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RATES OF SUCCESS IN THE REINTRODUCTION BY FOUR METHODS OF SEVERAL PERENNIAL PLANT SPECIES IN EASTERN MASSACHUSETTS

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ABSTRACT. To prevent species from going extinct and to restore locally extinct species to conservation areas, conservationists have been attempting to create new populations of rare and endangered species. Such efforts are still at an early stage, with the basic methodology still being developed and many efforts resulting in failures or only modest success. The purpose of this work was to develop some general rules about how to carry out reintroduction efforts using four methods to create many new populations of eight perennial species. Our results demonstrate that the chances of success were greater when planting seedling and adult material rather than sowing seeds on the sites. Using larger adult material was more successful than using seedlings. Adult transplants also flowered and fruited right away, in contrast to plants derived from seeds, which rarely flowered even after several years. Digging up the site to expose the soil and reduce competition prior to sowing seed did not result in a greater establishment of seedlings. At many sites no plants survived at all, or success was low. These results emphasize the difficulties of establishing new plant populations. To increase the rate of success, attempts should utilize many sites, numerous seeds or plants, and various methods in order to develop a workable methodology for the species in question. Because of the difficulties of establishing new populations, conservation of rare and endangered species should first protect existing populations and only secondarily rely on reintroductions to ensure species survival.

Key Words: reintroduction methods, conservation, population re-establishment, restoration ecology

It has been estimated by the Center for Plant Conservation that perhaps 4200 of the 20,000 plant species of North America are under threat of extinction to some degree (Center for Plant Conservation 1993). A recent survey of the New England flora found 576 taxa judged to be "in need of regional conservation" (Brumback and Mehrhoff, et al. 1996; Stevens 1998). Worldwide, perhaps 25% of vascular plant species may become extinct in the coming 50 years (Raven 1987).

A primary cause of species extinctions is direct damage to the populations, whether by destruction of habitat, over-exploitation, or from competition from introduced plant or animal species. In addition to these acute effects, however, there is also a mounting chronic pressure on many species owing to a combination of human factors that alter species' environments in ways that inhibit or interrupt reproduction, dispersal, and colonization of new sites and thus the establishment of new populations. Local or regional anthropogenic effects, such as the production and dispersal of ground-level ozone or acid precipitation, alter the chemical environment adversely for some species (witness the effects of acid rain on *Picea rubens* in New England, or the contribution of airborne sulfur compounds to Waldsterben in Germany; Schulze et al. 1989), killing or weakening individuals, thus rendering them more susceptible to pathogens, drought, or wind damage. Fragmentation of habitat can introduce changes in the biological and physical characteristics of a location that can accumulate dramatically over time (Bierregaard et al. 1992; Brothers and Spingarn 1992; Harris and Silva-Lopez 1992; Saunders et al. 1991). These changes can both cause the death of plants currently occurring there and prevent or largely inhibit the establishment of new populations, either by the creation of barriers to dispersal, by the local extinction of dispersers, or by the introduction of weedy species that compete with previously occurring species.

On a larger scale and over a longer period of time, global climate change, especially carbon dioxide (CO_2) enrichment of the atmosphere and attendant global warming, is likely to contribute as well to the cascade of plant extinctions, as the temperature and precipitation regimes render areas of the current distribution of many species inhospitable (Bazzaz 1996; Kutner and Morse 1996; Peters 1992). The rate of anthropogenic climate change currently projected (Houghton et al. 1996) would require an adjustment of species ranges at a rate higher than any known to have occurred during at least the past 10,000 years, and species often will not be able to migrate naturally across the human-fragmented landscape.

Rates of extinction of species across all five biological kingdoms are estimated by some to be as high as 0.5% per year worldwide (Wilson 1992; Woodwell 1990). Studies of local extinctions in areas in which human impacts such as habitat modification and fragmentation have been sustained over a long period are consistent with this estimate (Drayton and Primack 1996; Newmark 1991; Robinson et al. 1994; Turner et al. 1994). As much as one third or more of the native species have been eliminated from some small and high-impact conservation areas. In the face of the local and global threats to biological diversity, the basic conservation response has been site protection: setting aside habitat that is maintained relatively undisturbed, in order to allow threatened populations to survive with no further damage (Primack 1998).

This protection is necessary but probably not sufficient as a conservation strategy (Buttrick 1992; Falk and Olwell 1992; Pressey 1994). It can prevent further direct disturbance of a site, or the effects of overexploitation of the site or population. It does not, however, protect against the more subtle stressing effects of climate change or pollution. It also does not counteract the long-term impoverishing effects of habitat fragmentation, which inhibit or interdict the metapopulation dynamics necessary to the continued survival of a species at the local and regional scales—specifically the colonization of fresh suitable sites at a rate sufficient to offset the natural and human-induced extinction of local populations (Grubb 1977; Holsinger 1993; Hughes and Fahey 1988; Norton 1991; Peterken and Game 1984; White 1996).

Increasingly, *in situ* management includes the creation of new populations of taxa or the augmentation of existing populations (Falk et al. 1996; Primack 1996), despite some concerns about implications of the practice and the indifferent success of many programs. The restoration ecology and conservation biology literature now reports many projects in which plants are reintroduced to an area where they once occurred, or new populations are initiated near existing stands, or species are introduced at apparently suitable sites. This flush of reintroduction activity has opened up many areas of research both on the basic biology of the species under consideration (Drayton 1999; Primack 1996; Schemske et al. 1994), and on many aspects of technique that must be considered in relation to the biology: whether to undertake a reintroduction or augmentation plan (Gordon 1994), how to define success for a reintroduction (Pavlik 1996; Sutter 1996), how to select suitable sites (Fiedler and Laven 1996), and how to design the actual introduced "population" (Guerrant 1996; Havens 1998; Husband and Barrett 1996; Primack 1996). In addition, there is still much to be learned about which techniques are most effective in restoration and reintroduction, including the relative value of seeds versus propagated material for introduction, and the extent and nature of appropriate site preparation and aftercare.

Choosing material for reintroductions: Seeds or plants? Because the germination and seedling stages of growth are periods of high vulnerability and high mortality, and because rare plant material must often be used with great care and economy, the majority of reintroductions of perennials have proceeded by the propagation of plants *ex situ,* and then transplanting into the target site (Guerrant 1996). Transplants of material in forms such as seedlings, cuttings, or bulbs arrive at the target site already past the most vulnerable stage of life. Individuals translocated in these forms tend to survive at a higher rate than seedlings germinating *in situ* (Barkham 1992; De Mauro 1994; McEachern et al. 1994; Ray and Brown 1995; Rochefort and Gibbons 1992; Vora 1992) and initiate flowering or asexual reproduction faster than individuals propagated from seed (Seliskar 1995; Vasseur and Gagnon 1994). In cases where the site cannot be characterized quantitatively, transplants that survive provide evidence that the site is suitable for the species and that its absence there may be due to lack of dispersal (Barkham 1992; Lee 1993; Primack and Miao 1992).

