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RESTORATION AND REINTRODUCTION OF ENDANGERED PLANTS: A NORTH AMERICAN PERSPECTIVE

Marlin L. Bowles
The Morton Arboretum, Lisle, IL 60532 USA

ABSTRACT

The worldwide expansion of human populations and loss of natural vegetation has endangered thousands of plant species. In North America, cooperation between government and non-government organizations and scientists has facilitated an expanding number of in situ restorations designed to prevent further endangerment and loss of species. Botanic gardens and arboreta play a critical role in recovery programs by providing an ex situ setting for propagation research and a source of propagules for restoration. Attempts to restore viable populations of plant species to reserves and other habitats must consider biological, ecological, and demographic factors that can negatively affect small populations. The linkage between plant species genetics and breeding system (e.g. selfing vs out crossing) is a key factor affecting distribution of genetic diversity within and among populations and an important determinant for whether restored populations can reproduce. As a result, this information can serve as a template for genetic sampling and population restoration. Other reproductive factors such as genetic self-incompatibility, sensitivity to inbreeding, and pollinator requirements can directly affect reproductive potential and viability of small restored populations. Once biological information is clarified, ecological habitat requirements, such as plant community, soil conditions, and natural disturbance regimes to which species may be adapted, should be considered. Successful restoration will require replication of species habitat, and may be most feasible in naturally occurring conditions. Additional ecological requirements such as pollinators and mycorrhizal relationships are rarely considered in species restoration. Demographic analysis of plant mortality, survivorship, growth, and fecundity in restored populations is needed to determine critical life-cycle stages for each species and to assess affects of management treatments on restoration success. The importance of these factors to restorations is illustrated for several US-threatened plant species, including Hymenoxys acaulis var. acaulis (COMPOSITAE), a self-incompatible perennial herb of dolomite and limestone outcrops in the North American Great Lakes basin, Cirsium pitcheri (COMPOSITAE), a self-compatible monocarpic thistle adapted to dynamic shoreline dune systems of the Great Lakes, and Asclepias meadii (ASCLEPIADACEAE), a genetically diverse out crossing perennial milkweed of North American tallgrass prairie.

INTRODUCTION

The expanding human population and loss of natural vegetation have caused the extinction of about 600 plant species since the year 1600, and threaten over 22000 additional species of seed plants (9% of the world flora) with extinction (Smith *et al.*, 1993). For example, 3170 United States plant species are either critically imperiled or imperiled (Ehrenfeld *et al.*, 1997), and over 3000 Australian plants are considered rare or threatened with almost 1000 at risk of extinction (Cropper, 1993). This accelerating decline has led to development of the World Conservation Strategy against further loss of species and their habitats (IUCN, 1980; Lucus & Synge, 1981).

The most desirable strategy for long-term persistence of plant species as evolutionary units is the protection of natural habitats in large reserves (Pavlik, 1994). However, this strategy is no longer possible in many parts of the developed world and is becoming more difficult elsewhere as remote temperate and tropical areas are impacted by humans (Falk & Olwell, 1992; Maunder, 1992). This urgent situation has resulted in a need for increased *ex situ* conservation of rare species in botanical gardens (Given, 1987; Heywood, 1990; Maunder, 1994) and for greater numbers of *in situ* plant population enhancement, reintroduction and restoration efforts designed to reduce extinction probabilities (Maunder, 1992; Bowles & Whelan, 1994; Falk *et al.*, 1996). In the United States, federal recovery plans often provide for population restoration as one of many recovery criteria (Falk & Olwell, 1992; Bowles *et al.*, 1993; DeMauro, 1994; Bowles *et al.*, 1997). Botanic gardens and arboreta play a critical role in these recovery programs by providing *ex situ* settings for propagation research and a source of propagules for restoration (Falk, 1990; Falk & Olwell, 1992; Falk *et al.*, 1996). Museum collections at these institutions also can provide a viable seed resource for species whose seeds can be maintained under collection conditions (Bowles *et al.*, 1993).

