Planting State-Listed Endangered and Threatened Plants

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Abstract: The distribution and planting of state-listed endangered and threatened plants is outlawed in most states of the United States, yet listed species are commonly used in landscaping and restorations. There is a need to re-examine policy regarding planting and propagation of endangered and threatened plants outside of planned recovery efforts. Potential advantages associated with increased outplanting of rare species include: (1) improved public education and relations; (2) demographic security derived from creation of new populations; (3) provision of new, appropriate gene flow opportunities; (4) applied research opportunities; and (5) ability to regulate a currently uncontrolled activity. Potential disadvantages are: (1) confusion of natural and planted populations; (2) bureaucratic problems with protection of planted populations; (3) potential for inappropriate gene flow between natural and planted populations causing outbreeding depression and loss of genetic purity of natural populations; and (4) extension of the natural geographic and ecological range of the species. Policies, regulations, and nursery practices exist that would maximize the potential advantages and minimize the risks associated with the distribution of endangered and threatened plants. Policy considerations discussed include selection of appropriate species, production of appropriate and high-quality gene stock, and regulation of outplanting programs. I weigh the risks and benefits of a program that would allow the general public access to some state listed plants for natural landscaping. I conclude that a less restrictive but enforceable set of policies and regulations may be preferable to the status quo.

La plantación de plantas listadas como amenazadas o en peligro de extinción

Resumen: La distribución y siembra de plantas listadas como amenazadas y en peligro de extinción es ilegal en la mayoría de los estados de Estados Unidos; sin embargo, especies listadas son utilizadas comúnmente en parques o jardines y en la restauración del paisaje. Existe necesidad de re-examinar las regulaciones con respecto a plantar y propagar plantas amenazadas y en peligro de extinción en todas aquellas actividades que no están incluidas dentro de los esfuerzos de recuperación planeados. Las ventajas asociadas con la propagación de especies raras incluyen: 1) el mejoramiento de la educación y las relaciones públicas; 2) la seguridad demográfica derivada de la creación de nuevas poblaciones; 3) la provisión de oportunidades de flujo genético nuevas y apropiadas; 4) las oportunidades de investigación aplicada; 5) la habilidad para regular actividades; 6) el control sobre la actualidad. Las desventajas potenciales son: 1) la confusión entre las poblaciones naturales y las plantadas; 2) los problemas burocráticos con respecto a la protección de poblaciones plantadas; 3) el potencial para un flujo genético inapropiado entre las poblaciones naturales y las plantadas causando una depresión por escasez y la pérdida de la pureza genética de las poblaciones naturales; y 4) la extensión del área de distribución geográfica y ecológica natural de las especies. Existen políticas, regulaciones y prácticas de un vaho que pueden maximizar las ventajas potenciales y minimizar los riesgos asociados con la distribución de plantas amenazadas y en peligro de extinción. Las consideraciones de planes de acción discutidas incluyen la selección de especies apropiadas, la producción de stock genéticamente apropiado y de alta calidad y la regulación de programas de propagación. Evalúo los riesgos y beneficios de un programa que permitiría al público en general acceder a algunas de las plantas listadas para la decoración natural de parques y jardines. Concluyo que un conjunto de políticas y regulaciones menos restrictivas pero de mayor cumplimiento sería más preferible que el "status quo."

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Introduction

Use of native plants in restoration, reintroduction, and creation of new populations is practiced widely by both governmental agencies and private industry and is largely unregulated. Plants that are listed as endangered or threatened (ET) at either the state or the federal level in the United States are currently the only native species for which commercial use and distribution are controlled. Most states outlaw the sale or commercial use of ET plants. There is a public demand for ET species, however, especially native prairie species, for restorations and native gardens. Several ET plants are being commercially distributed (Janzen 1988). Some midwestern states (such as Wisconsin) are currently considering policies and regulations that allow regulated use of some ET species by the restoration and native-plant industry.

