

ment, still need to be determined. Whether stem straightness in the younger age classes of the wild parents was reliably assessed, and also, to what extent cuttings from the older age classes develop straight stems or suffer from plagiotropic growth, remains to be seen. For these reasons, experimentation will be continued and results will be described in subsequent papers.

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A Control Concept of Gene Conservation

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Summary

A new concept is introduced for the joint management of gene conservation and tree breeding programs. The control of yield in an environmental space is defined as the objective and multiple populations are described as the variable elements in both conservation of natural populations and developing breeding populations. The optimization of the array of populations is then suggested to be soluble by the method of control theory. A management strategy, based on these control concepts is then discussed, and includes the use of *in situ* and *ex situ* programs.

Key words: Multiple Populations, Conservation, Diversity.

Zusammenfassung

Es wird ein neues Konzept zur Verknüpfung der Durchführung von Gen-Erhaltung und Forstpflanzenzüchtungsprogrammen vorgestellt. Die Kontrolle des Ertrages in einer bestimmten Umwelt wird als Zielpunkt betrachtet und multiple Populationen werden als variable Elemente so-

wohl zur Erhaltung natürlicher Populationen als auch entwickelter Züchtungspopulationen angesehen. Die Optimierung einer Reihe von Populationen wird dann durch die Methoden der Kontrolltheorie lösbar. Eine Management-Strategie, die auf diesen Kontrollkonzepten basiert, schließt die Verwendung von *in situ* und *ex situ* Programmen ein und wird diskutiert.

Introduction

Current interest in gene conservation is largely based on economic, esthetic, or other human uses of the biota and not on any inherent values of non-human organisms themselves. While philosophers debate the moral issues surrounding gene conservation (REGAN, 1982), this topic is not treated in this paper. I do, however, include among the objectives of gene conservation, not only immediate economic utility, but also maintaining the evolutionary capacity of species to adapt to changing economic and ecological requirements and the viability of the supporting ecosystems.

For these objectives, the preservation of any particular allele, allelic combination, population, or even species may not be necessary as long as available alternatives exist. That is, we can consider the objective of gene conservation in this context to be managing the genetic components of an evolving biosphere in which extinction, mutation, recombination, etc. are natural genetic events. Genetic management, then, involves breeding for immediate goals and developing or maintaining populations that may be needed for future use as the environment changes and as pathogens and other elements of the biota evolve. It also involves managing or ensuring the coevolution of other interacting species and the evolution of species that may serve as substitutes or alternatives to currently used species. So far we have not done a very good job of ensuring the existence of viable alternatives. Instead, we have created conditions that threaten extinction of alleles and populations for many species, including critically important crop plants. At the species level, we have done little to develop useful alternatives for our currently domesticated crop species, if any should become unable to adapt to new conditions. For most of our important crop species, the dangers of allele and population loss are thus exacerbated by the lack of available substitute species. It would obviously be preferable to have greater genetic resources to create new variations to offset the inevitable extinctions at all levels. Greatly expanded but still inadequate programs exist for most of our major food crop species and for the much larger number of species that are of potential but largely unknown value (ANONYMOUS, 1982).

In forestry, the situation seems less desperate. Since most species have not yet been intensively cultivated for uniform performance, large samples of alleles, populations, and species are still available. However, despite frequent lip service given to the desirability of maintaining a broad genetic base, most tree breeding plans are short term (KANG, 1982) and, if iterated, will actually lead to rapid allelic and population losses. With few exceptions, such as the British Columbia Forest Service (YEH, *et al.* 1981), Texas A & M (VAN BUIJTENEN and LOWE, 1979), and the Zimbabwe Forest Service (BARNES, 1981), little provision is made for effective genetic diversity within breeding operations (NAMKOONG, 1983). For species with little current economic value as cultivated crops, still less attention is paid to maintaining and developing genetic diversity. Therefore, we are in danger of creating the same kinds of problems with the loss of genetic resources as in agronomic crops, but without the advantages afforded by short breeding cycles and intensive cultivation that are available to agronomic geneticists.

If it is true that programs for crop genetic resource development are underfunded, it is obvious that forest gene conservation will not often be funded at levels which permit intensive management for conservation purposes alone. Therefore, gene conservation programs will most often have to be coupled with other breeding or ecosystem conservation programs. They will have to rely on indirect methods of management and extensive monitoring to ensure the maintenance of allelic variations. Our management units typically contain collections of trees and control over allele preservation will have to be exercised mostly through the number and arrangement of individuals in ecologically defined areas and rarely through directly controlled reproduction. Therefore, the primary concern is the relationship between numbers of reproducing individuals, their groupings, and probabilities of having alleles and

populations available for an array of future environmental and economic conditions.