However, despite numerous attempts to restore populations of endangered species, no populations of North American plant taxa have yet been considered restored *in situ* (Pavlik, 1994). As a result, the growing science of restoration ecology must provide a proving ground for developing techniques and strategies for restoring viable populations of plant species (Bowles & Whelan, 1994; Falk *et al.*, 1996). The success of restorations hinges on understanding and integrating biological, ecological, and demographic factors that affect the abilities of species to reproduce, occupy habitat, and undergo population maintenance and growth. This paper reviews some of these factors, illustrating how they have affected restoration of several threatened plant species in the midwestern U.S.

FACTORS AFFECTING PLANT RESTORATION SUCCESS

Biological factors: interactions between genetics and plant breeding systems

Plant species genetics and breeding systems are closely linked factors affecting how natural populations are structured and have implications for designing and restoring populations. Assays performed by starch gel electrophoresis provide extremely useful comparative data on the partitioning of population genetic diversity by determining frequencies of genes that encode soluble enzymes (Schaal *et al.*, 1991). Plant breeding systems strongly affect the spatial and temporal distribution of this allozyme diversity (Karron, 1991; Weller, 1994). In general, widespread perennial out crossing species are genetically more diverse than other species groups, and this diversity is usually maintained within populations, as measured by the G_{ST} statistic, which ranges from 0-1 and is < 0.2 for out crossing species (Hamrick & Godt, 1990). Selfing species generally have lower levels of genetic diversity, which is usually partitioned among different populations, as indicated by $G_{ST} > 0.5$. However, selfing species with extremely low levels of allelic diversity can also have low G_{ST} values.

The partitioning of allozyme data within and among populations can serve as a template for sampling of genetic diversity from seeds for restoring populations (Brown & Briggs, 1991; Hamrick *et al.*, 1991). In general, genetically diverse out crossing species whose heterozygosity is maintained within populations (low G_{ST}) can be sampled from few populations; but, comparatively large samples may be needed. In contrast, for selfing species with low genetic variation, few samples may be needed to replicate individual populations, but if their genetic variation is partitioned among populations (high G_{ST}), multiple populations must be sampled to represent range-wide variation. The level of genetic diversity to be collected also depends on restoration goals. To preserve most allelic richness and heterozygosity, seed samples are needed from fewer individuals, usually ~1000 seeds from 10-50 individuals per population (Brown & Briggs, 1991). But larger samples are needed to obtain rare alleles and to represent the natural allele and genotype frequencies that may be needed for population growth and persistence (Hamrick *et al.*, 1991).

In small populations, out crossing species can be vulnerable to loss of heterozygosity and to inbreeding depression, or may suffer total reproductive failure (Schaal *et al.*, 1991). Thus, plants with breeding systems that incorporate genetic self-incompatibility (SI), or species that are highly susceptible to inbreeding depression, pose special challenges for seed collection and restoration. For SI species, a minimum number of genotypes containing different SI alleles must be present to allow compatible cross pollination (Weller, 1994). Under these circumstances, sampling among different populations may be required to insure that restored populations contain high numbers of SI alleles or high levels of heterozygosity (Les *et al.*, 1991; DeMauro, 1993). When populations of these plants are rare, widespread collecting is often required to obtain adequate numbers of genotypes, and subsequently restored populations could develop novel combinations of allelic diversity (*e.g.* Tecic *et al.*, 1997; Bowles *et al.*, 1977). Such combinations would have potential for out breeding depression by disrupting co-adapted gene complexes (Barrett & Kohn, 1991) or conversely, they may result in heterosis that enhances restoration potential (Fenster & Dudash, 1994). These contrasting conditions often lead to contentious restoration debates (Bowles & Whelan, 1994), with recommendations ranging from maximizing genetic diversity in novel restorations (Barrett & Kohn, 1991) to maintaining locally adapted populations (Hamrick *et al.*, 1991).

Ecological factors

Once plant genetics and breeding system issues are clarified, restoration projects must consider ecological requirements, primarily habitat conditions and plant community structure (Pavlik, 1994; Fiedler & Laven, 1996). For rare plants with narrow ecological requirements, the best guarantee for successful restoration is habitat that replicates conditions occupied by natural populations. Many rare plants do not occupy all potential habitat within their range (Harper, 1981; Rabinowitz, 1981), and the introduction of plant species into vegetation remnants that do not naturally contain the species may represent the best method for preventing species extinction in fragmented landscapes. If natural habitat is absent, restoration may involve creation of suitable habitat. However, historically, few self-sustaining ecosystems, let alone species populations, have been successfully restored (Zedler, 1996). Microsite-specialization is an important consideration for establishment of many plant species (Menges, 1991). At this level, analyses of soil texture, pH, and chemistry, and vegetation structure are crucial for comparing potential restoration sites to natural habitats to determine whether appropriate or suitable species habitat is present (Fiedler & Laven, 1996; Pavlovic, 1994).