Most state-listed ET plants of the central and northeastern United States are locally rare because they are at the margin of their range in the state. These species are often more common in other states located in the central parts of their range (Ayensu 1981; Gentry 1986). Marginal populations of species are worthy of preservation at the state level for several reasons: (1) maintenance of biodiversity at a state or regional level; (2) aesthetic appreciation of rarity afforded to the residents of the state; and (3) perhaps most important biologically, marginal populations, which are generally lower in genetic diversity than more central populations, may have a relatively high frequency of unique alleles, uncommon genotypes, and ecotypes adapted for extremes of environmental conditions (Lewontin 1974, Shumaker & Babble 1980; Rabinowitz 1981). The uniqueness of marginal populations is due to isolation, genetic drift, and extreme selection in marginal habitats. Marginal populations are worthy of preservation, therefore, because they may harbor a disproportionate amount of the genetic and allelic diversity of the species (Millar & Libby 1991). Wright's (1977) "shifting balance" theory suggests that such unique populations may play a critical role in long-term macroevolutionary and adaptive change.

Commercial distribution of ET plants within the state in which they are listed is illegal, but the laws are not often enforced and the plants are distributed widely by commercial nurseries and by well-meaning restorationists and native-plant enthusiasts. In fact, state ET protection status unintentionally encourages the importation of the "foreign" genotypes available in plant catalogues from states where the species does not have a protected legal status. In this case, what appears to be laissez faire may unwittingly be the most destructive type of intervention because of the tendency to encourage the use of inappropriate genetic stock (Frankel 1983).

There is a great need to examine and assess policies regarding the commercial use and distribution of state ET plants. We must critically examine the advantages and disadvantages associated with the outplanting of native species. This requires careful application of genetic and ecological principles to assess the risks of creating new populations of native species that are not part of a formally-planned recovery program. There are a wide variety of ways to select and utilize native genotypes and species for outplanting (Guerrant 1992). I attempt to list and discuss briefly the advantages and disadvantages of the translocation of native species. I then apply general principles from population genetics and ecology to the design of outplanting programs for use when our knowledge of the genetic structure, ecology, and population biology of the species is not very detailed.

Potential Advantages and Disadvantages of an Outplanting Program

Educational Value

Perhaps the greatest single benefit that can be derived from commercial use of some ET plants is in the potential for improved public education and relations. It has often been suggested that education of the general public is one of the most crucial roles for conservation biologists (Jacobson & Hardesty 1988; Schaaf 1988). Others have drawn attention to the need to inform and positively direct the passions and energy of environmental activists and the concerned public (Fleischner 1990; Kingsman 1991). Distribution of appropriate informational material with ET plants can directly connect members of the public with the species and with general issues related to the conservation of rare plants. A large portion of the concerned public is capable of grasping ecological and genetic issues related to the conservation of rare plants when given the opportunity with well-designed educational material. We should make an effort to empower the general public with this type of knowledge. When people "own" and care for a rare species, they develop an intimate and long-lasting connection with an organism and its environment. Furthermore, people concerned with conservation feel that they are doing something beneficial for the survival of a rare species when they plant it in a natural area or even a garden (James 1982).

Creation of New Populations

Demographic security is the primary consideration for the preservation of rare species (Lacy 1988). Behavioral, genetic, and ecological processes are important largely because they directly affect the demography of species (Lande 1988). Population viability analyses using demographic simulations show that environmental stochasticity, especially catastrophic mortality, generally exerts dominant influences on estimates of population viability.
(Menges 1986, 1990, 1992; Ewens et al. 1987; Quinn & Hastings 1987; Shaffer 1987). Risk of extinction as a result of catastrophic mortality is dramatically reduced when the species exists in several separate populations (Guerrant 1992). The creation of a metapopulation (a population of independent populations) can serve as an insurance policy against the extinction of natural populations (Pickett & Thompson 1978). Public perception of an endangered species program is also enhanced if the creation of new populations is successful. Public support for an endangered species program continues only if the program is perceived to be both successful and fair (Humphrey & Stith 1990).

The creation of new populations may also benefit the evolutionary potential of the species (Frankel 1983) if the species is placed in novel selective regimes that have the potential to produce rapid genetic changes (Clegg & Brown 1983). It may be preferable to create new populations when natural populations are still sufficiently large to contain considerable genetic diversity (Templeton 1991).

Opportunities to Learn More about the Species

Although intervention to assist the recovery of many ET species may not currently be required, it can become essential within a relatively short time. We know very little about propagation methods, environmental tolerance, and habitat preferences for most state-listed ET species, let alone the relationship between environmental heterogeneity and genetic variability (Barrett & Kohn 1991). In short, we often lack the practical knowledge to grow the species successfully. This lack of knowledge exists in most cases because we have not devoted the resources required to study the species. Allowing commercial nurseries and private enthusiasts to propagate and create populations of ET species can add substantively to our knowledge of how to establish ET species successfully in restorations and naturalized plantings. Information on garden techniques is valuable and applicable to the early phases of a recovery project. The most important lessons for conservation are learned after material is planted in the wild. Ability to learn from propagation experiments is valuable to the extent that conditions are known or controlled, the performance of outplanted populations is adequately monitored, and the outplanting habitats are well described.

