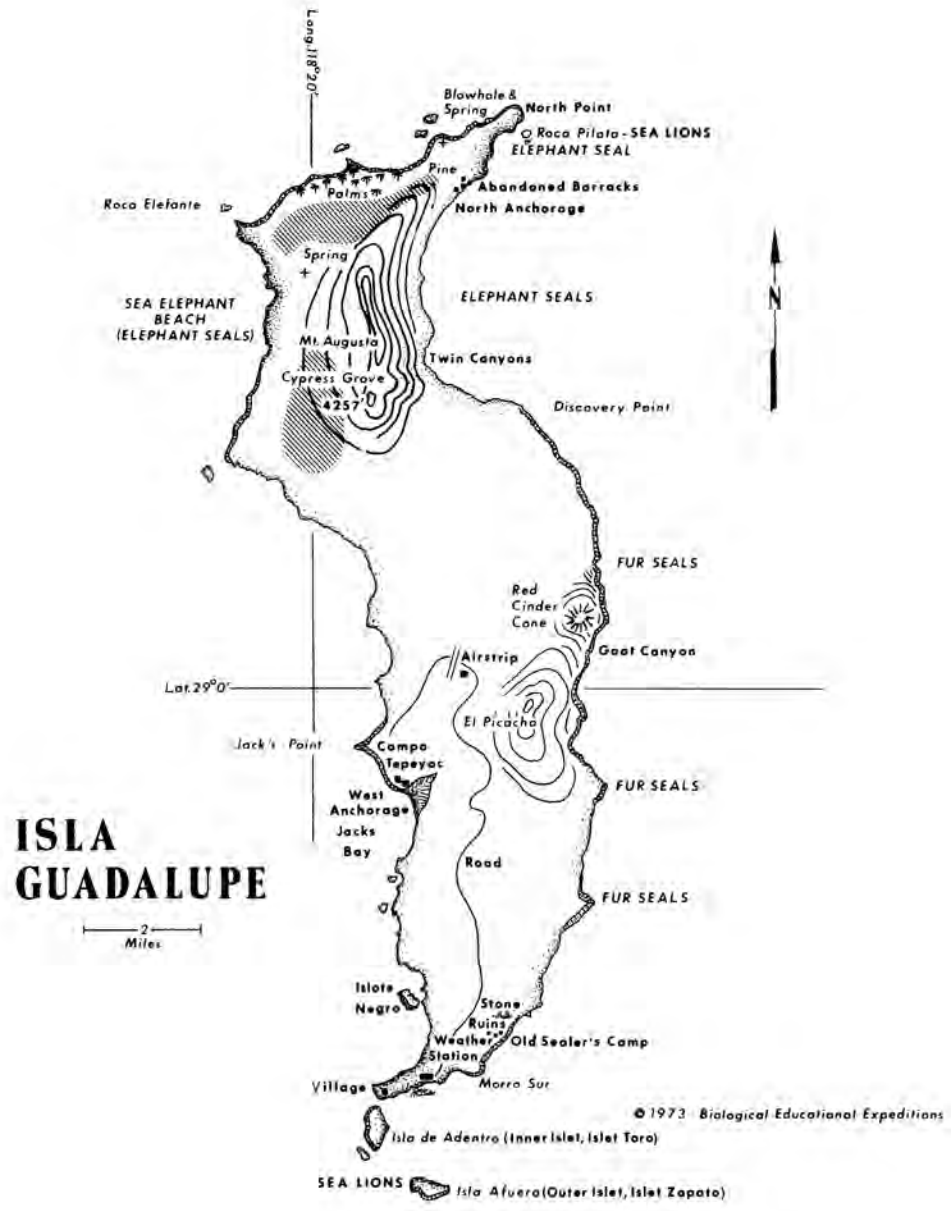


Figure 8. Map of Guadalupe Island (Bostic 1975). [Illustration credit: Robert Crim, Biological Education Expeditions, Inc., used by permission of Biological Education Expeditions, Inc.]

Guadalupe Island has a large number (34) of endemic plant species and subspecies relative to other California or Baja California islands. Several are thought to have gone extinct recently. Some of the endemics are the pink-flowered *Talinum guadalupense*, a yellow-flowered shrub (*Perityle incana*) reminiscent of dusty miller, and a yellow-flowered amaryllidaceous plant, *Triteleia guadalupensis* (Oberbauer 1986).

Rapidly dwindling numbers of Monterey pine, in an environment hostile to recruitment of seedlings, has led to a uniform opinion that this population of pines is headed towards extinction (FAO 1986; Oberbauer 1986; Ledig et al. 1998). The most recent census of the pines found only 220 (±20) mature trees remaining (Rogers et al. 2002). Although no records can be found of any census of the pines before the mid-1900s, an Italian horticulturist visiting the island in 1892 remarked that the all the northeast part of the island almost certainly had been clothed in dense pine forest (Moran 1996). By the mid-1960s, there were perhaps 400 trees (Bannister 1965b).The decline is the result of natural attrition

coupled with no regeneration—primarily due to the introduction of goats. Monterey pine grows in association with island live oak (*Quercus tomentella*) and the endemic Guadalupe Island fan palm (*Brahea edulis*). The Monterey pine forest occurs at the northern end of the island where there is more rainfall, less direct sunlight, and higher occurrence of fog banks than elsewhere on the island (Moran 1998). The pines grow on northwest slopes up to the crest of the ridges—presumably limited by drought stress on the hotter, drier, and fog-free southern aspects. Other species associated with the Monterey pines include the endemic Guadalupe cypress (*Cupressus guadalupensis* ssp. *guadalupensis*), island ceanothus (*Ceanothus insularis*), and island coffeeberry (*Rhamnus pirifolia*) (Axelrod 1980).

Cedros Island

Cedros Island lies about 23 km north of Punta Eugenia, the southernmost point of Bahía Sebastián Vizcaíno on the Pacific side of Baja California. It is about 34 km long and 4 to 14 km wide (Rico C. 1997c). The area of pine forest is fairly consistently reported in the relevant literature as 140 ha. This consistency is probably an artifact of both few visits to and reports of the island and few reported indications of recent influences that would dramatically change habitat area. The pines occur in two main populations: inland towards the center of the island and at the northern end of the island, separated by approximately 14 km (Figure 9). Their locations on the island may be moisture limited (Libby et al. 1968) because conditions are dry—lower elevations receiving less than 250 mm of precipitation annually. However, fogs and mist are common at higher elevations (Perry 1991).

Formation of the island has been described as due to a series of subductions—rock plates are driven beneath other plates, causing uplifting and debris distribution. An early subduction event in the late Jurassic-early Cretaceous was later followed by an uplift of three major structural blocks in the late Pliocene along a new set of faults. A general uplift during more recent Pliocene and Pleistocene, accompanied by development of marine terraces, created the current topography (Kilmer 1977).

The vegetation on the island is diverse, even in the dry southern areas, and includes perhaps 15 endemic species and varieties (Oberbauer 1986). The desert canyons contain such shrubs as the silver-leaved sunflower (*Viguiera lanata*), elephant trees or torote (*Pachycormus discolor*), bursage (*Ambrosia chenopodiifolia*), and the Cedros sage (*Salvia cedrosensis*) (Oberbauer 1986).

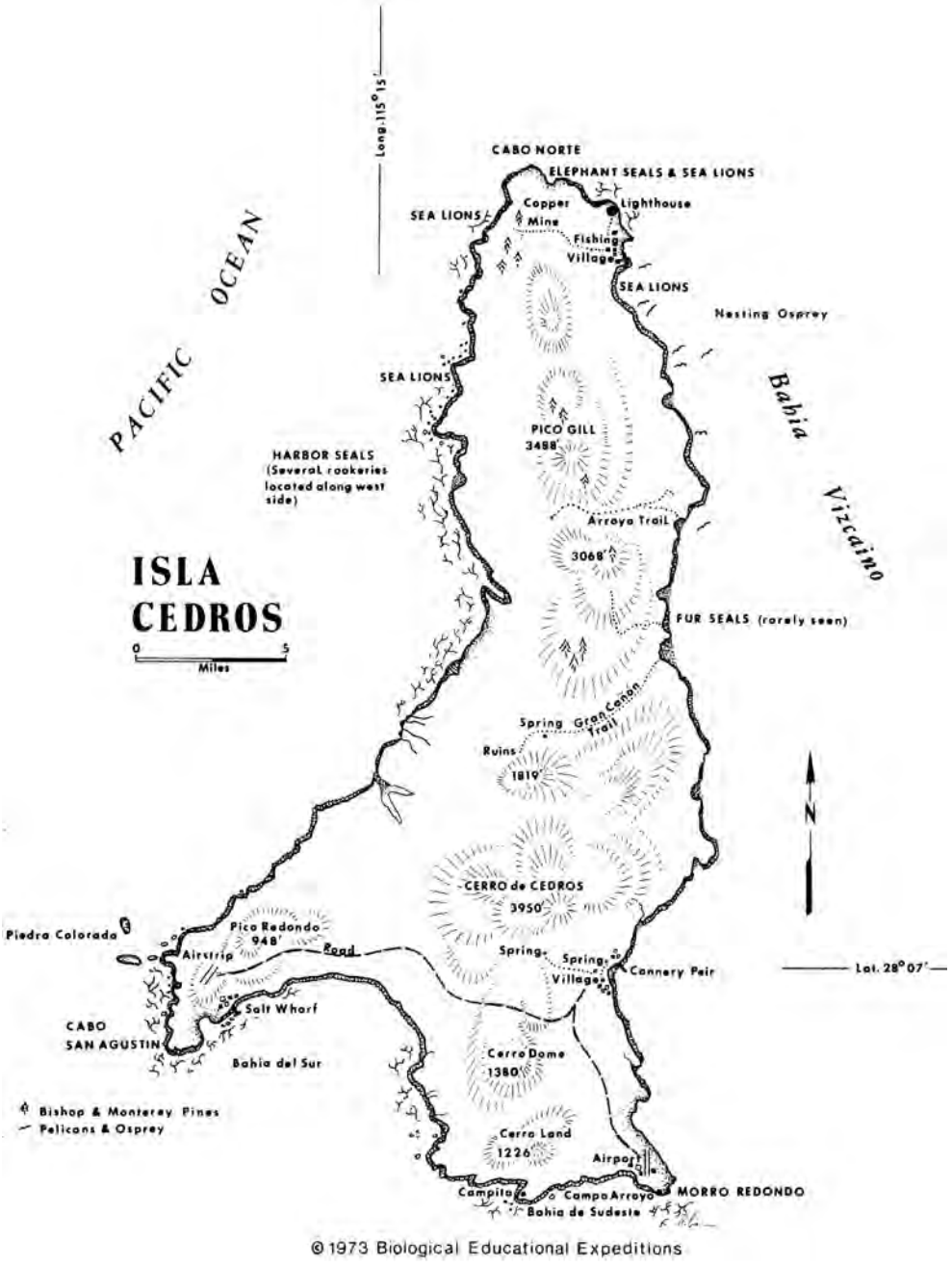


Figure 9. Map of Cedros Island (Bostic 1975). [Illustration credit: Robert Crim, Biological Education Expeditions, Inc., used by permission of Biological Education Expeditions, Inc.]

No census has been taken on the Monterey pines here—their numbers are far greater than those on Guadalupe Island—and no comprehensive map of their distribution has been made. Some general maps of the pines, based on a 1964 visit (reported in Bannister 1965b), indicate that the southern population—approximately half the area of the northern population—is mainly distributed along the windward side of the main ridge running north from Cedros Mountain. A few small stands have been noted several kilometers from the main forest area, with a total pine forest area of perhaps 130 ha (Bannister 1965b). The northern population is also mainly distributed along ridges, and notes from the 1964 visit indicate more mature trees and less recent reproduction as compared with the southern population. Similar to the southern population, there are also several stands apart from the main forest area. In both the southern and northern populations, outlying stands are reported to be less dense and composed of more mature trees than the main forest areas, presumably a function of having escaped more recent fires (Libby et al. 1968). This observation is consistent with that from a 2001 expedition (Box 3): the main northern and southern stands were composed of many, fairly young, trees. A small population, disjunct from and north of the southern stand, had the most mature pines seen on that trip. The small size, and apparently young age, of many of the pines, together with some direct fire scar and charred snag observations, suggested recent fires on Cedros Island.

The island is owned by the federal government of Mexico and home to approximately 4500 inhabitants (CONABIO 2000). It has no specific protection, although it lies close to a natural protected area in Baja California called 'Valle de los Cirios' and so receives some supervision (J.J. Vargas-Hernández, pers. comm.). Cedros Island is considered an important area for bird conservation by CONABIO.

Box 3. Biological expedition to Guadalupe and Cedros Islands, Mexico, May 2001.

A multinational group of 14 scientists and conservationists participated in an expedition from May 12 through 24, 2001 to secure cones from Monterey pine trees on Guadalupe and Cedros Islands, Mexico for conservation, restoration, and research purposes. Organized by the author with the University of California (UC) Genetic Resources Conservation Program (GRCP) in collaboration with two scientists from the Colegio de Postgraduados in Montecillo, Mexico (J. Jesús Vargas-Hernández and Jesús J. Guerra-Santos) and A. Colin Matheson from CSIRO in Canberra, Australia, this trip was motivated by concern for the status of the pines, especially on Guadalupe Island where there has been no successful pine regeneration for decades. The purpose was to collect seed from the pines, map the location and make detailed descriptions of the sampled trees, and determine the status of the pines. Genetic research on these seeds can provide insight into the genetic relationships among the trees, determine the level of inbreeding, and provide direction for restoration efforts.

Funding for the trip came from a variety of sources including UC MEXUS (a UC program aimed at increasing collaboration between UC and Mexican scientists); the Australian Department of Industry, Science, and Resources; the Australian CSIRO; UC GRCP; the Food and Agriculture Organization of the United Nations; and personal contributions from several of the participants. In addition to the four principal investigators, the participants included five conservation-spirited Americans who provided various resources for the expedition (David Bates, Richard Hawley, Carl Jackovich, Laurie Lippitt, and Nicole Nedeff), two Mexican scientists (Javier López Upton, also from the Colegio, and Ernesto Franco, California State University Monterey Bay and CICESE, Mexico), an American graduate student from UC Berkeley (Tadashi Moody), and two Mexican conservation authorities from the Área de Protección de Flora y Fauna (Ana Ma. Padilla Villavicencio and Celerino Montes). The author is Canadian, making this a multinational, Pacific Rim collaborative activity.

The expedition team reached Guadalupe Island on May 13 aboard the *Searcher*. This chartered vessel from San Diego, California and its crew served as home and support system for the team while they collected from and described the remaining pines. Assisted by local fishermen and a rancher who was on the island herding and transporting goats, the team was given a ride from the landing point at the south end of the island to the north end of the island, at the base of the ridges where the pines occur. Over the next several days, the team walked for hours from base camp over difficult and steep terrain to the sparse array of trees, which sometimes were separated from one another by a kilometer or more. Using a GPS (global positioning system) unit, the team mapped the trees, described their condition, and secured cones. Professional climber Carl Jackovich improved the seed collection success by climbing trees that were beyond the reach of the pole pruners. Cones were not collected from all trees, primarily because of the inaccessible location of some, on very steep slopes. David Bates led a team to make a comprehensive census of all the pines. Not including the few seedlings noticed, his estimate was 220 ± 20, allowing for some that were undoubtedly obscured by slopes or fog.

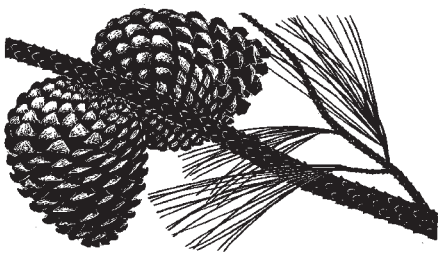
There was no definitive evidence that the pines here have contracted the introduced fungal disease (pitch canker) that has caused significant mortality in the pines along the California coast. All participants took considerable precautions to ensure that they did not inadvertently transmit the disease to these pines on their shoes or equipment. Samples of tree tissue were taken for laboratory analysis which has since confirmed that the disease was not present in the sampled trees. The pines seemed healthy, but were obviously nearing the end of their natural life span. With no young trees evident, the population seems headed for extinction without intervention.

After five days on Guadalupe Island, the team continued south to Cedros Island. Here, the pines have an entirely different character from their Guadalupe Island relatives and are more numerous. They still grow only in the upper elevations, along mountain ridges, and, in a few cases, in gorges of intermittent streams. But instead of individual and widely spaced trees, the pines here grow mostly in forest congregations, linked by smaller clusters of trees. There are several main populations that extend from the middle to the northern end of the island. Many of the pines are young and of the same age: indications that they have grown up quickly and uniformly after a fire. While goats are also present on this island, apparently as a result of deliberate release, they appear to pose no severe threat to the pines. The goat population has not thrived here as it has on Guadalupe Island.

Thanks to the contributions by many—particularly the participants themselves and the excellent support team—the trip was a success. The cones were deposited at a forest tree nursery of the Mexican Programa Nacional de Reforestación (PRONARE) in Ensenada and were later moved to a PRONARE facility in Mexicali. The seeds have been extracted and will remain at Mexicali until distributed to other locations for research and conservation purposes.

3

Current status of genetic information on Monterey pine



The genetic diversity information currently available for Monterey pine has been generated by four methodologies: 1) common-garden or provenance studies where differences in observable traits (e.g., phenotypic traits such as growth rate or insect resistance) are inferred to have a genetic basis because of the constancy of the environment (e.g., field or nursery trial) in which the plants are growing; 2) chemical composition studies, such as turpentine analysis; 3) allozyme studies; and 4) molecular studies of DNA or RNA. No matter which method has been used, there is much more information on genetic differences *among* the five populations than on genetic diversity *within* them. An additional source of information comes from descriptions of the pines *in situ*. Although phenotypic descriptions of trees in their native context do not necessarily reflect genetically based traits, a brief review of some phenotypic differences among the native populations is presented because these early observations provided clues about genetic differences which were often substantiated with subsequent genetic tests.

Different kinds of genetic information (or inferred genetic information) are appropriate for different issues or questions. For example, relationships between Monterey pine and other pine species (phylogeny) are perhaps better addressed by molecular and biochemical data than by morphological data (e.g., Wheeler and Guries 1982; Wheeler et al. 1983; Strauss and Doerksen 1990; Krupkin et al. 1996; Furman et al. 1997). Different DNA markers have differential strengths and weaknesses for the range of genetic questions. Microsatellite markers have proven useful in identifying among- and within-population genetic structure of forest tree species (e.g., Echt et al. 1998; Scotti et al. 1999); allozyme data continue to be useful in revealing levels of genetic diversity and genetic structure within and between populations. The great wealth of allozyme data for many forest tree species, particularly western conifers, allows the allozyme information on Monterey pine to be interpreted within an informed and comprehensive context. For some genetic questions—particularly those of amount or structure of genetic diversity—some context is required for interpretation such as the area of the genome that has been sampled and how genetic variability reflected by the particular method or marker varies across related taxa. Other questions, such as identification of foreign pollen or domestic cultivars, have a more restricted context for interpretation.

Phenotypic diversity

Phenotypic diversity—reflecting genetic and environmental influences and their interaction—is noted in early descriptions of Monterey pine. Considerable morphological diversity exists within Monterey pine, suggesting to some early taxonomists that these differences represented distinct species. One notable distinction between the island and mainland populations is the grouping of needles—generally grouped in fascicles of threes in the mainland trees and of twos in the island trees. The Cedros Island population, for example, was at one time called *Pinus muricata* D. Don or *P. muricata* var. *cedroensis* J.T. Howell (Moran 1996). Another characteristic with much variation within the species is cone morphology. Variation among populations is strikingly evident in average cone size (Figure 10). These differences have suggested several hypotheses. Population differences in cone size, cone symmetry, thickness of scales, and size and weight of seeds suggested that these characteristics are related to climate, and the length of the summer dry season in particular (Axelrod 1980). The differences among populations in the thickness of cone scales, cone attachment angles, and cone symmetry were suggested to be related to selective pressures from fire and squirrel predation (Linhart 1978).

Lindsay (1932) found the Cambria population to be distinguished from the other mainland populations in its larger

average cone size, faster height growth, better stem form, and tendency for foliage to be massed on the upper side of the side branches, giving a terraced appearance to the trees.

Considerable information is available on differences in needle and branch characteristics within and among the three mainland populations, based on trees directly sampled from the populations (Forde 1964b,c). Briefly, these studies showed that trees in the Cambria population, as compared with those in the Monterey population, have significantly longer and thicker needles with more widely spaced stomatal rows and marginal teeth. Trees from the Año Nuevo population are intermediate in these characteristics with the exception of the last characteristic: marginal teeth on needles of Año Nuevo and Monterey trees are significantly more narrowly spaced than on Cambria trees. Common-garden studies—that could differentiate between genetic and environmental effects—confirmed the existence of among-population differences in needle length and the observation that the Cambrian population has the longest needles. However, some disparities were noted between these results and the earlier field study. Specifically, the Monterey population was found to have longer needles than the Año Nuevo population, and there were no significant differences among populations in weight/length ratio of fascicles, indicating no population differences in needle thickness—in contrast to the findings of the earlier field study (Burdon and Low 1977).

Differentiation among populations of Monterey pine is also suggested by the geology and soils. Underlying the coastal California populations are different geologic substrates or soils that seem to confer some competitive advantage to the conifers over adjacent oak forests. The soils tend to be droughty or nutritionally poor. The unique substrates emphasize the fact that these populations represent island-like ecosystems, not just populations of trees (Barbour 1995).

Figure 10. Diversity in cone size among the five native populations of Monterey pine (Axelrod 1980, used by permission from University of California Press). Each cone represents the average size for that population. *Key:* 1 Cedros Island; 2 Guadalupe Island; 3 Monterey; 4 Año Nuevo; 5 Cambria.

Common-garden or provenance studies

Common-garden studies were established decades ago, many of them in Australia and New Zealand, and have since offered information on genetic diversity of many traits. There is evidence for substantial genetic differences among the five Monterey pine populations in their resistance to western gall rust, a disease caused by the fungus *Endocronartium harknessii* (Old et al. 1986). Specifically, the Guadalupe and Cedros Island populations are least susceptible. Of the three mainland populations, Año Nuevo is the most resistant. The island populations also are less susceptible to red band needle blight (Cobb and Libby 1968).

In glasshouse and field studies in Australia, considerable genetic variation in resistance to *Phytophthora cinnamomi* has been found both among and within populations of Monterey pine. Seedlings from the Cambria and Monterey populations showed the greatest degree of resistance. Seedlings from Año Nuevo and the two island populations generally were more susceptible (Butcher et al. 1984; Butcher and Stukely 1997). Also, there was large variation within the Monterey, Año Nuevo, and Guada-

lupe Island populations in family-level resistance (Butcher and Stukely 1997).

A California common-garden study containing clonal and seedling material from each of the three mainland populations showed that the Año Nuevo population suffered the least cold damage following an unusually cold 12-day period in December, 1972; the Cambria population showed the most damage; and the Monterey population had intermediate damage (Hood and Libby 1980). Subsequent studies have provided similar observations (Alazard and Destremau 1982; Burdon et al. 1992a).

The same common-garden study was also assessed for damage from black-tailed deer and porcupines—possibly a reflection of genetic differences in palatability. Significant differences in damage were seen among the three populations: the least porcupine damage was on trees from the Monterey population and the least deer damage (based on percentage of trees browsed) was to those from the Cambria population (Hood and Libby 1980).

Common-garden studies in New Zealand have been conducted since the 1950s, with significant new tests added in the mid-1960s and 1980. This long-term series allows insights into genetic differences of the populations expressed in a nonnative environment. In general, these studies suggest that the Año Nuevo and Monterey populations are better suited than the others to overall New Zealand conditions, with the caveat that Año Nuevo is much less adapted to phosphorus-deficient clay soils and better adapted to cold, snow-prone sites. In these same studies, the Cambria population has shown susceptibility to two foliage pathogens (*Dothistroma pini* and *Cyclaneusma minus*), shoot dieback, and frost and snow damage, but considerable tolerance to poor soils, and, in a Western Australian study, tolerance to *Phytophthora cinnamomi*. Trees from the Guadalupe Island population show modest overall adaptation to plantation conditions in New Zealand but have very straight stems and higher corewood density than the others. Similarly, trees from the Cedros Island population show less overall adaptation to these conditions than the mainland populations but interpopulation hybrids perform much better (Burdon et al. 1992a,b, 1997). The higher wood density of the Guadalupe Island population was also noted in a study in Australia—where island populations were noted to have higher wood density and thinner bark than mainland populations (Nicholls and Eldridge 1980). A summary of genetically based differences among populations as observed in these trials in New Zealand (with some supplementary information from other trials) is contained in Table 4. Note that the actual values for various populations (e.g., height superiority of one population versus another) are site dependent and thus may change were the trials to be located elsewhere. However, the fact of underlying genetic differences remains.