Yet even when it seems feasible from a logistical point of view, transplanting does have inherent risks, since there can be significant trauma during the transplant. Plants grown *ex situ* by definition have not grown *in situ,* so that the change in environment may subject the transplants to stress that affects their viability or results in high levels of herbivory (Cavers and Harper 1967). Poor horticulture or adverse conditions such as unanticipated drought can result in high mortality in the field (Fahselt 1988). Further, introduction of plant materials may inadvertantly introduce pathogens as well (Given 1994).

Beyond the biological considerations, however, is the factor of the cost of such an approach, which must be weighed against potential higher rates of success as compared with the use of seeds to initiate the new populations (Danielson 1996; Given 1994). For example, the cost of establishment of a single individual of Texas Ebony by tranplanted seedling (raised *ex situ*) was about $1.25, while the cost of establishment by seed was around $0.39 per individual (Vora 1992).

Reintroductions by seed offer some important advantages over transplants. In the first place, seeds can often be collected in large numbers. Collection of seed can usually be accomplished without damage to the individuals in existing populations, and this is especially important when there are only a few individuals of a taxon remaining. For example, in the case of the threatened Prairie Fringed Orchid (*Platanthera leucophaea*), populations are scattered and declining to the point that pollination is inhibited in some parts of its range. Little is known about the cultivation requirements of this species, so transplanting of existing individuals entails an unacceptable risk of mortality. The use of seeds for the creation of new populations of this species is the most useful short-term strategy for increasing the number of populations or for augmenting existing populations (Packard 1991).

It is possible that in a suitable site the individuals that germinate and grow *in situ* have a better long-term chance of success on that site than plants not "selected" by the microenvironment of the site. In some cases, seedlings from seeds sown *in situ* may have a more rapid growth rate than seedlings transplanted from elsewhere (Vora 1992), and rapid growth rate can be important if light is the limiting medium so that the production of photosynthetic tissue is decisive for survival in the face of aboveground competition or litter-fall.

Seeds can be dispersed soon after collection, thus ensuring that the propagules used for reintroduction are arriving at the target site in synchrony with the natural dispersal process. Seeds are also amenable to several kinds of experimental plantings which may provide important information about the biology of the species under study. This may improve the effectiveness of recovery or mitigation plans. For example, it may be important to design an introduced population to have maximal genetic diversity (Dole and Sun 1992; Fenster and Dudash 1994; Jacobson et al. 1994). It is easier to introduce multiple populations and multiple genotypes by means of seed than by means of transplanted material. Another important concern is the density of the population, but the optimal density and spatial arrangement of individuals in a population is known for rather few species. Reintroduction by seed allows for a variety of planting arrangements and densities.

In the case of species for which abundant seed is available, one can even design restoration or reintroduction plans at a landscape level using mixtures of seeds and seeding techniques (e.g., Jacobson et al. 1994), though this is perhaps most likely for grassland habitats.

Site preparation and post-translocation care. The concept of "safe sites" for establishment (Harper 1977), or the "regeneration niche" (Grubb 1977), provides an important rationale for careful site selection for the reintroduction of a species. The rationale includes a range of criteria, including biological criteria (e.g., specific nutrient or water requirements), logistical criteria (e.g., is the site accessible enough to the researcher to enable the operation to proceed and to enable appropriate monitoring, with "after care" or maintenance activities?), and "defensive" criteria (e.g., is the area vulnerable to human disturbance? Have management policies resulted in a high density of deer that might eat the plants?; Fiedler and Laven 1996). In addition, there may be other evidence to consider, such as the historical presence of the species. The autecology of many species is not well understood. If time and resources permit, one can conduct the studies needed to ascertain the answers to critical questions. As this is not always possible, some surrogate measures of site suitability may be required. A common example is the use of indicator species, species whose occurrence is highly correlated with the occurrence of the target species.

Initial experiments on which this study is based used little in the way of site preparation (for a summary, see Primack 1996). There is a strong *a priori* rationale for this, since most plants disperse the bulk of their seeds onto unprepared sites. Further, for many species it is not known what kinds of "preparation" might favor establishment by seed or the survival of seeds once germinated. Studies of germination requirements are not reliable guides to the requirements for establishment, as the ideal conditions for germination may not be ideal for the new seedling (Grubb 1977). This is likely to be the reason that studies show high laboratory germination rates but very low seedling survivorship in the field (Vora 1992), or high seedling emergence and also high seedling mortality (Barkham 1992; Bazzaz 1996).

For species whose establishment biology is not well understood, some approximation can be attempted based on dispersal mechanisms (Robinson and Handel 1993), germination requirements known or conjectured (Baskin and Baskin 1998), and on what is known of the disturbance regime of the species' habitat. For example, desiccation is an important cause of mortality in emergent seedlings (Larcher 1995). Sites can be prepared with mulches (Jackson et al. 1990; Rochefort et al. 1992) or shaded with branches, litter, or screens (McChesney et al. 1995) to minimize drying of the top layer of soil. Bringing seeds' emergent radicles close to mineral soil may require the removal of litter or the mowing or removal of vegetation (Gordon 1996; Rochefort and Gibbons 1992; Vasseur and Gagnon 1994; Vora 1992; Watson et al. 1994). Removal of over-shadowing vegetation can improve the light supply for early rapid growth of seedlings and can impair root competition, significantly improving seedling survival (Danielson 1995; Pavlik et al. 1993). Cultivation of the soil can also reduce below-ground competition (a decisive factor in the mortality of seedlings in many systems; Bazzaz 1996), aerate the soil, and facilitate root growth (Bainbridge and Virginia 1990). The site may be irrigated or enriched by fertilizers to facilitate rapid growth (Doerr and Redente 1983). A fire regime may be instituted, which can remove above-ground competition, remove thatch or litter that may prevent seeds' reaching the soil, and provide a nutrient pulse (Gordon 1996; Pavlik et al 1993). Finally, some species may require protection against seed predators or herbivory on the emergent seedlings (Bainbridge et al. 1995; Barkham 1992; Chambers and MacMahon 1994; Primack and Drayton 1997).

Post-reintroduction care ("soft release") may also be part of the reintroduction plan. Techniques reported from the literature include protection against seedling dessication with mulching, screening, or irrigation (Bainbridge and Virginia 1990; Doerr and Redente 1983; Jackson et al. 1990). Sites can be weeded (Jackson et al. 1990) or clipped (Danielson 1995; Gordon 1996) to continue to prevent competition during early growth.