Control over Currently Unregulated Practices

In many states, growing or distributing ET species is currently prohibited, but the laws are unenforced or even unenforceable. In other states it is legal to grow and sell state or federally threatened species as long as the propagules are derived from a horticultural source. These regulations inadvertently encourage the importation of foreign genotypes into many states. Responsible commercial nurseries of native plants don’t grow or sell species outlawed within their state. Thus, enthusiasts who desire those species purchase them from growers in other states where the species is not listed. Other local nurseries may sell listed species illegally, but there are no regulations in place governing the source of the genotypes propagated in the nurseries. Finally, the unavailability of commercial sources for some listed species may encourage enthusiastic amateurs to collect from local relict populations, potentially reducing their viability. The unregulated distribution of ET species is clearly undesirable. Permitting the distribution of some ET species and enforcing regulations regarding their use and distribution is clearly more desirable than allowing their unregulated use by failing to enforce existing laws.

Confusion of Natural and Planted Populations

Relict or remnant populations of ET species are generally considered to have a higher value than planted populations of the species for at least three reasons: (1) natural populations have a relatively unaltered genetic structure, possibly including local adaptive genotypes that may have taken a long time to evolve; (2) because of their relatively unaltered genetic structure and ecology, natural populations offer potential for research and understanding lacking in created populations; and (3) created populations of ET species are not given the same degree of legal protection that is given to natural populations. There is danger that creation of successful new populations could confuse the distinctions between created and natural populations in the long term. Only a very well-designed and well-managed database and monitoring program would be capable of recording the location of all created populations over the long term. Management of such a database may prove to be a bureaucratic nightmare. Uncertainty as to whether relict populations are natural or created could jeopardize their legal protection, and, by extension, protection of the habitats in which they grow. In the long term, success in creation of populations of an ET species may lead to delisting of the species (and is often an explicit rationale for their establishment). There is the danger that species could be delisted because of a recovery program that is inappropriately or prematurely deemed successful. Protection of ET species is often our only powerful tool for habitat protection.

Possibility of Extending the Range of the Species

Creation of new populations of state-listed ET species could extend their ranges within the state—enough to represent extensions of historic ranges of the species. Extensions of the “environmental” range of the species are also likely when populations are created in habitats
that were previously unknown for the species. There are both philosophical and biological reasons why it may be undesirable to extend the historic range of ET species. On the philosophical or social side, there is the potential for future confusion of the natural and planted range and the fact that a species outside of its historic range is an exotic. Knowledge of the current and historic range of natural populations reduces the likelihood of confusion. If the natural and planted ranges of a species are eventually confused, however, the potential for some types of research with the species will be reduced. A species planted outside of its historic range is an exotic, and it could be argued that use of an exotic is contrary to the intention of most restorations and naturalizations.

Potential threats to the biology of the ET species that could result from range extension, and threats to the integrity of natural communities in the area of range extension, seem unlikely to occur for most species. Risks to natural areas outside the historic range of the species include the possibility that plant communities could be disrupted by the introduction of a new species. The species could even become a pest outside of its historical range. This seems improbable because the range extension would be small, and most ET species have little likelihood of becoming aggressive. Threats to the ET species itself include the possibility of hybridization with a closely related species with which it previously had little or no contact (Rieseberg 1991) and the potential that increasing the range of the species may expose it to new predators or pathogens from which it had escaped by virtue of its limited distribution (Strong et al. 1984). These threats seem unlikely for short-range extensions of the vast majority of species.

Enhanced Opportunities for Gene Flow

The possibility of gene flow between relict and created populations can constitute either a positive or a negative force in an effort to conserve an ET species locally. The relative benefits of gene flow depend on the genetic structure of the species, the genetic constitution of the created populations, the level of gene flow, and the nature of selective forces over time (James 1982; Frankel 1983).