There are fewer reports of within-population genetic diversity but some of these show significant genetic differences among subpopulations. A physiological study suggests that, paradoxically, stands on coastal areas at Año Nuevo and Monterey have a lower salt tolerance as compared with inland stands in the same populations. No such differences were noted among the samples from the Cambria population but only three areas there were sampled. These results were explained as adaptations within subpopulations—the coastal areas at Año Nuevo and Monterey experiencing lower temperatures, lower evaporation, more frequent fog drip, and less salt accumulation within the soil profile than in areas further inland (Cromer et al. 1982). Common-garden studies in New Zealand show significant differences among five selected subpopulations of the Año Nuevo population in height growth (measured at 2.5 and 8 years), diameter, and incidence of forking (Burdon et al. 1992a). In this same study, genetic differences in branching pattern were noted among subpopulations of the Monterey population, and in 8-year height growth among subpopulations of the Cambria population. In this common-garden study, subpopulations were artificial groupings of sampled trees, based on locality, and hence may not have a clearly elucidated spatial genetic structure within populations. A series of eight provenance trials in New South Wales, Australia revealed significant height or basal area differences among some subpopulations within the three mainland populations (Johnson et al. 1997). Also, as noted above, there were considerable differences found within the populations (i.e., family-level) of Monterey, Año Nuevo, and Guadalupe Island in resistance to *Phytophthora cinnamomi* (Butcher and Stukely 1997). Genetic differences among families (i.e., open-pollinated progeny from the same female parent tree) have been noted for some seed and germination characteristics within the Cedros Island population (Quiroz V. 1998).

Chemical analyses

Additional genetic information comes from studies of turpentine composition (e.g., Bannister et al. 1962; Bannister and McDonald 1983) and seed protein (e.g., Murphy 1981) differences among the populations of Monterey pine. For both types of traits, considerable genetic diversity has been noted.

An early study of the turpentine composition of cortical oleoresin collected directly from trees of the three mainland populations showed differences in the proportion of alpha-pinene. Monterey and Cambria were quite similar in this feature, and different from the Año Nuevo sample (Bannister et al. 1962). However, because the trees were sampled directly from the forest, the results could not be strictly interpreted as genetic differences. In a later study, turpentine composition from samples from the two island populations showed differences between the two populations, as well as considerable differentiation from the mainland populations (Bannister and McDonald 1983). However, again, environmental effects could not be ruled out. More recently, Burdon et al. (1992d) provided more direct evidence of genetic differences in turpentine composition among populations with samples from planted trees in New Zealand field trials. In a comparison of Guadalupe Island material with that from the three mainland populations, clear differences were found among all populations in at least two of the monoterpenes assayed. When all monoterpenes were considered simultaneously, populations were again shown

as distinct, and Cambria and Monterey appeared the least different, consistent with the earlier (1962) observation. In a separate substudy within the same report, Cedros and Guadalupe samples were compared and strong differences were noted between the two island populations (Burdon et al. 1992d). Other studies have confirmed, using clonal material, the high degree of genetic control of monoterpene composition in this species (Burdon et al. 1992c).

Seed proteins from samples from each of the five Monterey pine populations have been compared using immunochemical assay techniques. Significant antigenic differences were noted between populations (Murphy 1981). These

Table 4. Summary of phenotypic characteristics of the native populations of Monterey pine in field trials in New Zealand (Burdon 1992). *Symbols:* + denotes superiority; – denotes inferiority; o denotes average; and • indicates no data were located.

		Population				
Attribute	**Weight of evidence†**	**Año Nuevo**	**Monterey**	**Cambria**	**Guadalupe Island**	**Cedros Island**
Growth rate	a	+	+	+	–	– –
Ease of transplanting	bc	+	o	–	+(+)	– –
Resistance/tolerance to:						
Frost	b	+ +	+	–	o?	– –
Snow damage	c	+	o	–	•	•
Boron deficiency	b	+	+	+	– –	– –
Phosphorus deficiency	b	–	+ +	+ +	–?	– –
Dothistroma pini	ab	+ +	+ +	– –	o	– –
Cyclaneusma minus	a	+	+ +	– –	–	– –?
Diplodia pinea	b	+ +	+ +	– –	– –	–
Phytophthora cinnamomi	b	– –	+	+ +	•	•
Endocronartium harknessii	b	+	–	– –	+ +	+
Pineus pini	c	+	+	–	– –	+
Damage by mammals:						
Deer/rabbit browse	bc	o	o	o	–	+
Deer browse	b	–	o	+	•	•
Porcupines	b	+	+	– –	—	—
Soil salinity	bc	o	+	+ +	– –	-
Tree form:						
Overall	a	– –	o	+	+	– –
Stem straightness	a	– –	o	+	+ +	+
Forking (lack):						
Early	a	– –	o	o	+ +	+
Later		–	+	+	–	–
Branch habit:						
Early	a	– –	o	o	+ +	+
Later		–	+	+	–	–
Butt straightness	a	– –	– –	+	+ +	+ +
Wood properties:						
Basic density	a	–	o	– –	+ +	+ +
Compression wood (lack)	c	–	o	+	o?	?
Grain spirality (lack)	c	–	+	+	–	?

†*Key:* **a** denotes a large body of solid experimental evidence (many sites); **b** denotes good experimental evidence but from limited number of sites/pot trials; **c** denotes slender evidence; and two letters denote intermediate weights of evidence.

differences strongly correlate with cone-length differences among populations. Also, these data suggest that the two island populations are more closely related to each other than to the mainland populations (Murphy 1981).

Allozyme diversity

The tremendous amount of allozyme literature for plant species indicates that pine species are among the most genetically diverse plants (e.g., Hamrick et al. 1979). Allozyme studies may reasonably be interpreted as reflecting relative levels of whole genome variation (e.g., Woodruff and Gall 1992). Not atypically, different statistics and different studies show somewhat different patterns (Table 5). For example, depending on which statistic and which study are considered, the Monterey, Cambria, or Cedros population has the highest diversity. For most allozyme measures of genetic diversity, though, the Monterey population shows the highest genetic diversity.

Compared with other western conifers, the genetic diversity of Monterey pine, as measured by certain allozyme statistics, is modest to average (Table 6). Overall genetic diversity (Nei 1973), including monomorphic loci, is estimated as H_t=0.117 (Moran et al. 1988). However, as compared with other western pine species, the within-species diversity is mid-range. As compared with other California closed-cone pines (knobcone, H_t=0.087, Strauss and Conkle 1986; bishop, H_t=0.085, Millar 1983), it is high.

Expected heterozygosity (H_e) under Hardy-Weinberg equilibrium ranges from 0 to approximately 0.33 for the 48 pine species for which data are available for 10 or more allozyme loci (Ledig 1998). The modal value lies between 0.13 and 0.16. The H_e values from studies of Monterey pine (0.098, Moran et al. 1988; 0.127, Plessas and Strauss 1986; 0.141, Millar et al. 1988) show both that genetic estimates can vary considerably depending on sampling design and that Monterey pine lies in the normal (modal) range for pine species generally. These values suggest that most individuals of Monterey pine are expected to be heterozygous at about 10 to 14% of their loci (not adjusting for population differences).

Table 5. Allozyme diversity for the native populations of Monterey pine from three studies: number of trees sampled per population (N), mean number of alleles per locus (A), percent polymorphic† loci (P), and expected heterozygosity (H_e).

Population	N	A	P	H_e
Moran et al. 1988				
Año Nuevo	50	1.47	33.1	0.088
Monterey	72	1.74	50.5	0.097
Cambria	50	1.58	38.7	0.110
Guadalupe Island	50	1.46	35.5	0.089
Cedros Island	50	1.56	38.7	0.092
Millar et al. 1988				
Año Nuevo	15	1.8	44	0.13
Monterey	15	2.4	91	0.15
Cambria	15	1.8	50	0.14
Guadalupe Island	15	1.7	47	0.13
Cedros Island	14	2.0	56	0.16
Plessas and Strauss 1986				
Año Nuevo	96	1.62	29.8	0.125
Monterey	77	1.87	32.4	0.122
Cambria	84	1.78	37.9	0.131

†With the exception of data from Plessas and Strauss, the criterion of polymorphism is 99%, meaning a locus must have a second allele with at least a frequency of 1% for that locus to be considered polymorphic. For the Plessas and Strauss data, the criterion is 95%, thus these data are an underestimate relative to the other data in the table.

Molecular diversity

Monterey pine has a fairly large genome of approximately 10^{10} bp (Smith and Devey 1994). As compared with 82 other pine species for which nuclear DNA content has been recorded, Monterey pine is average (Murray et al. 2001). For example, Monterey pine has considerably more nuclear DNA than pitch pine (*Pinus rigida*) but much less than sugar pine (*P. lambertiana*) (Dhillon 1980). Montery pine at 22.00 pg of nuclear DNA (Murray 1998) is intermediate to bishop pine (20.28 pg, Hall et al. 2000) and knobcone pine (25.05 pg, Murray 1998).

Many of the approaches for assessing diversity at the DNA molecular level have been employed with Monterey pine. Three of the most useful types of markers have been RAPDs (random amplified polymorphic DNA markers), RFLPs (restriction fragment length polymorphism markers), and microsatellites (simple sequence repeat markers). Genetic linkage maps have been constructed for Monterey pine using all three (Devey et al. 1996, 1999).

RAPD markers have revealed somewhat higher genetic diversity and stronger among-population differentiation than an analysis with allozyme markers carried out with the same populations (Wu et al. 1999; Table 7). In this study, only trees from Año Nuevo, Cambria, and Guadalupe Island were included. Other studies of different plant species support the observation that RAPD data reveal more genetic diversity than allozyme data. This may result from several conditions (reviewed by Aagaard et al. 1995), including the reasoning that allozyme data reflect only a very limited part of the plant genome and a part that may evolve more slowly or be under stronger selection pressures than the genome at large (Wu et al. 1999).

A study of microsatellite sequences confirmed the finding that dinucleotide repeats are abundant in the Monterey pine genome, albeit seemingly less frequent than has been reported for some other species (Smith and Devey 1994). The reasonably high levels of heterozygosity found in two microsatellite loci provide a basis for developing a fingerprinting strategy for Monterey pine.

No significant chloroplast DNA diversity was found among the populations (Hong et al. 1993). However, chlo-

roplast DNA in general is highly conserved and thus may not be a sensitive marker for distinguishing populations within species.

Population genetic structure

Genetic structure—the pattern of distribution of genetic diversity within and among populations—is important in conservation planning because it defines the rate and spatial scale at which populations can evolve in response to environmental perturbations (Porter 1999). Genetic structure is, to a large extent, spatial structure. Most plant populations have substantial spatial structure—limitations in the distances that individuals (or propagules) disperse will result in relatives mating due to close proximity and consequently the buildup of genetic isolation by distance (e.g., Epperson and Li 1997).

Genetic structure (often measured with the statistic F_{ST}) is generally increased by local selection and genetic drift and decreased by gene flow. Wright (1931) derived an equation to express the opposing relationship between gene flow and genetic drift ($F_{ST} = \frac{1}{4N_e m + 1}$). In this relationship, m is the number of migrants per generation (a measure of gene flow) and Ne is the effective population size. It can be seen that even a low amount of gene flow would greatly reduce the divergence among populations caused by genetic drift. However, this equation assumes that the populations are at equilibrium—a condition not often satisfied in nature. Others have attempted to evaluate the relative historical influences of gene flow and drift on regional population structure by comparing the relationship between genetic and geographic distances, with good success (e.g., Hutchison and Templeton 1999).

Genetic structure is often interpreted as a function of genetic and ecological processes including natural selection in local environments, mating system, geographic distribution, seed dispersal mechanism (e.g., Hamrick et al. 1993), successional status, population size, and natural disturbance regime of habitat. These generalizations are supported by population genetic theory (e.g., Mitton 1995) and much allozyme literature (e.g., Hamrick and Godt 1989). However, a review of genetic structure studies across a range of plant species reveals many exceptions to expected genetic structure based on genecology, suggesting that genetic structure may be more a reflection of the contingencies of evolutionary history than ecology, life form, distribution, or breeding system (Rehfeldt 1997). This view is supported by a review of genetic differences among the populations of Monterey pine, many of which are not well (or at least, not easily) explained by natural selection, but are more likely a result of founder effects from repeated local extinctions and re-colonizations (Burdon et al. 1992a). These lessons caution us about infer-

Table 6. Allozyme diversity in western conifer species native to California: mean number of alleles per locus (A), percent polymorphic† loci (P), and expected heterozygosity (H_e).

Species	A	P	H_e	Reference
Thuja plicata	1.0	—	—	Copes 1981
Pinus torreyana	1.0	—	0	Ledig and Conkle 1983
Cupressus macrocarpa	1.2	61	—	Conkle 1987
P. muricata	1.5	25	0.077	Millar 1989
Sequoiadendron giganteum	1.5	50	—	Fins and Libby 1982
P. attenuata	1.6	40†	—	Wu et al. 1999
P. radiata	1.8	46	0.098	**Moran et al. 1988**
***P. radiata*‡**	1.8	48	—	**Wu et al. 1999**
P. radiata	—	58	0.141	**Millar et al. 1988**
Larix occidentalis	1.8	58	—	Jaquish and El-Kassaby
Chamæcyparis lawsoniana	1.9	65	—	Millar and Marshall 1991
Taxus brevifolia	2.0	68	—	Wheeler et al. 1995
P. ponderosa§	—	68	0.155	Niebling and Conkle 1990
Calocedrus decurrens	2.5	50	—	Harry 1984
P. albicaulis	2.6	85	—	Jorgensen and Hamrick 1997
P. contorta	2.7	89	0.185	Conkle 1981
	—	66	0.17	Yang and Yeh 1993
P. lambertiana	2.8	80	0.275	Conkle 1981
Sequoia sempervirens	3.1	92	—	Rogers 2000
Pseudotsuga menziesii	3.9	74	—	Conkle 1981

†With the exception of data for *P. radiata* from Wu et al., the criterion of polymorphism is 99%, meaning a locus must have a second allele with at least a frequency of 1% for that locus to be considered polymorphic. For the Wu et al. data, the criterion is 95%, thus these data are an underestimate relative to the other data in the table.

‡Calculated from samples of Cambria, Guadalupe, and Año Nuevo populations only.

§*P. ponderosa* var. *ponderosa.*

Table 7. Comparison of RAPD and allozyme markers in a study based on three native populations of Monterey pine (Año Nuevo, Cambria, Guadalupe Island): mean number of alleles per locus (A), percent polymorphic† loci (P), expected heterozygosity (H_e), and among-population differentiation (G_{ST}, Nei 1986) (Wu et al. 1999).

Marker	A	P	H_e	G_{ST}
Allozyme	1.76	48	0.14	0.12
RAPD	1.50	50	0.17	0.26

†The criterion of polymorphism is 95%, meaning a locus must have a second allele with at least a frequency of 5% for that locus to be considered polymorphic.

ring cause and effect relationships where only correlations exist. Evolutionary history, geographic distributions, population demographics, and their associated features must all be considered to understand the basis for specific genetic structures and then interpret this pattern for conservation purposes.

Genetic structure is often used as a means of identifying unique populations for conservation attention. Thus, attention is given to such measures as the proportion of total genetic variation that is due to among-population differences (G_{ST}, Nei 1973) and Nei's genetic distance between individual populations and others within the species (e.g., Jaquish and El-Kassaby 1998).

Genetic differentiation among populations of Monterey pine (based on allozymes) has been estimated as 16.2% of the total genetic diversity (Moran et al. 1988)—a rather large proportion compared with other western North American pine species (Table 8). In fact, the value of 16.2% for Monterey pine is among the highest values presented by Hamrick (1983) for conifers or by Ledig (1998) for pine species. Using Nei's genetic distance measure, the Cedros Island population is most strongly differentiated from the others, and the Monterey and Año Nuevo populations are most similar to one another. Genetic isolation by distance is suggested (r=0.88, P=0.05) if the Guadalupe Island population is excluded from the analysis (Moran et al. 1988).

These interpretations are largely, but not completely, mirrored by a similar allozyme study (Millar et al. 1988). Here, the five populations were strongly differentiated (13% diversity among populations) and the Cedros Island population was found to be the most genetically distant from all others. However, the loci assayed in this studied suggested that Monterey and Cambria were the most closely related pair of mainland populations.

These studies underscore the distinctiveness of the island populations. Indeed, both have been given varietal names, prior to most of the genetic studies, based on their substantial morphological differences from the mainland populations and each other (see Taxonomy section in Chapter 2).

Table 8. Estimates of proportion of total genetic variation among populations (PGV), based on allozyme data, in rangewide studies of western North American pine species.

Species	PGV	Reference
	(%)	
Pinus albicaulis	3.4	Jorgensen and Hamrick 1997
P. longæva	3.8	Hiebert and Hamrick 1983
P. contorta	6.1	Wheeler and Guries 1982
P. attenuata	12.0	Millar et al. 1988
P. jeffreyi	13.8	Furnier and Adams 1986
P. monticola	15.0	Steinhoff et al. 1983
P. radiata	16.2	Moran et al. 1988
P. muricata	22.0	Millar et al. 1988
P. torreyana	100.0	Ledig and Conkle 1983

Additional perspectives on genetic structure come from studies of the cytoplasmic organelle genomes—mitochondrial and chloroplast DNA. We might expect studies based on mitochondrial DNA (mtDNA) to show stronger differentiation among populations possibly as a result of lower rates of sequence mutation, small effective population size, and limited gene flow for maternally inherited organelles (e.g., Birky 1988). Indeed, a recent study of mtDNA among the Año Nuevo, Cambria, and Guadalupe Island populations showed a strong level of population differentiation (G_{ST} = 0.79) (Wu, J. et al. 1998). This was considerably higher than a similar study conducted on Douglas-fir (Hong et al. 1995). Furthermore, this estimate of population differentiation for Monterey pine may have been an underestimate since the population that is apparently most strongly differentiated from the others—Cedros Island—was not included.

Fine-scale genetic structure, or genetic patterns *within* populations of Monterey pine, has not been well studied. The few available studies used few stratified samples per population and thus did not comprehensively explore possible structuring associated with local selection regimes (e.g., elevation, microclimate, and soil type). Strong local genetic structure associated with soil type has been noted in some other pine species. For example, abrupt changes in genetic variation are known in bishop pine due to changes in soil fertility (Millar 1983) and in ponderosa pine (*Pinus ponderosa*) due to serpentine/nonserpentine soils (Ledig 1998).

Some common-garden studies have, though, shown considerable differentiation among subpopulations of the natural populations. For example, significant differences in the incidence of stem forking among subpopulations were noted in a series of common-garden studies conducted in Chile (Jayawickrama and Balocchi 1993). Strong local differentiation based on monoterpene levels has been noted within the Año Nuevo population (Burdon et al. 1997a). The reason for this differentiation has not been determined. Some of the possible causes include local adaptation, genetic contamination from planted nonlocal trees, introgression with nearby knobcone pine, founder effects, or a combination of all of these. The study's authors favor the founder effect explanation. In this case, trees near the edge of the main population could have experienced a more restricted pollen cloud than those at the core, leading to some genetic differentiation over time (Burdon et al. 1997a).

Mating system effects

The mating system of plants usually refers to the level of inbreeding and outcrossing. Monterey pine is largely outcrossing, typical of the genus. Given that neither spatial nor temporal separation of the sexes is strong (e.g., placement of male and female structures on the tree and timing of pollen shed and seed cone receptivity), that related trees tend to be clustered, and that self-incompatibility seems to be lacking in most species of pines, the level of outcrossing must be maintained by some other mechanisms. Partial self-sterility resulting from inbreeding depression may be a major part of the explanation for many pine species (Ledig 1998). In-

breeding depression may be expected in pine species because of the high frequency of recessive lethal genes that are found throughout the genus (Ledig 1998). Of course, inbreeding depression can have a variety of expressions, not all of them the result of poor self-fertility due to recessive lethals. The expression of deleterious but nonlethal genes can be manifest as low viability in offspring that result from self-fertilization, for example (R.D. Burdon, pers. comm.).

A recent study suggests that the overall outcrossing rate for Monterey pine may actually be quite low relative to many other conifers. The overall rate estimated from samples from the five populations was 0.75, and for the island populations was even lower: 0.67 and 0.45. The lower outcrossing rates observed in the island samples could, in theory, be a result of less outcross pollen reaching the seed cones or lower numbers of embryonic lethal equivalents relative to mainland populations (Savolainen et al. 2002).

There is considerable evidence of inbreeding depression in Monterey pine, from lowered seed viability, to slower growth rates among seedlings, to smaller heights and diameters of more mature trees. For example, there is evidence of lower viability of selfed embryos relative to outcrossed—one study showing approximately 40% filled seed in self-pollinated cones versus 80% filled seed in open-pollinated cones (Griffin and Lindgren 1985). The reduction in proportion of full seed after selfing is due to embryonic mortality, because conifers have no self-incompatibility system (Savolainen 1994). However, the selfing effect shown in that study is less dramatic than that found in some other pine species. For example, viability is reduced from 90.5% (open-pollinated) to 14.4% (self-pollinated) in piñon pine (*Pinus edulis*) (reviewed in Lanner 1998). In a controlled-pollination study, there were significantly fewer selfed seedlings produced than expected. This could have been the result of either lowered fertilization success with self pollen or reduced survival of inbred embryos (Matheson 1980). More recently, a single recessive lethal allele, associated with the death of Monterey pine seedlings (progeny of selfing) in their first month after germination, has been identified (Kuang et al. 1998).

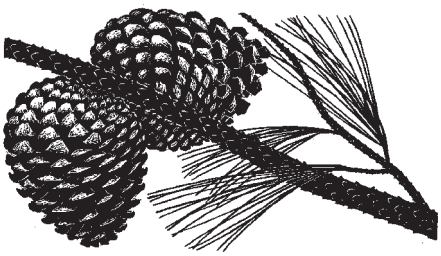
Nursery and field studies conducted in New Zealand, in which comparisons were made between artificially cross-pollinated and selfed progeny of Monterey pine, provided further evidence that selfing can be detrimental. Selfed progeny were generally slower growing, had more crooked stems, displayed less desirable branching habit, and were more susceptible to needle diseases as compared with the cross-pollinated progeny (Wilcox 1983).

More evidence of selection against selfed genotypes in Monterey pine is apparent from a study that compared genotypes from embryos, seedlings, and more mature trees. In this allozyme study, homozygosity (i.e., indicative of selfing) is highest at the embryo stage, less at the sapling stage, and least in mature trees (Plessas and Strauss 1986). In another comparison of inbred (selfed) and outcrossed seedlings, the inbred genotypes grew only 80 to 90% as well as the outcrossed genotypes over an 8-year period (Pawsey 1964). The effects of inbreeding on growth were measured over 13 years in a field study of pedigreed Monterey pine in Australia (Wu, H.X. et al. 1998). Outcrossed material was compared with full siblings, half-sib matings, and first- and second-generation selfs. Inbreeding depression was shown to be a dynamic process, being greatest at the initial stage of stand development (four years), lessening for several years, and then increasing again with a secondary peak at the end of the study (13 years). In summary, in pines in general and Monterey pine more specifically, there is a fairly high expected true genetic load—which would tend to lead to inbreeding depression and drive the species towards outcrossing.

Understanding the genetic basis of inbreeding depression is important for appropriate conservation decisions. For Monterey pine, we do not know how many loci mutate to lethals. We do not know whether inbreeding depression is due to a few highly deleterious alleles or a large number of less deleterious alleles. If the former, then the unfavorable alleles could be quickly purged; if the latter, they could become fixed in the population (Savolainen 1994). Understanding the nature of the genetic load in Monterey pine, then, is critical to choosing the appropriate management response for inbred populations and for managing risk in the others.

