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BOSTON UNIVERSITY
GRADUATE SCHOOL OF ARTS AND SCIENCES

Dissertation

THE EXPERIMENTAL ECOLOGY OF PLANT REINTRODUCTIONS

by

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THE EXPERIMENTAL ECOLOGY OF PLANT REINTRODUCTIONS

(Order No.)

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ABSTRACT

To deal with the accelerating, worldwide loss of plant species, conservation biology investigates species loss and effective methods for preserving species diversity. This thesis reports on three experiments in plant conservation biology, conducted in eastern Massachusetts.

1. Starting in 1993, 8 perennial species were introduced by 4 methods into experimental quadrats. The methods were: transplanting seedlings; transplanting mature plants; and sowing seeds on sites dug up with a shovel and on undisturbed sites. There was a low rate of success per seed sown (0.47%) and few of the resulting plants have reproduced. Transplanting of mature plants shows more success: 23% of the transplants survived, and plants on 25% of the quadrats reproduced. Thus, the most reliable method of establishing new populations of woodland perennials is by transplanting mature plants.

2. Garlic mustard, introduced by seeds, was used to examine the relative importance of genotype and site characteristics in colonization success. These

experiments also provide an indication of the maximum rates of success to be expected from species introduction by seed.

Only 6.5% of the seeds produced seedlings. Genotypes did not differ significantly in rates of germination or reproduction; site characteristics were the determining factors in establishment success. The experiments provided useful demographic information such as rates of survival to flowering, average seed production, and rates of extinction of new populations.

3. Finally, the thesis reports on an experimental attempt to cause local extinctions of wild populations of garlic mustard. Understanding the process of population extinction is crucial to preventing species extinction and is a poorly understood aspect of population biology. Control populations were compared to experimental populations in which all reproducing individuals were removed for 3 years. Twenty-one percent of the experimental populations went extinct, in contrast to only 5% of the controls; the populations that went extinct were all initially small. Fifty-two percent of experimental populations were in decline at the end of the study, as compared with only 3% of the controls.

The thesis results are of interest for conservation biology, in the design of species reintroductions, and in the control of aggressive weeds. Finally, the thesis suggests several lines of new research in plant ecology.

Preface

The four papers constituting this thesis form a thematic series, exploring aspects of plant demography of special interest to conservation biology — the birth and death of populations. Each chapter has an applied and a theoretical aspect, since the questions at their core arose in the context of plant conservation, but concern matters of plant population biology that are not widely studied.

When I conducted research on changes in the flora of the Middlesex Fells Reservation, I saw species turnover — that is, species extinction and species colonization — on the scale of a century. Yet in most cases this takes place as a series of population extinctions, a series of population originations, and the frequency of these must be much higher than once in a century— but how often do populations arise, or disappear, in fact? The experiments reported here attempted to make some quantitative sense of this question, while exploring techniques of interest for the reintroduction of species of interest.

Chapter 1 looks at the reintroduction — i.e. the experimental origination of populations — of several perennial species chosen from the New England flora. These experiments showed that for species reintroductions, the more expensive technique of transplantation of wild-collected or propagated plants is the most reliable. It also suggests, however, that the founding of a new population in the wild may be a rather rare event, which is of interest in understanding the demography and life-history of such species. Chapters 2 and 3 contrast these results with studies of reintroduction by seed of a "weed" species currently spreading rapidly in the study area. Garlic mustard populations were definitely easier to establish by seed than were the woodland perennials, yet even here the rate of success is less than 7%. In addition to establishing this "upper limit" of success that can be expected for reintroductions by seed, the initiation of garlic mustard populations provided valuable data on the development and behavior of newly-founded populations of the species. Garlic mustard may also present an example of a species that has different life-histories in different parts of its current range, and this opens the way to further interesting research on the species' evolution during migration

Chapter 4 then uses this model species to explore the process of population extinction, which is a fundamental feature of species persistence in the landscape. It makes sense that smaller populations of a species are probably more vulnerable than larger populations, but is size the most important factor? Garlic mustard populations were hard to extinguish at any size, and the likely reasons are relevant for the conservation of other species in temperate forests. For species which form a seed-bank, the disadvantages of small population size may be outweighed by the effects of population age: in effect, a population may be augmented by migration from other populations in space, but also from "migrations in time" through the germination of buried seeds from previous years.

In addition to the information gained about plant reintroductions, then, these experiments suggest that for many species in this flora both colonization and extinction may be surprisingly rare events, and thus provide a little more insight into rates and processes of floristic change.

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Chapter 1

Rates of success in the reintroduction by four methods of several perennial plant species in eastern Massachusetts.

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" (Stevens 1998; Brumback and Merhoff 1996); 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 which alter species' environment 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 (Harris and Silva-Lopez 1992, Brothers and Spingarn 1992, Bierregaard *et al.* 1992,Saunders *et al.* 1991, Kapos 1989, Wilcove 1987, Diamond *et al.* 1987). 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, or by the local extinction of dispersers, or by the introduction of weedy species which 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 (Kutner and Morse 1996, Bazzaz 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 will often not be able naturally to migrate 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 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, Robinson et al 1996, Kattan et al. 1994, Turner et al. 1994, Matlack 1994, Holland and Sorrie 1989, Peterken and Jones 1987, Peterken and Game 1984). 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 1993).

This protection is necessary, but probably not sufficient as a conservation strategy (Pressey 1994, Falk and Olwell 1992). It can prevent further direct disturbance of a site, or the effects of overexploitation of the site or the 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 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 extinction of populations (White 1996, Holsinger 1993, Fiedler and Ahouse 1992, Norton 1991, Grubb 1977).

Increasingly, *in situ* management includes the creation of new populations of taxa, or the augmentation of existing populations (Primack 1996, Hamilton

1994, Falk 1992), despite some concerns about implications of the practice, and the indifferent success of many programs (Fahselt 1988, Hall 1987). 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 (Falk et al. 1996). This flush of reintroduction activity has opened up many areas of research both on the basic biology of the species under consideration (Primack 1996, Schemske *et al.* 1994), and on many aspects of technique which 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" (Havens 1998, Guerrant 1996, Husband and Barrett 1996, Primack 1996, Guerrant 1992). 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 vs propagated material for introduction, and the extent and nature of appropriate site preparation and after-care.

Choosing material for reintroductions: Seeds or plants?