Population Size and Structure

NAMKOONG (1980, 1982) estimated minimum population sizes necessary to ensure allele conservation in samples of random mating populations. Considering more general allele frequency distributions and nonrandom mating populations, GREGORIUS (1980) derived somewhat larger minimum sample sizes. These studies indicate that a few hundred to a few thousand trees would be adequate to ensure with high probability that low frequency alleles will be saved. For a locus with several alleles at 0.01 frequency, the probability of loss in a sample of around 600 can be kept below 0.01 (NAMKOONG 1980, 1982). With unknown levels of inbreeding or population structure, sample size should be approximately doubled. For any level of inbreeding and for multiple alleles at a locus, GREGORIUS derives this minimum sample size to be 916. The major effect on this requisite sample size is the frequency of the rarest allele we wish to ensure being saved. If we take 1,000 trees as a rough guideline for the above situation, then the number of trees required to save alleles at loci with frequency q is approximately $10/q$. Another way of stating the effect of risking loss is that if the loss probability is 0.01 per locus, then we incur an expected loss of 1 allele at any of 100 independent loci which are in the same risk situation. NAMKOONG (1980) assumed that about 100 loci might have alleles at risk, but even expanding the number of loci does not greatly affect the required sample sizes. An order of magnitude increase in the number of loci only doubles the necessary number of trees to ensure the same probability of losing any allele at any locus.

Since the geographic distribution of alleles is not uniform, we can sometimes improve our chances for capturing genes by sampling populations that we have some reason to believe contain alleles not present elsewhere. Such populations may be in isolated pockets or in extreme environments. Hence, it is preferable to sample species margins to capture any locally concentrated alleles. With such sampling, the probability of capturing widely distributed alleles is insensitive to sample locations.

Once alleles have been captured in one or another population sample, the next problem is to ensure the capability of the collection to adapt to evolving requirements. Arguing on the basis of mutation rates on a trait basis, FRANKLIN (1980) estimates that effective population sizes of at least 500 can maintain the genetic variances in quantitative traits. However, this figure would have to be boosted if the rate of useful mutations is lower than 0.001 per trait as it would be for traits affected by few loci and for mutation rates on the order of 10^{-5} per locus. But again, total populations of a few hundred to a few thousand trees seem large enough for subsequent maintenance of allelic variations. This size is insufficient for any particular allele since it is clear that low frequency alleles have high probability of eventually being lost from the population. In fact, without selection favoring the allele, the probability of eventual loss is the complement of its initial frequency. For alleles favored by selection, the probability of inclusion is increased, and for those disfavored by selection, the probability is decreased. Therefore, one must be concerned about alleles that are of no selective importance at this time, but that may be disfavored by selection due to an unfavorable linkage disequilibrium. For such alleles, the pop-

ulation sizes need only be doubled over the requisite sizes under neutrality to free them from the effects of unfortunate linkage. Alleles that start at low frequency are still in danger of eventual extinction, and while their loss may not be noticed at the mean performance level of traits or in the variance, their loss can mean that a certain capability for adaptation is lost. For such alleles, it is particularly useful to diversify selection in separate, multiple populations so that they may be increased in frequency in some population units. That is, by practicing a form of disassortative mating and disruptive selection, allele frequencies are allowed to diverge, and if these units are the progeny generations of any original divergent population sampling, their probabilities of existing at high frequency in some population are improved. Therefore, with approximately the same total effective population size as in an original population sample, not only can genetic variances and all but the lowest frequency alleles be maintained, but with subdivision and selection emphasizing natural diversity, alleles can be better conserved.

With almost total ignorance of the effect of individual alleles and equal ignorance of the kinds of trait combinations wanted for a variable and uncertain future, there is little guidance on the selection criteria to use for creating and diversifying these multiple populations. For alleles with little effect, the directions of selection are irrelevant if total population sizes are kept large. But where selection can affect allele frequencies and traits, a strategy for choosing selection directions is needed.

A Control Concept

In one trait dimension it has already been demonstrated that expected gain is increased by splitting populations into multiple breeding units (NAMKOONG, 1976). Whenever there is a variance in the environments and a variance in genotypic yields or fitnesses, there is an optimum level of deviation between subpopulations that maximizes the combined gain of all populations over all sites. Two cases have been considered for the manner in which the populations are placed in the environments. MAY (1974) considers a model of evolution where all individuals from two populations are placed randomly on all sites and the individuals compete in the sites where both populations are adapted. NAMKOONG (1976) considers a model where the environments are split and only the one population that is better adapted to each part of the environmental range is planted in that part of the range. The difference between the two models in the evolutionarily stable level and the optimum level of population mean divergence is very small, indicating that regardless of how one manages the planting of genotypes, it is always better to have diversified populations, and there is an optimum level of divergence.