4

Status of conservation for Monterey pine



The range of genetic conservation activities is traditionally divided into two basic approaches: *in situ* and *ex situ* methods. *In situ* conservation has been defined as the continuing maintenance of an existing, wild population within the community of which it forms a part, in the environment to which it is adapted (Plucknett and Horne 1992). *In situ* genetic conservation is conservation of genetic resources on site—in the natural and original population, on the site formerly occupied by that population, or on the site where genetic resources of a particular population developed their distinctive properties. Thus, this approach involves preserving not only associated flora, fauna, and ecosystem processes but maintaining the populations within a dynamic environment in which the genetic variation can continue to respond to natural influences. *Ex situ* conservation refers to the suite of activities that involve removing genetic material from the natural populations and maintaining it outside of the natural habitat in such conditions as seed banks, clone banks, seed orchards, or plantations. Both types of conservation are dynamic—the genetic resources change over time—but differ in the degree and influences of change. *In situ* genetic conservation favors genetic changes that are related to natural selection and regeneration. Genetic changes in *ex situ* reserves may be more artificial (e.g., loss of seed viability over time in seed banks, artificial selection in nurseries). However, this distinction is not absolute. For example, a plantation that is allowed to regenerate naturally could be considered an *ex situ* reserve yet still respond to natural selection.

A critical feature of the *in situ* approach is the conservation of those associated populations and species, those natural disturbances, and those underlying processes that work to maintain genetic structure and diversity within a normal range of variation. Not only is an understanding of these coevolved organisms and processes important to the effective genetic conservation of the target species, but, by safeguarding the opportunity to understand the web of ecological interactions similar to those under which Monterey pine evolved, there may be some valuable guidance for silvicultural, breeding, and genetic engineering efforts of those with interests in the commercial values of Monterey pine (e.g., Tewksbury et al. 1999). Without concurrent conservation of the pine forest ecological community, adult plants may be maintained for some time, but genetic diversity in future generations may be compromised. A case in point is the dawn redwood (*Metasequoia glyptostroboides*) in China, which has been protected as a species since the 1940s but without the attendant protection of its habitat. As a result, ongoing human activities have impacted regeneration such that only mature trees—perhaps the last generation—remain (Barbour 1995).

The focus of this report is on *in situ* genetic conservation. However, given that a comprehensive and effective genetic conservation program should embrace both types of conservation methods, *ex situ* conservation will also be reviewed and considered—to the extent that it enhances the goals of *in situ* genetic conservation. That latter caveat is important: given the tremendous and historical economic importance of Monterey pine, there are many genetic collections of Monterey pine worldwide, in various life forms and degrees of separation from the original collections. A comprehensive review of all of these reserves is far beyond the scope or intent of this report. Many, perhaps most, of these collections would have little or no value to *in situ* conservation goals. The treatment of *ex situ* conservation in this report will be limited to those collections that could play a supportive role in *in situ* conservation or restoration.

Ex situ genetic collections are an important parallel conservation activity to the conservation of natural populations *in situ*. *Ex situ* collections can play a variety of roles including conservation support, research, education, and commercial applications. To play a meaningful support role for

in situ conservation, however, genetic collections should represent the genetic diversity within the species or target populations, maintain the genetic diversity (e.g., seed life) over long periods of time, and be accompanied by strategies for using such collections to establish self-sustaining populations under natural conditions (e.g., Guerrant and Pavlik 1997).

Individually, *ex situ* reserves are ephemeral and vulnerable to loss. Some *ex situ* genetic resources of Monterey pine have been lost due to lack of funding (e.g., Guadalupe Island nursery, Ledig et al. 1998; Monterey pine collections at the University of California, Libby 1990). Others have been reduced or lost due to more natural disasters.

Many weaknesses in relying on *ex situ* collections for genetic conservation have been cited. A major problem is the lack of knowledge about how to sample genetic diversity appropriately—how it is distributed within the population and what alleles may be useful in future and uncertain environments. It has been suggested that there are declining increments of genetic variation collected for increasing sample size. However, under neutral theory, any allele no matter how rare may become evolutionarily significant (Hamilton 1994). Some types of rare alleles may confer large fitness advantages under conditions of frequency-dependent selection (e.g., Holsinger and Gottlieb 1991). Thus, the sampling design and intensity required to represent adequately the genetic diversity of a species have not been convincingly established.

In situ conservation is critical: it cannot be replaced with *ex situ* conservation activities. The purpose of *in situ* conservation is to maintain the evolutionary genetic adaptability of populations and species over many generations (Koski et al. 1997). This approach is the only means of achieving both genetic conservation objectives: maintaining the amount and the structure of genetic diversity. Therefore, genetic reserves are selected and managed for genetic conservation purposes, typically chosen to reflect the range and spatial structure of genetic diversity within a species (and thus, reserves are chosen to be representative of areas that are genetically differentiated). The reserves are sufficiently large to harbor effective populations of a size that would not encourage inbreeding.

Status of *in situ* reserves

Current Monterey pine protected areas have not been selected with genetic values in mind, and thus do not necessarily contain representative genetic variation, represent sufficient habitat size or effective population size, or reflect conditions that allow ongoing regeneration and adaptation. Thus, current protected areas are not necessarily *in situ* genetic reserves, but some may offer the potential for including genetic values in their management.

The protected areas described in this section are those areas that have some official status—conferred by law, agency objectives, or management policy of the landholder—that restricts direct impacts on the Monterey pine forests, such as removal of trees for any other but conservation-related purposes. However, restrictions on the type of land use do not in themselves necessarily confer protection of genetic integrity. For example, nonlocal Monterey pine trees, planted outside of but close to a reserve, can still be a source of genetic contamination to the *in situ* reserves. Some forms of recreation may also be incompatible with conservation objectives. In most reserves, the natural processes controlling the ecosystem's composition and structure may not be restorable if degradation has proceeded too far (Cropper 1993). Data from South Africa on the pressures causing extinction or threatening the survival of a species indicate that even after creating a reserve, over half of the threats are likely to continue (Hall et al. 1980). Equivalent data from Australia suggest that about half of threats are likely to continue after reserve status has been conferred (Leigh et al. 1984). Accordingly, genetic reserves must be selected with genetic diversity and structure, ecosystem health, and restoration potential in mind.

Averaged over four native populations, approximately 25% of the extant Monterey pine area has some kind of protected status. This figure excludes Guadalupe Island because of the few trees there and difficulty in converting this to area. These protected areas are not evenly distributed over the native populations. For example, the pine population on Cedros Island has no specific protection. In contrast, the California populations each have some protected area that ranges from approximately 3% to perhaps 45% of their total respective pine forest area. However, there is no standard here for 'protected area' and hence little comparability among populations for this value. Some protected areas are simply narrow greenbelt areas or small parks, or highly developed or degraded areas that conserve few genetic values. Guadalupe Island has protected status but there are grave problems there with invasive exotic species—both plant and animal. Similarly, some areas that currently do not have protection may be more suitable as genetic conservation areas than some protected areas. More information is required to ascertain which currently protected areas may also serve as genetic conservation areas. More detailed information on each of the Monterey pine populations follows.

Año Nuevo

Approximately 12 ha have some kind of protected status. Using a total pine forest area of 400 ha, this translates to three percent. In addition, a large, privately owned ranch in the area—the Swanton Pacific Ranch—was donated to California Polytechnic State University in 1993 to be managed for educational purposes. A mixture of agricultural and forested areas, much of the forest is dominated by coast redwoods and Douglas-fir. There is also a significant component of Monterey pine, but separating this from the redwood and Douglas-fir forest type is subjective. There are perhaps 50 ha that contain some natural Monterey pine forest (W.R. Mark, pers. comm.). Because harvesting is included in the management practices, and educational value is a primary determinant in property management, this property has not been included within the protected area calculation for the Año Nuevo population. Nevertheless, it is owned and managed by a public institution and may have some conservation value using different criteria.

Most of the Monterey pine forest here is privately owned. There has been some planting of nonnative trees in this population. The Big Creek Lumber Company and others have planted some trees in this area for forestry purposes—some with local origins, but others from seedlings or clones from New Zealand or other nonnative sources (Libby 1990). Approximately 4 ha of Monterey pine forest are protected within Año Nuevo State Reserve and Park, along the coast. The pine trees here, often with a prostrate phenotype, have been particularly affected by pitch canker and mortality is high (B.D. West-Bourke, pers. comm.). In the only other publicly owned Monterey pine forest here—approximately 8 ha within the Big Basin Redwoods State Park—Monterey pines grow together with knobcone pine along ridgetops towards the eastern (inland) extent of Monterey pine's natural range. Natural interspecific hybrids *(P. attenuata* × *P. radiata*), and advanced generations of these hybrids, have been observed in and close to this same area (B.D. West-Bourke, pers. comm.; Griffin and Critchfield 1972).

Monterey

According to a comprehensive review of this population conducted in 1996 (Jones & Stokes Associates, Inc. 1996), approximately 22% of the current Monterey pine area had some kind of protected status. The protected area then consisted of approximately 20 properties, collectively amounting to about 849 ha, and existed as undeveloped pine forest in parks, open spaces, and scenic easements (Jones & Stokes Associates, Inc. 1996). The purchase in 2002 of a previously privately owned ranch (the 'Palo Corona Ranch'), by the Big Sur Land Trust and The Nature Conservancy, added approximately 62 ha of Monterey pine forest to the total protected area (L.W. Overtree, pers. comm.). Therefore, this new area brings the portion of forest with protected status to approximately 24% for the Monterey population. Ownership of the protected areas is diverse: state, county, and city governments; land trusts; and foundations. Management regimes and usage patterns are equally diverse. Most properties are essentially noncontiguous and many are surrounded by urban areas. None have been selected for, or managed as, genetic reserves. Again, protected status is not synonymous with natural or undisturbed condition. Many of the protected areas have been previously harvested, affected by pitch canker, planted with nonlocal Monterey pine, invaded by exotic invasive species, or affected by other management activities.

One assessment uses a combination of vegetation type, soil development, and climate to suggest a stratification system for selecting ecological reserve types for Monterey pine in the Monterey area (Jones & Stokes Associates, Inc. 1996). Of the 14 categories developed using this system (including an 'unknown' category for unclassified Monterey pine forests), it was determined that only three categories (prequaternary shale, prequaternary granitic, and other types) had sufficient reserves. Whether this classification system is an adequate proxy for within-population genetic structure has yet to be tested.

Cambria

Until recently, only approximately 35 ha within this Monterey pine population had some kind of protected status. At time of publication of this report, approximately 430 ha (48% or less of the total forest area, depending on which estimate for total forest area is used) have some form of protection. Purchases, acquisitions, and conservation easements of forest by landtrusts, environmental organizations, the University of California, and others during 1999–2000 increased the amount of protected area dramatically. Recently, The Nature Conservancy purchased a conservation easement on a 590-ha parcel, formerly known as the 'CT Ranch' and more recently referred to as the Cambria Coast Ranch. Of this area, approximately 325 ha are Monterey pine forest (K.W. Smith, pers. comm.). Another area, with approximately 28 ha of pines and known as the 'East-West Ranch', was purchased as a park. The University of California's Natural Reserve System has signed a memorandum of understanding (MOU) with the private owner of a pine forest property (approximately 162 ha of which perhaps ⅓ is pine forest) to manage the property as a reserve. The property is known as the Kenneth S. Norris Rancho Marino Reserve (D.C. Canestro, pers. comm.). Greenspace—The Cambria Land Trust recently purchased an additional 5 ha of pine forest (R.H. Hawley, pers. comm.).

The Rancho Marino Reserve, privately owned, will be managed as a University of California reserve during the agreement period—until April 2006. After this period, the reserve status is uncertain (D.C. Canestro, pers. comm.). Exact pine forest coverage is somewhat uncertain, but estimated at 46 ha. The pine forest canopy is fairly open and no recent fires (since early- to mid-1900s) have been recorded (M.R. Stromberg, pers. comm.).

Prior to these recent acquisitions and agreements, the only pine forest area in the Cambria population over 20 ha in size that had some protection was at the San Simeon State Park with ownership and management by the California Department of Parks and Recreation. The park encompasses 220 ha of which approximately 30 ha are Monterey pine forest. Two notable pine forest types occur here, differentiated by aspect, elevation, soil type, moisture regime, tree age and density, and co-dominant and understory vegetative species. Los Osos loam soils are found along the hilltop ridge, while San Simeon sandy loam is located along the north-facing slope. The elevation of the Monterey pine forest within the park ranges from 6 to 50 m. Fewer than 20 California live oak are scattered within the Monterey pines along the ridge top, while no oaks or other tree species are found with the Monterey pines on the north-facing slope. Sycamore (*Plantanus racemosa*), alder (*Alnus rubra*), black cottonwood *(Populus trichocarpa*), and willows (*Salix* spp.) are found in the riparian channel just below the pine forest. The shrub and herb layers are dominated by toyon (*Heteromeles arbutifolia*), canyon gooseberry (*Ribes menziesii*), poison oak (*Toxicodendron diversilobum*), and California blackberry (*Rubus ursinus*) (R.M. Orr, pers. comm.). Management policies include fire suppression and the most recent known fire

in this park was approximately 100 years ago (D.S. Hillyard, pers. comm.). There is no evidence of logging within this Monterey pine stand. Absence of logging history is confirmed by the Whitaker family—descendents of the Washburn family who owned this area prior to its conversion to state park status (S.A. Hamill, pers. comm.). Some planting of Monterey pine has occurred in nearby campground areas, including the Washburn (Upper) Campground and the San Simeon Creek Campground. Seedlings planted in the late 1980s were grown from seed collected in Cambria. A few Monterey pines that were planted earlier at the Washburn Campground were grown from local seed collections (H.W. Elliott, pers. comm.). Hence, there is no evidence that any planting of trees from outside of the Cambria population has occurred within or nearby this park. Some trees within this area are known overwintering sites for migrating Monarch butterflies.

Some smaller pine properties are owned and managed for conservation purposes by Greenspace—The Cambria Land Trust and the Land Conservancy of San Luis Obispo County. Collectively, these properties amount to approximately 4 to 5 ha (R.H. Hawley, pers. comm.).

Guadalupe Island

Although the island is officially under the control of the Ministry of the Interior, Mexico and is a protected area under SEMARNAT, Monterey pine has no specific protection here. Furthermore, there are no specific genetic reserves for Monterey pine. The number of mature trees has dropped dramatically since the informed estimate of 400 (±20) in 1964 (Bannister 1965b). Few seedlings were noted in the 1978 seed collection expedition and predation by goats introduced in the 19th century was continuing. The expedition in 2001 found approximately 220 (±20) trees (Rogers et al. 2002), all of them large and presumably very old. A few seedlings were seen, but are expected to be eaten by goats in the near future.

In situ conservation is challenging because of the stressful environmental conditions, continued heavy predation pressure from feral goats, and the small number of seed trees (Ledig et al. 1998). Key to the maintenance of remaining genetic diversity of the pines and the success of any natural regeneration or restoration efforts is the effective control or removal of the introduced goats. This proposal has been made at various times by different parties and may finally be making progress (Box 4). In the last two years, several thousand goats have been removed by Mexican ranchers and a binational not-for-profit organization has organized fence construction in some critical areas, including three exclosures around some of the pines.

Genetic research on a portion of the seed collected in 2001 is planned. This research will provide information on the remaining amount of genetic diversity and the level of inbreeding—information critical to appropriate conservation or restoration decisions for the pines. An additional question is whether or not microenvironmental conditions remain that would support natural regeneration in the pines. Given that small seedlings were seen in May 2001 in the immediate vicinity of mature trees, at least germination and initial growth is still possible. Fog condensation on pines produces a considerable amount of moisture, so natural regeneration may still be possible within the drip zone of existing trees as long as the goats are removed or controlled before the remaining trees die.

Cedros Island

The island, under the control of the Ministry of the Interior, Mexico, has no official overall protection or specific genetic reserves for Monterey pine. Two fires have occurred on Cedros Island between 1964 and 1978. According to a 1978 visit to the island, reproduction of Monterey pine following the fires was abundant, leaving a scientist to conclude that "Cedros Island remains the least endangered of the five native radiata populations." (Libby 1978). During the 2001 expedition (Box 3), recent regeneration was noted in much of the pine-covered area, suggesting another fire within the last decade. Although the pines are largely restricted to ridge-top areas, natural regeneration seems abundant. Genetic studies that are planned for some of the seeds collected in May 2001 may provide information on differences between the extremes in the pine range and levels of inbreeding within stands. There could be some influences on the genetic diversity and integrity of the Monterey pines on Cedros Island—

Box 4. Removal and control of goats on Guadalupe Island.

Many of the islands off Baja California have experienced negative effects from introduced mammals (Oberbauer 1986; McChesney and Tershy 1998). Guadalupe Island is particularly impacted. It has been recommended at various times that the harmful introduced fauna on Guadalupe Island be removed (e.g., Moran 1996; Rico C. 1997b). Since their introduction, the goat population has fluctuated dramatically, both from climatic and associated vegetation cycles, and from their slaughter. There are reports of over 34 000 goats being removed in 1971 alone—over 20 000 of those slaughtered and the rest removed live and taken to Ensenada, Mexico (Moran 1996). However, a goat-removal effort must be large scale, comprehensive, well funded, and well coordinated if it is to be effective in terms of island conservation.

In 1980 a small temporary nursery was fenced on the island to raise Monterey pine seedlings but none were planted in the natural stands because of lack of funding. By 1994, only six young trees survived in the nursery (Ledig et al. 1998).

Two ranchers from Sonora, Mexico recently obtained permits from SEMARNAT to remove goats from the island. As of October, 2001, several thousand have been removed (J.A. Sanchez Pacheco, pers. comm.). The Island Conservation and Ecology Group (ICEG)—a binational nonprofit organization dedicated to preventing extinctions and protecting natural processes on the more than 250 islands in northwest Mexico—has long-term plans for conservation on the island. One of the first steps they took, in 2001, was the erection of fenced enclosures to keep goats out of the most sensitive areas of the island until eradication can be realized. (J.A. Sanchez Pacheco, pers. comm.).

such as tree removal or browsing by introduced animals—but these are not obvious or extreme, nor have they seriously affected regeneration.

Status of e*x situ* reserves

Ex situ collections may be held in a variety of states: planted collections, stored seeds, preserved tissues, and DNA and DNA products. Seed collections are typically distinguished from field-based plantings, but both are dynamic states and experience selection pressures. The type of collection and its management or preservation conditions affect its utility in various conservation roles.

As previously mentioned, an exhaustive review of all the *ex situ* reserves of Monterey pine, worldwide, is beyond the scope and not supportive to the objectives of this report. First, such a review would be a massive undertaking in its own right: for example, a review of the genetic reserves of Monterey pine in Australia alone was an ambitious project (Eldridge 1998a,b). Second, and more importantly, only a fraction of the *ex situ* reserves worldwide would be relevant to the goals of *in situ* conservation in the native populations. However, it is important to describe the relevant portion of those reserves—particularly those that could be used in restoration of native populations or those that predate some of the current influences on the native populations and thus could be useful for comparison purposes (e.g., collections that predate pitch canker infestations or collections from trees on Guadalupe that are now dead). Finally, some of the domestic reserves are described in some detail to make a more public and permanent record of their location and composition. *Ex situ* reserves of Monterey pine are selectively reviewed here.

Seed collections

The first European record of a specimen of Monterey pine collected from mainland California dates back to the La Pérouse Expedition of the 1780s (Lavery and Mead 1998). Collections continued, sporadically, of all populations in the 1800s and early 1900s (Fielding 1957b; Eldridge 1998b). The collections recorded in this document are those that are relatively recent—so as to have still viable seed in storage or resulting trees in cultivation—and with fairly large samples (Table 9). Most of the seed collections and other *ex situ* reserves of Monterey pine meeting those criteria originated from a seed collection trip in 1978 primarily financed and organized by Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO) and trips organized and financed by the Central America and Mexico Coniferous Resources Cooperative (CAMCORE) in 1991 and 1992 (with some financial assistance from CSIRO).

CAMCORE and Carl Jackovich (with assistance from Laurie Lippitt) made a seed collection of the three mainland populations, thirty trees each, in March 1991. Seeds were distributed to Chile and South Africa and most of this material has been outplanted into the field for the purpose of genetic testing and conservation banks. Several recent seed collections (1999–2001) have been made from the mainland populations specifically for use in studies for resistance to pitch canker or for a source of possibly resistant seedlings for mitigation plantings in residential areas (R.H. Hawley, pers. comm.).

In general, Monterey pine seeds have good storage life under appropriate temperature and moisture conditions, particularly as compared with many deciduous tree species. Seed can perhaps be stored for decades without significant loss of viability (L.A. Lippitt, pers. comm.). However, a seed collection event does not provide safe, perpetual protection of genetic resources. "It is also risky to consider seed banks as 'insurance' against extinction in the wild. As with most insurance policies, you must continually pay the premiums in order to be covered. We must avoid thinking that seed banks are a one-time collecting effort if *ex situ* methods are to be useful in preserving genetic variation." (Hamilton 1994). Germination tests done in 1995 on seeds collected from the three mainland populations in 1978 and stored at CSIRO facilities (Australia) show a considerable reduction in germination from 1978 (91%) to 1995 (64%). There is also some suggestion of population variability in germination rate (or storability), with the Cambria population showing lower percentage germination in 1995 (54%) than either the Monterey (68%) or Año Nuevo (65%) populations (Eldridge 1998a). Because of notable differences in mean seed weight among the five populations, it is important to recognize these differences when estimating the number of seeds in any particular collection (Box 5).

Table 9. Major sampling events of Monterey pine populations since 1950 (adapted from Burdon 1984 and Eldridge 1997)†.

Population	1958	1961	1964	1978	1991	1992	2001
	—— (Number of trees sampled per year) ——						
Año Nuevo	–	100	–	179	30	–	–
Monterey	–	100	–	244	30	–	–
Cambria	–	100	–	99	30	–	–
Guadalupe Island	51	–	77	48	–	76	80
Cedros Island	–	–	100	51	–	–	101
Reference‡	1	2	3	4	5	6	7

†In addition, there have been several expeditions by Mexicans to Guadalupe Island and Cedros Island with the objective of collecting seeds for both potential restoration of the natural populations and *ex situ* conservation. During the period of 1975–1982, at least four expeditions to Guadalupe and Cedros Islands were made by faculty and students from the Universidad Autónoma Chapingo to collect seed from Monterey pine (Ravest Santos 1983). However, only a few seeds remain in storage (most probably with a very low germination percentage) from those collections (J.J. Vargas H., pers. comm.).

‡*Key:* 1 Moran (Bannister 1958); 2 Forde (Forde 1964); 3 Libby, Bannister, and Linhart (Libby et al. 1968); 4 Eldridge and others (Eldridge 1978a,b; Libby 1978); 5 CAMCORE (Dvorak 1991); 6 CAMCORE (Dvorak 1993); 7 Rogers, Matheson, Vargas Hernández, and Guerra Santos (Rogers et al. 2002)

Some seeds from the 1978 and 1990 seed collections remain in storage in various locations in California (Table 10). Late in 2000, individuals involved in maintenance, conservation, and research (e.g., USDA Forest Service, California Department of Forestry and Fire Protection (CDF), and University of California) met to discuss appropriate care and use policy for these remaining genetic collections in California. One outcome from this assembly was consolidation of some seed collections: the collection previously held at the Pacific Southwest Research Station of the USDA Forest Service (Albany, California) was transferred to the CDF seed storage facility at Davis, California.

Existing collections from Cedros and Guadalupe Islands are of particular interest because of the protected status of Guadalupe Island, the real or potential decline of the populations since previous collections, and the considerable expense involved in making new collections in these remote locations. The existing seed collections from Guadalupe Island, in particular, are in part irreplaceable because of the serious decline in parent trees and apparent genetic erosion since the 1978 collection. The fate of seeds from these islands that were taken to Australia and New Zealand is described in Box 6.

Seed collections can play a supportive role, but do not in themselves constitute a long-term genetic conservation strategy. "For sustained genetic conservation through stored seed, old seed would have to be grown out in plantations before it loses its viability (to prevent the seed store from becoming a seed morgue) and replaced with pure seed of equal genetic variability without loss of rare genes." (Eldridge 1998b).

Concern over introducing diseases either from or into the native populations of Monterey pine puts another constraint on the transfer of seed for *ex situ* conservation or restoration purposes. For example, the apparent nonexistence of pitch canker disease on Guadalupe and Cedros Islands suggests caution in moving seeds stored in California to those islands for any restoration activities. Risks are too high, currently, to allow seeds from California to be transferred to Australia or New Zealand.

