Forest Ecology and Management, 14 (1986) 77—90
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

CONSERVATION STRATEGIES FOR FOREST GENE RESOURCES

F. THOMAS LEDIG

Institute of Forest Genetics, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Box 245, Berkeley, CA 94701 (U.S.A.)

(Accepted 17 September 1985)

ABSTRACT

Ledig, F.T., 1986. Conservation strategies for forest gene resources. *For. Ecol. Manage.*, 14: 77—90.

Gene conservation has three facets: (1) the maintenance of diversity in production plantations to buffer against vulnerability to pests and climatic extremes; (2) the preservation of genes for their future value in breeding; (3) the protection of species to promote ecosystem stability.

Maintaining diversity as a hedge against damaging agents is a simple strategy in theory. In practice, economic forces tend to favor genetic monocultures to maximize short-term gain.

Genes are the raw material from which new strains will be constructed, but only if they are preserved. Gene resources can be preserved in situ in reserves or special management areas or ex situ in seed banks or arboreta. Because timber harvest and gene conservation are compatible, in situ preservation can be quite inexpensive. However, viable reserves depend on the maintenance of adapted gene complexes, not just the preservation of genes. Ex situ preservation is a prudent back-up system. Studies of genetic architecture are necessary to optimize the sampling strategy for ex situ preservation or the size and location of reserves for in situ preservation.

Extinction results in the loss of genes, but even more important, it has the potential to undermine entire ecosystems. Even rare species may serve as keystones, upon which entire, coevolved systems may depend.

The technical aspects of gene conservation are relatively simple, compared to the socio-economic aspects. The real problem for gene conservation is the competition for land and economic resources, and the solutions are social and political.

INTRODUCTION

> Conservation is sometimes perceived as stopping everything cold, as holding whooping cranes in higher esteem than people. It is up to science to spread the understanding that the choice is not between wild places or people. Rather, it is between a rich or and impoverished existence for Man.
>
> *Thomas E. Lovejoy* (1980)

Foresters are concerned about gene conservation for three distinct reasons: (1) genetic uniformity increases vulnerability to pests and climatic

0378-1127/86/$03.50

extremes; (2) genetic variants are important for their potential breeding value some time in the future; and (3) the loss of diversity by local or global extinction of a species may reduce the stability of entire ecosystems. These concerns give rise to three objectives: promote genetic diversity, preserve and evaluate variability, and protect endangered species.

Each objective demands its own strategy and, in fact, each concern is unique to entirely different types of forest stands, or populations: (1) the natural forest, or resource population, (2) the breeding population, and (3) the commercial, harvestable stand or plantation. The question of vulnerability is not a practical consideration applied to natural forest. Natural forest may prove vulnerable to new pathogens, like American chestnut (*Castanea dentata* (Marsh.) Borich.) was to the introduced blight (*Endothea parasitica* (Murr.) P.J. et H.W. Anderson), but geneticists or foresters can do little or nothing if a species does not already have pre-adapted variants able to resist the new threat. Likewise, the preservation of genetic variants has little meaning in terms of commercial forest plantations. Whether rare variants are included in commercial plantations that are cut and replanted has no practical importance; such plantations are genetic dead ends.

Gene conservation strategies in trees will differ from those employed in agricultural crops, or even other wild plants, primarily because of the great longevity of trees. Because trees are long-lived, genes can be stored "on the stump", with no change or loss, for very long periods of time. In annuals, in situ populations must be regenerated every year. However, a long life cycle can also be a disadvantage in commercial plantations because it compounds the problems of crop vulnerability.

This paper explores the problem of genetic vulnerability and gene conservation, the strategies for saving genes and preserving endangered species and populations, and the economic and social problems of conservation. Many of the ideas expressed here were developed during a U.S.D.A. Forest Service workshop on gene resource management. The reader is directed to the proceedings, particularly to Kang (1980), Nienstaedt (1980), and Theisen (1980) who provide a fuller discussion, especially of the role of tree breeding in gene conservation.