Because the germination and seedling stages of growth are periods of high vulnerability and high mortality (Harper 1977), and because rare plant material must often be used with great care and economy, the majority of reintroductions have proceeded by the propagation of plants *ex situ*, and then transplanting into the target site (Guerrant 1996, Hall 1987). 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* (Ray and Brown 1995, McEachern *et al.* 1994, De Mauro 1994, Vora 1992, Barkham 1992, Rochefort and Gibbons 1992, Cavers and Harper 1967) 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 which survive provide evidence that the site is suitable for the species, and its absence there may be due to lack of dispersal (Lee 1993, Primack and Miao 1992, Barkham 1992, Hughes and Fahey 1988, Howe 1984).

The logistical demands of transplanting are such that most reintroductions by this method focus on one or a few species, rather than on a species assembly. For some grassland species, at least when locally abundant, transplantation by sod makes possible the translocation of substantial portions of a community surrounding the target species (Revel 1993). In a project conducted in an area near Calgary, Alberta, parts of which are under active development, sod strips of rough fescue grassland were moved to areas safe from development. In the course of this experiment, several herbaceous species have appeared in the new areas, apparently from the remnant "seed bank" in the transplanted sods.

Yet even when it seems feasible from a logistical point of view, transplanting has inherent risks as well, since there can be significant trauma during the transplant, and 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 (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, Vora calculated that 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 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 limiting medium so that the production of photosynthetic tissue is decisive for survival in the face of above-ground competition or litter-fall (Roché *et al.* 1997, Larcher 1995).

Seeds when collected 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, which in turn 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 (Fenster and Dudash 1994, Jacobson *et al.* 1994, Dole and Sun 1992). It is easier to introduce multiple populations, and introduce multiple genotypes by means of seed, than by means of transplanted material. Another important concern is the density of the population, and in this case 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, and 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) provide 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 and if necessary "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. In practice, 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, but this is not always possible. In that case, some surrogate measures of site suitability may be required; a common example is the use of indicator species, species whose occurrance is highly correlated with the occurrance of the target species.

Initial experiments on which this study is based used little in the way of site preparation (see for a summary 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, since 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 (Bazzaz 1996, Barkham 1992).

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 (Rochefort et al 1992, Jackson et al. 1990) or screened with various mechanisms (McChesney *et al*, 1992) 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 Vasseur and Gagnon 1994, Watson et al 1994, Gibbons 1992, Vora 1992). 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, which is 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 fertlizers to facilitate rapid growth (Doerr and Redente 1983). A fire regime may be instituted, which can remove above-ground competition, remove thatch or litter which may prevent seeds' reaching the soil, and can provide a nutrient pulse (Gordon 1996, Pavlik et al

1993) Finally, some seeds may require protection against seed-predators or herbivory on the emergent seedlings (Primack and Drayton 1997, Bainbridge *et al.* 1995, Chambers and MacMahon 1994, Barkham 1992).

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 (Jackson *et al.* 1990, Bainbridge and Virginia 1990, Doerr and Redente 1983). Sites can be weeded (Jackson et al 1990) or clipped (Gordon 1996, Danielson 1995) 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, for example in order 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 new, 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 in terms of biomass (Shaw 1996, Doerr and Redente 1983), per cent cover (Jackson et al 1990), or presence-absence (Revel 1993 , Packard 1990).

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 non-endangered status as a result of a restoration plan (Pavlik 1996). In part this statement can be explained by the length of time often needed in order 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 which require further research. The recent history of reintroduction work shows a swift development of understanding of the challenges facing such conservation work, as researchers attempted various approaches, developed criteria for assessing results, and collected results from a range of different studies and species.

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?

Methods

Starting in 1993, we identified eight perennial species which are not present but formerly attested, or whose distributions are highly restricted, in two conservation areas in the Boston area. None of these species is endangered or threatened in Massachusetts, but their ranges appear 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 population's distribution is shrinking, so that its (presumed) genetic diversity is diminishing, or if there are 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 attempting 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 marylandica*)
Spikenard (*Aralia racemosa*)
Cardinal flower (*Lobelia cardinalis*)
Sweet Cicely (*Osmorhiza claytoni*)
Bluets (*Hedyotis caerulea*)

Marsh Marigold (*Caltha palustris* L., Ranunculaceae). This species of slow-moving or standing fresh water is found throughout New England. Occurs in restricted distribution in Hammond Woods, and in the Middlesex Fells, locally abundant. Hollow stems bear cordate leaves, and in early spring multiple axillary or terminal flowers each with 5-9 bright yellow sepals. Pollinators include flies and solitary and bumble-bees. Multiple (2-12) free follicles when dry dehisce to drop the seeds around the base of the plant; since the plants often are standing in or near water, secondary dispersal by water is common.

Columbine (*Aquilegia canadensis* L., Ranunculaceae). Widespread in New England, most often in dry woods and on outcrops or ledges. No longer occurs in the Hammond Woods. In the Middlesex Fells, it occurs in widely scattered patches, most of a few individuals. The erect stems bear compound, lobed leaves, and terminal nodding flowers. The regular red and yellow flowers, with simple sepals, but spurred petals, are humming-bird pollinated, but also visited by bumble-bees. The seeds mature in (4-6) follicles, which when dry drop the many small seeds to the ground.

Bloodroot (*Sanguinaria canadensis* L.) A species of rich woods, widespread in New England. Occurs in the Middlesex Fells in three widely separated patches, one large (over 200 individuals), the other two much smaller (25 individuals or fewer). Deeply-lobed leaves arise in early spring from the perennial rhizome, which over time may branch and give rise to several ramets. The single, white, many-petalled flower terminates a scape which often elongates through the unfolding leaf. The fruit is an elongate capsule bearing a few to 18 arillate seeds, which fall to the ground upon the capsule's dehiscence, and are often removed by ants.

Early Saxifrage (*Saxifraga virginiensis* Michx., Saxifragaceae). A widespread herb of open woods and ledges. Occurs in the Middlesex Fells in two large populations in the northeast region of the western half of the reserve. A basal rosette of ovate leaves gives rise in April and May to a scape topped with a raceme of small, 5-merous, white-petalled flowers. Multiple minute seeds are dispersed by wind and gravity from dry capsules.

Spikenard (*Aralia racemosa*L, Araliaceae). A large (often > 1 m in height) herb of rich woods and margins, widespread in New England. Does not occur in the Hammond Woods. One population of 6 individuals occurs in the Middlesex Fells. The pinnately compound leaves arise basally, and below their canopy appears in mid-summer the cylindrical panicle of white flowers in small umbels. Fruit is a small, dark-purple berry, eaten by song-birds and small mammals (Martin et al. 1951).