CSIRO (Australia) has approximately 30 kg of Monterey pine seed in storage, with an average germination of 64% when last tested in 1995. A detailed description of the Monterey pine seed in storage in Australia (mainly from the 1978 seed collection event for the five native populations) is contained in a 1998 report (Eldridge 1998a). This collection contains more than 600 seedlots from the five populations. The report, commissioned by the CSIRO Australian Tree Seed Centre, contains recommendations on the best conservation strategy for this seed resource. A major recommendation is that the seed in storage be outplanted (with the exception of some seed in special long-term storage at Black Mountain, Canberra) within the next two to three years in well-designed genetic conservation plantings. It is suggested that, based on previous germination tests, germination may be low for many of the seedlots within as little as ten years. The seed in storage is considered irreplaceable—with the uncertainty of safe quarantine procedures for new seed collections from the native populations and the uncertainty of the current and future integrity of the genetic diversity in the native populations. Therefore, restoration of the current pure seed supplies may only be possible through expensive controlled pollinations of the outplanted seed reserves (Eldridge 1998a). A recent update of this report shows that seed germination percentage has declined dramatically—to about 37% (average of California populations) in 2001 (Eldridge 2002).

Box 5. Differences in mean seed weight among the five Monterey pine populations.

Differences in cone characteristics were one of the first differences noted among Monterey pine populations in native conditions. Later, controlled studies confirmed a genetic basis for such characteristics as cone dimensions, number of scales, and mean seed weight (e.g., Burdon and Low 1973). However, the relative (mean) seed weight among populations will vary according to the protocol for the sampling procedure (number of trees sampled per population and number of seeds weighed in total and per tree), moisture content (and so, maturity of the seed, fresh or stored, amount of time in storage, and storage conditions), environmental conditions, and other factors. Two reports on mean seed weight per population show almost a twofold difference in mean seed weight between the lightest and heaviest seed weights, but differ in the ranking of the (lower three) populations. Because both sets of weight estimates are based on seeds taken directly from the native populations, these ranking differences reflect differences in the composition of the samples (e.g., number of trees sampled per population and number of seeds weighed per tree) and possibly other factors such as those described above.

To convert *ex situ* seed collections from a weight basis to numbers of seeds per population (i.e., when numbers of seeds are large), these conversion estimates may be useful. However, in making such conversions to number of seed in storage, to inform conservation policies or seed management decisions, it is important to consider how the estimates were derived and whether the population differences have been reflected in these estimates.

	Mean seed weight (mg) per population	
Population	Burdon 2001b†	K.G. Eldridge pers. comm.‡
Año Nuevo	42	34.5
Monterey	23	24.5
Cambria	48	36.4
Guadalupe Island	29	32.4
Cedros Island	29	20.0

†Based on weighing approximately 600 seeds per population, except for Cedros Island for which 850 seeds were weighed (R.D. Burdon, pers. comm.).

‡Based on weighing one hundred seeds per tree for each of the trees collected from the source populations in 1978.

Planted domestic reserves

Most of the genetic conservation plantings for Monterey pine in California were planted on University of California (UC) property as a result of the initiative of W.J. Libby. During the 1960s and 1970s, Libby and colleagues made collections from native populations, conducted controlled pollinations, and established seed and hedge orchards and other research and conservation plantings at several central and northern California sites. Some of these plantings have already been removed; many others are at risk for removal for other land uses. For example, two hedge orchards on University of California property containing clones from all five native populations were removed in 1987 and 1988

Table 10. Monterey pine seed in storage in California in 2000.

	USDA Forest Service Albany, CA†		L.A. Moran Reforestation Center Davis, CA‡		USDA Forest Service Placerville, CA	
	Seedlot§	Seedlot size	Seedlot§	Seedlot size	Seedlot§	Seedlot size
	(count)	(seeds/seedlot)	(count)	(kg)	(count)	(seeds/seedlot)
Año Nuevo (AN)	21	10–700	1	2.7 IT	174	40–100
Monterey	21	40–1000	1	1.7	237	40–100
			1	2.4 IT		
Cambria	22	60–1000	3	2.6	96	40–100
			1	3.4 IT		
Guadelupe Island (GI)	16	10–60			47	100
Cedros Island (CI)	41	5–90			50	100–400
Date of collection	1978#		1990 & 1991¶		1978#	
Within-population crosses††						
AN × AN	88	0–300				
Monterey × Monterey	69	0–200				
Cambria × Cambria	54	0–200				
GI × GI	101	0–200				
CI × CI	70	0–200				
Among-population crosses‡‡						
Assorted crosses	60	0–200				
Unknown or mixed	1	2000				
	1	5000				

†Germination tests conducted in 1999 show germination for open-pollinated seedlots (i.e., seeds collected from native stands) of 80 to 100% and for control-pollinated seedlots of approximately 50% (D.L. Delany, pers. comm.). In 2001, these collections were moved from the facilities at USDA Forest Service, Albany, CA to the California Dept. of Forestry and Fire Protection's L.A. Moran Reforestation Center, Davis, CA.

‡A unit of the California Dept. of Forestry and Fire Protection (CDF).

§The term 'seedlot' as used here stands for 'unit of stored seed'. How such units are defined, measured, stored, and inventoried varies with the institution. A seedlot could mean in one case a bulked collection of seed from many individual trees and in another case a collection of seed from individual trees, the seed from each tree packaged and kept separate from the others, but regarded altogether as one unit. The latter case, when known, is denoted by the letters IT (for individual tree) in the seedlot size field.

#Seedlots are from the 1978 seed collection trips (D.R. Johnson, pers. comm.) by Eldridge and others (Eldridge 1978a,b; Libby 1978).

¶Individual tree collections (IT) are from 1991 CAMCORE collections, while all others are from 1990. There are also small amounts of seed in cold storage at North Carolina State University from the 1991 CAMCORE collections. There are also small quantities of seeds in storage from six individual trees at Año Nuevo, collected by Dave Adams (CDF). Four of the trees appeared resistant, at time of collection, to pitch canker; the other two appeared susceptible (L.A. Lippitt, pers. comm.).

††Within-population crosses were made in 1978 through 1980 by W.J. Libby.

‡‡No further information is available for this material.

Box 6. Fate of Australia and New Zealand collections from native Monterey pine populations from Guadalupe and Cedros Islands.

Australia: "In long-term -18°C secure storage at CSIRO Plant Introduction Laboratory, Black Mountain, Canberra there are about 30 seeds of each of about 515 mainland families, 50 Cedros, 48 Guadalupe, and also 30 of each of 76 Guadalupe families from the 1992 collection. We expect all this old seed will germinate well, after stratification, as it was extracted under relatively benign conditions and has not had the quarantine treatments of sodium hypochlorite dip and methyl bromide fumigation.

"In the cold room at CSIRO Forestry and Forest Products Laboratory at Yarralumla, Canberra there is more than 20 kg of the 1978 seed which probably has low germination due to inappropriate quarantine treatment in 1978 and imperfect storage since. Within this collection, there is plenty of Monterey and Año Nuevo, very little Cambria, no Guadalupe, and a little of Cedros." (K.G. Eldridge, pers. comm.; more details in Eldridge 1998a)

New Zealand: "We received 42 Guadalupe families (from the 1978 collection trip) which went out into a pedigreed planting in Kaingaroa Forest. From a combination of this planting, and earlier plantings ('Genetic Survey', i.e., provenance-progeny trial) from 50 families collected by Reid Moran (in 1958) and five by Libby et al. (in 1964), about 80 good phenotypes have been selected and are being intercrossed (in archives) to maintain pure Guadalupe material. There is also controlled crossing being done to produce F_1 hybrids with our local, mainland origin, stock as a pilot commercial operation.

"In addition, we have a small block of pure but unpedigreed Guadalupe material, which produces a mix of purebred and hybrid seed, the purebred component being at least free of most of the inbreeding of *in situ* seed.

"Regarding the Cedros material from the 1978 collection, of which Ken Eldridge sent some to New Zealand, we have a tale of total loss, in which the final, decisive chapters stemmed indirectly from our institutional changes. However, we do have some material, representing less than 15 families, plus some unpedigreed trees, left from the Libby et al. collection in early 1964. Ten or so clones have been archived and are being used for some crossing.

"No seeds from the 1978 trip remain: we have sown everything and planted out what resulted." (R.D. Burdon, pers. comm.).

(Libby 1990). In addition to pressures from competing land uses and uncertain funding provisions, the UC collections remain at risk from western gall rust, pitch canker, and, at some locations, fire.

At the University of California's Russell Reservation, near Berkeley, California, several Monterey pine plantings are maintained. Three breeding orchards were established here in 1963–1965. One orchard was planted in 1965 with open-pollinated seedlings from 98 trees on Cedros Island (from a 1964 seed collection trip). Another was planted with seedlings from 73 trees sampled from Guadalupe Island. A third was planted with close to 270 clones from trees in the three mainland populations (90 from each). These trees originated from a 1962 collection of eight trees within ten selected stands of each of the three mainland populations. These orchards are not sufficiently distant from one another for genetic isolation and controlled crosses would be required to be assured of pure-population progeny. A hedge orchard was established here, originally with 940 clones. It was repropagated in 1974, but an informal UC 1984 report says it was then dying of western gall rust. Various other plantings occur at this site, including an exhibit with representatives of all five native populations plus some interpopulation hybrids. A series of field studies were installed here in the early 1980s to determine family and population differences in resistance to western gall rust (e.g., Old et al. 1986).

Another set of field trials at the Russell Reservation, planted in 1988, contains material from all five native populations, mainland × island crosses, and selected families from Australia and New Zealand. A total of 32 clones are replicated on four sites. The four field trials, established with rooted cuttings, were intended to test for differences in resistance to western gall rust. The difference in response is dramatic after 12 years. The field trials are expected to be continued for perhaps three more years. As the original hedge orchard from which these cuttings were derived has been destroyed, the principal investigator for this experiment, Detlev R. Vogler, plans to 'reconstitute' the hedges by taking cuttings from the ramets in the field. If successful, this source of germplasm may be perpetuated (D.R. Vogler, pers. comm.).

At another UC property in Albany, California (Gill Tract), part of the mainland population breeding orchard was replicated. In 1988, approximately 90 clones were removed to install a sewer line. A 940-clone hedge orchard was also established here that occupies approximately 0.1 ha. Neither planting is well maintained and the future of the material here is uncertain (M.A. Diegan, pers. comm.).

Ramets from half of the 270 clones in the mainland population breeding orchard at the UC Russell Reservation were planted in northern California. The property, near Korbel, California, is owned by the Simpson Timber Company.

International *ex situ* reserves and interest in the native populations

For well over a century, there has been much international interest in Monterey pine, particularly from the southern hemisphere (Box 7). Monterey pine is grown as a plantation species in Chile, New Zealand, Australia, and to a lesser extent in Argentina, South Africa, Spain, and several other countries. Combined, the countries that have commercial plantations of Monterey pine have more than 4 million ha in production (Table 11). This is over six times the plantation area recorded in the mid-1950s (Scott 1960). Current trends suggest that the Pacific Rim countries are increasing their dominance in Monterey pine plantations (Lavery and Mead 1998).

More detail on the history and nature of Monterey pine plantations worldwide is available elsewhere (e.g., Lavery and Mead 1998). The focus here is on providing a brief description of the commercial context of Monterey pine, to the extent that there are genetic resources internationally that could be considered *ex situ* reserves with relevance to genetic conservation of the native populations. Summaries and comparisons among countries are complicated because breeding and conservation programs in these countries differ considerably in the extent of documentation of the original collections that form the basis of their programs, the degree of recording the breeding histories of existing material, and the units and variables by which the plantings are described. Much of the information provided here is derived from responses to a 1998 questionnaire (a list of respondents is provided in Appendix B), supplemented by several specific reports on the Australian and New Zealand reserves and information offered through recent personal communications.

Genetically pure reserves—having not been shaped by artificial or natural selection in the host (nonnative) country—are not only in the minority among germplasm reserves in these countries, but are the most valuable towards conservation or restoration of native forests. There is an important distinction here between germplasm that can serve as an *ex situ* genetic reserve for the native populations versus that for plantation purposes. Substantial genetic reserves for Monterey pine exist internationally, but pure-population reserves are a small proportion (i.e., perhaps a few hundred ha of provenance trials and stored seeds) and are at risk from a variety of threats. At some point, the stored seeds must be grown out and, in so doing, are subject to selection pressures different from those in the native populations and, in some cases, genetic contamination. "The option of maintaining pure native-population stocks as gene resources in New Zealand is threatened by ubiquitous pollen contamination from plantations, unless massive controlled-crossing operations are practiced." (Burdon et al. 1997b). Planted reserves are vulnerable to a variety of risks and are difficult and expensive to maintain in the long term. "[In Australia] it is clear that, in a time scale of several rotations, the present *ex situ* radiata pine genetic conservation plantings must be regarded as EPHEMERAL [*sic*]. There will be a considerable challenge to continue to have such uncontaminated 'wild' material still available in 100 years, and it seems likely that most of it would disappear in the next 20–30 years unless determined action is taken now to recognize its value, preserve the best of the present plantings beyond the normal rotation age, and plan for their replacement." (Eldridge 1998b).

Argentina. The area of Monterey pine plantations is approximately 15 000 ha and has not changed significantly in the last decade or so. One of the main limitations is finding appropriate sites with sufficient moisture, especially during the summer months. Some plantations, established 50 to 60 years ago in areas with annual precipitation of over 2000 mm, now lie within the boundaries of national parks. These plantations show very good growth. The other plantations in Argentina are mainly in Cordoba province and along some Altantic coastal areas in Buenos Aires province (L.A. Gallo, pers. comm.).

Australia. Sources of information on the Australian breeding program for Monterey pine include Matheson and Brown (1983), Cotterill (1984), Eldridge (1985), Boomsma (1997), Matheson et al. (1997), and many others. The description here will focus on the genetically pure *ex situ* reserves. The major organization with research and conservation interests and historically and currently making large investments in these activities is the Division of Forestry and Forest Products, CSIRO.

An excellent summary of much of the outplanted Australian germplasm is provided in an annotated catalogue of Australian provenance trials and genetic conservation plantings (Eldridge 1998b). There are 67 such trials in Australia, the earliest planted in 1933. Of these, 12 no longer exist (i.e., harvested, burned, abandoned, or lost). The total area of the remaining plantings, as of 1998, is approximately 237 ha. There is good representation, among the remaining trials, of all five native populations.

Forty-five of the remaining trials contain trees derived from the 1978 seed collection effort organized by CSIRO, most having been planted between 1979 and 1981. A recent field inspection of six of these plantings revealed both conservation opportunities and problems (two in Gippsland, Victoria on Australian Paper Plantations land and four near Tumut on State Forests New South Wales (NSW) land) (K.G. Eldridge, pers. comm.). Because these field plantings are now approximately 20 years old, and were planted at a spacing that required some selective thinning, they are not well designed for long-term growth comparisons. The tests were planned not only for genetic conservation but also for shorter-term genetic testing. Thus, some trees have been, or will be soon, removed. Natural mortality is not random within the plantings. For example, the Cedros and Guadalupe Island trees, at two of the NSW areas, have suffered heavy mortality and thus some plantings do not have the same conservation value as they did when planted for all five populations. Active management and thoughtful consid-

Box 7. Early observations on the commercial significance of Monterey pine.

"This is probably the most important conifer from the view point of commercial afforestation that has been introduced to countries of the southern hemisphere, Australia, New Zealand and South Africa. Planting of the species has now been going on for 40 to 50 years and a very considerable amount of capital, both State and private, has been invested in these operations. Quite insignificant in its native habitat, on the coast of California, its rapidity of growth and adaptability to a wide range of conditions in many countries of the southern hemisphere, render it an invaluable species in providing softwood supplies to meet the shortage in that region." (Lindsay 1932).

eration of these plantings will be required to maintain some of their genetic conservation potential in the long term. Most of the plantings from the 1978 seed collection—in both Australia and New Zealand—are due for clear-cutting within the next 20 years (K.G. Eldridge, pers. comm.). A report that provides an update of the status of both CSIRO field plantings and seed reserves of Monterey pine and recommendations for their management has been recently published (Eldridge 2002).

There is continued strong interest in the conservation of the native gene pools *in situ*. Because of the many problems associated with *ex situ* conservation of pure-population genetic resources, Australian plantation managers and owners value the native populations as a source of new genes. It is acknowledged that technologies and biosafety protocols would be required to prevent introduction of disease (such as pitch canker) into Australia if new collections were made. Also, there is concern about genetic contamination of the Monterey and Cambria stands due to the planting of trees raised from New Zealand seed (thought to be largely of Año Nuevo origin), the uncertainty of property owners allowing future seed collections, and the serious decline of the Guadalupe Island population (Eldridge 1997).

Australia's interest in and commitment to the conservation of the native gene pools in Monterey pine has been expressed for decades in such activities as sponsoring expensive seed collection expeditions (e.g., 1978), provision of funds to the University of California for genetic conservation (e.g., Libby 1990), establishing numerous provenance trials, conducting considerable genetic research, and organizing workshops and meetings to discuss the importance of genetic conservation and appropriate policies and procedures for *ex situ* genetic conservation collections.

Chile. Monterey pine was introduced to Chile in the late 1800s. Later, there was interest in using this species to help stop erosion problems that threatened the Coastal Range. The first commercial plantations were planted in the early 1940s and today Monterey pine constitutes the basis of the Chilean forest economy. Exports from these plantations contributed over $1.5 billion USD in 1994 to the national economy (Toro and Gessel 1999). Little is known about the source of the seed used for early plantations (Jayawickrama and Balocchi 1993). Because the cone sizes and seed weight from the plantations are similar to those found in New Zealand landraces, it has been suggested that the seed source of the Chilean Monterey pine is the same as that for New Zealand, namely the Año Nuevo and Monterey populations (R.D. Burdon, pers. comm.).

Several provenance trials, comparing the growth of Monterey pines from the five natural populations and several foreign and domestic seed orchards, may be considered *ex situ* reserves. Measurements show differences in volume among the various source populations. The good growth rates of some of the subpopulations, and the desirable straight stems shown by the material from Guadalupe Island, suggested to researchers that it may be desirable to incorporate material from the natural populations directly (rather than just continuing with domesticated material) into Chilean tree improvement programs (Jayawickrama and Balocchi 1993).

Table 11. Estimate of plantation area of Monterey pine internationally.

Country	Area in plantations	Reference
	(ha)	
Argentina	15 000	Rogers and Ledig 1996
Australia	745 000	From 1998 survey (unpublished data)
Chile	1 500 000	Rogers and Ledig 1996
Great Britain	270	C.J.A. Samuel, pers. comm.
Ireland	300	D.G. Thompson, pers. comm.
New Zealand	1 540 000	From 1998 survey (unpublished data)
South Africa	71 840	DWAF 1996
Spain	237 400	From 1998 survey (unpublished data)
Turkey	2 800	B.N. Cengel, pers. comm.
Total	**4 112 610**	

Breeding and selection has contributed to shaping a genetic resource that is more appropriate for the plantation conditions and market needs in Chile. These localized genetic resources are important for commercial conservation purposes, but less valuable in relation to conservation of the native Monterey pine forests. A breeding program that began in 1976 has resulted in more than 200 ha of seed orchards, more than 1000 full-sib families in progeny trials, as well as clone banks and hedge orchards. The response to a 1995 survey suggested that the genetic reserves were considered adequate for the future of the breeding program in Chile. However, long-term genetic conservation is not institutionalized here because the plantation property and reserves are all privately owned: forest industries own approximately 70% of the Monterey pine plantation area and smaller private landowners the rest (Rogers and Ledig 1996).

Great Britain. There are currently almost 300 ha of Monterey pine plantations in Great Britain, approximately evenly divided between public (Forest Enterprise) and private ownership. Most of the publicly owned Monterey pine plantations are located in Wales or the southwest England peninsula. Monterey pine is also used as an ornamental tree, particularly common along the south coast of England.

Species and provenance trials of Monterey pine have been planted, particularly in the Bournemouth area. One of these field trials, planted in 1980, contains trees from seeds collected from planted Monterey pines in southern England as well as samples from the three California native populations and some Australian-source material from Guadalupe Island (i.e., Guadalupe *ex* Canberra). The California mainland and Guadalupe material was obtained from CSIRO. Thirteen-year results show that the best height growth and survival are found among the home-collected seed sources, showing that a single generation within Britain can have a

beneficial effect. This observation has also been made for other exotic conifers in which a comparison is possible between directly imported germplasm and first-generation domestic seed collections (C.J.A. Samuel, pers. comm.). The Guadalupe material also showed good survival and growth. Among the three mainland populations, the Año Nuevo material generally had the best survival. (C.J.A. Samuel and R.L. Jinks, pers. comm.)

Greece. The first recorded introduction of Monterey pine to Greece was in 1913 as a addition to the Arboretum of Vytina. Monterey pine is currently a minor plantation species here and is limited to particular sites that have sufficient moisture and microclimate (Varelides 1996).

Ireland. Monterey pine is a minor but important plantation species in Ireland, currently growing in plantations of total area of approximately 300 ha. It adds to species diversity, has among the highest wood production rates of forest plantation species there, and grows on less fertile sites than Sitka spruce (*Picea sitchensis*)—another favored plantation species with similar yields. Guadalupe Island is the seed source of most interest for the plantations, primarily due to its lower (relative to other populations) severity of symptoms from *Cyclaneusma* disease (D.G. Thompson, pers. comm.). Plantation area of Monterey pine—Guadalupe source in particular—may increase, particularly in the south near Cork, as some of the practical and technical limitations are overcome (Box 8).

New Zealand. Although records have not been exhaustively searched, it appears that Monterey pine—as germplasm rather than a wood product—was introduced in the late 1850s (R.D. Burdon, pers. comm.). As with Australia, there is a sophisticated and long-established breeding, genetic research, and germplasm conservation program here for Monterey pine, much of it provided by the New Zealand Forest Research Institute, based in Rotorua, New Zealand. Some sources of information on the breeding programs include Shelbourne (1970), Shelbourne et al. (1986), Jayawickrama et al. (1997), Shelbourne (1997), Shelbourne et al. (1997), Sorensson et al. (1997), and many others. As with Australia, the description of genetic reserves will focus on those that are the most genetically pure derivatives from the native populations.

Box 8. Commercial significance of Monterey pine in Ireland.

"Forestry in Ireland is divided between Coillte Teoranta—the Irish Forestry Board (i.e., forests established under state forestry 1905–1989)—and privately planted, owned, and managed forests. For Coillte, we have 261 ha of Monterey pine in our inventory out of a total of 325 000 ha or about 0.08% of our forests. No current details of Monterey pine in the private sector exist, but a survey done in 1973 found only 21 ha.

"The genetic base is rather unclear because although there is a register of all seed imports for the period 1930 to 1980, there was little attention paid to the exact origin of imported seed until perhaps the 1960s or 1970s. Therefore, the seed source is generally recorded as 'western North America' or 'California'.

"The average yield class (i.e., volume of wood produced per ha per year) of Monterey pine in Ireland is 16.5 cubic meters which is among the highest species production rates recorded here. Nevertheless, Sitka spruce (*Picea sitchensis*)—which has about the same yield class—grows on a much wider range of sites than Monterey pine and therefore is the major commercial species.

"There has always been an interest in Monterey pine in Ireland because of its productive potential. One of my colleagues says: 'Every generation of foresters rediscovers Monterey pine'. The main problems with Monterey pine in Ireland have been: 1) determining the site requirements; 2) determining the right seed origin; and 3) development of quality nursery stock.

"We now know on what sites it performs well and they are typically nutrient-poor soils where sitka spruce requires large amounts of repeated fertilization. It also provides variety to forest plantations, both visually and perhaps ecologically, providing unique habitats for different plants and animals. Provenance trials established in the early 1980s identified Guadalupe Island as the most productive seed source, mainly because we have found much lower levels of *Cyclaneusma* disease in this seed source. The *Cyclaneusma* infection greatly reduces needle area which results in greatly reduced wood production. We have tested some of the 'Guadalupe *ex* Canberra' material from Australia and unfortunately find that it has considerable yellowing due to hybridization with local Monterey pine. This is the reason why we are interested in obtaining a source of pure Guadalupe island material. We also had a programme of collecting seed and scions from local individuals of unknown origin that did not exhibit the yellowing problems, but they also are not as productive as the pure Guadalupe Island material.

"Given that we have identified appropriate sites, and assuming that we can develop a reliable source of Guadalupe seed, the question of producing high-quality planting stock is the remaining limiting factor. Instability or 'toppling' of young, container-grown plants is the major problem at present. It appears that there is an inappropriate allocation of photosynthate to shoot growth relative to root growth. Monterey pine has the reputation of being difficult to transplant so containerized planting stock seems to make sense. Cultural practices such as sowing date, fertilizer rates, and other nursery practices are probably critical in the production of high-quality planting stock. I do not think that the production of bare-root plants will overcome these problems.