GUARDING AGAINST VULNERABILITY

> **If uniformity be the crux of genetic vulnerability, then diversity is the best insurance against it.**
>
> *U.S. Committee on Genetic Vulnerability of Major Crops* (1972)

The threat of uniformity

Breeders in the United States focused on genetic vulnerability of agricultural crops after the corn blight (*Helminthosporium maydis* Nisik. et

Miyake) epidemic of 1970. About 75% of the maize (*Zea mays* L.) crop was of single cross hybrid type, which has less diversity than the double cross hybrids used almost exclusively prior to 1955. All of the single cross hybrids could trace their ancestry back to a single mutant that was particularly susceptible to the blight (U.S. Committee on Genetic Vulnerability of Major Crops, 1972).

Vulnerability increases with the uniformity of the crop. A forest plantation composed of a single clone would represent the extreme lack of variability in forest trees. Certain clones of cryptomeria (*Cryptomeria japonica* (L.F.) D. Don.) have been planted for 400 years in Japan, but their widespread cultivation is no longer recommended because of the high risk of fungal and insect attack (Toda, 1974). Many geneticists have warned about the dangers of monoclonal plantings (e.g., Libby, 1973), and it has been decades since Schreiner (1939) advised the use of multiclonal varieties for production plantings. However, there is still a temptation to plant single clones because some clones are surpassingly good and because compatible mixtures are difficult to design. Plantings of single families are not quite as vulnerable as plantings of single clones. For example, families of full-siblings are expected to have half the additive genetic variation found in the entire population, and three-quarters of the dominance genetic variation. Nevertheless, dense plantings of single families may provide conditions suitable for epidemics and, therefore, the potential for catastrophe.

Diversity is advised by some agronomists even in annual plants (Browning, 1974), and is all the more important for long-lived perennial trees. Agronomists can tolerate more uniformity than foresters because they have more options for pest control. Agronomists can combat pests by cultural treatments (e.g., the application of insecticides and fungicides) or by rapid shifts to new cultivars. Foresters are limited in their choice of cultural practices by topograpy, by the relatively low value of the product compared to the costs, by concern for the environmental consequences of widespread pesticide applications, and by the length of the rotation.

Because pests produce multiple generations for each generation of a tree species, virulence can evolve more rapidly than resistance, increasing from year to year. Each tree may have its own population of pests specifically adapted to it. Individual ponderosa pines (*Pinus ponderosa* Dougl. ex Laws.) were more susceptible to black pineleaf scale (*Nuculaspis californica* Coleman) when reinoculated with insects from their own branches than when inoculated with insects from other trees (Edmunds and Alstad, 1978). Infestation increased as trees became older, suggesting that natural selection on the host had improved the insect's ability to overcome the tree's defenses.

Other examples of the swift evolution of virulence come from pathology. Fusiform rust (*Cronartium fusiforme* Hedge. et Hunt ex Cumm.) inocula collected from galls on a resistant loblolly pine (*Pinus taeda* L.) family produced more than four times as much infection as "wild" inocula when

placed back on the resistant family (Snow et al., 1976). This difference demonstrates the presence of virulent races that might increase in frequency and create havoc in plantations of limited diversity. Sugar pine (*Pinus lambertiana* Dougl.) that had remained free of blister rust (*Cronartium ribicola* J.C. Fisher ex Rabenh.) for 14 years because they had been selected for a dominant gene conditioning a hypersensitive reaction to the fungus were suddenly infected by a new, virulent race (Kinloch and Byler, 1981). Because of the diversity of genotypes, other mechanisms of resistance were present in some individuals. The lesson from all these examples is obvious: plantations of genetically similar or identical trees will encourage the evolution of pests that are specifically adapted to overcome their defenses. The result is enhanced probability of catastrophe.

Genetic monotypes are also susceptible to climatic fluctuations; presumably a frost, drought, or other damaging factors could devastate an entire plantation of a monotype, while in a stand of diverse types, some trees would escape.

Strategies for the maintenance of diversity

Vulnerability is a problem of production forestry, and diversity is a form of bet-hedging, preventing total loss while accepting the loss of some individuals. Narrowing the genetic base provides opportunity for great gain, but also opportunity for great loss. Diversity increases crop reliability; i.e., the chance of a reasonable harvest at rotation age, although never the maximum possible.