Criteria for success of a reintroduction. Increasingly it has been recognized that a reintroduction effort must be evaluated with reference to its original goals, and that these will vary considerably from case to case (Pavlik 1996). These goals may specify an extension of a species' range by the creation of new populations or by increasing the size of existing populations in order, for example, to reach a threshold of attractiveness to pollinators. In most cases, success will be achieved stage-wise, first by the presence of individuals on the target site, then by their reaching reproductive stage, then by their dispersing viable seed, and perhaps finally by their establishing secondary populations. A longer-term goal may be a minimum viable population size, a target developed on the basis of demographic modelling.

Long-term monitoring of new populations or reintroductions can serve several critical purposes, yet systematic monitoring past the initial stages of establishment is a surprisingly rare feature of published reports on reintroductions. Measures of success are often expressed in terms of biomass (Doerr and Redente 1983; Shaw 1996), per cent cover (Jackson et al. 1990), or presence-absence (Packard 1991; Revel 1993).

Despite the large amount of attention that plant reintroduction has received in recent years, it is still possible for a leading researcher to state that there is no example of a taxon's having been conserved or brought to nonendangered status as a result of a restoration plan (Pavlik 1996). In part this statement can be explained by the length of time often needed to assess the outcome of a reintroduction, especially when working with perennials. In part the statement also reflects the state of our understanding of many aspects of the reintroduction process. In each section above, one sees open questions that require further research. The recent history of reintroduction work shows a swift development of understanding of the challenges facing such conservation work as researchers have attempted various approaches, developed criteria for assessing results, and collected results from a range of different studies and species.

The literature and examples of restoring populations of rare and endangered species have grown considerably over the last 10 years, but the development of general approaches has been inhibited by a variety of factors. First, most attempts to restore species are done with a single species, so it is unclear if the result would be applicable to another species of different growth form, family, or basic biology. Second, most attempts involve a single approach rather than conducting experiments in which several approaches are contrasted. Third, most attempts do not replicate the approach, so it is unknown how consistent the reported results are. Fourth, the results of many, if not most, such projects are never published, and in particular it is quite likely that most unsuccessful attempts to create new populations are never published at all. This may lead to literature biased in favor of successful and optimistic results. The purpose of the work presented here is to develop generalizations on the most effective way to establish new populations of rare, declining, and endangered species. We used many species, several techniques, and many replicates to develop generalizations that could be widely applicable. In this research we focused on perennial wildflower species, as many New England plant species are in this category, and our earlier research investigated annual species (Primack 1996; Primack and Miao 1992).

The present experiment was intended to answer the following questions with regard to eight native perennial species:

1. How frequent is the establishment of new populations of perennial species in relation to the number of propagules arriving on a site?
2. Is transplantation of seedlings and adults more or less effective than reintroduction by seed?
3. Does site preparation increase the success of reintroduction by seed?
4. Finally, is the establishment of new plant populations in the wild a realistic goal for perennial wildflower species?

MATERIALS AND METHODS

Starting in 1993, we identified eight perennial species that were not present but formerly attested, or whose distributions were highly restricted, in two conservation areas in the Boston area. None of these species was endangered or threatened in Massachusetts, but the number and population size of most of them appeared to have declined substantially over the last century. Such species may be of conservation interest in themselves—and thus the subject of reintroduction efforts—if the populations' distributions were shrinking so that (presumed) genetic diversity was diminishing, or if there were other biological, cultural, or aesthetic values to the species' continued presence in a particular locale (Hunter and Hutchinson 1994). In addition, such species can serve as model systems for the purpose of exploring the values and limits of conservation techniques before attempts are made to apply such techniques to endangered species.

The species used for this study were as follows (nomenclature follows Gleason and Cronquist 1991; geographic information from Seymour 1993): Marsh Marigold (*Caltha palustris*); Columbine (*Aquilegia canadensis*); Bloodroot (*Sanguinaria canadensis*); Early Saxifrage (*Saxifraga virginiensis*); Spikenard (*Aralia racemosa*); Cardinal Flower (*Lobelia cardinalis*); Sweet Cicely (*Osmorhiza claytonii*); Bluets (*Hedyotis caerulea*).

These species are well-known, even "characteristic," elements in the New England flora. All species were present in the Middlesex Fells, and all were uncommon except Bloodroot, Bluets, and Sweet Cicely. Only Marsh Marigold was present in the Hammond Woods, where it existed as a single large population. While each species has its distinct requirements, there are a few features that should be noted. Columbine and Cardinal Flower are hummingbird-pollinated, whereas the other species are insect-pollinated. Marsh Marigold and Cardinal Flower are wetland species, while the others grow in forests, fields, and disturbed areas.

Sources of plant material. In the summer and fall of 1994 seeds of all species were collected from populations in eastern Massachusetts, in most cases within 2 km of the experimental sites. Seeds to be sown on quadrats were collected at the time of natural dispersal, cleaned, counted, and placed on quadrats within a week of collecting; they were stored to ensure viability in the meantime (Baskin and Baskin 1998). In the winter of 1994, samples of the seeds of all species were sown in flats, cold-stratified at 4°C for 10 weeks, and germinated in growth chambers to test for viability and if necessary to provide material for transplantation. All species showed germination rates in the laboratory > 50%, except for *Saxifraga,* for which seeds germinated at a rate of approximately 10%.

Seedlings and adults for transplantation (see below) were obtained in the spring of 1995, when possible from wild populations in the area that were of sufficient size to allow removal of plants for transplanting (*Sanguinaria, Osmorhiza, Caltha, Saxifraga, Hedyotis* seedlings). In cases where this was not possible (*Lobelia, Hedyotis* adults, *Aquilegia, Aralia*), seeds were collected from naturally occurring sites in eastern Massachusetts and propagated first in the laboratory, then in suitable sheltered areas outside for hardening until transplantation.

Study sites. Experimental sites were established in the Hammond Woods (Newton, MA) and the Middlesex Fells (Medford, MA). The Hammond Woods is a conservation area approximately 80 ha in area. It comprises a mixture of deciduous woods, swamps, parking areas, meadows, ledges, and roads. The Middlesex Fells is approximately 800 ha in area, in two roughly equal sections isolated from each other by major highways; the reserve overlaps five municipalities. The park is dominated by mixed deciduous woods, but includes large and small bodies of water, stream courses, maintained and abandoned fields, gravel carriage roads, and hiking trails. It is used heavily for hiking, mountain biking, picnicking, and similar recreational purposes.