"We plan to increase planting of Monterey pine in the southern part of the country around the Cork area because of the warmer temperatures and the availability of sites where Monterey pine does well with only modest fertilization (i.e., nutrient-poor, old, red, sandstone-derived soils). If we can overcome the toppling problem and have a verified seed source, I expect that planting of Monterey pine will increase. It will never become our major commercial species, but in light of the current emphasis on biodiversity, it could play an important role in certain parts of the country." (D.G. Thompson, pers. comm.).

Seed collections from 1958, 1961, and 1978 (Table 9) are represented in breeding-population parents from field plantings for Año Nuevo, Cambria, Monterey, and Guadalupe populations. However, there are now some dramatic differences between the original collections and the remaining trees. Some field plantings have been felled or thinned. Also, natural selection for New Zealand conditions (disease and general local adaptation) has removed some of the trees, and thus, truncated genetic diversity. Approximately 50 to 75% of these original collections of the three mainland populations have been lost in the field from a combination of thinning and natural selection. Representatives from up to 92 parent trees from Guadalupe Island have been installed in field plantings. One-third to one-half of these trees has been lost either from planned harvesting or disease or other natural selection. Approximately one hundred parent trees from Cedros Island were represented, via seeds collected, in field plantings. Probably the majority of these have been lost. In general, material collected from the 1961 seed collection trip (from mainland populations) has been partially harvested and the remainder will be removed in the foreseeable future. Plantings from the Cedros Island population, in particular, have largely vanished owing to a combination of suppression by trees of faster-growing material and low interest in the genetic resources from this source for the breeding program (R.D. Burdon, pers. comm.). In addition to these pure population collections, some breeding-population selections have been made from these collections and planted in new field sites.

Risks of low to moderate levels include fire, climate change, and ash eruptions from active volcanoes. Pollen contamination is potentially a major (if poorly quantified) risk in connection with any attempt to maintain reasonably large native-population entities in New Zealand without controlled pollination. New diseases or pests, whose behavior in New Zealand conditions is unpredictable, present additional risks. Perhaps the most pressing and most certain risk comes from institutional and political conditions: despite policy protection for these reserves, institutional upheavals may generate both human error and a lack of funding which undermines effective, long-term conservation strategies (R.D. Burdon, pers. comm.).

Although there is a sophisticated tree improvement program here with advanced domesticated generations and local landraces, native gene pools are still considered valuable. For example, Monterey germplasm may improve edaphic tolerances and Guadalupe germplasm may be useful in improving stem form and wood quality and possibly snow resistance (Burdon et al. 1997b). Currently, there is strong commitment to maintaining the New Zealand plantings of Guadalupe as a pure population that can be used to produce F_1 crosses with local, improved stock for commercial plantings (R.D. Burdon, pers. comm.). Conservation and introgressive use of the Cedros Island and Cambria populations may also be of real value because of unpredictable benefits of completely new gene combinations and to help meet unforeseen selection criteria that might emerge in the future (Burdon 1992). Monterey gene pools are also of interest as they are underrepresented in landrace stocks in New Zealand (as compared with Año Nuevo) and because of the general adaptedness of trees from this population, particularly in the north of the country. Año Nuevo is well represented in the landrace stocks, tending to reduce interest in the native population. However, its general adaptedness to New Zealand conditions, particularly in the south, could refocus interest on the native germplasm if landrace stocks and the breeding population could not meet some need that arose. These native genetic resources are difficult to maintain *ex situ*. Perhaps the greatest concern is that the native populations remain in a condition that enables them to continue to regenerate, maintain diversity, and give rise to trees that are resistant to pitch canker or any other pest that might reach California before eventually reaching New Zealand (R.D. Burdon, pers. comm.).

South Africa. Monterey pine is very important for the Cape region, particularly the Monterey population. Provenance trials, containing material from the three mainland populations and some Canberra-collected seed of Guadalupe origin, have been replicated on six sites. Assessments have shown that there are not significant differences among provenances within populations (of the traits assessed), but the superior population varies by trait and by trial site (Falkenhagen 1991).

Aside from the provenance trials, much of the germplasm has been shaped in some way towards local conditions, and is less valuable as an *ex situ* genetic reserve relative to the native populations. A Monterey pine breeding program initiated in 1962 by the South Africa Department of Forestry has been taken over by the South African Forestry Company Ltd. (SAFCOL). The basis for this program was a selection of 562 superior trees from close to 16 000 ha of Monterey pine plantations in the Cape Province. These plantations contained a mixture of trees from some of the native populations. Of these, 466 were approved for use in the breeding program, and were supplemented with some trees from Australia and New Zealand. Open-pollinated seed orchards were established with the best of these selections. Seventeen progeny trials were established with representation as follows: 484 selections from open-pollinated progeny from the seed orchards, 108 open-pollinated and 24 full-sib families from Australia, 30 open-pollinated families from New Zealand, and 86 full-sib families from local breeding efforts. Selections were then made from these progeny trials to form the basis of a breeding population. Two second-generation progeny trials (210 selections) and a second-generation seed orchard (100 selections) were established (D.J. Steyn and H. Rossouw, pers. comm.). There is a high degree of risk to germplasm from fire and a moderate risk from disease (C. Bester, pers. comm.).

Spain. There are three seed orchards established with material from the Año Nuevo population, each with approximately 100 trees. There are also three progeny tests with seedlings from the plus trees (i.e., trees selected, based on phenotype, for desirable traits) from these seed orchards. For each of

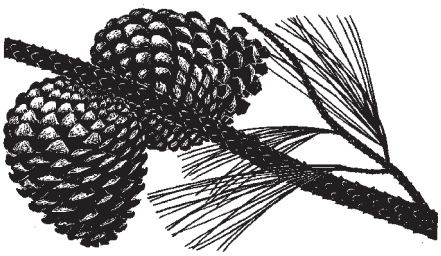
the Cambria and Monterey populations there is one seed orchard, each with approximately 250 trees. There is also one small seed orchard with trees of unknown origin.

Monterey pine is a very important species in the north of Spain. It grows in over 162 000 ha in the Basque country (Espinel et al. 1995). The Monterey population, in particular, is of great importance in the Basque country because this population shows growth performance superior to the other three mainland populations in field tests here.

Turkey. The Monterey pine plantation area is approximately 2800 ha. The genetic source for these plantations is known in some, but not most, situations. The only genetic reserve is a plantation in northwestern Turkey, near Adapazari, that is growing well and protected as a seed production area. Interest in Monterey pine as an exotic plantation species is not increasing. In 1984, many plantations suffered damage from *Evetria buoliana* and interest was lost in Monterey pine as a result. However, some trees have almost totally recovered (B.N. Cengel and Z. Kaya, pers. comm.).

5

Models of genetic conservation plans



The United States does not have a comprehensive strategy for conserving forest genetic resources or a national program for long-term *ex situ* conservation of forest genetic resources (Riggs 1990; Ledig et al. 1998). Some European countries are more proactive and have some level of national planning for forest genetic conservation. Many European countries are members of a coordinated effort to ensure the effective conservation and the sustainable use of forest genetic resources in Europe. This organization—the European Forest Genetic Resources Programme (EUFORGEN)—was established in 1994 as an effective means of promotion and coordination of *in situ* and *ex situ* conservation of genetic diversity, exchange of reproductive materials, and monitoring progress in these areas (Turok et al. 1998). The organization is coordinated by the International Plant Genetic Resources Institute (IPGRI), in collaboration with the Department of Forestry of the FAO. Much of the work is conducted through smaller groups—known as networks—that focus on genetic conservation issues for a particular species (e.g., *Picea abies*, *Quercus suber*, *Populus nigra*) or groups of species. Through this coordination, complementary conservation activities can be undertaken and much or all of the natural range of a particular species can be considered.

A similar type of cooperative—the South Pacific Regional Initiative on Forest Genetic Resources (SPRIG)—aims to provide coordination and support for planning genetic conservation and management of forest tree species in this region. For example, general strategies for the conservation, management, and utilitization of Highlands Yuka (*Dacrydium nausoriense*) in Fiji and Santo kauri (*Agathis silbæ*) and whitewood (*Endospermum medullosum*) in Vanuatu have recently been produced (Tuisese et al. 2000; Corrigan et al. 2000a; Corrigan et al. 2000b; respectively). All three are economically valuable species and more research has been recommended towards the development of comprehensive and scientifically sound conservation strategies.

Some European countries have overall plans for their forest tree species or plans for some species of particular economic importance. A strategy for the conservation of the genetic resources of 75 tree and shrub species in Denmark was prepared in the early 1990s (Graudal et al. 1995). This strategy was based on the recognition of the historical and continuing influences on genetic diversity in these species, and the need to make a focused and systematic effort to conserve the adaptability and utility of these species in the long term. A guide for planning national programs for conservation of forest genetic resources has been developed by geneticists in Denmark (Graudal et al. 1997). This is an excellent guide, particularly for situations when there are numerous species that are widespread in their natural ranges, thus requiring the setting of priorities and the selection of conservation opportunities such as determination of genecological zones, socioeconomic values, and conservation methods. Another example is the Finnish network of *in situ* gene reserve forests for their major commercial forest tree species (Koski 1991). In general, though, there are few comprehensive networks of reserves dedicated to *in situ* genetic conservation of forest tree species, although there are many examples, worldwide, of reserves to conserve the genetic resources of a particular population of a taxon (Kanowski and Boshier 1997).

Few cases exist that can serve as a direct and complete model for a genetic conservation plan for Monterey pine—concerning a single forest tree species, covering the entire natural range of the species, containing both *ex situ* and *in situ* elements, and focusing on the genetic structure, underlying principles, and opportunities for genetic conservation. Existing single-species conservation plans are more general and often do not include a comprehensive description of genetic variation or enunciate genetic principles. Many plans are concerned with a threatened or endangered species with little natural habitat and few opportunities for specific

genetic conservation (e.g., species recovery plans of the U.S. Fish and Wildlife Service). Existing genetic conservation plans are often only concerned with *ex situ* resources (e.g., Spencer et al. 1998) or are restricted by jurisdiction (e.g., state or agency) and thus do not consider the full natural range of the species (e.g., Wilson 1990).

In North America, perhaps one of the highest-profile forest tree species with considerable attention provided to conservation of its genetic resources is Douglas-fir. Like Monterey pine, this is a commercially valuable species. But unlike Monterey pine, Douglas-fir has a wide natural range that extends from western Canada through many western states in the USA and into Mexico. Although there is no rangewide overall genetic conservation plan for Douglas-fir, particular reports and activities have been undertaken in specific regions. An assessment and conservation plan for the genetic resources of Douglas-fir in California were prepared in the early 1980s (California Gene Resource Program 1982). Another regionally focused effort is the establishment of gene pool reserves of Douglas-fir in the state of Washington (Wilson 1990). This *in situ* conservation plan is restricted to that part of the species' range that occurs on public (i.e., State of Washington Department of Natural Resources (DNR)) forests in Washington state and focuses on *in situ* reserves. These reserves were established in recognition of concern over genetic contamination of natural populations of Douglas-fir due to increasing areas planted with genetically improved seeds that were derived from a fraction of the species' natural genetic variation and concern for the largely unknown effects from selection pressure due to forest management practices. Reserves (areas protected from harvesting) were established according to elevation and seed zones—the latter reflecting genetic differentiation among populations. As of 1988 over 100 gene pool reserves had been located and designated, amounting to 1050 ha or 0.19% of DNR forest land. Although selection criteria favored the designation of old-growth areas, this was not always possible due to historical harvesting practices. Thus, some gene pool reserves, particularly those in lower-elevation and higher-access forest areas, were second generation. However, records were checked to ensure that the regeneration in these areas was natural. These reserves were designed and selected with the best available information. Ongoing concerns include genetic contamination from adjacent (and artificially regenerated) forests and loss of gene pools by natural disturbances such as fire.

The DNR gene pool reserves for Douglas-fir also provide experience on the challenges of maintaining an *in situ* genetic conservation program over time. Since implementation, approximately 25% of the reserves have been administratively lost—that is, traded or transferred to different ownership. Some of those reserves affected can still function as genetic reserves under the new ownership but the coordination and management necessary to achieve specific genetic outcomes have been lost or lessened. The DNR maintains a strong commitment to their genetic conservation policy. However, over time, decisions about land transfers and management necessarily consider the institutional values and responsibilities with which DNR is charged, which are broader than genetic concerns (J.D. DeBell, pers. comm.).

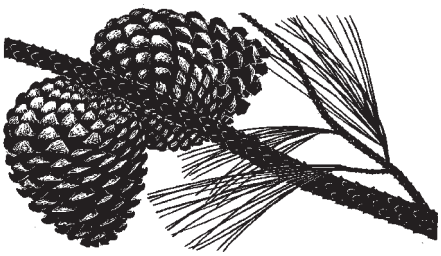
Internationally, there are examples of forest tree species that are of particular conservation concern and have attention focused on the conservation of their genetic diversity. A genetic conservation plan has been developed for *Leucæna salvadorensis*, a threatened tree species native to El Salvador, Honduras, and Nicaragua (Hellin and Hughes 1993). It has a largely contiguous distribution in the seasonally dry, deciduous tropical forest association on south-facing Pacific slopes. Its genetic resources have been severely degraded as a result of habitat loss to farming. *In situ* conservation methods are compromised because very little natural habitat remains. However, farmers have traditionally maintained some trees of this species around houses and in fields and fencelines, meaning that the species has more presence than would be indicated by the loss of forest cover. There is, therefore, an opportunity here to encourage the interest and traditional protection by farmers, involving them in seed collection, planting, and protection efforts. *L. salvadorensis* can grow on shallow soils and under drought stress, producing high-quality wood. Accordingly, its genetic resources are valued as a possible means of improving the widely cultivated congeneric species, *L. leucocephala*, as well as other species with domestication potential in their own right.

English yew (*Taxus baccata*) has a natural distribution throughout most of Europe, yet remains as part of a natural plant community in only a few stands and is generally considered to be a declining species. It is also cultivated for ornamental purposes. One of the largest protected areas—the Wierzchlas Reserve in Poland—has suffered a major loss in number of living yew trees in the last 80 years. Genetic analysis showed that this loss is not a direct result of low genetic diversity in this population (Lewandowski et al. 1995), as previously thought. In fact, there is apparently high genetic diversity within this species as compared with other conifers. The genetic study turned attention over the species' decline towards environmental factors that limit natural regeneration, such as soil pathogens. Thus, the value of the Wierzchals Reserve as a gene pool reserve and the need for a longer-term genetic strategy, including *ex situ* conservation, have been recognized.

The conservation of wild relatives (usually congeneric species) of agricultural crop varieties has become a shared priority of agricultural geneticists and conservation biologists (Frankel and Soulé 1981). Because the domestic use of improved germplasm far exceeds the census of the natural populations, conservation of the native populations of Monterey pine could be considered in this light. From this perspective, the value of conserving the native gene pools is not only to protect the genetic source of derived families, but to safeguard the opportunity to understand the web of ecological relationships and coevolved species and thus to provide unique (i.e., unavailable in *ex situ* repositories) opportunities to improve the breeding or management of domestic germplasm (Tewksbury et al. 1999).

6

Principles and recommendations for *in situ* genetic conservation of Monterey pine



This chapter contains a review of genetic principles that are most relevant to genetic conservation of Monterey pine, a description of issues and influences (mostly anthropogenic) on native gene pools, and a set of recommendations for genetic conservation. The selection of principles and issues has been undertaken from an inclusive, species-level perspective, although some issues and recommendations are more (or exclusively) relevant to certain populations than to others, and this is noted where pertinent.

Issues and influences have been discussed within discrete topics, but it should be kept in mind that they are interactive, cumulative, and context-dependent in impact. Some influences may have immediate genetic impacts; others may only exhibit their impacts after many generations. Given the interactions, cause and effect may be difficult to discern. Thus, for example, habitat fragmentation may lead to population sizes that are below those adequate to maintain genetic diversity, which may lead to inbreeding, which may lead to inbreeding depression, which may lead to loss of seedling recruitment, which may lead to lower population size, and further inbreeding, etc. In this case, most of the steps in the sequence are both causes and effects of genetic decline.

This section has been organized by the general categories of activity associated with *in situ* genetic conservation of Monterey pine: Planning, *in situ* management, outreach needs, and research. Within each general category, several issues or activities that are relevant to or appropriate for Monterey pine are discussed. Most, but not all, of these discussions include some specific recommendations. In a few cases, the issue or activity is discussed to provide the background or rationale for other recommendations. For example, some description of the concept of 'minimum viable populations' is needed to appreciate many of the recommendations related to *in situ* conservation. In some cases, the recommendation that pertains to an issue has already been provided in an earlier section and is not repeated in subsequent sections.

Recommendations can be meaningless, or even counterproductive, if taken out of context. Considerable care has been taken in providing an appropriate context for the recommendations provided here. The specific recommendations are offered as one set of expressions of underlying principles of genetic conservation but are by no means exhaustive to all possible situations. Good guidance—perhaps even more valuable than specific recommendations—can be derived from an understanding of the principles and rationale used in developing recommendations. This understanding will allow readers to better translate the information to their particular context and update their understanding and practices over time as new information becomes available.

Planning

Monterey pine is a conservation challenge. Historically, its natural range included natural disturbances (e.g., fire) and was dynamic in its response to environmental change—conditions that are difficult to maintain in urban and semi-urban environments (e.g., Hillyard 1997). Interestingly, although we restrict the movement of the host species (Monterey pine), we facilitate the movement of some of its pathogens. Therefore, it is important to conserve as much of the natural diversity as possible to allow adaptation *in situ*.

Amount of genetic diversity is not a sufficient conservation standard in its own right: it must be referenced to adaptability, long-term evolutionary potential, or natural levels and structure. For example, the amount of genetic diversity could be increased by genetic contamination, but this is not necessarily a positive contribution.

Conserving genetic diversity can be a cost-effective management tool in the long term. Healthy, functioning ecosystems require fewer inputs on an ongoing basis than stressed ecosystems. Genetic diversity allows a 'response system' to environmental change.

For planning purposes, the definition of 'Monterey pine forest' changes according to the intended use. For example, the criteria appropriate for siting *in situ* genetic reserves will differ from those for buffer areas or seed collections for *ex situ* reserves.

Demographic and genetic characteristics are tightly coupled but one cannot serve as a proxy for the other. For example, genetic diversity obviously cannot persist, *in situ*, without regeneration. But simply ensuring regeneration success does not guarantee maintenance of genetic diversity. So, for example, encouraging regeneration with mechanical methods may have different genetic consequences than fire-influenced regeneration.

One planning tool for projecting the genetic influences of particular activities is to consider the potential impact of the activity on the genetic processes of migration (gene flow), natural selection, and genetic drift. For example, will the activity significantly affect pollen production or flow, seed dispersal, distance between stands of trees, or local adaptation?

Recommendation 1: *Biologically significant losses of genetic diversity within the species overall and within each of the five native populations of Monterey pine should be avoided.*

Recommendation 2: *Native Monterey pine populations should not be allowed to become further domesticated, meaning uncoupled from natural processes and thus requiring constant input and management to ensure standard biological functions such as growth and reproduction.*

Minimum viable population size

It has been shown, with studies of many different species, that the expected longevity of a population increases with its size (Hanski et al. 1996). Small populations are expected to become extinct rapidly. Thus, many theoretical and empirical studies have attempted to determine the minimum number of individuals required to maintain a population for a given length of time. This concept—minimum viable population size—is useful in risk analysis of population extinction. This quantity will be affected by genetic, ecological, and demographic features, in particular. Lande (1988) emphasizes the extreme importance of the demography of populations in determining their minimum viable sizes. In a review of more recent work, Nunney and Campbell (1993) conclude that both stochastic demographic models and population genetic theory lead to very similar conclusions about minimum viable population size, at least under panmictic conditions.

For species with metapopulation structure, and hence the expectation of local extinctions and recolonizations, a somewhat parallel concept of 'minimum viable metapopulation size' has been defined as "the minimum number of interacting local populations necessary for the long-term persistence of the metapopulation" (Hanski et al. 1996). Because recolonization is so critical to this long-term dynamic, the amount of suitable habitat for recolonization is simultaneously considered; otherwise known as the minimum amount of suitable habitat (MASH) necessary for metapopulation persistence. Thus, for a species with presumed metapopulation structure, there are minimally three considerations for population size: minimum number of populations, minimum viable size of each population, and minimum amount of suitable habitat. The last-mentioned will be necessarily larger than the current occupation of habitat if the species is not to become extinct.

A recent review of models pertaining to MASH for species with metapopulation structure found that some of the assumptions in these models were unrealistic, likely leading to an underestimate—and possibly a severe underestimate—of MASH. For example, the assumption that metapopulations occur at a steady state is probably not realistic for many species due to the high rate of habitat loss, fragmentation in many landscapes, and lack of opportunities for recolonization. Therefore, the authors caution that scores of rare and endangered species may already be 'living dead', committed to extinction because extinction is the equilibrium toward which their metapopulations are moving in the present fragmented landscapes (Hanski et al. 1996).

In situ genetic reserves

Because existing parks and other 'protected areas' of Monterey pine were neither established nor specifically managed for the purpose of protecting genetic diversity, there may be a need for additional genetic reserves. The selection of genetic reserves is best guided by a knowledge of within-population genetic structure, as well as other factors such as potential for buffers and size required for natural processes related to natural regeneration potential. A conventional process involves siting of core reserves, determination of buffer areas, and development of genetic management and monitoring guidelines. An excellent discussion of reserve principles and issues is provided by Hawkes et al. (1997). However, much of the conventional process may be inapplicable to Monterey pine owing to restriction of opportunities. For example, although a debate exists over whether it is preferable, in theory, to have a single large or several small reserves, this may have little application to Monterey pine where large, contiguous genetic reserves are not possible for some or most populations.

The process of selecting genetic reserves for Monterey pine may differ from that used for other more widespread or less impacted species in that:

- Opportunities for selecting genetic reserves may be severely limited owing to previous loss of habitat, fragmentation of existing habitat, and other land-use impacts.
- Opportunities for buffer zones around genetic reserves may be limited in some populations. This may indicate a need for larger core reserves or possibly may be mitigated through creative interventions such as planting buffers.
- The loss of considerable habitat and attendant genetic diversity means that the baseline for genetic

conservation has been obscured. Therefore, a higher-than-normal retention level for genetic diversity may be warranted.

- Given the limitations on native populations for migration in response to climate change by both natural (e.g., ocean) and constructed (e.g., urban areas) borders, reserve sizes should take into account the need for adaptation in place.
- Genetic reserves, in this case, might include some potential (new?) habitat for Monterey pine adjacent to native populations to allow some freedom of movement, recognizing the movement would most likely be in a north-south direction rather than further inland.
- There may be proxies for knowledge of genetic structuring: for example, the USDA Forest Service seed zones are based on a two-tiered system of physiography and elevation (i.e., don't move seed between zones). Zones are quite well supported by genetic test results. Elevation is usually the more reliable clue to genetic differentiation.
- Outlying trees may have more value and importance than is the case for many other forest tree species. In some populations, the outlying trees (on edges of the forest) may represent adaptations to extreme (i.e., edge of range) conditions and may harbor important genetic diversity. Because of habitat loss, trees near the extant edge of the current range may actually represent diversity at a more core position prior to habitat reduction. Also, or alternatively, they may harbor diversity that is particularly relevant to occupying new environments.

Risk from catastrophic events plays a large role in determining *in situ* conservation strategy. A discussion of population viability theory and evidence from empirical studies concludes that local extinctions—for example, of conserved populations—are far more common then we would be led to believe by some prediction models that exclude catastrophic events (Mangel and Tier 1994). Furthermore, Mangel and Tier (1994) suggest that minimum viable population sizes are almost certainly larger than those predicted from a theoretical basis that ignores catastrophes. Their conclusion is that even when conserved populations are large, we should expect local extinctions; they are likely events. Therefore, conservation plans should acknowledge this and include contingencies for catastrophic events.