Tree improvement programs generally promote diversity in seedling plantations to a degree, perhaps, not attained even in natural stands. In high intensity programs, selections from scattered stands are brought together in seed orchards. The progeny, produced by cross pollination, have gene combinations that could never have occurred in nature, where their parents were widely separated. Production plantations established with seed from an orchard of several, say 40, different selections should be in little danger from reduced diversity (Rawlings, 1970), especially if the breeding program has been managed to control inbreeding and reduce the chance loss of genetic variability. Even in low intensity tree improvement programs, the genetic base is usually maintained. For example, in the National Forest System's tree improvement program for California, the policy is to collect seed from trees in at least 20 stands within a seed zone and bulk it for planting (Kitzmiller, 1976). The seed zones themselves are narrow latitudinal and elevational bands, so there is a high probability that the planted seedlings will be as well adapted as natural regeneration.

New pests or environmental change may eventually require a shift in cultivars. Most tree improvement programs have maintained a large breeding population, usually preserved in clone banks. A clone bank is essentially a holding area in which all selections or accessions are preserved as grafts

even if they have been rejected for use in the initial seed orchards. The North Carolina State—Industry Tree Improvement Program has preserved over 8000 selections of loblolly pine, forming a substantial pool of genes for the production of new cultivars (McConnell, 1980). Similarly, the U.S.D.A. Forest Service Tree Improvement Program for California maintains over 200 selections for each species in each of several breeding zones, even though only 50 selections will be used in the orchards that produce seed for commercial plantings (Kitzmiller, 1976). Even better than single, large breeding units, are multiple breeding units managed to maintain diversity in improved populations (Kang, 1980). Most breeding programs have maintained sufficient diversity to shift cultivars to counter new threats. But that is small comfort. In forestry with its long rotations, switching to new cultivars is not a realistic, short-term option. The safest option is to maintain diversity in commercial plantings. Diversity can be maintained by a mosaic of different cultivars or by intimate mixes of genetic variants in the same plantation. Both reduce the risk of catastrophic, region-wide losses. However, within a block of a single cultivar, the spread of pests, and perhaps their evolution, becomes easier than in a plantation with a mix of cultivars.

SAVING GENES

> Genetic conservationists are not interested in preserving a representative sample of the target species, where representative is defined in as many senses as possible. Rather, they are interested in preserving at least one copy of each of the different alleles in the target species.
>
> *D.R. Marshall and A.H.D. Brown* (1975)

The threat of loss

Conservation is a poor term to describe the maintenance of genetic resources (Kang, 1980), because genetic resources can be used without ever using them up. Preservation is a more realistic term than conservation. Although genetic resources can be used in breeding without destroying them, they can be destroyed by thoughtless exploitation. Generations of loggers felled the straightest, defect-free trees because they were of high value, and left the crooked, diseased, and runty. Selective cutting of the best trees on short rotations may have degraded pitch (*Pinus rigida* Mill.) and loblolly pines in the eastern United States (Ledig and Fryer, 1974; McConnell, 1980). And the poor form of several Mexican pines is attributed to similar exploitation (Jasso, 1970). In some parts of the Caribbean and Central America, mahogany (*Swietenia mahagoni* Jacq.) has been reduced to a shrub because of the high demand for its timber (Styles, 1972). Good silvicultural practices, therefore, are the first step in gene conservation.

Does the loss of part of the genetic resource make any difference? Obviously it does, if prime native forests regenerate to more slowly-growing, less

valuable stands. But it is also important to prevent more subtle losses of genetic variability. Genetic variants that are of no value today may be useful in the near future. They may have utility to the breeder to combat future pests or to provide adaptation in case of climatic changes. And they may enable forestry to respond to changes in demand. For example, at one time consumers preferred milk with high butterfat content, and breeders produced dairy cattle that gave high-fat milk. Today's market demands low-fat milk, so it was necessary to shift breeds. Without a reservoir of variability, shifts would be impossible. The answer to the question "Does genetic loss make any difference" is "yes". Genetic resources should be maintained because of their potential utility; no one can predict their actual utility. The genetic resources of noncommercial species may be as important as those of our most valuable timber trees.

Genetic engineering dramatically highlights the value of genetic resources. The new recombinant DNA technology makes it likely that genes can eventually be transferred among individuals and species that do not normally cross. Genetic engineering will proceed by picking and choosing among what is available, not by creating genes de novo. The implications for forest tree breeding are enormous; gene transfer offers the possibility of engineering new combinations of genes in months rather than decades or centuries (Sederoff and Ledig, 1985). However, the genes must be preserved now, so that they can be drawn on when needed.