The historical rarity, or lack thereof, of ET species affects the likelihood that enhanced gene flow will be beneficial. Most rare species exist in isolated and often small populations. There are many causes of rarity in plants (Rabinowitz 1981; Fiedler 1987), but most plants currently considered rare have suffered to some extent from habitat destruction. Genetic variance is reduced in small, isolated populations by genetic drift and directional selection (Karron 1987, 1991; Lacy 1987; Barrett & Husband 1989; Barrett & Shore 1989). Small populations also become inbred and can suffer lowered seed set because of reduced pollinator visitation (Harper 1981; Jonkersten 1988), or reduced germinability (Menges 1991), due perhaps to biparental inbreeding. Populations maintained at a small size or going through periodic bouts of inbreeding may become purged of deleterious recessive alleles (their genetic load is reduced) and may tend therefore not to suffer as much from inbreeding depression as historically outbred populations. It has often been claimed that purging is effective in inbreeding inbred populations of their genetic load, but empirical studies have done little to support this supposition (Ågren & Schmieske 1993; Dole & Ritland 1993). Wolfe (1993) found that inbreeding depression actually increased after a second generation of inbreeding. Even without effective purging, drift combined with selection in small, isolated populations can cause the development of coadapted gene complexes and locally adapted ecotypes (Barrett & Kohn 1991).

On the other hand, populations that were historically less isolated but have been made rare by habitat destruction are more likely to suffer inbreeding depression when inbred and less likely to exhibit outbreeding depression upon hybridization with other populations than historically isolated populations would be (Polans & Allard 1989; Barrett & Kohn 1991). Species that have always been rare are more likely to exhibit little inbreeding depression but more severe outbreeding depression. Plant species that historically occurred in much less isolated populations are, therefore, likely to derive more benefit from enhanced gene flow opportunities with created populations (Frankel 1983) than species that have historically survived as small, isolated populations (James 1982).

The genetic constitution of the created population is even more important than the genetic structure of the relict populations in determining the relative advantages and disadvantages of creating gene flow opportunities. Mild outbreeding depression has been shown to occur with crosses of individuals separated by relatively short distances within single populations (Price & Waser 1979). There is reason, however, to expect severe outbreeding depression when plants from different ecoclimatic regions are hybridized. Hybridizations between widely separated populations are likely to perform poorly because they would produce hybrids with respect to a wide range of ecological characters (such as drought and cold tolerance, response to day-length cues, and flowering and fruiting phenologies) (Liu & Godt 1983). In addition to outbreeding depression, there is the possibility that foreign genotypes could swamp local relict populations and destroy the unique aspects of local adaptations (such as adaptation to extreme environmental conditions at the margins of a species' range).

The relative advantages and disadvantages of increased gene flow opportunities also depend on the
magnitudes of gene flow. High rates of gene flow could prevent populations from developing locally adapted ecotypes through differential selection in different habitats. A low-to-moderate level of gene flow prevents differentiation due to genetic drift but allows development of local adaptations through selection. A level of gene flow that prevents drift could increase the genetic variance within relict populations and enhance their potential to evolve in response to changing environmental conditions. In the absence of natural selection, the exchange of one reproductively successful individual per generation is sufficient to prevent the loss of alleles and genetic divergence of populations through drift (Kimura & Ohta 1971; Allendorf 1983), but it is not sufficient to affect the allele frequencies in demes under natural selection. For many long-lived perennial plants, the exchange of one individual per generation is equivalent to a very low rate of gene flow on an annual basis. As a general rule, it is inappropriate to allow the augmentation of existing relict populations except as part of a well-planned recovery effort. For many species, however, it may be appropriate to allow the creation of new populations separated from relict populations by distance (say 1 km) to reduce the probability of gene flow and genetic swamping.

In summary, there are potential genetic advantages derived from allowing the creation of new populations of an ET plant (1) if populations of the species were once less isolated but the plant has been made substantially more rare by habitat destruction, (2) if the genotypes used in the created populations are locally derived, and (3) if only the creation of new populations, separated by some distance from relict populations, is allowed. Creation of new populations is potentially destructive to the target of our conservation efforts (or at least more risky) (1) if the species has always existed in very isolated populations, (2) if foreign genotypes are used to create new populations or if sources of genotypes for new populations are uncontrolled or unknown, and (3) if the augmentation of existing, natural populations is allowed.

Maximizing Advantages, Minimizing Disadvantages

I have attempted to explore the advantages and disadvantages of permitting the private, institutional, and commercial outplanting of state-listed plant species outside of an organized recovery effort. The profit from such a program obviously depends on regulation of the application of the outplanting process. Our challenge is to design a workable and enforceable policy that will maximize the advantages and minimize the risks for both the target ET species and regional natural areas.