Recommendation 3: In situ *genetic reserves should be designated for each of the five native populations, guided by within-population genetic structure. They are critical to genetic conservation and research objectives. A management plan to guide the protection of genetic values and a framework for genetic monitoring should also be established for these reserves.*

Empirical and theoretical studies show that peripheral populations are often genetically and morphologically different from more central populations, and that in some cases their conservation may be beneficial to the long-term evolutionary flexibility of the species (Lesica and Allendorf 1995). Peripheral populations or individuals—given their edge-of-range conditions and possibility of harboring rare alleles—may be particularly important in providing the capacity to adapt to climate change (e.g., Gunter et al. 2000). For Monterey pine, with its few extant populations, this translates to a finer scale—peripheral stands and individuals, rather than populations. Additionally, the conservation of habitat adjacent to peripheral stands and individuals may be important to dispersal and colonizing opportunities for this dynamic species.

Recommendation 4: *'Outliers' (trees at edges of populations) should be conserved because some may contain genetic diversity important for adaptation to new environmental conditions and may represent opportunities to expand the natural range or allow the populations some movement.*

Information on within-population genetic structure should guide the siting of genetic reserves. The size of reserves can be guided by the considerable amount of theoretical and empirical information available. In addition to the minimum viable population size discussed earlier, which gives an indication of population viability over time, there has been much investigation of the specific requirements to maintain genetic diversity in the long term. The parallel concept, when the primary focus is on long-term genetic conservation, is minimum genetic reserve size. This, of course, requires the minimum population and habitat sizes discussed above, but in addition considers the amount and distribution of genetic diversity. Generally, the number of trees required for long-term genetic conservation in a population is typically expressed as the 'effective population size' (N_e). This value is *not* the actual number of trees in the population but a smaller, theoretical number based on the number of unrelated trees, and is affected by the mating system and demographic profile of the species. Until recently, a generally accepted rule of thumb for long-term genetic conservation was that an effective population size of approximately 500 is necessary (i.e., 500 unrelated, randomly interbreeding individuals) (e.g., Franklin 1980; Frankel and Soulé 1981; Graudal et al. 1995). A review of such calculations found much variation in the recommended effective population size, ranging from 50 to 50 000 individuals (Brown and Moran 1981). In these calculations, there are numerous assumptions, including the way genetic diversity is distributed in the population (e.g., the frequency distribution of rare alleles) and the acceptable level of risk to losing certain alleles. For example, Gregorius (1980) calculated that 754 individuals would be required to ensure that all alleles at a locus (i.e., all the alternative forms of a single gene) with frequencies greater than or equal to 1% are detected, with probability of 95%.

In the mid-1990s, the availability of empirical evidence and the further development of genetic theory led to the recommendation that the general rule for effective population size should be closer to 5000 than 500 (Lande 1995).

This revision was largely related to consideration of the role of mutation, and that the potentially adaptive variance is an order of magnitude smaller than the total mutational variance. Thus, with new information, the desirable size of genetic reserves has recently increased considerably.

Translating the effective population size into a genetic reserve size requires insight into how genetic diversity is structured in the population, demographic structure, physical distances between trees, and pollen dispersal distances. Generally, the actual or census number of trees required is considerably larger than the effective population size. For example, assume that a reserve 8 ha in size has been proposed. Using an assumption that trees within a 50-m radius may be related, it is estimated that this hypothetical reserve might contain only eight unrelated trees (Box 9). Extrapolating to a more desirable number of unrelated trees, we find that genetic reserves might be recommended that are considerably larger than individual existing protected areas in some populations. For comparison, a USDA Forest Service project identified potential genetic conservation areas (GCA) for five commercially significant conifer species: ponderosa pine, sugar pine, incense-cedar (*Calocedrus decurrens*), Douglas-fir, and white fir (*Abies concolor*). Depending on stand conditions and the status and management of adjacent areas, recommended sizes of GCAs were from 500 to 3000 ha (Millar 1999b). The shape of the genetic reserve is also important because it influences the opportunities for trees to breed with one another, as well as physical considerations such as shelter of seedlings and windthrow of adults.

Recommendation 5: *The establishment of* in situ *genetic reserves should be guided by theory such as desirable effective population size. However, given that theory might suggest reserves larger than areas available, efforts should be made to extend the boundaries of genetic reserves through appropriate genetic management of surrounding urban or recreation areas.*

Introduction, reintroduction, or extirpation of Monterey pine populations

As discussed earlier, the dynamic evolutionary history of the species and sensitivity to climatic triggers, combined with the current limitations on the movement of Monterey pine, suggest that maintenance of genetic diversity may be highly important to the species' ability to evolve essentially in place. Monterey pine's evolutionary history may also suggest creative opportunities for genetic (and broader) conservation. One such application could be, for example, artificially introducing Monterey pine into areas that could have been naturally founded (introduction) had the opportunity not been prevented by human barriers or into areas that had been occupied by the species at some earlier time (re-introduction) (e.g., Millar 1998b). This thought deserves objective and careful consideration of the risks and benefits. Some of the risks include possibilities such as displacing some extant populations of other native species, providing an artificial bridge for introduced disease (such as pitch canker) into other native species, and affecting fire risk or current disturbance regimes in the potential introduction areas. However, there may be considerable ecosystem accommodation, over time, to such introductions. For example, planted Monterey pines on a southeast facing slope at Muir Beach (north of the current northern limit of the natural range of Monterey pine) serves as an overwintering site for monarch butterflies (Tuskes and Brower 1978).

Any such intentional introduction of Monterey pine would require a case-by-case consideration of the genetic and ecological consequences, not only for Monterey pine but also for the new host ecosystem. At present, such historical introductions of Monterey pine beyond its native range, into some California state parks and reserves, are considered unfortunate. Indeed, in some parks and reserves, planted Monterey pines have naturalized and are considered an invasive exotic, competing with the native vegetation. For example, large numbers of Monterey pine seedlings were planted in the Jug Handle State Reserve (a 300-ha reserve along the northern California coast in Mendocino County) decades ago, and they have spread by natural regeneration. A large-scale effort in the late 1980s removed many of the trees, but there is still natural regeneration—a condition that will continue until there are sufficient resources available to complete the removal (C.M. Fabula, pers. comm.) It is the current policy of the California Department of Parks and Recreation to manage the state parks and reserves not only in a manner that would maintain and encourage native species, but to match the local gene source for planting stock. Consistent with this policy, exotics—including Monterey pine planted outside its current natural range—are removed to the extent possible with the resources available for such activities (S.R. Bakken, pers. comm.). Thus, intentional introductions of Monterey pine, or maintenance of existing naturalized plantings, would not only have to be well considered, but negotiated and rationalized within the appropriate management structure.

Another and more conservative approach to conserving and possibly expanding the species range is conservation of areas adjacent to the extant populations to allow movement via

Box 9. Genetic sampling for *ex situ* or *in situ* reserves: How much is enough?

"In the 1978 seed collection in California we collected in fairly dense forests from trees about 100 m apart to be sure we were not collecting from closely related trees. After an old tree is killed in a wild fire most of the seed falls near the tree so that a family group is established in an area perhaps 50 m diameter, and one group overlapping with the next to some extent. By that sampling standard there would be only about eight unrelated trees in each of the proposed 8-ha reserves, and 40 for the whole population, a small number, but far better than having no secure reserve. Of course there would be many other trees in each reserve and they would also contribute to genetic conservation, as well as to æsthetic and habitat values." (K.G. Eldridge, pers. comm.).

natural regeneration. Indeed, some recent conservation activities embrace this view by protecting areas adjacent to Monterey pine forests in addition to the current forested area (e.g., recent conservation easements, conservation management agreements, and land purchases in the Cambria area).

The rationale for founding new Monterey pine populations is strengthened by, although not entirely dependent on, embracing the concept of metapopulation structure for this species (see Box 1). Metapopulation structure would include not only natural occurrences of new populations being founded but of existing populations going extinct (i.e., extirpation). One must be careful, though, not to make illogical applications of our understanding of the species' evolutionary history. For example, local population extinctions that may have happened over evolutionary time scales should not be encouraged or viewed as normal species' dynamics within our human time scales. Obviously, the loss of populations over evolutionary time in response to climatic triggers when the species has many populations and is recolonizing is a very different situation from the present—where the species is reduced to a few populations (S.P. Harrison, pers. comm.).

Climate change

Temperatures rose in the 20th century at a rate unprecedented in the last millennium. Atmospheric CO_2 concentration is now higher than at any time in at least the last 420 000 years and it will almost certainly double within the next century (Bradley 2000). Changes in the normal range of temperatures, patterns of precipitation, concentration of CO_2, and other atmospheric characteristics affected by recent and continuing climate change, will affect forest dynamics and possibly species' ranges (e.g., Peters 1990). Globally, these effects are expected to be more pronounced in temperate (including the Monterey pine native range) and arctic forests, where temperature increases are projected to be relatively large. Coastal ecosystems may be more immediately and critically affected, given that global mean sea levels are expected to rise about 6 cm per decade (Kappelle et al. 1999). Given that climate change will surely exert significant pressures on Monterey pine, that its precise environmental tolerances are not known, and that historical migration routes for populations are largely limited by human developments, it is desirable to conserve as much extant genetic diversity as possible to allow the best opportunity for adaptation in place.

Predicting the effects of climate change on ecosystems is complicated and requires baseline data on the status and trends of a vast array of species across all taxa, and effects may differ across spatial scales and with the assumptions about the nature of climate change (Root and Schneider 1995; Bachelet et al. 2001). In one study, future species distributions were simulated for a future climate scenario (2090–2099, 10-year mean) for 15 tree and shrub species in North America (including Douglas-fir and ponderosa pine). Predicted range shifts were in all directions (i.e., not simply northward) and characterized by increased fragmentation (Shafer et al. 2001). Certainly, degraded or fragmented forest ecosystems are less resilient or resistant to climate change effects than are diverse and healthy ecosystems (Noss 2001). Minimally, these climatic changes will provide different or more pronounced selection pressures on populations of Monterey pine. In particular, climate may be expected to affect its phenology. Possibly, the changes would be sufficient to decrease current habitat. Prior to human settlement, species theoretically would have had opportunities to migrate in response to climatic pressures. However, given the developments and land uses surrounding Monterey pine habitat, this is not an option in most areas. In situations such as this, where the species cannot avoid an increasingly stressful environment by shifting its geographic distribution, adaptation or extinction will rely decisively upon the ability of the species to mobilize sufficient genetic variation to track the environmental change (Rodríguez-Trelles et al. 1998).

The potential to adapt to strong directional selection, such as that imposed by rapid climate change, could be limited either by limitations in the amount of genetic diversity (i.e., additive genetic variance for selected traits becomes exhausted) or because of counterbalancing selection by other influences (Rodríguez-Trelles et al. 1998). Both the amount and the structure of genetic diversity will influence the capacity of a species to adjust to environmental stress associated with climatic warming (Gunter et al. 2000). Given the evolutionary history of a dynamic natural range that is responsive to climatic triggers, and a current natural range that is highly constrained by development, it is critical that the genetic diversity of Monterey pine should be conserved so as to allow continuing evolution in place (*in situ*). The predicted effects of rapid climate change underscore the need for maintaining diverse gene pools and avoiding further forest fragmentation (Noss 2001).

Ex situ genetic conservation

Ex situ genetic collections are important not only as a parallel conservation strategy to support *in situ* conservation, but also for research, education, and commercial breeding activities for industrial plantations in other countries. Guerrant and Pavlik (1997) summarize factors germane to genetic sampling for conservation collections of endangered plants. Monterey pine has attributes corresponding to eight of the ten highest priority criteria for genetic sampling (e.g., experiencing rapid decline, biological management required, recently or anthropogenically reduced, feasibility of successful maintenance in cultivation or storage, and economic potential). It is desirable to conduct further rangewide collections of Monterey pine seed from the five natural populations. There is some urgency to this because of the attrition of old trees on Guadalupe Island and the recent mortality within the California populations from pitch canker that may remove some significant genetic diversity. In response to the concern about loss of genetic diversity in the pines on Guadalupe Island, a multinational expedition was organized and seeds were collected on this island and on Cedros Island in May 2001 for conservation, possible restoration, and research purposes (Box 3). Care must be taken to collect

seeds at a time that coincides with maturity and maximum viability of the embryos (e.g., Rimbawanto et al. 1989). Collections may at least provide a reservoir of some of this diversity to be used at a later time for regeneration, restoration, research, or other purposes. Additional seed collections are also warranted as seeds have finite lifetimes (i.e., one of the most comprehensive and rangewide collections is now 24 years old) and former seed supplies have been diminished through use. Also, existing seed collections do not necessarily represent the range of genetic diversity. For genetic research that could offer more scientific information towards conservation, additional seed collections can offer the opportunity to study specifically the pattern of genetic diversity in each population.

Recommendation 6: *Additional seed collections should be undertaken in the five native populations using genetic sampling criteria.*

Given the value of *ex situ* collections for research, education, conservation, and commercial activities, their viability should be supported with the best available facilities and professional stewardship. Emerging technologies and information from recent studies should be routinely evaluated for relevance to the maintenance of collections (e.g., Siregar and Sweet 2000). Although seeds of temperate zone pine species typically have good long-term storage capability, there can also be losses in viability over time and genetic changes due to chromosome damage or nonrandom loss of seed viability (Bonner 1990). The physiological condition of the seeds when stored and the storage conditions also influence the shelf-life of seeds. Research on long-term storage for Monterey pine seeds, including cryogenic storage, could provide valuable enhancement to the role of seed collections in genetic conservation.

The status of *ex situ* reserves of Monterey pine in California should be determined, including recommendations for maintaining the conservation values of the various seed collections and outplanted reserves. Seed collections, for example, can vary considerably in their value for conservation purposes, depending on the sampling design for the collection and the seeds' viability. Old or even nonviable seed collections could still be useful. For example, some types of genetic research can make use of DNA from seed that have lost viability and are not of use for restoration purposes.

Given recent or potential significant losses in genetic diversity within the native Monterey pine populations, existing *ex situ* collections of Monterey pine may not be completely replaceable because the genetic source may be gone, depleted, or contaminated. Therefore, it is important to treat *ex situ* collections as valuable and finite. Use of these collections should be guided by a policy that considers the value of the proposed use and the benefits and risks of reducing the *ex situ* collection for this purpose. Some uses of genetic collections are nonconsumptive (e.g., educational activities such as tours of breeding orchards and genetic field tests). Some parameters that could be considered in making decisions about the use of limited genetic collections are presented in Table 12.

Financial support is often a limiting factor in long-term conservation of *ex situ* genetic collections. Genetic collections are particularly concentrated in the public sector and are disproportionately affected by government cutbacks in budgets. The true value of genetic collections has not been

Table 12. Factors to consider in deciding appropriate use of *ex situ* genetic collections† for research or restoration purposes.

	Factor	
Type of use	**Favoring use**	**Against use**
General		
	Use is nonconsumptive	Use is consumptive
	Collection easily replaced	Collection wholly or partially irreplaceable
	Collection inexpensive to replace	Collection very expense to replace
	Multiple uses/applications	Restricted use/application
Specific research		
	Research is novel	Research not novel
	Methods are parsimonious in germplasm use	Methods unnecessarily consume germplasm
	Objectives require specific genetic material	Objectives could be satisfied with less valuable genetic collections or *de novo* collections
	Outcome likely to support conservation of *in situ* populations	Research has little to no conservation application
	Germplasm or DNA products can be reused for other purposes	Germplasm completely consumed or contaminated
Conservation/restoration		
	Natural regeneration unlikely	Natural regeneration still possible
	Little risk of genetic contamination of natural populations	Significant risk of genetic contamination of natural populations

†It is assumed, for the purposes of this table, that the genetic collections are pure collections (i.e., reflecting the genetic attributes of the native gene pools, without contamination), still valuable for restoration or native-population research purposes.

calculated or internalized in activities—such as research—that make use of them (e.g., Hoagland 1996). To mitigate this problem, pricing schedules could be developed to suggest financial contributions by researchers who use genetic collections of Monterey pine. These expenses could become normalized in research proposals.

Other than seed collections, Monterey pine genetic collections exist in various genetic trials, breeding orchards, and other living collections in California. Often established in the 1970s and 1980s, they require a current and focused assessment because of changes over the last few decades that include introduction of pitch canker, changes in principal researchers and staff associated with these collections, changing priorities or emphases in the host institutions or companies, and changing requirements of the genetic collections due to their age (e.g., aging seed collections or mature seed orchards).

Recommendation 7: *Protocols for any extant* ex situ *genetic reserves should:*

i. *Determine the maintenance strategy for that collection, including risk management by subdividing the collection among several location;*
ii. *Recommend and preferably secure a long-term or perpetual sponsor or steward for the collection(s);*
iii. *Establish priorities for the most appropriate use of the collection (i.e., decision-making criteria for seed distribution for uses such as research, commercial, restoration, or mitigation); and*
iv. *Recommend a pricing structure for returning support to the collections based on their use.*

In addition to these considerations, plans for any future genetic collections should include an assessment of the effect of the collection on the genetic diversity of the sampled natural population (e.g., risk assessment).

In situ management

Harvesting influences

Historical harvesting practices, at least on the mainland of California, have affected habitat of Monterey pine and probably its genetic composition. Several cycles of logging over much of the pine forests of Cambria and Monterey, in particular, occurred in the 1700s and 1800s. The Año Nuevo population was perhaps less affected by logging owing to the availability of coast redwood and Douglas-fir in that area. Although all harvesting does not necessarily have a negative genetic impact, it can be detrimental if it is extensive and causes narrowing of the genetic base in future generations or if it is selective of certain trees which carry genes that are absent or less frequent in the remaining trees. Good reviews of the human settlement activities and logging practices in these areas are provided by Forde (1966) and Libby (1997).

Much of the Monterey pine forest in Monterey County has been harvested at least once (e.g., McDonald 1959). For example, some pines near the Carmel River were felled and used in establishment of the Carmel Mission in 1769. During the mid-1800s, other documented uses of Monterey pines were the building of a fort and blockhouse near Monterey, the export of timber to the Hawaiian Islands, and the establishment of a sawmill near Point Cypress that rapidly thinned out the forest. Brick kilns established in the area also promoted harvesting because of the need for fuel (McDonald 1959). This historical use of much of the Monterey population may have had an impact on genetic diversity. Without an unharvested, natural forest stand in the area with which to compare, it is difficult to assess the genetic effects of harvesting practices. However, a recent comparison of genetic diversity in old-growth populations of eastern white pine (*Pinus strobus*) with partially harvested nearby stands provides some insight. Pre- and post-harvest genetic diversity were measured in each of two study areas—approximately 0.7 ha each in size—within larger areas of old-growth eastern white pine. In this study—conducted in Ontario, Canada—genetic erosion occurred as a result of harvesting. The total and mean number of alleles were reduced by approximately 25%, the percentage of polymorphic loci dropped by about 33%, and about 40% of the low-frequency alleles and 80% of the rare alleles were lost because of harvesting. This suggests that the ability of the postharvest gene pool to adapt to changing environmental conditions may have been compromised (Buchert et al. 1997).

Given the historical harvesting practices that occurred throughout much of the mainland California populations of Monterey pine, care must be taken in describing 'natural' levels and structure of genetic diversity. Knowledge of management history is needed to make decisions about site selection for research and for context in interpretation of scientific studies involving the current Monterey pine forests.

Recommendation 8: *Management history, for the mainland populations in particular, should be well documented to allow appropriate site choices and data interpretations for scientific research and for support in forest management.*

Habitat loss and fragmentation

Loss and fragmentation of the natural habitat of forest tree species have been so long term and widespread that there is considerable theoretical and empirical evidence of the significant genetic impact for some species (e.g., Ledig 1992; Huxel and Hastings 1999). Reduction in the natural range of Monterey pine provides two physical consequences which, in turn, could precipitate genetic consequences: loss of habitat at the margins of the existing populations increases the distance among populations; loss of habitat within populations can cause fragmentation. Both types of habitat loss can change the pattern of pollen and seed dispersal (and their efficacy) and gene flow. For example, fragmentation of forest populations can create habitats that promote interspecific hybridization (e.g., Harrison 1990). The genetic consequences of fragmentation depend on the breeding system and type of pollination (e.g., Nason and Hamrick 1997).

Estimates of a tree population's mating system (rates of self- versus outcross-fertilization) and breeding structure (spatial patterns and relative frequencies of effective pollen transfer between plants) are also indicative of pollen dispersal patterns (Nason and Hamrick 1997).

Fragmentation can lead to other effects, indirectly affecting genetic diversity and structure. Fragmentation creates more forest edge which can alter the sunlight and wind effects on the forest fragment (relative to the former contiguous forest), which can, in turn, affect forest structure, leaf fall, turnover in the plant community, seedling recruitment patterns, and distribution of animals (Gascon et al. 2000). In some studies of tropical forests, fragmentation has had major impacts, very quickly changing the tree composition from climax to pioneer species, and a cascade of associated impacts (Gascon et al. 2000).

Although the naturally occurring distance among populations and the genetic substructuring within populations can enhance genetic integrity because they may reflect underlying processes such as adaptation (e.g., Chambers 1995), forced distance or fragmentation—such as that caused by housing or transportation developments—can have detrimental effects on genetic integrity by interrupting these processes. Fragmentation may lead to artificially small subpopulations which may increase the effects of genetic drift—the random process of gene sampling from one generation to another. Small populations tend to lose genetic variation by genetic drift more rapidly than will larger populations. In fact, a study comparing the effects of such processes as genetic drift, mutation, immigration from outside populations, and directional and balancing selection, revealed that genetic drift was the overriding factor controlling the loss of genetic variation (Lacy 1987). These results were interpreted as a strong signal to managers that they should be concerned with the variation-depleting effects of genetic drift.

Reduction of population size or increasing the distance among populations can have significant genetic consequences. These trends may result in increased levels of inbreeding which genetic theory indicates may result in expression of deleterious recessive alleles which may cause lowered fecundity, higher seedling mortality, and reduced growth rates that could eventually drive a population to extinction (e.g., Wright 1977). As discussed earlier, there is considerable evidence of vulnerability to inbreeding depression in Monterey pine. Also, loss of heterozygosity (another consequence of inbreeding) may reduce a population's ability to respond to future environmental changes—thereby increasing the probability or rate of extinction (e.g., Franklin 1980). Examples of the consequences of extreme reduction in genetic diversity are found in agriculture. Early 19th century Irish farmers mostly grew a single clone of potato—a clone that proved vulnerable to the devastating potato blight. Similarly, by 1970, 75% of the United States' corn crop was composed of a single genotype that was vulnerable to the corn blight fungus (Ledig 1988).

Loss of habitat within populations—those five major areas of Monterey pine that we superficially call populations—may actually erode significant levels of genetic diversity and remove locally adapted subpopulations (Ledig 1992). Although the within-population genetic structure of Monterey pine is not well studied, suggestions of fine-scale structure are evident in a number of studies. Cromer et al. (1982) noted differences in salinity tolerance among subpopulations of the Monterey population. Toplu et al. (1987) found differences in six-year volume among subpopulations within mainland populations. Burdon et al. (1992a) found that one subpopulation from Año Nuevo grew much more slowly than the seedlots collected from other areas within this population. Johnson et al. (1997) found significant differences in height and basal area among some subpopulations within mainland California populations.

Recommendation 9: *Further fragmentation of remaining Monterey pine forests should be avoided.*

Fire suppression

The role of fire in Monterey pine forests may change over time, is dependent on the nature of the fire, and is affected by interactions with climate and other environmental and anthropogenic factors. Both social and ecological contexts are important considerations for management of Monterey pine forests as it pertains to fire policy. For example, in areas where Monterey pine intermixes with knobcone pine, fire may be given more ecological weight in management decisions because of the more intense heat required to open the cones of knobcone pine (Vogl 1973; Sigg 1987; Ornduff and Norris 1997). Given the urban and near-urban location of much of the remaining Monterey pine forests on the California mainland, suppression of wildfires is likely to continue in many areas. Public safety and protection of buildings and other developments are one issue; public acceptance of this natural disturbance and its ecological impact is another. For example, after the 'Vision Fire' (i.e., a massive wildlife ignited by embers of an illegal campfire on October 3, 1995 on Mount Vision in the Point Reyes National Seashore in Marin County, California), there was prolific natural regeneration of bishop pine, and many of the pine trees in the previously mature pine forest were killed (Ornduff and Norris 1997). Although this may be considered a natural regeneration cycle, the dramatic change in the landscape and abundance of charred dead trees may not be immediately understood and accepted by the public.