Genes and gene complexes

Should the objective of genetic resource conservation be the preservation of alleles or entire, co-adapted gene complexes? In breeding new cultivars, the objective will be to maintain as much variation as possible, but it is likely that the variants will be incorporated in new gene complexes. Therefore, in breeding new cultivars the genes themselves are important, not their present population context. The maintenance of gene complexes is important if the objective is the maintenance of naturally regenerated, native stands, an objective that requires a viable, vigorous population adapted to its environment. That goal represents the third problem area usually considered part of gene conservation. It also represents a tactic for the "storage" of potentially useful genes, in situ. Luckily, timber harvest does not necessarily conflict with the preservation of either genes or gene complexes.

Ex situ and in situ conservation

Preservation of genes can be accomplished either in situ or ex situ. Either way has both advantages and disadvantages (Johnson, 1980). Ex situ preservation includes storage of seed, pollen, scion, or tissue cultures in special facilities, or the preservation of trees in arboreta or provenance

plantations. There are many difficulties with ex situ preservation. Because storage life is limited, populations must be rejuvenated on a regular schedule to produce fresh seed or tissue. During the period in which samples are being grown to produce new material for storage, they are unavoidably subjected to selection, often quite alien in nature to that under which the original populations evolved. Thus, there is the potential for genetic erosion, or at least change in gene and genotype frequencies. Because genetic changes also occur in stored seed or tissue cultures, by mutation, it is difficult to guarantee genetic integrity by ex situ methods of preservation (D'Amato, 1975; Chaleff, 1983). Implementing a program of ex situ preservation requires knowledge of the optimum conditions for promoting longevity of stored materials and of ways to retard genetic change in storage.

In situ preservation requires management of populations in natural stands of sufficient size that they can maintain themselves and preserve a reservoir of genes of potential use in breeding. Preservation in situ is more effective and realistic than ex situ preservation because forest management for gene preservation is compatible with other uses, and populations are free to evolve in their native environment (Frankel, 1970). However, problems of genetic integrity may arise in natural reserves as well as ex situ, although not in the same form: natural populations in situ may be subjected to gene migration from artificially regenerated plantations not representative of the native population.

The problems of gene preservation in situ are problems of determining which populations to maintain, and of defining the size, distribution, and number of populations necessary to: (1) preserve an adequate sample of among- and within-population variation, (2) protect the genetic integrity of the local population from contamination, and (3) maintain the dynamic equilibrium between inter- and intraspecific competition, habitat availability, age distribution, and the breeding system that is responsible for a species' genetic structure. In situ preservation is probably less expensive and more reliable than ex situ, but whenever possible, ex situ methods should be used as added insurance against loss.

Strategies for gene conservation

Both ex situ and in situ preservation require decisions on which populations to save or sample. An optimal preservation strategy requires some knowledge of the pattern of genetic variation, but in many cases we only guess (Frankel, 1970). In the absence of genetic information, a common strategy is to preserve samples of populations inhabiting representative habitats because they will probably include a maximum of the species' genetic resources. But, marginal habitats should also be sampled because selection may have favored novel variants.

Ideally, the conservationist can map the patterns of geographic variation over a species range and measure the extent of variability within populations,

so that informed choice is possible. Electrophoretic separation of enzymes and analysis of their isozymes has proven to be the most rapid means of surveying genetic variation (e.g., Conkle and Westfall, 1984). Intensive sampling can be followed by reduction to a practicable number of populations for actual preservation (Allard, 1970). Because resources are usually limited, tradeoffs must be made between sampling many individuals per population versus sampling a few individuals in each of many populations (Marshall and Brown, 1975). With few exceptions, isozyme studies of conifers have indicated that 88—97% of the total variation within a species is among trees within stands (Ledig and Conkle, 1983), and would be captured by sampling many trees either from a few stands or distributed over many stands. However, the choice of preservation strategy depends on external factors as well as the internal genetic structure: Is the species rare or common? Is it exploited or nonexploited? Is its habitat secure or in jeopardy?