Cardinal flower (*Lobelia cardinalis* L., Campanulaceae). A tall (50-150 cm) herb of streams and riverbanks, frequent in New England. Cardinal flower does not occur in the Middlesex Fells, though one individual is reported from a watercourse adjacent to the western margin, approx. 2 km from the experimental site. It is formerly reported from the Hammond Woods, but did not occur there at the time of this study. Terminal racemes of scarlet, irregular flowers are borne from July through September, pollinated by hummingbirds and bees. The small seeds fall from dry capsules into late October, and are often secondarily dispersed by water.

Sweet Cicely (*Osmorhiza claytoni* (Michx.) C.B. Clarke, Apiaceae). A widespread plant of rich woods, with fernlike, ternately compound leaves. Does not occur in the Hammond Woods. Occurs in two disjunct populations in the Middlesex Fells. Umbels of small white flowers appear in May and June. Fruits are enlongated, ribbed, and somewhat hairy, so that they are probably at least secondarily dispersed by attaching to animals' fur (or clothes).

Bluets (*Hedyotis caerulea* (L.) Hook. Rubiaceae). Common or occasional throughout New England, in moist meadows and margins. Bluets do not occur in the Hammond Woods; they occur in small, very widely scattered populations in the Middlesex Fells. Forms low clumps or small mats of spatulate leaves, spreading by rhizome as well as seed. Small, lavender, heterostylic flowers appear in May through July; small seeds dropped from dry capsules in late summer.

Sources of plant material

Seeds were collected in 1994 for all species, 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 1995, when possible from populations in the area which were of sufficient size to allow 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 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 hectares in area. It comprises a mixture of deciduous woods, swamps, parking areas, meadows, ledges, and roads. The Middlesex Fells is approximately 800 hectares 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 current occurs in their nearest populations, including degree of canopy closure, soil moisture, and co-occurring, indicator species. In each case, the experimental species was either known to have been present at or near the area in the past (e.g. *Lobelia cardinalis*), or to be present at substantially similar sites now, but in very restricted distribution within the reserves.

In each case, apparently suitable habitat exists in these conservation areas, so that reasons for decline in populations are not known. A first hypothesis is that dispersal has limited the extent of occurrance. Further, human use of the areas may well have contributed to reduced dispersal (see Drayton & Primack 1996 and references there). Therefore, the design provided several useful kinds of information about the sites being explored: transplants that survived and seemed to establish well provide evidence that the site is suitable for the species, at least within the time frame of the study to date. Establishment of seedlings from seed provides 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 1994. Four treatments were used (Figure 1-1);one quadrat at each site was assigned at each site randomly to each treatment; the number of quadrats for each treatment for each species is shown in Table 1-1. The treatments were as follows:

Treatment 1. Seeds. A known number of seeds were sown directly on the quadrat in 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 & 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 [a] were sown in 1994;

Treatment 3. Seedlings. Seedlings were transplanted onto the assigned quadrat in 1995, within a radius of .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, owing to unusually dry conditions.

Treatment 4. Adults. Adult plants were transplanted into the assigned quadrat in 1995, within a radius of .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, owing to unusually dry conditions. For treatments 3 and 4, the same number of individuals (seedlings and adults) were 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 1-1.

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

- numbers 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.

After-treatment. 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. In the first place, are individuals of the subject species present on any of the experimental sites? In the second place, 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? 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. Transplanted 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.

Numbers of quadrats occupied

There were a total of 596 quadrats of all species, 149 per treatment (See Tables 1-1 and 1-2). Of these, by the end of the period here studied, there were 112 occupied by the subject species, thus an overall rate of 18.8%. Of these, 87 (78%) were reintroductions by transplant, and 15 (22%) were by seed. A χ^2 test shows these differences to be highly significant ($p < .001$).

Although the values vary from 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.

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 (Figs 2a-h). For *Osmorhiza,* in 1997 no prepared quadrats (Trt. 2) were occupied, while six of the unprepared quadrats (Trt. 1) had individuals on them. In 1996, three of the *Saxifraga* prepared quadrats (Trt2) 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 are four occupied quadrats for each of the two "seed" treatments by 1997. The unprepared quadrats show a significantly higher number of seedlings present in 1997; this reverses the situation in previous years. For *Hedyotis,* the prepared quadrats show a significantly higher rate of occupancy in all years; only prepared *Aralia* quadrats show 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 quadrats planted with mature plants were still occupied by 1997 than quadrats planted with seedlings (Figures 1-2a-h). The advantage was most marked for *Caltha, Aquilegia,* and *Aralia.*, all 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 adult quadrats were occupied, and 7 seedling quadrats. In one case, *Hedyotis,* there was the opposite result, with seedlings occupying significantly 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* were found.

Rates of success per propagule

Overall, 27,800 seeds were introduced on the experimental quadrats (half on prepared quadrats, half on unprepared), and 1312 transplanted individuals (including both young and mature plants). The rates of success per propagule introduced varied widely (Table 1-3), but in general they mirror the results for rates of quadrat establishment, in that 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 22.9% of the 1312 transplants (including both seedlings and plants) surviving to 1997. Species differed in the relative rates of success, with

Sanguinaria showing the least spread between seed treatments (about 4.5% for the two seed treatments) and transplants (about 44%); most species showed rates of establishment by transplants from seed at less than 1%, signifcantly less than rates by transplant. *Aquilegia* showed no individuals from seed present in 1997, but a survival rate of 9.7% for seedling transplants and 18.8% for adults (these rates significantly different). *Aralia* showed survival rates of 0.042% for the seed treatments, and 13.8% for the transplant treatements. *Caltha* showed few individuals from seed (0.16% and 0.042% for treatments 1 and 2 respectively), but 5.2% for seedlings, and 51.4% for adult transplants. In the case of *Lobelia* and *Caltha,* the sites necessarily were near moving water, and 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. These sizes are not defined in the literature, so far as we can determine, and this fact of life-history means that monitoring introduced populations must be a long-term effort, unpredictably long.

In the case of introduced material, however, initial results can be reported. We report all instances of individuals flowering in 1996 (Table 1-5) and 1997 (Table 1-6). 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, and in a few cases the seeds produced by those tranplants yielded 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 tranplants flowered, but a high percentage did so (71.5% in 1996, with a total of 11 fruits, on 47 flowering individuals, 69.8% in 1997 with a total of 42 fruits on 33 flowering individuals). *Saxifraga* showed a high percentage of adult transplants flowering (88.9% in 1996, 100% of 2 individuals in 1997), and essentially all flowers matured fruit, but no seedlings have appeared at these sites. *Sanguinaria* seedling 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(e.g. 12.5% of seedling transplants in 1996, 77.8% 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, at a lower rate, in 1997 (21.3%).