Sites within each area were selected on the basis of general topographical aspect by comparison with sites in which the species occurred naturally in their nearest populations. Criteria included degree of canopy closure, soil moisture, and co-occurring indicator species. For each species, apparently suitable habitat existed in these conservation areas, so that reasons for the absence or decline of populations are not known. A first hypothesis is that dispersal has limited the extent of occurrence. Further, human use of the areas may well have contributed to reduced dispersal (Drayton and Primack 1996 and references therein). Therefore, the design provided several useful kinds of information about the sites being explored: transplants that survived and seemed to establish well provided evidence that the site was suitable for the species, at least within the time frame of the study to date. Establishment of seedlings from seed provided evidence that dispersal may have been limiting. Relative success of individuals of different ages may also provide evidence about life-stages that are particularly vulnerable in these species, information that should be taken into account in designing a reintroduction plan (Schemske et al. 1994).

Experimental design. At each site, four quadrats were mapped and each marked with a numbered wooden stake in the summer and fall of 1994. Four treatments were used; one quadrat at each site was assigned randomly to each treatment; the number of quadrats (replicates) for each treatment for each species is shown in Table 1. The treatments were as follows:

Treatment 1: Seeds. A known number of seeds was sown di-

Table 1. Number of replicates (quadrats) of experimental design, number of seeds sown for treatments 1 and 2, and number of individuals transplanted for treatments 3 and 4. Treatments are described in Materials and Methods.

	# Replicates per Treatment	# Seeds Sown per Quadrat for Treatments 1 and 2	Total # Seeds Sown per Species	# Seedings and Older Plants per Quadrat for Treatments 3 and 4	Total # of Transplants
Species					
Aquilegia	24	100	4800	4	192
Sanguinaria	12	50	1200	4	96
Hedyotis	16	100	3200	5	160
Aralia	24	100	4800	6	288
Caltha	24	100	4800	4	192
Saxifraga	6	50	600	4	48
Lobelia	19	100	3600	4	144
Osmorhiza	24	100	4800	4	192
Total for all species	149		27,800		1312

rectly on the quadrat in the summer and fall of 1994 within a 25 cm radius of the marker. Nothing was done to disturb the site other than to introduce the marker.

Treatment 2: Dig and Seed. The quadrat was dug up within a 25 cm radius of the marker and to a depth of approximately 12 cm, removing possible competing herbaceous cover and superficial roots and exposing bare soil; then the same number of seeds as in treatment 1 was sown in 1994.

Treatment 3: Seedlings. Seedlings were transplanted onto the assigned quadrat in the spring of 1995, within a radius of 0.5 m of the marking stake, in holes prepared by trowel. The sites were not altered in any other way (e.g., by removal of overhanging vegetation). In the case of *Hedyotis,* seedlings were watered once soon after transplanting because of unusually dry conditions.

Treatment 4: Adults. Adult plants were transplanted into the assigned quadrat in the spring of 1995, within a radius of 0.5 m of the marking stake, in holes prepared by trowel. The sites were not altered in any other way. In the case of *Hedyotis,* adults were watered once soon after transplanting because of unusually dry conditions. For treatments 3 and 4, the same number of individuals (seedlings and adults) was used.

The number of replicates was determined by the number of seeds or potential transplants that were available. The number of seeds sown (for treatments 1 and 2) and of transplanted seedlings and adults is shown for each species in Table 1.

All sites were visited repeatedly during the growing seasons, and data were taken annually on:

- number of seedlings from seeds sown by researchers or dispersed by introduced individuals,
- number of survivors from transplants,
- number of plants flowering or setting seed in the summers of 1996 and 1997,
- number of fruits.

Although the seasons of 1996 and 1997 were quite dry in eastern Massachusetts, no transplants were watered, nor was there any other post-transplant care except as noted for the transplants of *Hedyotis* upon first planting in 1995.

Statistical analyses were performed using the Statsoft Statistica™ (Release 4.1) program and Microsoft Excel™ versions 4 and 5.

RESULTS

The success of a reintroduction can be assessed with reference to several questions. For perennials, these can be answered at least provisionally in chronological order. First, are individuals of the subject species present on any of the experimental sites? Second, what percentage of the original propagules have resulted in individuals surviving at the time of census? Third, are there any individuals reaching reproductive condition, and if so, are they setting seed? Fourth, is there evidence of a second generation at any site?

In overall terms, the results of this experiment emphasize the difficulty of successful reintroduction, the caution needed in generalization about methods, and the need for long-term monitoring. Transplanting material was by far the most reliable way to establish new populations when comparing the results for all species, but there was considerable variation among species in the rates of success as measured both by occupancy versus treatment and survivorship versus treatment.

Number of quadrats occupied. There was a total of 596 quadrats of all species, 149 per treatment (Table 1). Of these, by the end of the period here studied, there were 105 occupied by the subject species (Table 2), thus an overall rate of 19%. Of these, 87 (78%) were reintroductions by transplant, and 15 (22%) were by seed. The success rate of transplants was significantly greater than establishment by seeds (χ^2, $P < 0.001$; Table 3).

Although the values varied among the species in the study, for most species, transplants were clearly more successful than seeds in terms of survivorship. In three species, *Lobelia, Saxifraga,* and *Aquilegia,* no individuals from seed survived to 1997. By contrast, both *Sanguinaria* and *Osmorhiza* showed relatively large numbers of quadrats occupied by seedlings from introduced seeds: for *Sanguinaria,* 8 quadrats planted with seeds were occupied in 1997 (4 each for the two seed treatments); for *Osmorhiza,* 6 quadrats planted by seed were occupied in 1997. For *Hedyotis,* five quadrats planted by seed were occupied in 1997, which contrasts with the 8 quadrats occupied by transplants.

Table 2. Number of quadrats occupied in 1997, by species and treatment. Treatments are described in Materials and Methods.

Species	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Aquilegia	0	0	5	10
Sanguinaria	4	4	6	7
Hedyotis	2	3	7	1
Aralia	1	1	7	11
Caltha	1	1	2	18
Saxifraga	0	0	0	4
Lobelia	0	0	0	0
Osmorhiza	6	0	1	3
Total quadrats	14	9	28	54

Except for *Osmorhiza,* there seemed to be no significant difference in the success of seeds on prepared versus unprepared quadrats. This result in 1997 was surprising, because in the previous two years of the study for several species (*Sanguinaria, Hedyotis, Aquilegia*) the prepared quadrats showed higher numbers of individuals present. For example, in 1995 *Osmorhiza* showed seedlings at 63% of the prepared quadrats, versus 13% of unprepared quadrats. Although this was the largest disparity, emergence of seedlings from the first seed input on prepared quadrats was generally higher than on unprepared quadrats. Yet by 1997, this difference had diminished in all species (Figures 1 and 2). For *Osmorhiza,* in 1997 no prepared quadrats (treatment 2) were occupied, while six of the unprepared quadrats (treatment 1) had individuals on them. In 1996, three of the *Saxifraga* prepared quadrats (treatment 2) showed seedlings, as opposed to none of the unprepared quadrats, but in 1997 no quadrats sown with seeds showed any individuals present. For *Sanguinaria,* there were four occupied quadrats for each of the two "seed" treatments by 1997. The unprepared quadrats showed a significantly higher number of seedlings present in 1997; this reversed the situation of previous years. For *Hedyotis,* the prepared quadrats showed a significantly higher rate of occupancy in all years. Only prepared *Aralia* quadrats showed any individuals from seed present in any year. In general, the site preparation seemed to facilitate germination and initial establishment but not to affect longer-term persistence at a site.