Rare species should usually be protected from exploitation completely. Different populations of a rare species often have unique alleles, and the loss of any population would be an irreparable genetic loss. Torrey pine (*P. torreyana* Parry ex Carr.) is a case in point. Only two populations exist: one in San Diego and one on Santa Rosa Island, California. The two populations are each genetically depauperate but differ at an estimated 8.5% of their gene loci (Ledig and Conkle, 1983). Representatives of both populations must be preserved, either in situ or ex situ, to protect the known genetic resource. Preliminary results indicate that another of California's rare conifers, Santa Lucia fir (*Abies bracteata* D. Don ex Poiteau) also has relatively little variability. It grows in one of the Coast Ranges, scattered throughout a narrow band less than 100 km long. As in Torrey pine, populations differ, suggesting that representatives of each should be preserved.

Long term in situ preservation of genetically depauperate species may be difficult. Species endure either because they can evolve in response to environmental change or because they can escape to more favorable environments. Depauperate species are as vulnerable as cultivars that have a drastically narrowed genetic base, and furthermore, encroachment directly threatens habitat. Agriculture and urban development have tended to confine endemics to pockets from which there would be no escape to more favorable habitat should climatic changes occur. For most rare species, reserves are an absolute necessity to protect the genetic resource, but ex situ preservation is also necessary to reduce the risk of sudden loss by catastrophe.

Common species are often genetically variable but are generally exploited. The entire species is seldom subject to loss, but alleles could be lost if harvest methods do not consider effects on the genetic resource. The most productive sites are also most likely the first to be harvested and, in the United States, the native populations tend to be replaced by

plantations. Populations on marginal sites are likely to enjoy protected status in parks and wilderness areas, but their gene pool may not include all the alleles characteristic of populations on the best sites, so it is necessary to make special arrangements to protect sample populations on land of high site quality. Special management areas should be set aside on which natural regeneration is mandatory, employing harvest techniques that will minimize genetic change.

Reserves may be influenced by pollen migration from surrounding plantations regenerated with seedlings of off-site parentage. However, geneticists disagree strongly on the impact of pollen contamination (Nienstaedt, 1980). Some believe that a wide buffer strip is necessary (Yeatman, 1973), making reserves impractically large. Others believe that pollen migration will be ineffectual if the immigrants carry maladapted genes, because proper harvest can assure dense regeneration and natural selection can be relied upon to eliminate unfit progeny. On the other hand, if migration introduces selectively advantageous genes, then contamination poses no problem for preservation of adapted populations, albeit changed. The substitution of neutral alleles may be a problem if the management unit is so small that pollen influx swamps the local pollen contribution. However, many management alternatives can be devised to reduce the problem of pollen contamination: e.g., surrounding the management unit with plantations of a different species, resorting to mass pollination with an appropriate pollen, or controlled pollination and artificial regeneration with progeny known to have originated by crossing among native trees.

PRESERVING ENDANGERED SPECIES

> I am myself and what is around me, and if I do not save it, it shall not save me.
>
> *Jose Ortega y Gasset* (1914)

The threat of extinction

Extinction is a natural phenomenon, but the rate at which species are being lost has accelerated in the last century as a result of human activities. The loss of species is the penultimate loss of genetic diversity; the loss of entire ecosystems is the ultimate loss. The loss of species is not simply the loss of one potentially useful allele, but the loss of thousands of alleles and regulatory sequences. Furthermore, extinction may constitute a threat to the entire ecosystem, and the magnitude of the threat cannot be satisfactorily predicted. Even the loss of several species from an ecosystem may have no great influence, particularly in the north temperate latitudes where disturbance has been a major factor in evolution, but there are cases where extinction has had profound effects.

The domino effect is illustrated by the results of the World Health Organization's attempt to eradicate the malarial mosquito in remote villages

in Borneo. DDT sprays had the desired effect, but they also led to the extinction of the local cats (Holling and Goldberg, 1971). Cockroaches picked up the DDT, lizards that ate the cockroaches accumulated it, and the cats that ate the lizards died. The loss of the cats led to an invasion of woodland rats which carried parasites that, in turn, precipitated sylvatic plague. Another effect of the spray program was the destruction of the predators of a small caterpillar that fed on the thatch roofs. With the elimination of their predators, the caterpillars increased in number and caused the roofs to collapse. The impacts were primarily borne by the villagers. The damage was not irreversible, but the example indicates the intricate, interlocking pathways that can magnify disturbance to the system when key components are lost.