Seedling tranplants flowered vigorously in 1996 (93.8%), but less so in 1997 (13.3%). However, this lower proportion of flowering reflects the fact that there were more individuals present on these sites (58 in 1997 vs 16 in 1996). The increase apparently is 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 1-4 summarizes the number of quadrats with reproducing individuals per species for 1996-7, the estimated number of fruits for those two years, and the presence or absence of seedlings from dispersed seeds (a "second generation"). Only *Sanguinaria* and *Hedyotis* at present (as of the 1997 growing season) show quadrats with both mature, flowering individuals and new seedlings present. The few *Osmorhiza* seedlings derived from 1995 flowering transplants do 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, 1994). In one set of experiments with annuals and perennials, a single population of an annual species, and two populations of a perennial species, survived to reproduce and disperse seeds, out of 221 quadrats. 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 show comparable results. For example, Vora reports that rates for 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) report emergence rates in their experiment with *Allium tricoccum* vary widely from about 3% to 90%, but they do not provide data on the survival of recruits from seeds after germination. Barkham (1992) reports seedling survivorship of *Narcissus* sown in the field "rapidly declining to zero."

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, since suitability is not only a function of site 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 which may have important consequences for succesional 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 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.

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 does expose mineral soil and provides 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 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, unpublished), in which in addition to disturbance, site preparation included a nutrient pulse. Preliminary results suggest that in this very different forest 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* is a species which flowers 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, such as dispersal conditions, and also of horticultural practices which 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 for example in Vasseur and Gagnon 1994), and both abiotic conditions, and biotic ones 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 over 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 which can only be resolved by longitudinal studies. In any case, we can only conjecture how resilient a population will be all possible disturbances over any particular stretch of time (is the target 50 years? 500 years?) (Pavlik 1996, Howald 1996, Menges 1991, Gilpin and Soulé 1986).

In any case, 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, a large number, which 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 apprpropiate size and placement of introduced populations or subpopulations is not only a matter of "distributing the risk" across varying habitat, 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 showed the most flowering success in this study (*Sanguinaria, Hedyotis*), the fact that they are pollinated by generalist pollinators may promote fruiting success, while *Aquilegia,* which showed good flowering in both years, but relatively poor fruit set, may be pollinator-limited in the areas in which the plants now occur, being too widely spaced to attract hummingbirds. In the Hammond Woods, the flowering individuals are widely separated, and there are no other stations of the species present. In the Middlesex Fells, *Aquilegia* does occur, and it appears that fruit set is somewhat higher there; but further monitoring will be necessary to establish trends. The attraction of appropriate pollinators remains a critical factor for the success of introduced species which require animal or insect pollination vectors.

In the design of a reintroduced population, especially when site characterization may be approximate, or miss some critical factor, a plan which disperses the reintroduced propagules in more than one site is an attempt to build in the resilience which 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 *et al.* 1985, Prince and Carter 1985).

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 5,000 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. 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, since 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 to 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, and the next experimental site from 50 to 500 meters distant. In cases like *Caltha* or *Sanguinaria* where there are multiple occupied quadrats, the result in effect is 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, so that 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, 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.

This experiment 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, 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 (Lesica and Allendorf 1992, Falk 1991), and "mitigation" of habitats even with species that are not threatened should be done with caution.

Tables

Table 1-1. Number of replicates of experimental design, number of seeds sown for treatments 1 and 2, and number of individuals transplanted for treatments 3 & 4.

Species	#replicates	#seeds sown per quadrat for treatments 1 and 2.	Total # seeds sown per species	# seedlings and older plants per quadrat for treatments 3 & 4	Total # of transplants
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

Table 1-2. Number of quadrats occupied in 1997, by species and treatment

Treatment	Seeds	Digging + seeds	Seedlings	Plants
Species				
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	14	9	28	54

Treatment	**Seeds**		**Dig + Seeds**		**Seedlings**		**Plants**	
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	1	1.25
Aralia	1	0.042	1	0.042	20	13.8	20	13.8
Caltha	4	0.16	1	0.042	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	3	3	4	4
Total for all species	60^a	0.43	69^a	0.5	181^b	28	109^b	16.6

Table 1-3. Number of 1997 survivors per treatment, and rates of survival per propagule in each category. Superscripts indicate values differing significantly by χ^2 test.

Table 1-4. 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

Table 1-5. Percentage of individuals flowering, 1996, per treatment

Treatment	Seeds	Dig & seeds	Seedlings	Adults
Species				
Aquilegia	0	0	12.5	37.2
Sanguinaria	0	0	15.8	16.1
Hedyotis	100 (1/1indiv.))	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 1-6. Percentage of individuals flowering, 1997, per treatment.

Treatment	Seeds	Dig & seeds	Seedlings	Adults
Species				
Aquilegia	0	0	77.8	33.3
Sanguinaria	0	0	47.8	57.9
Hedyotis	0	21.3	13.3	100 (1/1 individual)
Aralia	0	0	0	0
Caltha	0	0	0	69.8
Saxifraga	0	0	0	100 (2/2 indivs)
Lobelia	0	0	0	0
Osmorhiza	0	0	0	0

Figures

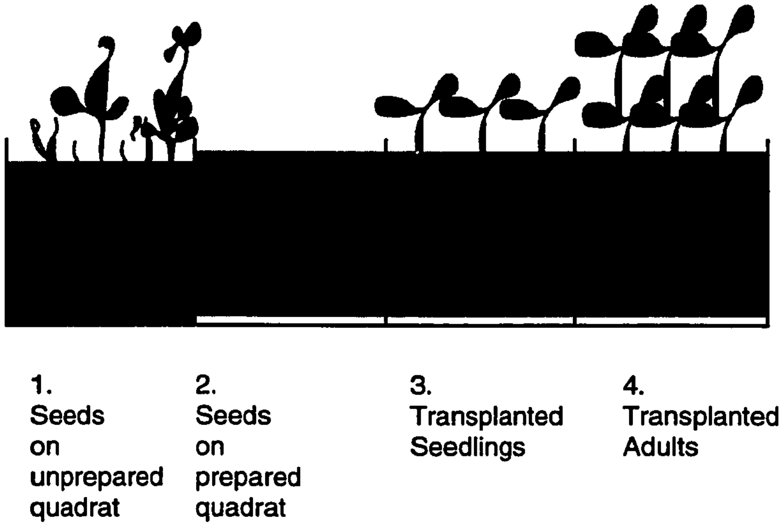


Figure 1-1. Schematic of the four experimental treatments: 1. seeds on unprepared quadrat; 2. seeds sown on prepared quadrat; 3. seedlings transplanted to quadrat; 4. adult plants transplanted to quadrat.