With respect to the relative success of the two transplant methods, with mature versus younger plants, for most species more

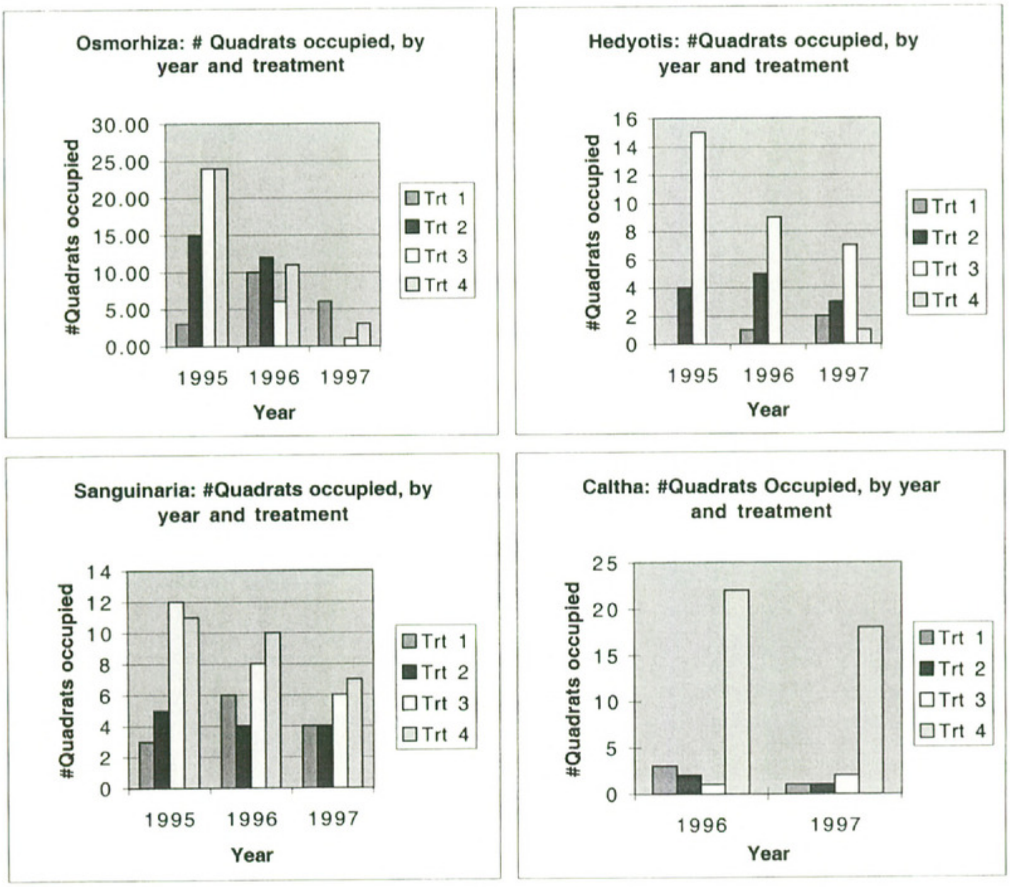

Figure 1. Number of quadrats occupied per year, by treatment, for *Osmorhiza, Hedyotis, Sanguinaria,* and *Caltha.* Treatments are described in Materials and Methods.

quadrats planted with mature plants were still occupied by 1997 than quadrats planted with seedlings (Figures 1 and 2). The advantage was most marked for *Caltha, Aquilegia,* and *Aralia,* with these differences statistically significant. For *Caltha,* 18 quadrats were occupied by mature transplants, while only 2 were occupied by seedlings. For *Aquilegia,* 10 quadrats were occupied by adults, 5 by seedling transplants. For *Aralia,* 11 quadrats were occupied by adults, 7 by seedlings. In one case, with *Hedyotis,* there was the opposite result with seedlings occupying more quadrats than mature plants in all years. For *Sanguinaria,* almost equal numbers of quadrats were occupied by plants: 6 seedling quadrats and 7 adult quadrats. For *Saxifraga* and *Lobelia,* only mature plants survived, and in the drought year of 1997, no *Lobelia* plants were found.

Rates of success per propagule. Overall, 27,800 seeds and

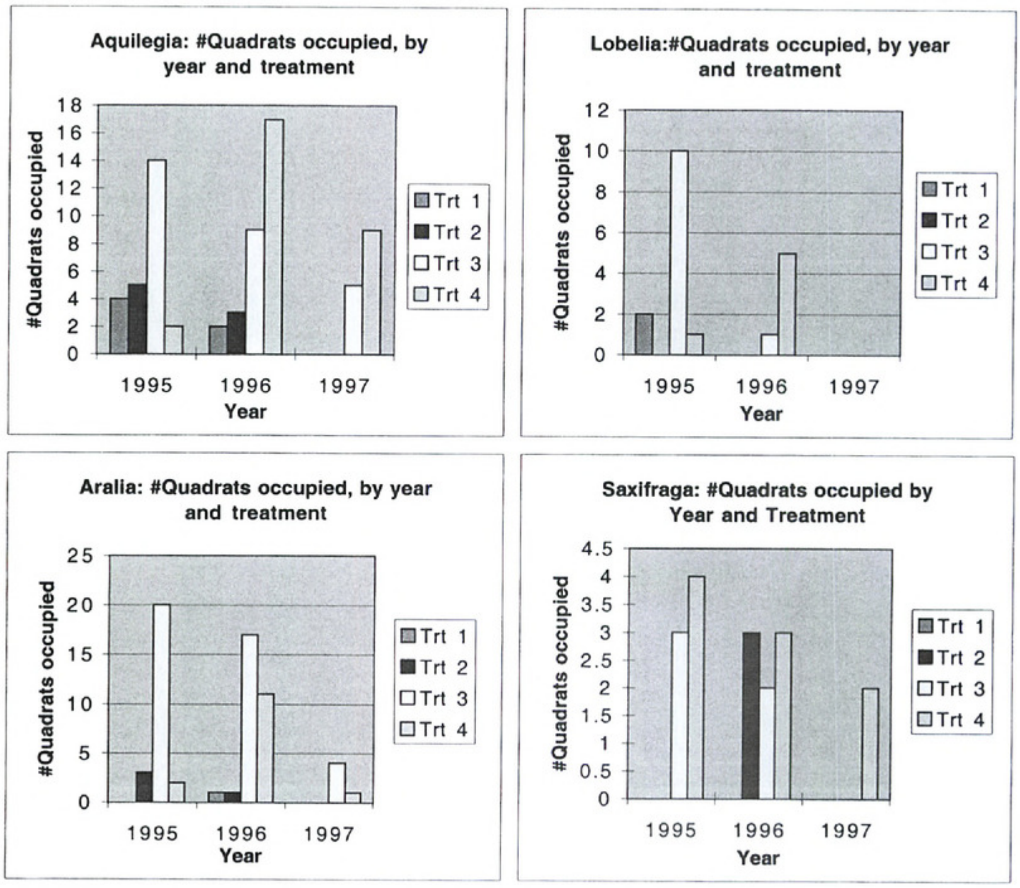

Figure 2. Number of quadrats occupied per year, by treatment, for *Aquilegia, Lobelia, Aralia,* and *Saxifraga.* Treatments are described in Materials and Methods.