Although the relationship between historical fire regimes and Monterey pine seed production, seed dispersal, and seedling establishment and recruitment is not well understood, the reality of fire suppression (for reasons of safety, investment protection, or public sentiment) has generated interest in finding substitute treatments for fire influence. One treatment that has been tried in some forest situations to enhance regeneration in the absence or near-absence of fire (and where fire was a part of the landscape prior to human influence) is mechanical creation of gaps or openings in the forest canopy. This treatment might be particularly effective in situations where shading, because of a mature and closed canopy, is a major limiting factor in germination

or seedling establishment. If other factors are limiting, this treatment may not be effective. For example, a study of the effects of harvesting trees to create openings in a giant sequoia forest near Mountain Home, California revealed that these mechanically created gaps were not successful—in this situation—in stimulating natural regeneration. This harvesting practice attempts to simulate the natural fire regime of forests (in this case, the southern Sierra Nevada mixed-conifer forest), but important ecosystem processes such as increased seed dispersal following patchy, high-intensity fire and large-scale nutrient cycling are not duplicated with mechanical treatments (Stephens et al. 1999).

In addition, the genetic impacts of using mechanical rather than fire- or other-stimulated regeneration are not known. An intense fire could simultaneously open the canopy for light penetration to the forest floor, release abundant seeds by opening cones, and remove much vegetative competition (for moisture and nutrients) for the Monterey pine seedlings. For example, in the absence of fire, forest conversion to a more oak-dominated forest has been noted in some areas (McBride and Stone 1976; White 1999). There could be abundant, even-aged regeneration after such a fire, which could allow a broad palette on which natural selection could act. In contrast, regeneration events that are more scattered, gradual, or lower intensity, would change the selection regime and potentially change the diversity, density, and dynamics of fire-related regeneration. These differences in regeneration dynamics, and selection regimes, have potentially significant consequences for the genetic diversity of subsequent generations of Monterey pine.

In summary, whether or not fire is needed for regeneration of Monterey pine is not the key question. Rather, we need to understand the interrelationship of fire with the ecology, reproduction, recruitment, and long-term health of the species and its ecosystem. That information will then inform forest managers as to whether and how other management options can simulate the effects of fire where its direct use is impractical. In general, more research is needed to understand regeneration dynamics.

Genetic contamination

Genetic contamination, simply, is the introduction of foreign genes into the local populations. In this usage, 'foreign' refers to genes from nonlocal individuals of the same species. This can occur directly—by planting seedlings from a nonlocal source in the local populations, or indirectly—from pollen or seeds blown in from sexually mature trees of nonlocal origin that were planted close enough to the native populations to influence them.

In general, the scope and impact of genetic contamination will derive from three conditions: the size of the 'contaminant' source relative to the native forests, the genetic diversity of the contaminant, and the degree of genetic matching between the contaminant and the native forests within gene flow range. In the first case, the larger the number of contaminant trees, and the greater their reproductive output (i.e., seeds or pollen) relative to that of the native forest, the greater is the potential for genetic contamination. If, for example, pollen production from the contaminant trees is very large, it can 'swamp' the proximate native forests. In the second case, even if the contaminant source is well matched genetically (i.e., it is from a local source), a kind of genetic contamination occurs if the genetic diversity of the native forests is lowered or changed by the overrepresentation of certain genes (alleles) in the introduced trees. For example, if a local seed source was used to produce a clone that was then planted in large numbers close to the native forest, its reproductive output could decrease the genetic diversity in the forest over time and cause inbreeding depression.

The third case—that of genetic mismatching—is the conventional condition for genetic contamination. In theory, genetic contamination can undermine fine-scale genetic structure and adaptation to local conditions. This potential has been demonstrated empirically for some woody Californian species, including the subshrub *Lotus scoparius*, where transplantation experiments showed lowered fitness for genetically mismatched populations, consistent with disruption of local adaptation (Montalvo and Ellstrand 2001). There can be a range of effects, depending upon how different or ill-adapted are the foreign genes and how they interact with resident gene pools. For example, if the introduced genes were directly expressed and very maladapted to local conditions, the seeds or seedlings might die soon. In this extreme case, the genetic contamination is self purging, over perhaps as little as one generation. However, there is still an ill effect in that the regeneration opportunities (within local gene pools) have been temporarily lost or compromised. Another scenario is that if the local population is inbred, outcrossing to a nonlocal source may lead to heterosis and genetic contamination may persist over several generations. More likely, the introduced genes have a less dramatic impact and may remain permanently in the population, contributing to future generations and probably lowering the fitness of that population to some extent, depending on how fine-scale are the adaptations to local conditions.

A committee formed to evaluate introduction of exotic genotypes into the University of California's nature reserves has outlined a number of documented effects from the scientific literature of such nonnative introductions (Endler et al. 2000). These effects include: disruption of natural patterns of geographic variation in genotype frequencies (which in turn affects the suitability of nature reserves as study areas for natural populations), introduction of genes that are poorly adapted to local conditions, disruption of local patterns of gene interaction, potential to affect the population's future ability to respond to environmental change, and cascading effects through the community (i.e., any genetic changes that alter a given species' ecological properties are likely to be felt in the community). Some or all of these effects are potentially applicable to the Monterey pine forests.

The opportunity for genetic contamination varies with time and conditions. Proximity of introduced trees to native trees is a large determinant. However, the transport of pollen, for example, will vary from year to year and among pine populations in relation to weather and topography. The annual variations may be more important in the early

stages of pollen production in a stand (R.D. Burdon, pers. comm.). Wind force, temperature, and humidity are key environmental factors influencing pollen dispersal (Fielding 1957a). Studies of the reproductive biology of Monterey pine (outside its natural range) suggest that there is considerable individual-tree and yearly variation in amount of pollen produced, timeframe for pollen dispersal, amount of seed dispersed, and dispersal distance (e.g., Fielding 1947).

The importance of using local plant sources to avoid genetic contamination has been recognized by the California Department of Parks and Recreation. Charged with the responsibility for protecting and preserving the State's natural heritage, the Department has a policy that specifically reflects the requirement to protect the genetic diversity of the State's rich botanical assemblage. Policy Number 7 of the California State Parks and Recreation Commission states that "In order to maintain the genetic integrity and diversity of native California plants, revegetation or transplant efforts in the State Park System will be from local populations unless shown by scientific analysis that these populations are not genetically distinct from populations being proposed for use." (Woodward and Harrison 1989).

Because of the decades-long use of Monterey pine as an urban landscape species and as roadside screens in coastal California (Box 10), there has been considerable opportunity for genetic contamination to occur in the three mainland populations. In fact, by the early 1970s it was noted that pollen and seeds were invading the native stands from widespread roadside and amenity plantings in the increasingly urbanized Cambria and Monterey native populations. These plantings were often Monterey pine seedlings from unknown or uncertain sources, or from known nonnative sources (Libby 1990). In the city of Carmel, at the edge of the Monterey area population of Monterey pine, over 36% of the city tree population is composed of Monterey pines—many planted by city personnel and of uncertain genetic origin (Nowak and McBride 1991). Nonlocal Monterey pines apparently were planted close to Asilomar State Beach and the Spanish Bay native stand (Libby 1990).

Genetic contamination could also result from planted field trials, *ex situ* reserves of Monterey pine, or Christmas tree plantations if nonlocal trees in these collections reached sexual maturity and were within pollen flow distance of native populations. The extent and severity of genetic contamination has not been studied comprehensively, either indirectly with a survey of planting records or by genetic testing of planted trees or directly with observation of genetic contamination in native forests.

Many California Christmas tree growers use nursery stock derived from New Zealand sources. However, genetic contamination from this use of Monterey pine has probably not been extensive, based on current conditions and practices within the California Christmas tree industry. First, genetic contamination would only be a potential issue when Christmas trees are grown within the pollen range of the native Monterey pine forests, thus excluding many current growers. Second, depending on the age at which trees are sold, pollen contamination may not be a significant issue. Based on the generally fast growth of farm-grown Monterey pine, they are often sold at three to four years of age, and not generally older than six years, even when grown on poor sites (S.E. Minturn, pers. comm.). Finally, another potential source of genetic contamination—that of people planting living Christmas trees in or near the native Monterey pine forest—has a very low likelihood of significant genetic effect. This is because the market for live Monterey pine Christmas trees is very modest, probably not more than a few hundred trees annually (S.E. Minturn, pers. comm.).

Recommendation 10: *The genetic and associated demographic risks from planted Monterey pines (e.g., roadside plantings, landscape trees, residential trees, and Christmas trees) within the current reproductive range of native Monterey pine populations should be evaluated. This evaluation should include an ex-*

Box 10. Planting of Monterey pine along California highways.

A cursory check with Caltrans (California Department of Transportation) personnel found that records were not sufficient to determine the seed source, nursery location, or year of planting for all projects within their considerable planting program of Monterey pines along California highways (D.T. Grinstain, pers. comm.).

It is not known when pines were first used by Caltrans along transportation corridors, but revegetation has been a part of the department's activities since shortly after its organization, approximately 70 years ago. Therefore, some of the planted Monterey pines may be quite old.

Planting stock was obtained, through contract, with a variety of private nurseries and some, if not much, of the material may have come from New Zealand or Australian sources. To the extent it is derived from New Zealand sources, the planted seedlings would very likely contain a significant portion of Año Nuevo ancestry (R.D. Burdon, pers. comm.) Research strongly indicates that the source material that forms the foundation of New Zealand commercial stock derives from only Año Nuevo and Monterey, with a disproportionate contribution from the former (Burdon 1988).

Because of increased mortality, largely from pitch canker, Monterey pine is no longer planted by Caltrans and has not been a regular part of their revegetation program for at least seven years. Prior to that, Monterey pine was planted along coastal highways, including State Route 1 and US 101, with a total in the thousands. The range of plantings on Caltrans right-of-way areas has been from Ventura/Oxnard northward through the Bay Area and as far inland as the Coast Ranges and in the Salinas Valley. Some particularly dense plantings exist along State Route 1 in the area between Monterey and Carmel. Here, it had been recommended to plant seedlings with a close spacing because of the expectation of high mortality. Many of the pines survived, however, and today provide a dense cluster of adult trees (D.J. Reeves, pers. comm.).

amination of geographic scope, timeframe over which trees have been planted, and genetic source of material.

It is desirable for many applications to be able to determine the geographic and genetic origin of planted trees. When this is not possible via records, some investigations have determined the feasibility of using various molecular markers for this purpose. For example, using allozyme frequency data, Moran and Bell (1987) determined that Monterey and Año Nuevo populations are most likely the major sources of original introductions in Australia. The origin of Basque populations of Monterey pine were investigated with RAPD markers. Results indicated that the Basque populations are most probably derived from the Año Nuevo population (Aragonés et al. 1997). However, there was no estimate of the power of the test. There is also the issue here of sample size. Determining the origin of a large sample of trees, knowing *a priori* that all are of the same origin, is a different and easier question than determining, with certainty, the origin of an individual tree. Strauss et al (1993) could differentiate among the five natural populations using mitochondrial DNA RFLPs. Nuclear microsatellite markers have been developed for this species (e.g., Smith and Devey 1994; Fisher et al. 1996) and, because they show a high level of polymorphism and Mendelian transmission, they may be useful in providing population identities for individual trees.

A technology that is being developed for application in commercial plantations of Monterey pine could have relevance to the reduction of genetic contamination of native Monterey pine forests. This technology is the generation of reproductively incompetent trees through genetic engineering. The advantages of this characteristic in commercial forestry include direction of more energy by the trees into vegetative growth, control of the invasive nature of the pines in some situations and hence less management directed towards removal of volunteer seedlings, and expansion of the range of plantation possibilities into residential areas without attracting criticism from those concerned about the potential for pollen-related allergies (Mouradov and Teasdale 1999). Although this technology has not been fully developed for Monterey pine, the potential has been fully demonstrated with the isolation and characterization of a gene family showing specific expression in immature male and female cone buds (Mouradov and Teasdale 1999). Near natural populations of Monterey pine, this technology could allow the extension of the ecological perimeter of the forest with Monterey pines that have specific characteristics of value to urban settings (e.g., pitch canker resistance or desirable shape) without presenting a genetic contamination threat.

An issue related to genetic contamination, but not considered here to be a genetic threat to the species, is interbreeding with other pine species—known more technically as introgressive hybridization. As with other species, this can only occur where two sexually compatible species grow close together and where the habitat allows an ecological niche for the establishment of the introgressive hybrids (e.g., Stebbins 1950). For Monterey pine, these conditions are both satisfied in certain areas with knobcone or bishop pines. As has been documented elsewhere in this report, naturally occurring hybridizations between Monterey pine and bishop pine have been observed at Monterey at low frequencies (less than one percent of the population, noted in the 1940s; Stebbins 1950). Similarly, a modest number of natural hybrids of Monterey and knobcone pine have been noted near Point Año Nuevo in Santa Cruz County (Lindsay 1932; Stebbins 1950; Bannister 1958). Historically, there has been some seasonal separation of phenology (i.e., pollen is shed later in knobcone pine and bishop pine than in Monterey pine), at least in these areas, which has perhaps prevented more recruitment into the population from these interspecific hybrids. As these are natural occurrences, this would not constitute a genetic threat unless conditions changed such that interspecific hybrids were becoming much more common and replacing the pure species to a large extent, or if planted knobcone or bishop pines were contributing interspecific hybrids to the native populations. Outside of natural occurrences, there has been considerable breeding and testing of artificial crosses between these species (Box 11).

Mitigation-, urban-, or recreation-related planting of Monterey pine

Genetic conservation concerns related to the planting of Monterey pine outside the natural forest depend first on whether or not the planted pines are within the seed dispersal and pollination region of natural forests. If so, then much of the rationale concerning planting is based on choice of material that does not constitute genetic contamination risk. If not, then planting decisions are wisely guided by the arboricultural considerations including growth rate, growth potential, light regime available and desired, soil type, disease vulnerability, leaf fall or retention, and proximity to structures.

When planting Monterey pine trees close enough to the natural pine forests such that it can reasonably be expected that seeds or pollen from the planted trees could mix with those of the forest when the trees are sexually mature, genetic implications should be considered. In addition to genetic contamination issues, discussed earlier, other genetic considerations are maintenance of natural levels of genetic diversity and local adaptations.

It is particularly important to consider genetic appropriateness when planting Monterey pines in areas where the boundaries between native forest and domesticated trees are not well defined. The reason is not only the high potential for genetic contamination of the native forest, but the confusion this presents for defining areas for conservation or for research on natural pine populations. Memories and records tend to deteriorate over time, lending to confusion over what is natural and what has been introduced. Given the limited availability of natural buffer areas for current or future conservation reserves of Monterey pine in some populations, the close vicinity and high level of interdigitation of natural and urban areas in the Cambria and Monterey pine populations in particular, the potential for large numbers of planted trees over time, and the potential for confusion over

planted versus natural trees in the long term, it is important that planted Monterey pines are genetically appropriate for the area. This includes street and residential plantings, mitigation plantings, artificial regeneration efforts, and restoration activities.

Recommendation 11: *For any planting of Monterey pine within an area where mixing with the native gene pool is possible, the planting stock should be locally adapted and contribute to maintenance of natural genetic diversity of the native pine forests. Seeds should be preferred to seedlings. Clonal material should not be used except in limited scope in situations where this is the only feasible or well-reasoned alternative. For large planting projects, the source for propagules should be chosen so as to create a large effective population size.*

Introduced biotic influences

Introduced biotic influences, such as diseases or insects that have evolved outside the native range of the host species, may have two types of genetic impact. If they have major effects on mortality or reproduction in the host (i.e., Monterey pine), they can reduce genetic diversity generally. If there is some genetic basis for resistance in the host then there can be selection within the pine populations, thereby losing some genetic diversity that is associated with vulnerability to the influence. With coevolved biotic influences (e.g., native insects and diseases), there is an evolutionary history that has resulted in some type of interaction that has allowed both species to persist. With introduced organisms, no such mechanisms are necessarily present and epidemics may result. A case in point is white pine blister rust *(*caused by *Cronartium ribicola*). Introduced to western North America in 1910, its impacts have resulted in one of the most catastrophic plant disease epidemics in history (Kinloch and Dupper 1987; Kinloch 1992).

Responses to artificial selection or human-induced factors (e.g., introduced diseases) may not follow the same 'adaptive model' as natural selection. Comparison of the results of some empirical studies demonstrates that specific empirical studies for the species and adaptive characters of interest are required to understand the genetic basis of the specific adaptation (Orr and Irving 1997).

Over 70 endemic diseases and insects have been described for Monterey pine (Offord 1964; Ohmart 1979, 1981; Old 1979, 1981; Ohmart and Voigt 1981; Old et al. 1986), but these natural influences are part of a functioning ecosystem and natural selection regime rather than a threat to the genetic diversity of the pine. However, introduced biotic influences may have a negative impact. For example,

Box 11. Artificial interspecific hybridization of Monterey pine.

In 1926 the USDA Forest Service began an interspecific crossing program for pines with the practical purpose of producing promising hybrids for extensive testing in forest plantings. Monterey pine has been hybridized artificially with knobcone and bishop pine, among other species (e.g., Righter and Duffield 1951). Hybrids between knobcone and Monterey pine produced in nursery conditions have proven vigorous and fertile (Stockwell and Righter 1946, Roy 1966). Characteristics of the interspecific progeny relative to the parental species are described in Stockwell and Righter (1946). Interspecific hybrids between bishop and Monterey pine could have some interesting traits, depending on which seed sources were used for the crosses (R.D. Burdon, pers. comm.).

The initial success of the knobcone × Monterey crosses prompted further investigation and hybrid seedlings were outplanted. Specimens of each parental species and 60 hybrids from controlled crosses growing at The Eddy Arboretum (USDA Forest Service, Placerville, California) and the nearby Camino Arboretum were studied in the late 1970s to determine parental contributions to the morphological and physiological status of the hybrids. With few exceptions, it was determined that the hybrids morphologically resembled knobcone pine more than would be expected. It was suggested that this may in part be due to maternal effects (Harrison 1980). Interspecific crosses, advanced generations, and backcrosses from these two species in cultivation at Placerville were analyzed for turpentine composition and the results suggested that the difference in turpentines of Monterey and knobcone pines was controlled by a single gene, with probable modifiers in Monterey pine (Forde 1964a).

The knobcone × Monterey pine hybrid has also shown potential for use in reclamation of some disturbed areas in California. Experiments with various tree, shrub, and grass species on Trinity Dam—an earthfill structure in northern California—showed the knobcone × Monterey hybrid to be one of the most promising revegetation choices. Numerous seedlings of this cross were planted on the site in the mid-1980s in a field test that also investigated the effects of added fertilizer and the use of bareroot versus containerized material (Walters and Medlicott 1990). Depending on which seed source was used, interspecific hybrids between Monterey and knobcone pines may also show improved resistance to snow damage (R.D. Burdon, pers. comm.). Superiority in cold hardiness of the hybrids was also noted in AFOCEL studies conducted near the Bourdeaux region in France (F.T. Ledig, pers. comm.).

The California Department of Forestry and Fire Protection (CDF) has collaborated in producing controlled crosses, using pollen collected from knobcones in the Santa Cruz area and pollinating Monterey pines growing in the Forest Service's Badger Hill Breeding Orchard. Seedlings from a specific cross (known as 'KMX') were installed in field tests in various counties in California (including San Bernardino, Humboldt, and Trinity) to observe long-term growth characteristics. Preliminary observations from some of these tests suggest a useful combination of the parental species has been captured in this particular cross: with the desirable growth characteristics of Monterey pine and the environmental hardiness of knobcone pine. Some second-generation seeds from these crosses (i.e., progeny from interspecific trees) are being held by CDF in controlled storage conditions. Although the production of seedlings from this cross by CDF has been halted because of the pitch canker epidemic, there continues to be some interest from areas outside California. (L.A. Lippitt, pers. comm.).

pitch canker, caused by the introduced fungus *Fusarium circinatum*, was first discovered in California in 1986, affecting thousands of trees in the summer of 1986 throughout Santa Cruz County, California (McCain et al. 1987). At that time, one strategy proposed was "to do nothing because it is thought that the fungus will not kill trees and infected trees will recover" (Tjosvold and McCain 1988). The pathogen then spread to Monterey pine populations at Año Nuevo and Monterey. Infestation in the Cambria population was discovered in 1994 (Adams et al. 1999). Twelve other pine species (eight of them native to California) and a Monterey × knobcone hybrid were quickly tested in greenhouse studies and found susceptible to the pitch canker fungus (McCain et al. 1987).

In California, the disease is often described as a 'pest complex': native insects such as twig and bark beetles act as vectors of the fungus, and fungal infections may weaken the tree and provide new habitats for the beetles. Though the exact relationships between the insects and the fungus are yet to be elucidated, the overall effect may be greater than the combined effects of the individual insects or fungus alone (Owen 1998). Given the high degree of mortality, and the evidence of some genetic basis for resistance, there may be a major genetic impact on the species from this epidemic. The degree and nature of genetic impact will depend on overall amount of mortality, the genetic basis for resistance or tolerance (and hence selection effects), and the age at which most trees are affected. If, for example, much of the mortality is among older trees, they would have already made, or had the opportunity to make, contributions to younger generations. However, because a healthy Monterey pine tree is reproductively active for decades, any curtailment in that reproductive period could have an effect on its overall genetic contribution.

Introduced disease issues stimulate debate and research concerning the most appropriate, if any, management response. At the time of publication of this report, the nature and genetic basis of resistance to pitch canker were not well understood. Results of controlled studies may vary according to the source of genetic material for the pines, the type of fungal isolates used, the infection protocol, and how resistance is measured. One greenhouse study found little resistance to pitch canker among samples from the native mainland and Cedros Island populations. As a species, Monterey pine was one of the least resistant among the 23 pine species studied for resistance to pitch canker (Hodge and Dvorak 2000). In other studies, variability in susceptibility among individual trees of Monterey pine suggests there may be some genetic basis (e.g., Storer et al. 1999). The diversity within the fungus (measured in one system as vegetative compatibility groups, VCGs, e.g., Wikler and Gordon 2000), coupled with evidence for recombination between VCGs of the fungus in the laboratory (Wikler et al. 2000), suggest that there is the potential for a dynamic relationship between host and pathogen. Furthermore, there is the possibility that different genotypes of Monterey pine may have different susceptibilities to infection by different strains of the pathogen (K.R. Wikler, pers. comm.), although there is no evidence of this to date for pathogen strains resident in California (e.g., Gordon et al. 1998). However, exotic strains (from Mexico and Florida) have been found that are more virulent than resident strains, based on growth chamber innoculations. Such strains could compromise genetic resistance in some Monterey pine genotypes (T.R. Gordon, pers. comm.).

Numerous laboratory, nursery, and field trials are in progress and planned which should elucidate genetic relationships. Therefore, it is not yet apparent what may be the most appropriate breeding and delivery systems—if any are to be recommended—for pitch canker resistance. Furthermore, as there may be differences between juvenile and mature resistance, studies need to be long term in nature before definitive information can direct management. Although development of selection and breeding programs in parallel with genetic research on pitch canker is a responsible strategy, actual deployment of any plants from such programs would not be advised until the genetic basis for resistance is understood and the need for such assisted regeneration is well reasoned and well informed.

For activities that are directed towards some specific goal (such as selecting trees that lack symptoms of pitch canker in the hope of finding pitch-canker resistance), there is an attendant loss in genetic diversity of the collection (because sampling is narrow). Unnecessary losses of genetic diversity in the sample can be minimized by keeping the genetic base as broad as possible (e.g., sampling from as broad an area as possible within the local adaptation zone, sampling from trees distant from one another, sampling from cones of different ages and locations in tree crown thereby perhaps sampling from different years of pollination or seed production). For such management-directed activities, natural—as opposed to human-determined—selection should be used and accommodated as much as possible, allowing as much of the selection of seedlings as possible to happen in the forest rather than the nursery.

Finally, there is good reason to be cautious in any management approach towards manipulating genetic diversity for resistance to an introduced agent. Artificial selection for resistance is generally only a short-term strategy that is not appropriate for long-lived species such as Monterey pine. Resistance can break down in annual plants, so it is not reasonable to expect that it would be durable in a long-lived species. The considerable history of experience in agriculture suggests there are relatively few cases where individual host plant resistance genes have maintained their efficacy for more than a few decades. In fact, the salient feature from the agricultural experience is the ability of the pathogen populations to evolve rapidly and adapt to genetic or chemical control measures (McDonald and McDermott 1993). However, most of the agriculture examples are based on major gene resistance, and while the basis of any pitch canker resistance in Monterey pine is not known, early results suggest that it is a quantitatively inherited trait. If this proves to be the case, prospects for durability are likely to be greater (T.R. Gordon, pers. comm.). A crucial factor is that disease resistance is almost always just one of many components of

fitness, and any selection for resistance is likely to incur a cost in the selection differential for other fitness components (Burdon 2001a).