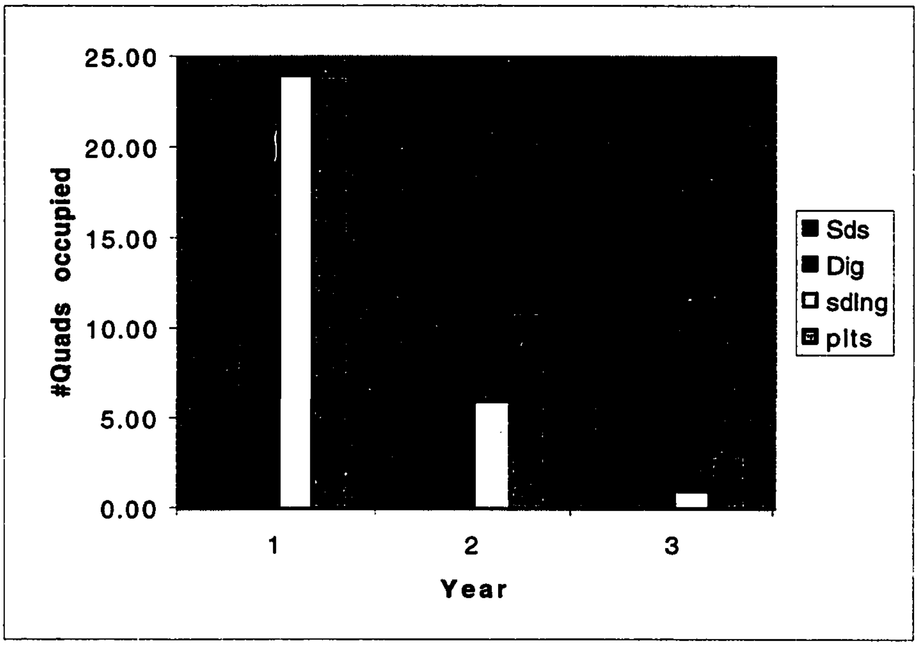


Figure 1-2a. Number of quadrats occupied per year, by treatment, for *Osmorhiza*.
Year 1 is 1995, Year 2 1996, Year 3 1997

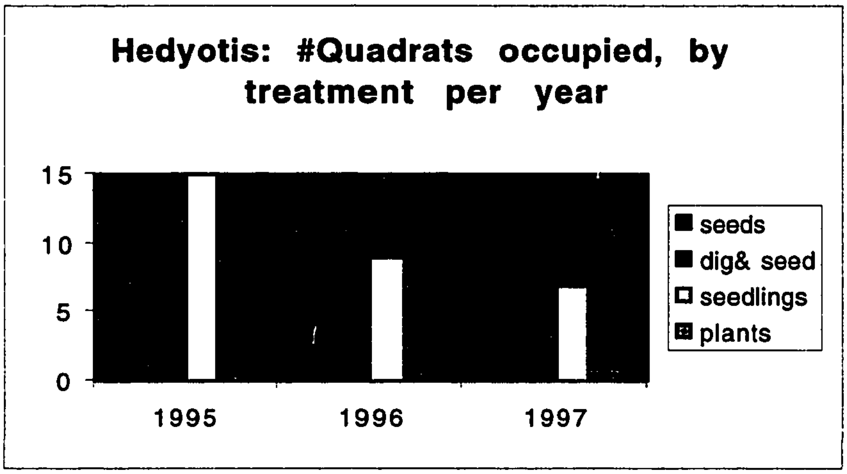


Figure 1-2b. Number of quadrats occupied per year, by treatment, for *Hedyotis*

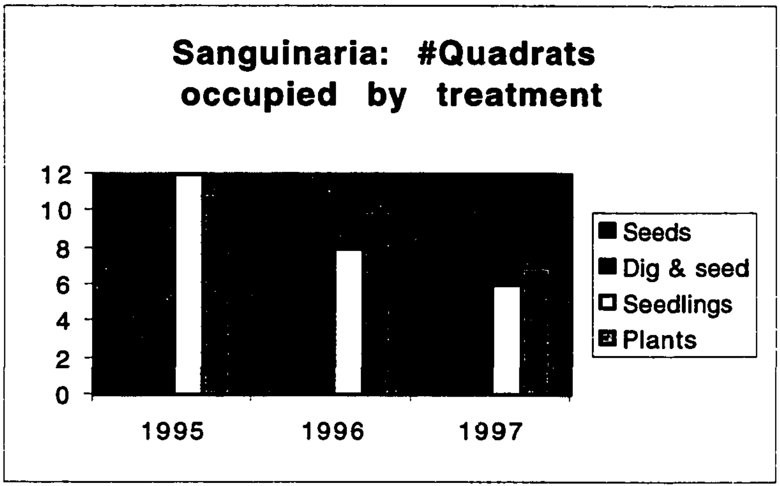


Figure 1-2c. Number of quadrats occupied per year, by treatment, for *Sanguinaria*.