State regulations could be enforced by requiring nurseries propagating state-listed ET species to have a permit for each species they hold. Permits should require that only plants or seed produced in the nursery be distributed, thereby reducing the risk of over-collection of relict populations. Species that cannot be successfully propagated in the nursery are poor candidates for such an outplanting program. A permit should specify the source of genetic stock used in the nursery and could require specific nursery designs or management practices. In short, the permit should be specific to each species, regulating those aspects of the process deemed important for the species in question. This regulation implies that some inspection and enforcement mechanism be in place and that there will be costs associated with regulation.

Production of Outplanting Stock

Selection of Species

A first step in designing policy for private outplanting of ET species is to select species for which the risks associated with outplantings are not too great. General guidelines for selection of species should rely on regional data on the historic and present range and on the distribution and abundance of the species. Excellent data are available for many species from the ET-plant programs of most states (for example, Natural Heritage databases).

The historic and present ranges within the state should be well known for those species considered for outplanting. All of the known remnant populations should be catalogued and monitored state-wide, and this data should be maintained in the same database. The judgment of state naturalists is required to define the level of confidence in this distribution and abundance data because it is impossible to be certain that all existing populations of the species have been located. These kinds of decisions should be made by the state ET-plant species program in conjunction with a technical advisory committee made up of knowledgeable biologists who are not employees of the regulating agency. Only after consensus is reached that at least some proportion (say 80%) of the existing populations are known should an outplanting program to create new populations be contemplated. Benefits to the demographic security of the species derived from the creation of new populations, and the advantages of public education and involvement, must be weighed against the long-term risks of becoming uncertain of the origin of some populations.

Selection of appropriate species for outplanting can substantially reduce the risk of damage to remnant populations caused by hybridization with created populations. For species that were historically less isolated and that occurred in larger populations, creation of new populations may actually restore a more natural level of gene flow opportunities. Restoring gene flow opportunities with appropriate created populations could help to
alleviate inbreeding depression in species with historically more continuous populations.

**Selection of Stock for a Nursery Population**

Permits for an outplanting program for ET species should require that outplanted seed or plants be produced in a nursery, either public or private, (1) to prevent overcollecting or damage to remnant populations, (2) to control the genotypes of the outplanted stock, and (3) to increase the likelihood that the selected ET species outplanting will succeed. The following discussion applies population genetic and ecological principles to the selection of nursery stock, although many of the principles would also apply to field collection for direct restoration.

**COLLECTION OF LOCAL STOCK**

With few exceptions, a state-regulated outplanting program should permit the planting only of local stock (from within the state or adjacent parts of a narrowly defined ecoregion). Use of local stock eliminates the potential for swamping of local genotypes by foreign genotypes and will also produce stock that is adapted to the general biotic and abiotic environment of the area. Most plant species probably have some optimal outcrossing distance. Crops of near neighbors suffer from some level of inbreeding depression, and crosses between plants too distant produce progeny exhibiting some outbreeding depression. While some outbreeding depression is possible in crosses of plants separated by a short distance (100 m; Price & Waser 1979), severe outbreeding depression is expected if widely separated populations (different ecoregions) are hybridized. Genotypes from distant populations are likely to be maladapted for a wide range of ecological and phenological characteristics necessary for success in the local environment. Artificial political boundaries are not ideal for regulating an outplanting program (for example, allowing only genotypes from within a state), but they may be necessitated by conditions of administration and ease of enforcement.

**SOURCE POPULATION**

Sampling from a single population to create a nursery eliminates the risk of severe outbreeding depression, but it increases the risk of inbreeding depression in created populations because of lower mean genetic variance in samples from single as opposed to multiple populations. Sampling from a single population may produce stock well adapted for specific habitats closely matching that of the source population but may not produce general-purpose stock capable of success across a range of potential habitats for the species. Sampling genotypes from multiple populations to obtain nursery stock increases the risk of outbreeding depression (Price & Waser 1979) but lowers the risk of inbreeding depression in the outplanting stock produced. The extent to which outbreeding depression can be a problem in the first-generation outplanting stock is in proportion to the degree of hybridization of the source populations that occur in the nursery. Sampling multiple populations has several potential advantages for the long-term evolutionary potential of the created populations. The stock produced as the result of hybridization of source populations will have a relatively high genetic variance (Hamrick et al. 1991) and will maximize the ecological range and tolerance of the species in new sites. Rather than attempting to recreate the genetic structure of an existing population, the use of multiple source populations will allow new genetic combinations to be formed (Templeton 1991). The potential will exist to form entirely new coadapted gene complexes and locally adapted ecotypes on the newly colonized sites (Templeton 1980, Goodnight 1987, 1988). Practical aspects of commercial nursery production require that outplanting stock have as wide an environmental tolerance as possible (Barrett & Kohn 1991).