Although examples may be found to illustrate adverse, neutral, or possibly even beneficial effects of extinction, the point is that they are not predictable with current knowledge. Certainly, many rare species might be lost with no detectable effect on ecosystem function, but in the end, loss of diversity must become a cascading effect, and catastrophe will be hastened by external stresses such as acid rain, gaseous pollutants, increased atmospheric CO_2, and changed climate.

The loss of a single species has a less visible aspect as well. An aesthetic and ethical sensibility is the mark of a civilized people. Species diversity is not only an important contributor to the moral and mental health of society, but an indicator of it. The loss of a species irreversibly impoverishes our lives, but it is immoral to tell a starving people that land can not be farmed because it is the last refuge of a vanishing species. It is incumbent on wealthier nations to share the cost of alternatives so that the quality of life can be improved without the loss of our global heritage.

Strategies for species preservation

Strategies for genetic management of endangered species are much the same as those for in situ gene preservation, except that preservation of coadapted gene complexes is the major objective. For some endangered species, genetic variation may be so low as to cause doubt about the long-term possibilities for a viable, vigorous, functioning population. Evidence in conifers suggests that vigor and fitness of individuals is related to variability (Ledig et al., 1983). Some analogue of captive breeding and replacement may be necessary for endangered plant species. Or, variation might be reintroduced from related species or by crosses among isolated populations.

FACING REALITIES

> One could hardly expect those people, in whose nations most of Earth's biological riches reside, to accept any plan that freezes them in poverty.
>
> *Paul and Anne Ehrlich* (1981)

The strategies for reducing vulnerability, preserving genes, and protecting endangered species are relatively simple. However, all strategies must be considered in their social and economic context, and when they are, the problem of gene conservation becomes incredibly complex.

The pressures operating against diversity and tending to increase genetic vulnerability are clearly economic. Often the pressure can be traced to a common human propensity — the willingness to gamble for the possibility of great gain. Large corporations, in particular, must necessarily think in terms of the quarterly dividend, a situation which is anathema to good land management practices.

But often the pressure against saving genes, populations, or species is a result of overpopulation. Jasso (1970) cited examples of loss of forest populations, and probably the loss of genes, in Chihuahua pine (*Pinus leiophylla* Schiede et Deppe) and false Weymouth pine (*Pinus pseudostrobus* Lindl.) as pine forest was replaced by maize and potatoes (*Solanum tuberosum* L.). Worse yet, it is the best-formed, most rapidly-growing trees that are lost first because they are growing in the lowlands on the richest, deepest soil, on sites that are most desirable for agriculture. As new farms move up the slopes, pines are restricted to more and more marginal habitat. The gene complexes that allow the lowland trees to respond to favorable habitat, ones that would be of most use to tree breeders, may be lost. The only solution is political; i.e., by affecting governmental policy on population growth and land use.

While population pressure makes it difficult to establish and protect reserves in the tropics, gene conservation in developed countries is also a problem, but for different reasons. For example, in the United States the National Forests are empowered to set aside Research Natural Areas that serve the function of in situ gene preservation. But, in the past National Forests have been reluctant to establish these areas on productive forestland because they reduce the timber harvest. Alternatives do exist. Areas managed for timber production can be valuable also for gene conservation if methods of natural regeneration, such as the shelterwood method, are used.

In the absence of social change, the practical alternative for foresters and geneticists is to sample as many gene pools as possible before they are destroyed in nature, and preserve them ex situ, probably in seed banks. Fortunately, the Institute of Commonwealth Forestry at Oxford and a new organization called CAMCORE are doing that for Mexican and Central American conifers (Andrew and Burley, 1976; Dvorak, 1981). In the United States and Canada, efforts are not as systematically organized, but hopefully, genes of major commercial conifers will be protected in breeding programs. Nevertheless, a North American seed bank for tree species could serve a real purpose.