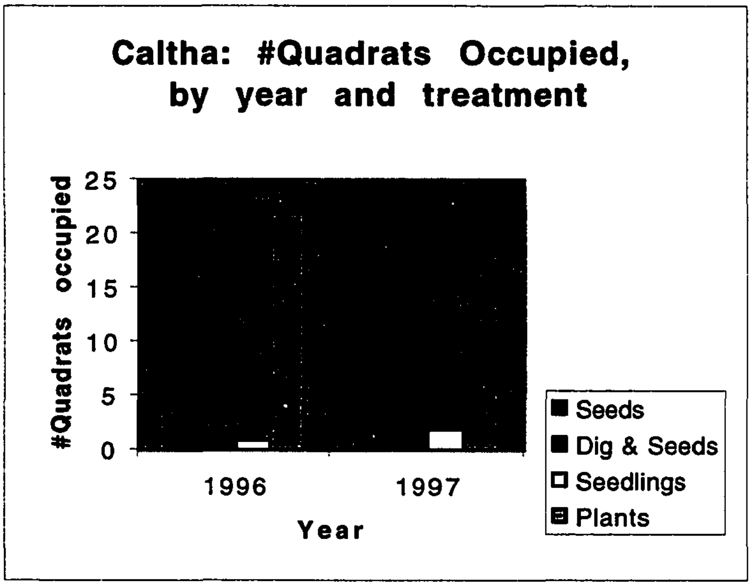


Figure 1-2d. Number of quadrats occupied per year, by treatment, for *Caltha.*

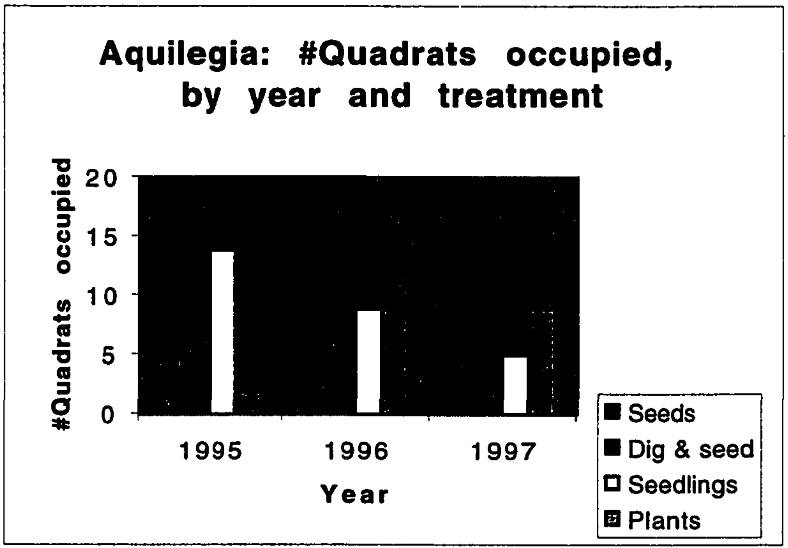


Figure 1-2e. Number of quadrats occupied per year, by treatment, for *Aquilegia*

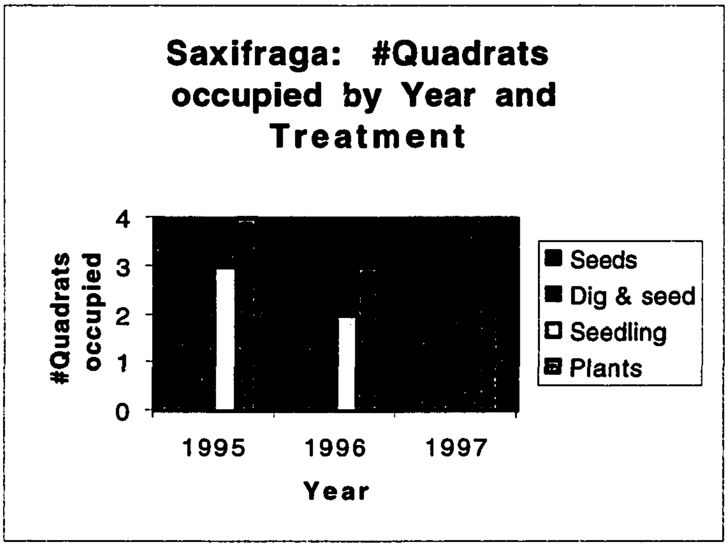


Figure 1-2f. Number of quadrats occupied per year, by treatment, for *Saxifraga.*

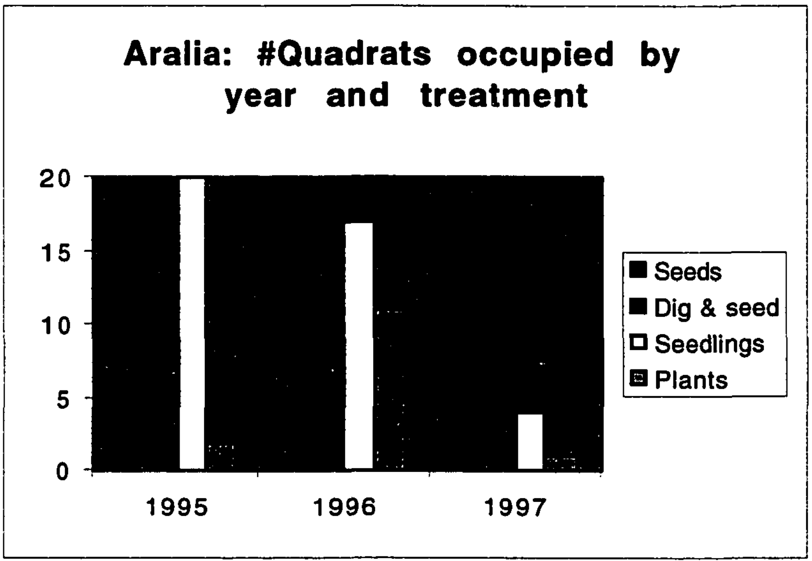


Figure 1-2g. Number of quadrats occupied per year, by treatment, for *Aralia*.

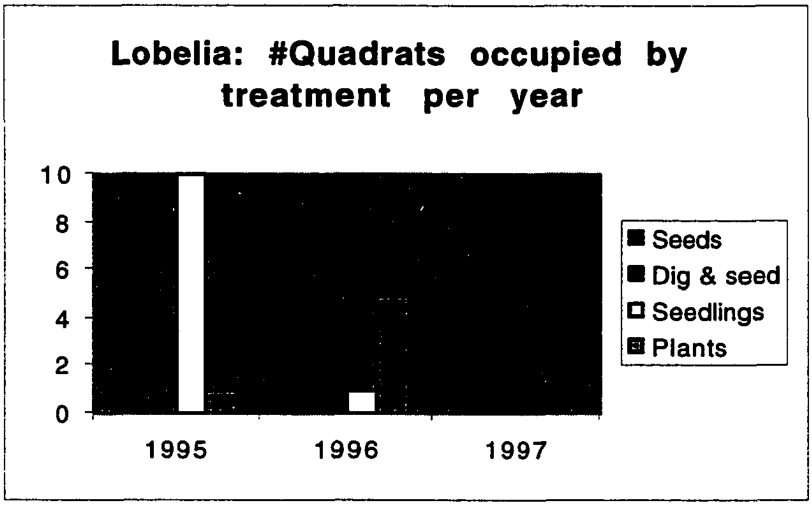


Figure 1-2h. Number of quadrats occupied per year, by treatment, for *Lobelia*.