Templeton (1991) argues that "Without knowledge of how the species' genetic diversity is divided within and between local populations, it is impossible to design a sampling program that is ensured to preserve a substantial portion of the species' genetic diversity." If the genetic structure is known, it is possible to design an efficient sampling procedure for obtaining both allelic diversity and preserving existing genotype frequencies. But even without knowledge of the genetic structure it is possible to ensure a high allelic diversity in the sample by sampling from multiple populations (Brown & Briggs 1991, Center for Plant Conservation 1991, Templeton 1991). Rare species with isolated populations tend to have a higher proportion of their total genetic variance among populations than within populations (Hamrick & Godt 1989; Hamrick et al. 1991), although this trend was not statistically significant in these two analyses. Sampling equally from several populations will ensure a high allelic diversity in the sample. If knowledge of the historic size of the populations is available, it would be advisable to sample more individuals from the larger populations that are likely to contain more within-population genetic variance (Brown & Briggs 1991).

**COLLECTING WITHIN POPULATIONS**

A general goal, both in seed collection and in the nursery, is to not impose artificial selection on the stock. Considerable effort should be invested to minimize intentional or unintentional artificial selection in the collection and nursery production of stock. Selection can occur only if there is differential survival or contribution
to the next generation. If family size—number of offspring—could be held constant, there could be no unintentional selection of traits. When collecting, it is easy unintentionally to select plants that appear to be more robust, and without a pedigree of plants growing in the collected population it is impossible to strictly equalize family size in the collection. Nonetheless, selection will be minimized by equalizing, as much as possible, the representation of seed-producing plants in the sample. There are several reasons for equalizing collection from individuals and avoiding selection at this stage: (1) if vigor (robustness) or showiness have any genetic basis, then selecting certain plants with like characteristics will reduce the genetic variance sampled; (2) selection of vigorous plants may favor those that are adapted to particular microhabitats or that reproduce well in years with particular weather patterns (for example, drought-adapted or mesic-adapted plants), and, again, the range of genetic variation sampled and the range of habitat conditions tolerated by the outplanted population may be reduced.

Ideal collection of stock within populations, which will maximize selection and maximize the genetic variance sampled (Center for Plant Conservation 1991), incorporates the following features: (1) Sampling of individuals should be stratified-random across the population. Collections are stratified across the population to sample as many microhabitats within the site as possible; individuals are chosen at random to avoid unintentional selection. (2) The same number of seeds are collected from every sampled individual to equalize representation in the sample. (3) If possible, sampling should span different years to include individuals that reproduce differentially because of variations in weather conditions. Keeping these general rules in mind could substantially improve the quality of the stock collected. Collection of seed to establish nurseries should be carefully regulated to avoid damage to relict populations. Ideally, all seed collection would be done by a state agency and the seed then provided to the nurseries with their permit.

Nursery Design and Management

The production of seed in a nursery should minimize the potential for selection of nursery or cultivation ecotypes and produce a high-quality, genetically diverse outplanting stock. Because nursery plants tend to be grown in an environment much more rich and less harsh than natural environments, there may be a negative correlation between fitness in the nursery and fitness in the wild for many plant species. Attainment of high-quality stock will be accomplished by producing stock that minimizes outbreeding depression and that has a high probability of surviving the demographic bottleneck at a new site and becoming established. This requires high-quality seed, in the traditional sense of being vigorous and having a wide environmental tolerance.

To minimize the potential for selection of cultivation ecotypes, several rules can be applied.

(1) Produce only one generation of perennial plants in the nursery. If nursery stock is always collected from natural populations, then there is only one generation of selection in the nursery. Eliminating the sexual reproduction of nursery plants to provide new nursery stock will lessen the potential for selection for nursery ecotypes. If annual ET plants are included in the program, this will not be a realistic goal because it will be outweighed by a requirement not to damage the seed-source population.