Thus, for an optimum breeding program, it is necessary to consider selection programs that maximize gain not only in a single environment but in specified environmental ranges. Selection for economic gain in trait performance in certain ranges of environmental variables therefore must be done in $n + 1$ dimensions. The value integral for selection may give weight to yield in some environments more than in others. Thus, even if yield is not as high for one genotype as for another in some environments, the genotype may have a higher value integral because it yields well in the more heavily weighted environments. For multiple, variable environments, the solution is not qualitatively different than for one environmental variable, and the only major problem for breeders is to decide how

many subpopulations the total population of a thousand or so individuals need be broken into. Since the more finely subdivided structures can more exactly fit an environmental distribution, the more subdivisions the better. However, to continue to increase yield in variable environments, that is, to be able to continue evolution in any of the $n + 1$ dimensions, the population sizes within units require sufficient size to avoid at least the short-term effects of inbreeding. For many plant species, this minimum size seems to lie in the range of 20—50 fully and equivalently reproductive individuals. Even smaller unit sizes can be considered if replicate populations of the type recommended by BAKER and CURNOW (1969) are maintained and if the effective population size is kept large by ensuring equal gametic representation of all selected individuals in succeeding generations.

For future generations where our uncertainty with respect to environmental or yield requirements is very high, another operational option becomes possible. Hybrid populations can be created to fill in the space between any set of breeding populations, hence, the value of a breeding population is also a function of the value it may have if crossed with other populations. In that case, the optimum interpopulational diversity for a few breeding or control populations would be increased and selection in the different breeding populations would more heavily emphasize yield responses in more extreme environments. The optimum divergence would depend heavily on how the interpopulational crosses behave with respect to their additivity, genetic dominance, epistasis, etc. as to how their hybrid populations yield as F_1 populations or as new breeding populations for re-crossing or for recurrent selection programs. A Maximum divergence for one generation might be bred by pair mating extreme individuals (LAND and MATTHEISS, 1983), but this would preclude any recurrent selection for continued future generation divergence.

Considered in this more comprehensive context, each breeding population contributes to the total value of the "meta-breed" in the sense of NAMKOONG *et al.* (1980), not only on its own, but in combination with the other populations. The value integral for the meta-breed then contains this more complicated function of the general component breeds, and the problem of optimizing the array of populations is a control theoretic problem. The value function, in such a problem, may be an integral of the summed values of the constituent populations or a sum of integrals over delineated parts of the environment. The control decision is how many populations are to be developed and how widely should they differ in adaptability. Thus, the new concept of controlling an environmental plus a yield space can be stated in terms of yield functions and their optimization, and the mathematical methods of optimization theory (see example, PETROV, 1968) can be applied. An array of populations thus constructed can be said to control yield in an environmentally defined yield space. The objective of gene conservation may then be to control a defined space by some optimal deployment of populations. Deployment may be designed to increase the boundaries of the space under control, or to fill in the interior of the space so that breeding can rapidly develop well adapted varieties.

A Management Strategy

If control of yield space is the objective, it is clear that in forestry it can be achieved only by indirect means and with high levels of uncertainty as to future values and

conditions. It seems unlikely that forestry will ever afford intensive breeding efforts in single, small populations such as are used for large mammals which are threatened by extinction. However, efforts of ordinary breeding in multiple populations form a simple foundation for gene conservation programs which can be coupled with *in situ* and *ex situ* conservation stand programs. Intensive breeding programs for species of high present economic value can conceivably be designed for feasibly controlling the same space that a conservation program would encompass. Conservation efforts would therefore need little or no supplement. For species that have been extensively studied and are already included in breeding programs, the major concern of conservationists will be best focussed on ensuring the existence of peripheral, supplementary populations of sufficient size.

There is clear economic justification for intensive breeding and conservation of known high value species. However, there are many less studied species, some of which may prove useful as part of a supporting ecosystem, as directly utilizable species, or as sources of genes for use with other species. The objective of control for such species can only be achieved by securing any present levels of diversity and by managing population units to encourage increased diversity. Thus, multiple population or ecosystem samples should be taken to span extremes of size and site conditions, and especially to include isolated populations. Treatment of these areas should then ensure the existence of continued reproduction of the species but under even more extreme conditions than presently exist. Only indirect genetic management by ecological means can be foreseen for these species (ANONYMOUS, 1982 and NAMKOONG, 1983).

Between these two types of species, a third type exists about which some knowledge has accumulated but with which little intensive work can be afforded. For such species at most a single population breeding effort may be justified, along with some opportunities for *in situ* and *ex situ* conservation stands. For these, some greater level of efficiency in identifying critical populations may be achieved by sampling specified stands and even creating stands on diverse sites to foster the diversity necessary for the control objective.

Thus, even with low-intensity genetic control, there are feasible sizes of programs and arrays of indirect ecological manipulations that can conserve alleles. Since the species constitutes the largest intermating unit capable of continuous evolution, a system is required for managing and monitoring the status of the species in an array of programs and management units. In the array of conserved

ecosystems, the array of species must be genetically managed, for genetically distinct objectives.

At present levels of funding, agencies such as the FAO cannot handle any but a very few species in the second and third classes of genetic management. Clearly what is needed is not more intensive breeding as much as simple gene conservation programs to save the natural legacy of diversity. Indeed, for these purposes, genetic research would be best directed towards increasing our knowledge of natural populations and efficient means for expanding diversity and not towards efficiency in eliminating variation through intensive breeding of small populations. The greatest needs are to support present efforts at *in situ* and *ex situ* conservation and to greatly increase research and development programs for saving and developing our natural diversity.

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