Chapter 2

Experimental Creation of Garlic Mustard populations

Ecology at its core is concerned with the distribution and abundance of organisms. The concerns of conservation biology place special emphasis on the processes which regulate distribution and abundance and their interactive product, biological diversity. Among these are the processes by which a population of a species becomes established in a location, and persists or goes extinct on that spot.

A better understanding of the factors that regulate colonization success is especially important for plans to reintroduce rare or otherwise desirable species to reserves, in which a goal is the creation of populations or even metapopulations that are viable over the long-term. Plant species reintroductions are increasingly used for conservation and mitigation purposes (Primack and Drayton 1997, Falk and Olwell 1992), but the success of these efforts overall is surprisingly low (Primack 1996, Pavlik 1994), and no plants to date have reached non-endangered status as a result of such efforts.

Reintroduction, especially reintroduction by seed, seems attractive on many counts, both in terms of biology and in terms of the practical or logistical considerations of restoration and reintroduction (Fiedler and Levin 1996). The harvesting of seed causes less disturbance to a sensitive population than transplants, and seed can be used directly, or to propagate seedlings for transplant. Sowing the seed into suitable field sites can be done quickly and at low cost, and site preparation or post-introduction maintenance should enhance success of the reintroduction. Yet to date these approaches seem disappointingly unproductive. More needs to be known about the establishment process itself, about the characteristics of particular species of interest, and about the interactions of the seed and the site (Guerrant 1996, Primack 1996, Prince and Carter 1985).

Site characteristics are generally taken to be a primary filter, perhaps the controlling factor, in the the success of colonization. Soil characteristics, existing vegetation, and weather conditions surely are important to the suitability of a site. From this point of view, a seed with finite resources arrives at a 'safe' site (Harper 1977) and either germinates or does not. It may or may not be 'established' as a seedling, and then may or may not make the transition to reproductive status. The likelihood of each of these life events is seen to be largely under the control of the environmental conditions pertaining at the time of dispersal or germination.

This environmental filter, however, interacts with other ecological factors, so that the "filter" is a complex of physical and biological dynamics. Dispersal can sometimes play a role in the local distribution of plant species in an area; the assumption that all potential suitable sites will eventually be filled may not be warranted (Primack and Miao 1992; Sauer 1988; Howe and Smallwood

1982). Further, the characteristics of the colonizer interact with site characteristics, which themselves vary in suitability with respect to a particular colonization event from season to season and from year to year. Genetic and maternal effects on seed and seedling vigor are known from agricultural and experimental literature (Miao et al. 1991; Harper 1977), and presumably the genetic variation present in a source population will at times result in genetic variation in characteristics that favor germination and establishment of seeds and seedlings under the particular conditions obtaining at the time of dispersal (Bazzaz 1996, Guerrant 1992).

One can expect that genetic variation in a plant population, as represented in its dispersed seed, will interact with the variation in colonization site quality. In cases of animal-dispersed seed, it has been suggested that the dispersal is more or less targeted, that is, that the dispersal vector increases the likelihood of the seed's reaching a suitable site for establishment (Howe 1986, Howe and Smallwood 1982, Culver and and Beattie 1980). For seed that is passively dispersed, that is, that has no adaptation to a particular dispersal vector, but merely falls to the ground upon release, the sampling of the habitat mosaic by the population's genetic mosaic will be more random.

The relation of genetic variation to colonization success is important in plant conservation, especially in reclamation or reintroduction efforts, in which the genetic make-up of the artificially created population(s) may be an important, perhaps decisive element of the design (Guerrant 1996). Usually, the genetic make-up of the design of such introduced material is aimed at preserving maximum genetic diversity, which may well increase the likelihood of the population's viability once established. It is not at all clear, however, how the variability which makes for colonization success is related to the variability that makes for longer-term population viability, and it may be that some genotypes will be more successful colonizers (under particular conditions) than others. Although there have been many studies of population genetic structure in new populations and metapopulations as a result of founding effects sand dispersal syndromes (e.g. Giles and Goudet 1997, Hamrick and Nason 1996), there has been little examination of genetic effects on founding or colonization events. This effect may play an important role in a plan to restore species to a site or in other conservation plans.

Yet research on perennial species can be very slow, with years passing before results can be assessed (Pavlik 1994), and in many cases a lack of understanding of the species' biology means that initiation of experimental populations from seed is rarely successful (Chapter 1; Primack and Drayton 1997, Primack 1996). For this reason, we have initiated several experiments on aspects of species reintroduction by seed, using a model species, the biennial garlic mustard (*Alliaria petiolata*). After being present in North America for approximately a century at low density, this European species is currently undegoing a massive expansion in density and number of sites occupied. New populations have become established in reserves in the Boston area over the past 15 years. Its population and metapopulation biology is of interest both to students of weedy species, and to conservation biologists concerned to understand and manage invasions of protected habitats. In addition, however, we believe that it provides a useful comparative model to explore the dynamics of population establishment and extinction experimentally. Although the usefulness of model species in ecology has been denigrated owing to the dangers of false generalizations among other problems(e.g. Peters 1991), we believe that in this case a model species, aggressively and successfully invading, can provide some valuable information about the maximum rates of success that can be expected in the creation of new populations of a species from seed, and in addition provide useful information about the conditions under which success can be expected (Mack 1985, and see Chapter 3 for further discussion of this point).

Furthermore, although the dynamics of weed populations have been exhaustively studied for several decades (Cousens and Mortimer 1995), this demographic work does not address sufficiently the dynamics on the local scale of weed colonization, especially of non-agricultural weeds. This is even true of recent studies of garlic mustard invasions, which have not been focused on these questions (e.g. Nuzzo 1996, 1991, Anderson and Dhillion 1991).

In this paper, I report on an experiment to explore rates of success of establishment of populations of Garlic Mustard (*Alliaria petiolata*), using seeds of different genotypes, at multiple sites in two conservation areas in Greater Boston. The experiment addresses the questions: Is there a discernible difference in colonization success of different genotypes of a species? And how likely is the founding of a new population of this species? In addition, what are the population dynamics of newly-estabished populations of this species, with respect to population growth rates, population structure, and extinctions?

Methods

Experimental organism

Garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande, Brassicaceae) is a European native, first recorded in North America in 1868, and in New England in the 1890s (Nuzzo 1993a). A biennial in North America, though a "winter annual" in Europe, adapted to wide range of conditions (Cavers *et al.* 1979, Anderson & Dhillion 1991) in some areas of North America it is displacing native vegetation (Nuzzo 1993b, White *et al.* 1993, Cavers *et al.* 1979). *Alliaria* outcrosses, but is self-compatible, and in fact may usually be selfing. In an experiment conducted in 1993 (Drayton, unpublished data), rate of fruit-formation per flower was essentially identical among (hand-pollinated) out-crossed, selfed, and non-pollinated plants, above 80%, and observations suggested that most flowers were self-pollinated before anthesis. Anderson *et al.* (1996) present evidence of pre-anthesis autogamy. They also report that the result of emasculation experiments exclude apomyxis; these observations are supported by the extensive studies of Cruden *et al.* (1996).

