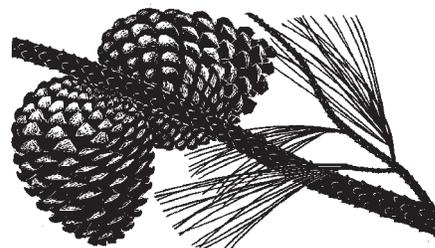


Principles and recommendations for *in situ* genetic conservation of Monterey pine



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 simul-

taneously 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 than 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 aesthetic 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 CO₂ 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 CO₂, 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.

Type of use	Factor	
	Favoring use	Against use
<i>General</i>		
	Use is nonconsumptive	Use is consumptive
	Collection easily replaced	Collection wholly or partially irreplaceable
	Collection inexpensive to replace	Collection very expensive to replace
	Multiple uses/applications	Restricted use/application
<i>Specific research</i>		
	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 <i>de novo</i> collections
	Outcome likely to support conservation of <i>in situ</i> populations	Research has little to no conservation application
	Germplasm or DNA products can be reused for other purposes	Germplasm completely consumed or contaminated
<i>Conservation/restoration</i>		
	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 di-

versity 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 wildfire 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. Grinstead, 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 nurser-

ies 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, leading 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 excep-

tions, 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 hardness 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 hardness 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. Lip-pitt, 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 inoculations. 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 suf-

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