1312 transplanted individuals (including both young and mature plants) were introduced on the experimental quadrats—half on prepared quadrats, half on unprepared. The rates of success per propagule introduced varied widely (Table 3) but in general they mirrored the results for rates of quadrat establishment. Thus the transplanting of material had a very much larger rate of success—that is, percentage of transplanted individuals surviving to 1997—than did introduction by seed. For all species, introduction by seeds (including both treatments) resulted in 131 individuals present for a success rate of 0.47%. Transplanted individuals fared better, with 23% of the 1312 transplants (including both seedlings and plants) surviving to 1997. Species differed in the relative rates of success, with *Sanguinaria* showing the most spread between seed treatments (about 4.5% for the two seed treatments) and transplants (about 44%); most species showed rates of estab-

Table 3. Number of 1997 survivors per treatment, and rates of survival per propagule in each category. Superscripts indicate values differing significantly by χ^2 test. Treatments are described in Materials and Methods.

	Treatment 1		Treatment 2		Treatment 3		Treatment 4	
Species	# Present 1997	% of Input	# Present 1997	% of Input	# Present 1997	% of Input	# Present 1997	% of Input
Aquilegia	0	0	0	0	9	9.4	8	18.8
Sanguinaria	35	5.8	20	3.3	19	39.6	23	47.9
Hedyotis	7	0.75	47	1.1	128	72.0	1	1.25
Aralia	1	0.042	1	0.042	20	13.8	20	13.8
Caltha	4	0.16	1	0.04	5	5.2	49	51.4
Saxifraga	0	0	0	0	4	8.3	4	8.33
Lobelia	0	0	0	0	0	3.9	0	9.2
Osmorhiza	13	1.0	0	0	3	3.0	4	4.0
Total for all species	60[a]	0.43	69[a]	0.5	188[b]	28.0	109[b]	16.6

lishment from seed at less than 1%, significantly less than rates by transplant. *Aquilegia* showed no individuals from seed present in 1997 but had a survival rate of 10% for seedling transplants and 19% for adults. *Aralia* showed survival rates of 0.04% for the seed treatments, and 14% for the transplant treatments. *Caltha* had a low survival rate from seed (0.16% and 0.04% for treatments 1 and 2, respectively), but 5% survival for seedlings and 51% for adult transplants. In the case of *Lobelia* and *Caltha,* the sites necessarily were near moving water, so it seems possible that many seeds were washed away from the experimental quadrats before germination. No seedlings of these species were noted downstream from the experimental sites, however.

Reproduction at experimental sites. The survival of introduced material is only the first level of success for a reintroduction effort, and the reintroduction can only be considered successful if some of the introduced individuals survive to reproduce and become a source of reproducing offspring in the target area. In the case of the present experiment, it is too early to assess this level of success with respect to individuals introduced by seed. In all cases except *Hedyotis,* which often flowers and sets seed during its first year, individuals of the perennial species in this study must reach a certain size, usually over several growing seasons, before they will reproduce. As these sizes are not defined in the literature so far as we can determine, this fact of life-history means that monitoring introduced populations must be a long-term effort.

In the case of introduced material, however, initial results can be reported. We recorded all instances of reproduction in 1996–97 (Table 4), and flowering individuals in 1996 (Table 5) and 1997 (Table 6). All but one species, *Aralia,* showed some reproducing individuals during the experiment to date. It appears that in the very dry conditions of 1996 and 1997 *Osmorhiza* was prevented from reproducing, even in the few sites where there were flowering transplants in 1995. However, in a few cases the seeds produced by those transplants did yield seedlings in 1996. *Lobelia* flowered in 1996 and two individuals set fruit (a total of 20 capsules between them), but no flowering individuals appeared in 1997. For *Caltha,* only the adult transplants flowered, but a high percentage did so (72% in 1996, with a total of 32 fruits on 47 flowering individuals; 70% in 1997, with a total of 42 fruits

Table 4. Number of quadrats with reproducing individuals, total number of fruits produced 1996–7, and presence/absence of second generation, i.e., seedlings from seeds dispersed by introduced material.

Species	# Quadrats	# Fruits	Second Generation?
Aquilegia	10	54	no
Sanguinaria	10	31	yes
Hedyotis	14	800	yes
Aralia	0	0	no
Caltha	19	263	no
Saxifraga	4	126	no
Lobelia	1	14	no
Osmorhiza	10	310	yes

on 33 flowering individuals). *Saxifraga* showed a high percentage of adult transplants flowering (89% in 1996, 100% of 2 individuals in 1997), and essentially all flowers matured fruit though no seedlings have appeared at these sites. *Sanguinaria* seedlings and adult transplants showed similar proportions of flowering individuals in both years (about 16% in 1996, around 50% in 1997), with a total of 31 fruits over those two years. *Aquilegia* showed increasing proportions of flowering individuals (12% of seedling transplants in 1996, 78% in 1997), but negligible fruit production until 1997 (22 fruits noted).

Hedyotis showed the most vigorous reproduction in both years although adult transplants showed only one flowering individual, in 1997. The individuals appearing from seeds sown on the prepared plots flowered starting in 1996 (83%) and continued in 1997 at a lower rate (21%). Seedling transplants flowered vig-

Table 5. Percentage of individuals per treatment flowering in 1996. Treatments are described in Materials and Methods. [1] Based on one individual.

Species	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Aquilegia	0	0	12.5	37.2
Sanguinaria	0	0	15.8	16.1
Hedyotis	100[1]	83	93.8	0
Aralia	0	0	0	0
Caltha	0	0	0	71.5
Saxifraga	0	0	33.3	88.9
Lobelia	0	0	100	42.9
Osmorhiza	0	0	0	0

Table 6. Percentage of individuals per treatment flowering in 1997. Treatments are described in Materials and Methods. [1] Based on one individual; [2] Based on two individuals.