Most plants are adapted to disturbance at some scale for regeneration, and identification of the regeneration niche (Grubb, 1977) required by rare species is critical for understanding whether restored populations can reproduce and persist (Pavlik, 1994). For disturbance-dependent species, natural disturbance regimes and community successional stages that are concordant with the species life-history stages are needed (Pavlovic, 1994). These requirements become complex for metapopulation species, where probabilities of individual population persistence in transient successional habitats are relatively low but independent, while metapopulation persistence is high and dependent upon landscape processes (Gilpin & Hanski, 1991; Goodman, 1987, McEachern *et al.*, 1994).

The ecological requirements of rare species for specific pollinators, fruit or seed dispersal agents, and mycorrhizal associates are often overlooked or poorly understood. These requirements may be critical for restoration success. For example, if specialist pollinating insects are absent from a restoration site, reproduction is either impossible and the restored population will decline due to attrition of established plants, or only autogamous pollination occurs and a population of out crossing heterozygous plants could shift toward homozygous plants with accompanying inbreeding and loss of evolutionary potential (Schaal *et al.*, 1991; Weller, 1994). Similarly, absence of organisms required to disperse or process seeds could limit or prevent seedling establishment and population maintenance. Mycorrhizae development is often needed to allow seedling establishment (*e.g.* in the Orchidaceae) or to provide essential soil nutrients in stressful, competitive, or successional environments; however, species-specific restoration of soil fungi necessary for such relationships is poorly understood and has not yet played a significant role in rare plant restoration (*e.g.* Miller, 1987; Miller & Jastrow, 1992).

Demographic factors and viability of restored populations

As species populations are reduced in size by habitat loss or fragmentation, they become vulnerable to extinction processes caused by interactions between stochastic demographic and environmental events, and genetic factors (Gilpin & Soule, 1986; Lande, 1988; Menges, 1991). Similar factors obviously affect the restoration of new plant populations, ultimately determining population characteristics, such as size thresholds, required for successful restoration (Fenster & Dudash, 1994; Weller, 1994; Pavlik, 1994, 1996; Gerund, 1996). To assess viability of natural populations, biologists have used demographic trend analysis of population growth rate using matrix projection of shifts between plant life states (Menges, 1986). For plants, this approach is complex, and must integrate multiple traits, such as genetic structure and breeding system requirements, interactions between phenotypic plasticity and microsite requirements, specialization for resources, regeneration niche and survival, vegetative growth and spatial aggregation (*e.g.* ramet and genet size), and adaptations to disturbance ecology, such as metapopulation structure, all of which affect demographic variables and the establishment of populations (Menges, 1991; Huenneke, 1991; Pavlik, 1994).

Because restoration usually involves planting of discrete numbers of propagules, experimental demographic monitoring can be used to assess population growth and to project viability. Here, non-integrated approaches to trend analysis can be used to interpret data on survivorship, reproduction, and establishment to assess which life-history stages are most vulnerable to environmental factors that affect viability, and how manipulation of these factors affects viability (Pavlik, 1994). For example, comparisons of intrinsic biological factors, such as levels of genetic diversity or different seed sources can be used to determine how to enhance restoration success. Furthermore, experimental comparison of ecological variables such as rainfall, plant competition, or herbivory, or management treatments (*e.g.* prescribed burning, grazing or mowing) can help identify critical factors that affect survivorship. Thus, experimental demographic monitoring can be used to tailor restoration to species requirements and habitat specific variables.

RESTORATION CASE STUDIES

Lakeside daisy (COMPOSITAE: *Hymenoxys acaulis* var. *acaulis*)

The U.S. threatened Lakeside daisy is a rhizomatous perennial herb restricted to dolomite and limestone outcrops or thin gravel soils in the Great Lakes basin of midwestern North America. Historically, this species occurred in three U.S. counties and on Manitoulin Island, Canada, and may have been introduced elsewhere in Canada (DeMauro, 1993). It became endangered due to habitat destruction, primarily mining for dolomite. The last Illinois population was destroyed in 1981. Federal recovery planning has called for establishing viable populations in protected suitable habitat within the species former range (DeMauro, 1994).