(2) Every plant (seedling) grown for the nursery should contribute equally to the production of seed for outplanting. Seedlings should be produced for the nursery without competition or intentional selection. Plants that are weak or less productive in the nursery should be horticulturally enhanced rather than replaced so that they will continue to produce outplanting seed.

(3) Species should be planted in blocks across some range of garden microhabitat types. In this way the unavoidable selection for cultivation ecotypes will occur across a range of microhabitats.

(4) Germination, propagation, and horticultural practices within the nursery should be varied. This would ensure that unavoidable selection would occur under a range of selective regimes, thereby maintaining the genetic variance of the outplanting stock.

Many nurseries may not be able to apply all of these rules strictly, but setting these goals could substantially improve nursery practices.

Nursery Layouts

When multiple populations are used to found a nursery, the outplanting stock produced in the nursery can be first-generation hybrids between the parental populations ($F_{1s}$), second-generation crosses between plants from within the parental populations ($P_{2s}$), or some combination of the two. Many of the ET species that will be produced in nurseries are long-lived perennial plants that will establish predominantly in the open conditions following a disturbance. Most establishment of individuals may occur during the initial planting. Those individuals established as the immediate result of the initial restoration seeding are, therefore, likely to play a dominant role in the population for a long time. The genetic makeup of the founding generation is likely to be important for the success of restoration.

First-generation hybrids ($F_{1s}$) between different populations may exhibit hybrid vigor (heterosis), mild outbreeding depression, or fitness comparable to that of within-population crosses. Crosses among plants from the same parental population ($P_{2s}$) are likely to be very
similar to progeny produced by the parental populations and are less likely to suffer outbreeding depression (Huenneke 1991). Production of first-generation hybrids may produce mild outbreeding depression. If the coadapted gene complexes that are disrupted by hybridization involve large portions of the genome, then adaptive gene complexes may never be reformed by selection (Templeton 1986). If, on the other hand, they involve only a small number of genes, selection will be very efficient at reforming adaptive complexes. Available evidence suggests that coadapted gene complexes tend to involve a small number of genes and that outbreeding depression is expected to be most severe in F₁'s and F₂'s and to ameliorate in subsequent generations (Templeton 1986). Hybridization of parental populations provides the potential for the formation of entirely new coadapted gene complexes, some of which may, by chance, be favored in the environment of the newly created population.

Perhaps the most conservative approach to producing outplanting stock suitable for a range of environments is to produce a mix of F₁'s and F₂'s. A mix of F₁'s and F₂'s not only maximizes allelic diversity but also produces the greatest variety of genome types. It produces a highly variable stock that has a high probability of containing some genotypes suitable for the environment of the new

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**Figure 1.** Nursery layout options for production of varying proportions of progeny from crosses among plants from the same parental (seed source) population (F₂'s) versus crosses among plants from different parental populations (F₁'s). Examples shown represent layouts with seed from five source populations (represented by letters A-E in the diagrams).
population (Lacy 1988). It is possible with different nursery layouts to produce all P2's, predominantly F1's, or a mix of the two, without performing hand pollinations (Fig. 1). If plants derived from different parent populations are randomized in the nursery, most of the seed produced in the nursery will be F1's, because most matings in an outcrossing species will be between nearest neighbors (Levin & Kerster 1974; Handel 1983) and most plants will be surrounded predominantly by individuals from other populations. If the nursery plants derived from different parent populations are planted in isolated beds, the outplanting stock produced will be entirely P2's. If, however, the plants from each parental population are planted as separate but adjacent rows (Fig. 1) the progeny produced will likely be roughly one-third P2's and two-thirds F1's assuming that the species does not have a mixed mating system, because self-pollination would increase the proportion of P2's.

A nursery layout producing such a mix of hybrid and parental-type plants may produce not just a variety of alleles but also the greatest variety of genotypes in the population of seeds to be used as outplanting stock. These seeds will be planted in a variety of environments. Some of the P2 types will be particularly well adapted to certain microhabitats they encounter in outplanting (Liu & Godt 1983). F1's in the outplanting stock are trials at the formation of new coadapted gene complexes well adapted for some of the new microhabitats encountered in outplanting (Hueneke 1991). Outplanting is likely to provide opportunities for microhabitat range extension of these ET species (Clegg & Brown 1983).

Regulation of Outplanting

Once policy providing for the production of appropriate stock has been formulated, it is essential that the outplanting process also be regulated. Regulation is mainly necessary in three broad areas: (1) distribution of planting sites, (2) education of the involved public, and (3) monitoring of outplanting sites.