Given the long-lived nature of Monterey pine and the uncertainty of how any resistance may play out over the lifetime of an individual tree, the potential for complex interactions between the pines and new variants of an introduced pathogen, and the potential to inadvertently screen out valuable genetic diversity, a cautious and conservative approach to any genetic manipulation motivated by introduced biotic influences is indicated.

The prospect and reality of introduced biotic influences reinforces the need for maintaining genetic diversity in native populations of Monterey pine. A large palette of genetic diversity, expressed in good levels of regeneration, will allow scope for strong natural selection to operate in a biotic crisis (R.D. Burdon, pers. comm.).

Recommendation 12: *Any breeding and delivery program aimed at providing disease-resistant trees for use within the genetic sphere of influence for native Monterey pine populations should be well informed about the genetic basis of resistance for that disease, the inheritance of the desired trait, its interaction with the environment, and the overall impact of artificially selected genotypes on the genetic diversity and population viability of Monterey pine and should not unnecessarily screen out potentially valuable genetic diversity.*

Other common, introduced biotic influences in native populations of Monterey pine are an array of exotic plant species. Exotic invasive plants can affect native ecosystems in numerous ways: directly displacing native species; changing drainage systems, microclimate, nutrient cycling, or light levels; and affecting pollinators and other interdependent species. Moran (1996) lists over 40 plant species that have been introduced to Guadalupe Island over the last two centuries, and another 15 that are probably introduced. Among the former list are tocalote or Malta starthistle (*Centaurea melitensis*), California bur clover (*Medicago polymorpha*), and tree tobacco (*Nicotiana glauca*)—all also introduced species to California.

In California, it has been estimated that invasive plants cost the State hundreds of millions of dollars annually (CalEPPC 2001). Although no comprehensive studies have been reported on their impacts specifically on Monterey pine forests, there is considerable evidence of exotic plant species in these forests. For example, pampas grass (*Cortaderia selloana*) is designated as one of the most invasive wildland pest plants in California, with Monterey pine forests one of the several habitats of concern (CalEPPC 2001).

Invasive plants can exert genetic effects on Monterey pine if, for example, they directly affect regeneration events such as seedling germination, establishment, or recruitment. They could also indirectly affect natural selection if they change microclimate or availability of soil moisture or nutrients.

A recent, informal survey (via questionnaire) of exotic, invasive plant species in native Monterey pine forests in California indicated that approximately 40 species are sufficiently common to have been noticed and identified (Table 13). This list is probably not comprehensive. Following Richardson et al. (2000), a species in Table 13 was considered invasive if it is not only surviving and regularly reproducing, but doing so some distance from the original site of introduction. Furthermore, the term invasive has been used here without any inference to environmental or economic impact. Approximately two-thirds of the species identified were also considered invasive in at least one of the three native pine populations. Five species were considered invasive in all three pine populations. Because this table represents the summary of several respondents for each population—each of whom commented on the area of the forest with which they were familiar, a species was designated as invasive for a pine population if one or more of the respondents identified it as such.

Recommendation 13: *The nature and extent of exotic invasive plants in the range of Monterey pine forests should be determined and an effective approach devised towards the control or elimination of those exotic species considered harmful.*

Finally, animals have been introduced to all five Monterey pine populations as livestock or pets that have become feral. The impact of introduced animals is most extreme on the pines on Guadalupe Island. This influence will be discussed separately in the following section.

The Mexican island populations

Because of the special conditions of islands in general, and because of the extreme current and potential impacts from exotic invasive species, the Guadalupe Island and Cedros Island populations of Monterey pine are of special concern and may require different or additional conservation activities relative to the mainland populations. In addition to exotic invasive plant species, cats, dogs, rats, and goats have been introduced to both islands (McChesney and Tershy 1998). Various possibilities for providing financial, professional, and genetic support exist, including involvement by concerned scientists in Mexico, Australia, and USA; the possibility of reintroducing some lost genetic diversity through use of seeds from earlier collections; and the possibility of doing some artificial regeneration if and when the situation (goat removal or control or soil erosion considerations) is conducive to seedling survival (Box 12). The proper sequence and duration of these various activities are such that *in situ* genetic conservation and restoration activities require long-term commitment, appropriate coordination, and agreement by both those affected (e.g., fishing communities on the island) and those responsible for administering management policies. To the extent that international involvement could provide support to the Mexican government for further protecting the Monterey pines and associated biota on Guadalupe and Cedros Islands, there is considerable interest in doing so.

Recommendation 14: *The international concern and interest for the Guadalupe Island and Cedros Island populations of Monterey pine should be used by Mexican authorities and*

scientists to provide support for conservation policies and practices.

There is particular concern for the Monterey pine population on Guadalupe Island. Here, there are in the order of 200 adult trees remaining, down from approximately 400 reported 40 years ago (Bannister 1965), and no effective natural regeneration. When a population is quickly reduced to a small fraction of its original census number, conventional wisdom suggests that random genetic drift will induce a massive loss of genetic variability which will be confounded through a subsequent increase in inbreeding and fixation of mildly deleterious alleles, thereby reducing evolutionary potential and increasing the probability of population extinction (e.g., Frankel and Soulé 1981; Luikart et al. 1998). Thus, the loss of trees on Guadalupe Island could push this population through a bottleneck. However, both empirical data and theoretical observations suggest that the genetic consequences are neither certain nor simple. Nei et al. (1975), using theoretical models, found that genetic effects are expected to depend on both the size of the bottleneck and how quickly the population expands subsequently. Reviewing several empirical studies, Carson (1990) finds that the genetic effects of bottlenecks depend on how long the population stays at the depressed census and whether the bottleneck is a single event or repeated. Thus, a single bottleneck event after which the population quickly expands in number is the least harmful. The more recent the bottle-

Table 13. Exotic plant species occurring in native Monterey pine forests in California.

Species		Presence†		
Scientific name	**Common name**	**Año Nuevo**	**Monterey**	**Cambria**
Acacia baileyana	Bailey acacia	—	P	—
A. melonoxylon	Blackwood acacia	—	I	P
A. longifolia	Sydney golden wattle	—	P	—
Ammophila arenaria	European beach grass	I	—	—
Arctotheca calendula	Capeweed	I	I	—
Arundo donax	Arundo, giant reed	—	—	P
Avena fatua	Wild oat	I	I	—
Briza maxima	Rattlesnake grass	I	I	I
B. minor	Small quaking grass	P	P	I
Bromus diandrus	Ripgut brome	P	I	—
Carduus pycnocephalus	Italian thistle	I	I	I
Carpobrotus edulis	Iceplant	I	I	P
Centaurea solstitialis	Yellow star thistle	I	—	P
Cirsium vulgare	Bull thistle	I	P	P
Conicosia pugioniformis	False iceplant	—	P	—
Conium maculatum	Poison hemlock	I	I	—
Cortaderia selloana	Pampas grass	I	I	I
C. jubata	Jubata	I	I	I
Cynodon dactylon	Bermuda grass	—	I	—
Cynosurus echinatus	Dogtail grass	I	—	P
Delairia odorata (= *Senecio mikanoides*)	Cape ivy, German ivy	I	I	I
Erechtites glomerata	Australian fireweed	I	I	—
E. mimima	Australian fireweed	I	P	—
Ehrharta erecta	Veldt grass	—	I	—
Festuca arundinacea	Tall fescue	—	P	P
Genista monspessulana	French broom	I	I	I
Hedera helix	English ivy	P	I	P
Holcus lanatus	Velvet grass	—	P	—
Hypericum canariense	Canary Island hypericum	I	—	—
Lolium perenne	Perennial ryegrass	P	I	—
Oxalis per-capræ	Bermuda buttercup	P	P	I
Pennisetum clandestinum	Kikuyu grass	—	I	I
P. setaceum	Crimson fountain grass	—	—	P
Phalaris aquatica	Harding grass	P	—	P
Polypogon spp.	Rabbit foot grass	P	—	P
Tetragonia tetragonioides	New Zealand spinach	P	P	—
Ulex europæus	Gorse	I	I	—
Vinca major	Periwinkle	I	I	P

†P=present, meaning that the species has been positively identified within a particular Monterey pine population. I=invasive, meaning that the species is not only present but has been identified as spreading some distance from its original site of introduction.

neck, the greater the probability that the deleterious effects of a bottleneck can be avoided or minimized by mitigative management procedures, such as habitat enhancement or introduction of immigrants (i.e., supplemental genetic variation from *ex situ* reserves) (Luikart et al. 1998). Furthermore, a bottleneck event may affect various kinds of genetic variation differently: although allozyme variation typically declines following a bottleneck, there may be an increase in genetic variance for quantitative traits. Dangerous genetic effects might be expected after a repeated succession of bottlenecks during which the population does not increase appreciably. This situation would be expected to erode not only allelic but quantitative variation. The genetically depauperate populations of the northern elephant seal (*Mirounga angustirostris*) and the cheetah (*Acinonyx jubatus*) appear to be cases in point (Carson 1990).

Of the five populations, Guadalupe Island excites the most suspicion of a bottleneck due to its current low census. Based on the levels of allozyme variation, Moran et al. (1988) suggested that the small population size on Guadalupe Island is relatively recent (in evolutionary time scales) and does not reflect repeated bottlenecks. A test to detect recent bottlenecks from allele frequency data (Cornuet and Luikart 1997) was used by the author with the same allozyme data tested by Moran et al. The test showed no evidence of recent reduction in effective population size. However, these results are based on seeds collected in 1978, when the census size was almost twice what it is today. In any event, a total population size of 200 trees, most of them reproductively isolated or in small groups, is cause for concern. It is important to apply to Guadalupe Island lessons gained from empirical and theoretical studies concerning bottlenecks. Specifically, it is important that the population expand quickly and soon, and that the possibility is considered of reintroducing some genetic diversity from *ex situ* collections (Box 12). The latter restoration tool, however, should only be used if genetic research on seeds collected in 2001 shows that considerable genetic diversity has been lost in the last two decades or if there are high levels of inbreeding. However, even if restoration activities are not justified by genetic criteria, there could be a need for intervention if natural regeneration is not successful for other reasons, such as soil erosion.

Recommendation 15: *The Guadalupe Island population of Monterey pine requires immediate attention including removal or control of the goats, an assessment of the impacts of the introduced flora and development of a plan to manage these effects, and a genetic assessment of the remaining pines to determine if direct restoration activities are required.*

Cumulative effects

Finally, it is important to recognize that effects on forest ecosystems act cumulatively and interactively. Habitat loss, fragmentation, and climate change collectively set the stage for major impacts on the ability of species to disperse and adapt and may lead to increased rates of extinction over those previously seen. For example, forest fragmentation has been shown to markedly affect the climate experienced by those fragments relative to a continuous forest (e.g., Saunders et al. 1993). Loss of forest habitat can contribute to climate change, which can further contribute to species decline, and so on. For example, the Intergovernmental Panel on Climate Change estimates that tropical deforestation was responsible for 20 to 30% of global, anthropogenic greenhouse gas emissions during the 1990s (Bonnie et al. 2000).

Outreach needs

Given the diverse array of conditions that Monterey pine inhabits through its five native populations, it is truly a conservation challenge. Effective and appropriate genetic management of Monterey pine requires a breadth of information and experience. Supportive science for this endeavor—though substantial—is far from complete, and application of science to management is complicated. Therefore, it is difficult to develop expertise in all aspects of genetic conservation of Monterey pine. Ongoing discussions and education are critical conservation tools. A recent initiative through the University of California, framed as the 'Monterey Pine Forest Ecology Cooperative', is intended to improve the use of scientific information in Monterey pine forest conservation, encourage more research on these forests, and provide a supportive network for science-bawsed conservation activities (Box 13).

Box 12. *Ex situ* conservation reserve of the Guadalupe Island population of *Pinus radiata*.

"An important and successful *ex situ* conservation planting was made in Australia in 1994 to conserve the Guadalupe Island population of *Pinus radiata* which is threatened with extinction. The Southern Tree Breeding Association Inc. (STBA) planted 23 ha of Guadalupe seedlings, at 5.0 × 5.0 m spacing, near Tantanoola, north of Mount Gambier, in the state of South Australia. The seed came from 44 families collected on Guadalupe in 1978 and 76 families collected in 1992. Basilio Bermejo found only about 150 native trees alive on Guadalupe Island when he collected there in 1992 with CAMCORE. Bill Libby and I (and several other enthusiasts for conservation of forest genetic resources) counted [approximately 350] in 1978 (Libby 1978). Libby et al. (1968) counted 383 in 1964. So the population is definitely on the way to extinction—there is no regeneration, due to the grazing pressure of numerous goats.

"It is planned that seeds for the next generation will be collected in the centre of the block when the adjacent routine plantation of radiata pine is felled and regenerated at about age 30 years. There will be a 'window of opportunity' for a few years when unwanted pollen from routine plantations is at a minimum. The Tantanoola planting is intended as a long-term replacement for the native forest on Guadalupe Island.

"The *ex situ* reserves in South Australia may be a source of seed for restoring Guadalupe Island pine should the dire prediction of extinction be fulfilled." (Eldridge 1996).

Recommendation 16: *An educational forum on Monterey pine should be organized that provides ongoing opportunities for exchange of ideas, presentation of scientific information, and discussion of applications among managers, scientists, and conservationists.*

Public attitudes almost certainly influence the suite of options for conservation-related management of Monterey pine. Genetic literacy among the general public, including its relevance to conservation and management of Monterey pine, is probably low. There is lack of understanding of the long-term consequences of using a small genetic base (which is superficially appealing because of uniformity) for planting purposes. This lack of understanding may reduce forest managers' opportunities to practice genetically appropriate activities. For example, one possible manifestation of genetic illiteracy could be public intolerance of diversity in planting stock or intolerance to accepting some survival risk (e.g., in the seedlings) by using an array of individuals rather than clones. Although it may be appealing to plant clonal Monterey pines that have some particular feature, doing so may—if planted in many copies over a broad area for a long period of time—contribute to lower genetic diversity in natural Monterey pine forests because of the lower genetic diversity in the pollen and seeds of these clonal trees. There is considerable evidence for inbreeding depression in Monterey pine. The public could assist in good genetic conservation strategies by using locally adapted Monterey pine planting stock (rather than trees from a different geographic area or an unknown geographic source), by using seedlings rather than clonal material, and by planting a larger number of trees each with some survival risk rather than trying to install a few trees with perhaps lower individual survival risk but with less genetic diversity. This would allow more opportunity for natural selection, maintenance of genetic-environmental relationships, and maintenance of genetic diversity.

This issue is very much related to earlier discussions on genetic contamination and on mitigation and other plantings of Monterey pine. Similarly, standards and practices will vary depending on context—such as whether the activity is within the genetic sphere of influence for native Monterey pine forests.

Recommendation 17: *Public outreach, particularly on the importance of maintaining local adaptations in native Monterey pine forests, is critical to enabling an appropriate suite of options for genetic conservation of Monterey pine and should be aggressively pursued.*

Research

Much basic research, and primarily ecological and genecological research, remains to be done for the native Monterey pine forests. It is important to recognize the continuum between genetic diversity and other species attributes in discussing the critical research needs. For example, the dynamic nature of Monterey pine has been emphasized throughout this report—its evolutionary history of movement and response to climatic triggers, and its current situation which seems to demand adaptation in place. Therefore, studies that explore the species' ecophysiology, ability to colonize environments at the margin of its current range, and enhance stress tolerance may be very important. For example, it has been demonstrated for some pine species that mycorrhizæ can enhance nutrient uptake, resistance to toxicity, and resistance to fungal pathogens (Read 1998).

In addition to some critical research needs, there are also some applied studies—surveys or reviews—that would support genetic conservation goals or forest conservation in general. Because of differences in site history, ecological or genetic attributes, or environment among the five Monterey pine populations, some of the recommended research or surveys are population specific. The topics are not listed in order of priority.

Recommendation 18: *Research, surveys, or reviews that should be undertaken for Monterey pine are:*

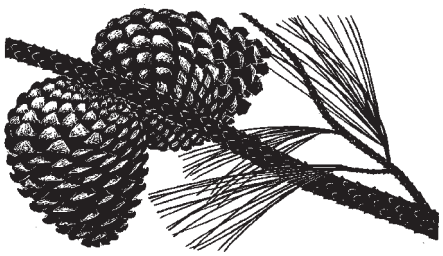
Box 13. The Monterey Pine Forest Ecology Cooperative.

Conservation planning and conservation-directed management of forests is best assured of long-term success if based on science. However, science does not make its way from refereed journals to conservation practice without considerable selection, interpretation, and application. In fact, deciding what scientific information is most relevant, and how to interpret and apply this information, is a critical but weak link in the process of science-based forest management.

The Monterey Pine Forest Ecology Cooperative was organized in 2001 by the University of California (UC) (Deborah Rogers, Genetic Resources Conservation Program) to act as a politically neutral, science-based, support group for Monterey pine forests to assist in providing scientific information for conservation planning, conservation management, research, and educational efforts for native Monterey pine forests. This organization is a cross-boundary entity, with members from the Monterey pine land-holding government agencies and land trusts, policy-administering agencies, private companies with large forest holdings, nongovernmental organizations, universities with faculty who are actively doing research on Monterey pine forest ecology and genetics, and other research or conservation organizations as appropriate. The Cooperative received generous financial support from The David and Lucile Packard Foundation for its first year of activity.

During the inaugural year, Cooperative activities included five meetings for scientific presentations and field tours, a workshop on control and prevention of exotic invasive plant species in Monterey pine forests, a seminar on Monterey pine as a plantation species in Australia, the awarding of four research grants for studies on Monterey pine forests, and many contributions to articles, decisions, and management plans related to Monterey pine. More information about the objectives and activities of the Cooperative can be found at its website (URL http://www.grcp.ucdavis.edu/projects/MPFECdex.htm).

- *A comprehensive vegetation survey of native Monterey pine forests, including associated plant species and extending to the geographic limits of the species.*
- *Mycorrhizal studies that will illuminate the relationship between forest ecosystem health and mycorrhizal dynamics, and the specificity of this relationship—if any—among the five populations.*
- *Soil/vegetation/ecological surveys for all populations, acknowledging that much of this has been done for the ecological staircase area of the Monterey population.*
- *Examination of relationship between microclimate or 'distance from ocean' effect and genetic diversity within the Monterey population.*
- *Determination of whether the 'outliers' near the Año Nuevo population are planted or naturally occurring.*
- *Investigation of genetic differences between the main Cambria population and the Pico Creek stand.*
- *Investigation of phenological differences within and between Monterey pine populations* in situ.
- *Determination of the effects on genetic diversity and structure from various enhanced or artificial regeneration techniques (e.g., mechanical creation of gaps).*
- *Investigation of the viability of seeds* in situ *over their temporal and spatial range, including persistence and viability in the 'canopy seedbank' over time and the effects on seed viability of site conditions and microclimate.*
- *Determination of optimum species-specific seed storage conditions that maintain viability and genetic integrity for long-term conservation.*
- *Research on the amount of genetic diversity in the Guadalupe Island population, losses of genetic diversity since goat introduction, and current level of inbreeding.*
- *Research on the relationship between fire and function of the Monterey pine forest ecosystem, including the effects of fire on nutrient cycling, litter removal, soil sterilization, seed release and germination, seedling recruitment, age structure, and genetic composition.*
- *Identification of an array of private or semi-private DNA marker alleles for the three mainland populations to enable identification and quantification of genetic contamination.*
- *Research on population dynamics including the role of adaptation in genetic structure, the genetic interactions of extant populations, and dispersal rates and efficacy.*



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Appendix A

Participants: Monterey pine genetic conservation workshop

Workshop held April 25–26, 2000 in Big Sur, California.

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Appendix B

Respondents to the survey on *ex situ* reserves and international interests

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Glossary

Bottleneck: a sharp reduction in the number of individuals of a species or population in a particular place or time.

Cline: a gradient of genetic variation within a population or between populations which often corresponds with an environmental gradient such as elevation.

Endemic: native to a given geographic area (i.e., not exotic, introduced, or naturalized).

Extirpation: locally extinct (e.g., an extirpated population).

Fascicle: a close cluster or bundle of parts, such as flowers, leaves, needles, or stems; in pines, the number of needles per fascicle is often a diagnostic character.

Gene flow: the movement of genes over space through seed or pollen movement, for example.

Genetic bottleneck: a reduction in the number of individuals of a species or population that is accompanied by a significant loss of genetic diversity.

Genetic drift: random changes in genetic composition (i.e., allele frequency) in populations over time; also called random genetic drift. Genetic drift occurs more quickly and dramatically in small populations.

Genetic integrity: the natural condition of a gene pool; freedom from genetic contamination (i.e., genes introduced from nonnative or nonlocal populations).

Genetic load: the proportion of a population that does not survive or reproduce because of genetic reasons (i.e., lack of adaptation); a measure of the deleterious portion of genetic diversity in a population.

Genome: the total DNA of a cell's nucleus or of a cellular organelle, such as a mitochondrion or chloroplast.

Half-sib: having one, and only one, parent in common. Thus, half-sibs can usually only be determined for sure when the fertilization has been controlled, so that the parentage of the resulting seedlings is known. In nature, with open pollination, seeds coming from one tree could have both parents in common (i.e., as a result of self fertilization) or one parent in common (if the pollen parent differed between the two).

Homozygosity: at a particular genetic locus, the presence of two identical alleles; the degree to which an individual has identical alleles at chromosomal loci.

Inbreeding: mating between relatives. Inbreeding increases the homozygosity in a population, and affects all genes.

Inbreeding depression: loss of fitness in a population that results from unnaturally high levels of inbreeding; more commonly manifested in typically outbreeding species.

Landrace: a group of individuals that have become adapted to a specific area to which they were (artificially) introduced. Therefore, two steps are required for development of a landrace: introduction of some plants to a new area (outside of their natural range) and subsequent reproduction and natural selection. The group of best-adapted individuals that result over time is referred to as the landrace.

Locus/Loci: the position on a chromosome occupied by a gene (or set of alternative alleles).

Microsatellites: also called *simple sequence repeats* or *SSRs*, lengths of DNA that consist of tandem repeats of short sequences of nucleotides (for example, AAT repeated 15 times in a row). When polymorphism for the number of repeats is found among individuals, the microsatellite can serve as a genetic marker and a measure of genetic diversity.

Mitigation: an act that is done to soften or compensate for an act that destroys or compromises habitat or individuals (generally plants and animals). Thus, mitigation may involve protection of habitat in exchange for destruction of other habitat, translocation of individuals, etc.

Panmictic: complete randomness in mating. A panmictic population is one in which every individual is equally

likely to mate with any other individual.

Phenotypic: referring to the observed characteristics of an individual, which may be the result of its genes, the environment, or a combination of the two.

Polymorphism: as applied to a gene, it is one that has more than one allelic form. However, technically, the definition also embodies the concept of frequency. Thus, a polymorphic gene, technically speaking, is a gene for which the most common allele has a frequency of less than 0.95 (some prefer a less stringent cutoff of 0.99). Polymorphism is also a term used to describe the proportion of genes that are polymorphic by the above criterion, for an individual, population, or species.

Population: a group of individuals of the same species living within a sufficiently restricted geographical area that any member can potentially mate with any other member. In this report, the term is also used loosely to refer to each of the five geographic occurrences of Monterey pine, regardless of the mating relationships among the trees within each location.

Ramet: a genetically identical copy or propagule taken from a single individual plant. This term is commonly used in forestry, in relation to plants generated by vegetative reproduction from one plant.

Riparian: pertaining to habitats, or species occupying those habitats, that border or are associated with streams and rivers.

RAPD: acronym for random amplified polymorphic DNA, which can be used as a genetic marker based on its differential PCR amplification from the DNA of individuals. Variation among individuals for a specific RAPD marker can be a measure of genetic diversity.

RFLP: acronym for restriction fragment length polymorphism, detected in the DNA of an individual as variations in DNA fragment sizes that are generated by cutting the individual's DNA with special (i.e., 'restriction') enzymes. These enzymes can cut only at specific DNA sequences, so variation in the pattern of these sequences in the genome results in fragment size variation. Thus, RFLP markers can be used to detect genetic diversity among individuals.

Serotinous: requiring fire or extreme heat to open; commonly used in reference to cones of certain tree species where the cones are assisted in opening (semi-serotinous) by fire or require fire or very high heat to open the scales and release the seeds (serotinous).