Almost no one is involved in gene preservation in tropical deciduous tree species; their gene pools are in greatest danger. For example, Mexico

has 46 250 000 ha of tropical vegetation and it is being deforested at an annual rate of 1.3% (U.S. Office of Technology Assessment, 1984). Only 28% of it is undisturbed and only 1% of it is preserved in parks. For species preservation, the realities are grim. The gene pool can be preserved for future generations by ex situ methods, but that will not protect the ecosystem from the impact of extinctions. Mexico is only one example. If the pressures of expanding population and uncontrolled exploitation continue, the world will lose thousands of species before the end of the century.

The problems of gene and species preservation are acute. Responsible scientists and land-use professionals must renew their efforts at gene conservation if we are to preserve the major fraction of our present biological riches. A massive sampling effort for in situ and ex situ preservation are called for throughout the world. We are all the potential beneficiaries of the earth's biological riches, and should all bear the costs of protection. For the developed nations this may mean not only supplying expertise in less-developed countries but economic relief as well, to compensate for the loss of agricultural production in forested reserves.

ACKNOWLEDGMENTS

I thank William B. Critchfield, Stanley L. Krugman, and Hans Nienstaedt for helpful reviews of an earlier draft of this manuscript.

REFERENCES

Allard, R.W., 1970. Population structure and sampling methods. In: O.H. Frankel and E. Bennett (Editors), Genetic Resources in Plants — Their Exploration and Conservation. Int. Biol. Prog. Handb. No. 11. Blackwell Sci. Publ., Oxford, pp. 97—107.

Andrew, I.A. and Burley, J., 1976. Information storage for conservation and improvement of tropical tree species. In: J. Burley and B.T. Styles (Editors), Tropical Trees: Variation, Breeding and Conservation. Linnean Soc. Symp. Ser. No. 2. Academic Press, New York, NY, pp. 217—221.

Browning, J.A., 1974. Diversity — the only assurance against genetic vulnerability to disease in major crops. In: Proc. Ninth Cent. States For. Tree Improv. Conf., Ames, IA, pp. I—XVIII.

Chaleff, R.S., 1983. Isolation of agronomically useful mutants from plant cell cultures. Science, 219: 676—680.

Conkle, M.T. and Westfall, R., 1984. Evaluating breeding zones for ponderosa pine in California. In: Progeny Testing. Proc. Servicewide Genet. Workshop, Charleston, South Carolina, 5—9 December 1983. Timber Manage. Staff, U.S. For. Serv., Washington, DC, pp. 89—98.

D'Amato, F., 1975. The problem of stability in plant tissue and cell cultures. In: O.H. Frankel and J.G. Hawkes (Editors), Crop Genetic Resources for Today and Tomorrow. Int. Biol. Prog. 2. Cambridge Univ. Press, Cambridge, pp. 333—348.

Dvorak, W.S., 1981. CAMCORE is the industry's answer to coniferous preservation in Central America, Mexico. For. Products J., 31(11): 10—11.

Edmunds, G.F., Jr. and Alstad, D.N., 1978. Coevolution in insect herbivores and conifers. Science, 199: 941—945.