After repeated seed collection from the last Illinois Lakeside daisy population failed to obtain viable seed, genetic analysis determined that the species has a strong, functional sporophytic self-incompatibility system; lack of multiple SI alleles had prevented seed production in the small fragmented population (DeMauro, 1993). Restoration of Illinois populations required sampling that would provide a high number of different S alleles to prevent self-incompatibility from inhibiting seed production. DeMauro (1994), obtained 5000 Lakeside daisy seeds from extant Ohio and Canada populations, and from

F1 crosses with Illinois plants. Seedlings, representing 25 maternal families, from these seed sources were propagated at the University of Illinois at Chicago, and first-year plants were translocated to establish three restored populations. Each restoration was targeted at 1000 plants, a number assumed large enough to buffer against vulnerability of small population size (DeMauro, 1994). Potential habitats were within the former range of the species and consisted of dolomite outcrops and gravel substrate supporting grassland habitat similar to habitat with extant populations in Ohio and Canada. A fourth *ex situ* population was established on constructed habitat on the grounds of The Morton Arboretum.

Stochastic environmental factors strongly affected the outcomes of these restorations (DeMauro, 1994). Only 5% of an initial spring planting of 3000 plants survived the summer of 1988, which underwent the worst recorded drought in Illinois history. However, a second planting of 1300 plants in the fall of 1988 had 60-80% over-winter survivorship. Insect, rabbit, and deer herbivory have damaged or removed as much as two-thirds of all inflorescences. Despite these impacts, successful reproduction has occurred at all restoration sites, and population size has doubled at the most successful site. The long-term viability and success of this recovery program continues to be evaluated to determine if the restored populations fall within ranges established for site, populations and demographic variables (DeMauro, 1994).

Pitcher's thistle (COMPOSITAE: *Cirsium pitcheri*)

Pitcher's thistle is a U.S. threatened herbaceous monocarpic perennial herb that is endemic to the North American Great Lakes shoreline dune systems. These dune systems are structurally variable and dynamic, ranging from linear beaches and foredunes to extensive dune complexes, and their vegetation is a series of early- to late-successional plant communities (McEachern *et al.*, 1994). Pitcher's thistle occupies early- to mid-successional graminoid dune vegetation, where it requires at least 60% open sand. As this vegetation succeeds toward higher grass or tree cover, thistle populations are lost. As a result, this species requires metapopulation dynamics for persistence, with relatively high probabilities of local population extinction, but a high probability of metapopulation persistence (McEeachern *et al.* 1994). This thistle has low allelic diversity throughout its range, but with genetic dissimilarity between widely separated populations (Loveless & Hamrick, 1988). Pitcher's thistle is self-compatible, with a mixed mating system in which flowers excluded from insects produce fewer viable seeds. Plants flower after reaching a threshold size, produce seeds, and die. Because they are monocarpic, seed production is required to produce new cohorts that will replace reproductively mature plants and maintain populations.

Human use and occupation of lakeshore habitat has endangered Pitcher's thistle. Federal recovery planning calls for restoration of populations to portions of its range from which it had been extirpated, including a 20-kilometer long shoreline dune system in Illinois where the plant was apparently lost due to human impact in the early 1900's (Pavlovic *et al.*, 1993). Multivariate analysis was used to compare potential Illinois habitat with habitat of extant populations to determine where this species could be experimentally re-introduced (Bowles *et al.*, 1993). Areas of human-induced shoreline erosion were excluded from restoration, and establishment of multiple populations that could provide metapopulation persistence was an important objective (McEeachern *et al.*, 1994). Restoration was initiated in 1990 by collecting seeds from the two nearest extant thistle populations, 170 km and 100 km distant. To enhance seedling survivorship and to accelerate cohort development, seeds were glasshouse-propagated (>20% germination) at The Morton Arboretum in spring 1991, and were out planted after four months. Direct planting of seeds was also conducted (1-4% germination), and all plantings have been enhanced annually and experimentally monitored. Initial treatments included fencing of first-year seedlings and comparison of different seed sources across ecological gradients. Because of the lack of genetic diversity in the species, no differences were expected in performance between seed sources. However, plants differed morphologically between seed sources, and the 70 km closer seed source had greater survivorship and flowering rates (Bowles & McBride, 1996). Planted cohorts have a Deevy Type III survivorship curve, with about 70% first year mortality, followed by high survivorship until flowering. Seedlings from directly planted seeds had almost 100% mortality due to late summer drought. The first flowering cohort appeared in 1992, and 18 plants have flowered and produced seed through 1996; however, more than half have been browsed by white-tailed deer. Naturally produced seeds have been harvested and propagated to accelerate population growth, leaving a proportion for monitoring of natural seed germination. Late summer drought in 1995 and 1996 increased mortality rates, and the population has persisted at about 100 plants. In 1997, a cohort was spring-planted after being overwintered *ex situ*, and had > 95% survivorship. This method appears to have potential for more rapidly increasing cohort size and will be continued until natural seedling establishment surpasses mortality.