Species	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Aquilegia	0	0	77.8	33.3
Sanguinaria	0	0	47.8	57.9
Hedyotis	0	21.3	13.3	100[1]
Aralia	0	0	0	0
Caltha	0	0	0	69.8
Saxifraga	0	0	0	100[2]
Lobelia	0	0	0	0
Osmorhiza	0	0	0	0

orously in 1996 (94%), but less so in 1997 (13%). However, this lower proportion of flowering reflects the fact that there were more individuals present on these sites (58 in 1997 versus 16 in 1996). The increase apparently was largely due to the establishment of new seedlings from seeds dispersed the previous year. These seedlings were all very small and did not flower, but persisted through the growing season.

Table 4 summarizes the number of quadrats with reproducing individuals per species for 1996–97, the estimated number of fruits for those two years, and the presence or absence of seedlings from dispersed seeds (a "second generation"). As of the 1997 growing season, only *Sanguinaria* and *Hedyotis* showed quadrats with both mature flowering individuals and new seedlings present. The few *Osmorhiza* seedlings derived from 1995 flowering transplants did not appear to be of flowering size yet.

DISCUSSION

Plant reintroductions are considered an important tool in the work of plant conservation, but there remain many unanswered questions about techniques for reintroduction and the biology that underlies them (Allen 1994).

The present experiment, still in progress, reinforces previous work in which reintroduction by seed has shown very low rates of success in establishment of new populations at even the most basic definition of "success," that is, presence of individuals of the species. The rates reported here, ranging from 0% to about 6%, are similar to rates reported in a series of experiments by

Richard Primack for many species in eastern Massachusetts (Primack 1996; Primack and Miao 1992). In one set of experiments with annuals and perennials, out of 221 quadrats, a single population of an annual species and two populations of a perennial species survived to reproduce and disperse seeds. Those experiments showed short-lived appearances of seedlings, as reported here, but the passage of time saw these "populations" extinguished.

Similar experiments in quite different habitats have shown comparable results. For example, recruitment from seeds of 8 different species sown in the field in the semi-arid Rio Grande Valley ranged from 11% to less than 1%, except for a single species (Vora 1992), despite several steps taken to improve the chances for success both by site preparation and after-care. Vasseur and Gagnon (1994) reported emergence rates in their experiment with *Allium tricoccum* to vary widely from about 3% to 90%, but they did not provide data on the survival of recruits from seeds after germination. Barkham (1992) reported seedling survivorship of *Narcissus* sown in the field as "rapidly declining to zero." In the New England area, repeated attempts have been made to establish new individuals and new populations of the endangered perennial *Potentilla robbinsiana* in the White Mountains of New Hampshire (unpubl. report). Some success has been achieved using transplants of adults, but sowing seed in a variety of locations has had no success whatever.

There can be many reasons for this kind of result. Many plants need some kind of disturbance to establish successfully. Thus the "safe site" at which the propagule must arrive is not only a particular locale, but a place in time as well. Site suitability is not only a function of characteristics such as soil composition and the presence of competitors and predators, but also the interaction of these with temperature and precipitation conditions.

The work of David Foster and others (e.g., Foster and Boose 1992; Whitney and Foster 1988) has shown how, on an ecological time scale—from a few decades to a few centuries—an ecosystem is likely to experience recurrent though unpredictable major disturbances that may have important consequences for successional processes, including the establishment or extermination of populations of plant species. In New England, a prime example of such a disturbance is hurricanes, whose effects on northern hardwood forest systems have been studied now for some years. In light of this work, Primack (1996) extended his experiments to an area artificially disturbed to recreate some of the features of a hurricane disturbance. The radically altered light and temperature regimes of such a disturbance can enhance or trigger seed germination, and the removal of competing vegetation and the exposure of mineral soil might be expected to foster a flush of germinations. In the event, no such response was seen for 15 perennial species sown on the experimental site, suggesting that other factors besides, or in addition to, disturbance affect establishment.

The present experiment follows on from these, with a change in the site preparation, and the addition of a comparison with transplants of two different sizes. Seeds were sown in some quadrats with no preparation, this being the most common fate for the seeds of these species. This unprepared sowing was compared, however, with small-scale site preparation, which imitated in its effects a very common type of disturbance, the uprooting of a tree or sapling (Runkle 1985). A disturbance on this scale will not materially alter the radiation regime of a microsite, but will expose mineral soil and provide a site largely free from root competition in the upper soil layers, and from shading by plants nearby.

This level of site preparation may have some positive effect on the rate of emergence of seedlings, but in these experiments it had no discernible effect on longer-term presence on a site. Similar results are reported from a series of experiments with a different set of species in sandhill conifer forests of South Carolina (Primack and Walker, unpubl.), in which in addition to disturbance, site preparation included a nutrient pulse. From the Cape Cod area as well, attempts to create new populations of the endangered Sandplains Gerardia, *Gerardia acuta,* in grassland sandplains, are enhanced by a carefully timed program of mowing and burning (P. Somers, unpubl. data). Preliminary results suggest that in this very different biological system as well, local disturbance does enhance the emergence of seedlings, while fertilizer does not. The long-term consequences for survivorship remain to be seen.

In fact, the point made by Grubb (1977) that the "regeneration niche" is more than a good site for germination is quite apposite here. Germination is the first and essential condition for a new colonization event by seed, but the conditions must also be conducive to the survival of new seedlings, so that some reach the next period of dormancy in good enough condition to survive the winter. For a species that takes some years to reach reproductive maturity, this second stage of recruitment lasts through several growing seasons, with their attendant risks of adverse climatic conditions, herbivory, and disease. The length of this "probationary period" will vary with conditions and with the species. In the present study, *Hedyotis* was a species that flowered in its first or second year, but seedlings of the other species still have not reached reproductive size.

These experiments suggest that establishment of new populations of these species may be a very rare event, and thus successful human reintroduction by seed will also be rare. There is a need for more exploration of the biology of the particular species involved, which may lead to the specification both of dispersal conditions and of horticultural practices that could protect the seedlings that do emerge. Some species in this experiment, with a single input of seeds, performed better than others. The interaction between seed-colonist and the environment at the time of arrival means that performances are likely to differ from year to year (as seen in Vasseur and Gagnon 1994), and that both abiotic and biotic conditions, including competition with other species, are important factors (Berger 1993). It is clear in any case that, given the low percentage of emergence for most species in the field, reintroduction by seed requires the use of a large number of seeds and probably more than one year. The number of propagules used (assuming that the supply is plentiful) will depend in part upon the ultimate population size deemed desirable for viability in the reintroduction site. What size is sufficient for "viability" is a subject of current research, though it is safe to say that generalizations are perilous at the moment, since regardless of the definition of viability used, there remain major areas of uncertainty that can only be resolved by longitudinal studies. In any case, we can only conjecture how resilient a population will be, given all possible disturbances over any particular stretch of time (is the target 50 years? 500 years?; Howald 1996; Menges 1991; Pavlik 1996).