Ehrlich, P. and Ehrlich, A., 1981. Extinction. Random House, New York, NY, 384 pp.
Frankel, O.H., 1970. Genetic conservation in perspective. In: O.H. Frankel and E. Bennett (Editors), Genetic Resources in Plants — Their Exploration and Conservation. Int. Biol. Prog. Handb. No. 11. Blackwell Sci. Publ., Oxford, pp. 469—489.
Holling, C.S. and Goldberg, M.A., 1971. Ecology and planning. J. Am. Inst. Planners, 37: 221—230.
Jasso, M.J., 1970. Impact of silviculture in forest gene resources. Unasylva, 24(2-3): 70—75.
Johnson, L.C. (Chairman), 1980. Committee report: in situ and ex situ strategies. In: Proc. Servicewide Workshop on Gene Resource Management. Timber Manage. Staff, U.S. For. Serv., Sacramento, CA, pp. 336—340.
Kang, H., 1980. Examining the rationale for gene conservation. In: Proc. Servicewide Workshop on Gene Resource Management. Timber Manage. Staff, U.S. For. Serv., Sacramento, CA, pp. 42—55.
Kinloch, B.B. and Byler, J.W., 1981. Relative effectiveness and stability of different resistance mechanisms to white pine blister rust in sugar pine. Phytopathology, 71: 386—391.
Kitzmiller, J.H., 1976. Tree improvement master plan for the California Region. U.S. For. Serv., San Francisco, CA, 123 pp.
Ledig, F.T. and Conkle, M.T., 1983. Gene diversity and genetic structure in a narrow endemic, Torrey pine (*Pinus torreyana* Parry ex Carr.). Evolution, 37: 79—85.
Ledig, F.T. and Fryer, J.H., 1974. Genetics of pitch pine. U.S. For. Serv. Res. Pap. WO-27, 14 pp.
Ledig, F.T., Guries, R.P. and Bonefeld, B.A., 1983. The relation of growth to heterozygosity in pitch pine. Evolution, 37: 1227—1238.
Libby, W.J., 1973. Domestication strategies for forest trees. Can. J. For. Res., 3: 265—276.
Lovejoy, T.E., 1980. Foreword. In: M.R. Soulé and B.A. Wilcox (Editors), Conservation Biology: an Evolutionary-Ecological Perspective. Sinauer Assoc., Sunderland, MA, pp. ix—x.
Marshall, D.R. and Brown, A.H.D., 1975. Optimum sampling strategies in genetic conservation. In: O.H. Frankel and J.G. Hawkes (Editors), Crop Genetic Resources for Today and Tomorrow. Int. Biol. Prog. 2. Cambridge Univ. Press. Cambridge, pp. 53—80.
McConnell, J.L., 1980. The Southern Forest— past, present and future. In: Proc. Servicewide Workshop on Gene Resource Management. Timber Manage. Staff, U.S. For. Serv., Sacramento, CA, pp. 17—26.
Nienstaedt, H. (Chairman), 1980. Issue Group 1: categories of resource management. In: Proc. Servicewide Workshop on Gene Resource Management. Timber Manage. Staff, U.S. For. Serv., Sacramento, CA, pp. 315—322.
Ortega y Gasset, J., 1914. Meditaciones del Quijote. Publ. Residencia de Estud., Ser. II—Vol. 1, Madrid.
Rawlings, J.O., 1970. Present status of research on long and short-term recurrent selection in finite populations — choice of population size. In: Pap. presented at Second Meet. Working Group on Quant. Genet., Sect. 22, IUFRO. Raleigh, NC, pp. 1—15.
Sederoff, R.R. and Ledig, F.T., 1985. Increasing forest productivity and value through biotechnology. In: Forest Potentials — Productivity and Value. Weyerhaeuser Sci. Symp. 4. Weyerhaeuser Co., Tacoma, WA, pp. 253—276.
Schreiner, E.J., 1939. The possibilities of the clone in forestry. J. For., 37: 61—62.
Snow, G.A., Dinus, R.J. and Walkinshaw, C.H., 1976. Increase in virulence of *Cronartium fusiforme* on resistant slash pine. Phytopathology, 66: 511—513.
Styles, B.T., 1972. The flower biology of the *Meliaceae* and its bearing on tree breeding. Silvae Genet., 21: 175—182.

Theisen, P.A., 1980. Maintenance of genetic diversity and gene pool conservation of commercial or potentially commercial tree species in the Pacific Northwest Region, United States Forest Service. In: Proc. Servicewide Workshop on Gene Resource Management. Timber Manage. Staff, U.S. For. Serv., Sacramento, CA, pp. 61—186.

Toda, R., 1974. Notes on the Japanese State Government forest tree breeding project. In: R. Toda (Editor), Forest Tree Breeding in the World. Government Forest Experiment Station, Meguro, Tokyo, pp. 161—169.

U.S. Committee on Genetic Vulnerability of Major Crops, 1972. Genetic Vulnerability of Major Crops. Nat. Acad. Sci., Washington, DC, 307 pp.

U.S. Office of Technology Assessment, 1984. Technologies to Sustain Tropical Forest Resources. U.S. Congr., Off. Technol. Assessment, OTA-F-214, Washington, DC, 344 pp.

Yeatman, C.W., 1973. Gene conservation in relation to forestry practice. In: D.P. Fowler and C.W. Yeatman (Editors), Proc. Thirteenth Meet. Comm. For. Tree Breeding Can. Part 2. Symp. on the Conserv. of For. Gene Resources. Prince George, B.C., pp. 19—24.