Mead's milkweed (ASCLEPIADACEAE: *Asclepias meadii*)

Asclepias meadii is a formerly widespread perennial self-incompatible forb of midwestern North America that is imperiled by habitat destruction and population fragmentation (Betz, 1989). Most populations occur in native prairie haymeadows in the western part of its range in Kansas and Missouri, where annual mowing prevents seed production and induces cloning of few genotypes. The few remaining small populations in Illinois, Iowa, and northern Missouri preserves comprise single clones that no longer produce seeds and are vulnerable to stochastic extinction processes (Bowles *et al.*, 1997). Although this species occupies grassland soil conditions ranging from acid to calcareous, it does not differ genetically across its range, and most allelic diversity (G_{ST} = .2) is found within large populations (Tecic *et al.*, 1997). Federal recovery planning calls for restoration of viable populations in the eastern part of the species range that replicates the genetic diversity found in naturally reproducing populations (Chaplin *et al.*, 1997).

To enhance recovery objectives, The Morton Arboretum has developed a genetically diverse Mead's milkweed garden population for experimental restoration. This has required sampling among different populations to represent the different genotypes needed to avoid inbreeding in small restorations, and has resulted in crossing of geographically distant seed sources (Bowles *et al.*, 1997). In initial greenhouse and garden experiments, greater performance has occurred in artificially out crossed seedlings, supporting the idea that such crosses could result in a beneficial heterosis effect. More than 500 milkweed seedlings and juveniles have been experimentally out planted in seven fire-managed prairies in Illinois and northern Indiana between 1994-1996. Experimental demographic monitoring has found significant variation in the germination, survivorship, and growth of these plants caused by weather, differences among sites, and site management practices (Bowles *et al.*, 1997). Seedlings are vulnerable to drought, with about 10% survivorship when rainfall is below normal, but with about 40% survivorship when rainfall is 200% of normal. In comparison, planting of juvenile milkweeds achieved more than 50% survivorship over three years. Greater growth and survivorship occurred in burned than in unburned plots at three sites, but not in all life-stages. Propagated plants from different seed sources also differed in size in the garden, but not in the field. Continued work is needed to determine if restored populations can become viable, and if there are negative effects of crossing and translocating genotypes.

SUMMARY AND CONCLUSIONS

To combat the global decline and loss of plant species, government and non-government agencies and groups are cooperating to conduct *in situ* rare plant restorations. These efforts can benefit from scientific knowledge gained from studies of genetic, environmental, and demographic factors affecting survival and extinction in small populations. No North American restorations have yet been determined to be successful, and continued experimental demographic monitoring will be crucial in developing a restoration science that will benefit these efforts. Restorationists currently face a lack of knowledge concerning demographic success of *in situ* restorations, unknown genetic consequences of restorations, continued climatic change, and potentially long time periods required for recovery (Pavlik, 1996). As a result, human intervention with seed storage and maintenance of *ex situ* collections of living plants will play an increasingly important role in plant conservation. Repeated *in situ* introductions of propagules also may be required to maintain plant populations in a modified world in which maintenance of viable populations becomes more difficult. Botanic gardens should expect to play an increasingly more important role by helping to blend *ex situ* and *in situ* rare plant conservation into a unified effort to maintain extant populations of imperiled plant species and prevent the further loss of their genetic diversity.

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