The most important regulation of outplanting by the general public will be a prohibition of plantings that augment any existing natural population. Augmenting natural populations should be part of a well-planned and approved recovery effort only after thorough study of the genetics and demography of the populations. In addition to possible adverse genetic effects from mixing native and planted genotypes, augmenting a population (or supportive breeding) can actually reduce the effective population size below that before intervention (Ryman & Lalkre 1991). Regulations should, therefore, provide a minimum distance separating planted and known populations of ET plants. A minimum distance of 1 km (Handel 1983) may be appropriate as a separation between planted and natural populations.

Other issues could be considered for regulation with respect to selection of planting sites. For example, will distribution of the species outside of its historical range be allowed? The state may prohibit distribution of ET plant material to another state to avoid violation of laws or conflicts with programs in other states. In most cases, restrictions of the historic range of a species within a state may be of little risk to the species. To provide for a high rate of success of outplanted populations, regulation of outplanting habitats may be considered. Placement of plants in appropriate habitats may be more effectively accomplished, however, by the distribution of educational materials with the plants. While some plant material will be wasted on inappropriate habitats, it will be material produced in a nursery and will therefore not be at the cost of remnant populations.

Other policy issues that must be addressed by the regulatory agency include (1) policy on use of public versus private lands as outplanting sites, (2) requirements for access to the population for monitoring, (3) provisions for long-term management of the population, and (4) legal implications pertaining to the protection of created ET-plant populations. The state must consider whether regulation of each of these aspects of site selection and control is required. It may be appropriate to make some of these decision on a species-by-species basis. I suggest (1) that voluntary compliance with regulations achieved through an educational program will be more effective and less costly than compliance achieved through enforcement, and (2) that if the advisory committee and state staff feel that a great deal of strict regulation is required to prevent damage to a particular species, then perhaps that species is not an appropriate candidate for the program.

Education of the public and generation of support for ET-species programs are the most important potential benefits of an ET-outplanting program. Distribution of educational materials should be required with any commercial use of ET species. State biologists and their technical advisory committee should produce a flyer describing the importance of protection programs for ET species. For every ET species permitted for commercial use in the state, there should also be a flyer providing information about that plant. Commercial enterprises that use the ET plant in restorations or that sell stock of the species should be required to distribute the informational material to the new owner of the ET plant.

Well designed educational material will provide the new steward of the ET plant with the background necessary to feel a real connection with the species. These educational efforts will generate supporters of ET-species preservation and of programs aimed at their preservation (Jacobsen & Hardesty 1988; Humphrey & Smith 1990). Clear explanation of the regulations and of the rationale for the regulations placed on the outplanting of ET species will encourage voluntary cooperation with
the guidelines. These educational activities should reduce the likelihood of inappropriate use of ET species below that which currently exists under the total legal ban on their distribution. Lack of information causes many amateur conservationists to view the ban on ET species as unnecessary regulation preventing them from accomplishing something positive for conservation and recovery (Fleischner 1990). Reporting of outplanting sites and monitoring of populations is essential to gathering information on locations for the species database, for learning which factors influence its distribution and abundance, and for assessing the effectiveness of the program. Reporting of planting sites should be mandatory. This would require a cooperation among three groups involved: the state agency that would issue permits for the outplanting program and maintain records and a database, the permitted commercial grower or restorationist who would distribute reporting forms and report sales, and the landowner who purchases and/or plants the ET species. Forms should be available both for the reporting of planting sites and for the subsequent annual or biennial monitoring of the planted populations. Monitoring of the planted populations is the only way to determine the conservation value of the outplanted material and will provide valuable applied information for the development of recovery plans. Formal applied research would also be enabled by the maintenance of such records for the planted ET populations. Reporting of planting locations will help to avoid confusion of natural and planted populations. While data obtained through monitoring is one of the most biologically valuable parts of an outplanting program, it may be difficult to achieve through enforcement of regulations. Every effort must be made to educate the public about the importance of their compliance.

Conclusions

The potential risks and benefits of an outplanting program must be weighed separately for each ET species (World Conservation Union 1987; Griffith et al. 1989). Conservative tendencies suggest that we should never move native plants (Maguire 1991), but that is already being done on a large scale. Careful evaluation of benefits and risks and consideration of appropriate and responsible production of stock could lead to a policy that is a marked improvement over the status quo (Murphy 1989, 1990).

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Literature Cited