The present experiments show (over the course of three years' data collection) rates of "establishment" (in a limited sense) from seed dispersal ranging from about 6% to far less than 1%, with an average around 1%. Using that figure, if the goal is a population of 50 individuals, one would use 5000 seeds. This large number of seeds would only grow larger if one's target population was, for example, 500, as suggested by some researchers, in order to provide a population that might be resilient to disturbance and environmental stochasticity over some length of time. In fact, several of the species in this study were introduced in numbers approaching this figure. In the short term, only two species might be said to be present in the numbers desired (*Hedyotis* and *Sanguinaria*), but they are present not in one population but several.

This raises another design consideration that has entered the design of plant reintroduction plans only recently, that of metapopulation structure (McEachern et al. 1994). Metapopulation theory has formalized the insight that species often exist in populations of populations, patchy concentrations in the landscape at varying distances from each other, joined by gene flow in various forms at a low rate. It is thought that this structuring of a species' population provides resilience to disturbance not provided even by a very large single population. The appropriate size and placement of introduced populations or subpopulations is not only a matter of "distributing the risk" across varying habitats but also of ensuring that there are enough individuals to support cross-pollination when the species is not self-compatible. In the case of the species that have shown the most flowering success in this study (*Sanguinaria, Hedyotis*), the fact that they are pollinated by generalist pollinators may have promoted fruiting success, while *Aquilegia,* which showed good flowering but relatively poor fruit set in both years, may have been pollinator-limited in the areas in which the plants occurred, being too widely spaced to attract hummingbirds. In the Hammond Woods, the flowering individuals were widely separated, and there were no other stations of the species present. In the Middlesex Fells, *Aquilegia* did occur naturally, and it appears that fruit set was somewhat higher there, but further monitoring would be necessary to establish trends. The attraction of appropriate pollinators remains a critical factor for the success of introduced species that require animal or insect pollination vectors.

In the design of a reintroduced population, especially when site characterization may be approximate or missing some critical factor, a plan which disperses the reintroduced propagules in more than one site is an attempt to build in the resilience that the metapopulation may provide. In addition, the reintroduction does not risk all its resources on one or a few sites' viability at the time of reintroduction, thus "sampling" the landscape for a wider range of safe sites (Harper 1977). This assumes as part of the reintroduction plan that the multiple sites of introduction will show varying rates of success and persistence, as in any colonization beyond a population's area of concentration (Prince and Carter 1985; Prince et al. 1985). Despite the best efforts of trained ecologists, it may be difficult to identify the critical environmental factors that allow or prevent the establishment of new populations. Selecting several or many sites for initial attempts increases the chance that at least some will be successful. The sites that show initial promise can then become target sites for more extensive reintroduction efforts.

This raises another point, however, which is relevant to reintroduction efforts: the "sampling" of the topography of time as well as space. The strategy of very large inputs at one point in time is convenient in the construction of emergency rescue plans for threatened species, and for the creation of research programs for doctoral theses, but it may be well to structure reintroductions by seed to include the axis of time in the population structure. Thus, a particular *Hedyotis* or *Sanguinaria* individual may disperse at most two dozen seeds in a year. Perennials, however, are iteroparous, that is, they will under most conditions disperse seeds year after year. Thus their dispersal "shadow" will take into account the interactions of site with climate. The plant conservationist may well wish to do the same, thus adding repeated dispersals to the same sites over the course of several years. In this case, the 50 or 500 plants in the final target metapopulation would not be the result of a single dispersal of 5000 or 50,000 seeds, but of a smaller annual deposit continued for several years.

The experiments reported here, however, show that where transplantable material is available for use, one is much more likely to achieve success in a reintroduction by means of transplanting of individuals past the seedling stage. This is supported by the results of experiments with *Potentilla robbinsiana* mentioned earlier. As discussed in the introduction to this paper, there are important advantages to the use of seeds as the method of reintroduction. Nevertheless, success rates are generally much higher with established individuals than with seeds. The number of individuals required is smaller than the number of seeds, though the cost per individual is higher: to reach a population of

50 to 500, with a success rate of 25% (plausible, based on the results reported here), would require an input of 200 to 2000 individuals, again probably distributed over multiple sites. The higher rate of success per propagule makes it more possible to "structure" something like a metapopulation. With even as few as four individuals per quadrat, a series of 100 quadrats spread across a target location could produce several populations separated by enough distance to provide some protection against disturbance, but close enough for occasional long-distance seed dispersal or exchange of pollen. In the present experiments, sites were usually clustered, with three or four replicates of the experimental unit in one general area, separated by no more than 10 meters. The next experimental site was from 50 to 500 meters distant. In cases like *Caltha* or *Sanguinaria* where there were multiple occupied quadrats, the result in effect was a metapopulation.

Yet there is still the question of the definition of success. For these experiments, success cannot be determined as yet, because for these perennial species, time to reproductive maturity may be as much as five years or more. Thus individuals established from seed, or from the transplant of young plants, will not begin to reproduce for some time, if they survive. Even for reproducing individuals, though, the monitoring time must be on the order of a decade or more. This is in part because of the dormancy of seeds and in part because of the relatively small number of seeds dispersed per plant per year. If the locale is suitable for the species (as may be deduced prima facie from the survival and reproduction of transplants), it may not always be suitable for seedlings, as demonstrated by these same experiments. Thus if a *Sanguinaria* is dispersing 15 seeds per year, with a success rate of perhaps 6% it may take 2–5 years for these seeds to result in new seedlings that persist for more than a year or two. The need for a long time-horizon is emphasized by the attempts to create new populations of the endangered orchid, Small-whorled Pogonia (*Isotria medeoloides*) using wild-collected adult transplants (Brumback and Fyler 1996). While there was a good rate of survival for the first 5 years after the transplants, after 8 years virtually all plants had died out and the remaining plants were no longer in flower.

The experiment reported here suggests that a reintroduction program should include reintroduction by more than one method since, as argued above, reintroduction by seed and by transplant each has its advantages. Further, the reintroduction should be designed when possible to provide new information about the biology of the species under consideration. Although the species used in this study are common features of the New England flora, there is little information available about their population biology and demography, about the applicability of the metapopulation model to them, or about the frequency and conditions under which new populations arise. Finally, it is clear that given the numerous hurdles that a reintroduction effort may encounter, protection of existing populations remains the fundamental ingredient in any conservation plan (Falk 1991; Lesica and Allendorf 1992), and "mitigation" of habitats even with species that are not threatened should be done with caution. If attempts are made to create new populations, these attempts should involve examining multiple sites and methods over a period of years to increase the chances of success.

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