The species has no known dispersal vector (Cavers *et al.* 1979), which is a common characteristic of plants in deciduous forests and margins where this plant is largely found (Hughes et al. 1994; Chambers and MacMahon 1994; Willson et al. 1990). The seeds fall to the ground upon the dehiscence of the siliques, and the majority of seed fall no further away than the height of the mother plant. Dispersal in the study areas was largely down slopes and along paths and roadways, suggesting that some secondary dispersal occurs by tracking of fallen seeds by human and animal feet and vehicle tires, and occasionally by surface water run-off and similar agencies. This dispersal can in fact be very long-distance, as exemplified by the existence of isolated populations in southern New Hampshire (Hillsborough Co.) and central Maine (Kennebec Co.) with no discovered seed source nearby (Drayton, pers. obs.).

Seeds dispersed in late summer overwinter, and germinate early in the following spring, forming a rosette of two, three, or more leaves which persist through the winter. In the second spring following dispersal, rosettes bolt regardless of size, and produce racemes of small white flowers on one or more leafy stems.

Recently established garlic mustard populations show a marked "dimorphism" in their population structure noted in other strict biennial species (Kelly 1985). Thus, the first year after seeds arrive on a site, only seedlings (first-year rosettes) will be visible. The following year, only reproductive individuals will be visible. The third year, again only rosettes from seeds dispersed in Year 2, and so on. This alternation continues for several generations.

Experimental sites

Twenty sites were identified, ten each in the Hammond Woods in Newton, and the Middlesex Fells in Medford, MA. The Hammond Woods is a conservation area approximately 80 hectares in area. It comprises a mixture of deciduous woods, swamps, parking areas, meadows, ledges, and roads. The Middlesex Fells is approximately 800 hectares 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.

These reserves were chosen because they provided a range of suitable habitat, and because many parts of both areas were already subject to invasion by garlic mustard during the previous five years. Sites for experimentation were chosen in advance of the invading fronts of the plant, on the basis of visual inspection of the sites for suitability. Sites chosen were along paths, roads, and forest edges, with moist ground, moderate to full shade, and the presence of species usually co-occurring with garlic mustard in the area ("indicator species"). Such species included poison-ivy (*Toxicodendron radicans*), jewelweed (*Impatiens capensis*), and wild-geranium (*Geranium maculatum*). Sites were situated at sufficient distance from naturally occurring *Alliaria* populations to make dispersal from those populations extremely unlikely; yet sites were likely to be invaded by *Alliaria* within 5-10 years.

In 1992, we attempted to create experimental populations of Garlic Mustard by sowing seed at sites in the Hammond Woods and the Middlesex Fells. Seeds were collected from 16 mother plants in several populations in Newton and Medford, MA, and sown within a few weeks of collection. Separate samples from each seed source were cold-stratified and germinated in growth-chambers (Baskin and Baskin 1992), showing germination percentages for all sources of above 60%.

Seeds were sown in 200 quadrats set in groups of 10 ('sites'), 100 quadrats in the Hammond Woods, and 100 quadrats in the Middlesex Fells. Quadrats at each site were 3-5 meters apart, and sites were at least 100 meters apart, and at least 20 meters from any naturally occurring population. Each quadrat was marked with a wooden stake, and seeds were dropped within a 50 cm radius of the stake. Seedlings all came up within that radius, indicating that there was minimal movement of seeds once sown. Seedlings did not appear in the areas adjacent to sites, nor between the quadrats, indicating that there was essentially no seed-rain nor seed-bank population before the experiment. The site was not disturbed or prepared in any way beyond the placement of the stakes.

Twenty seeds were sown by hand on each quadrat, thus at each site a total of 200 seeds were sown. At each site, 4 quadrats were sown with 20 seeds of one of 10 genotypes (thus 4 genotypes per site), and six quadrats were sown with seeds from one of three bulk lots (seeds from Newton, from Medford, and from both sites). The total number of seeds used in the study was thus 4000, (2 reserves x 10 sites per reserve x 10 quadrats per site x 20 seeds per quadrat).

Sites were visited annually during flowering periods. Number of seedlings and flowering individuals were censused at each quadrat. Statistical analyses were performed using the Statsoft Statistica™ (Release 4.1) program, and Microsoft Excel™ versions 4 and 5.

Results

The most striking result of this study is the difficulty of establishing a population of this aggressive invader. Of the 4000 seeds sown, 256 seedlings were observed in the first two years, before any individuals reached reproductive stage. Thus only 6.4% of seeds survived to rosette stage. The results show much variation from one site to another between the Middlesex Fells sites and the Hammond Woods sites, among the sites in each location, and among the quadrats within each site. A Wald-Wolfowitz runs test to see if the Fells and Hammond Woods sites should be treated as separate groups was highly significant ($p < 0.00001$), so in what follows the results will be presented for each locale separately.

The quadrats and the sites (groups of 10 quadrats) fall into three general categories, as follows:

1. Failures. No individuals present on the site in 1996, four years after seeds were sown, and few if any present in the intervening years.
2. Successful establishments. On these sites, there are 5-10 or more flowering plants in 1996, usually also a fair number of seedlings, and the mean population has increased markedly since 1994. These populations are producing seed, rosettes are surviving to flower, and the population is likely not to be vulnerable to a single disturbance event.
3. Vulnerable establishment. There are a few individuals, perhaps 1-5 flowering plants, few or no seedlings along with these. Population means have not increased dramatically over the course of the study. Transition probability from rosette to

flowering plant is relatively low (< 30%), and often seed production is low. These populations seem (on the basis of the extinction studies reported elsewhere) to be quite vulnerable.

These categories can be exemplified by reference to some specific sites and quadrats; the distribution of plots by category is displayed in Table 2-1. The success rates by genotype will be discussed in later sections.

1. Failures. Site #2 in the Hammond Woods showed a total of five seedlings on three quadrats in 1994, and nothing thereafter. Site #6 in the Middlesex Fells showed only one seedling, on quadrat 57, in 1993. This seedling survived to flower in 1994, but no other seedlings or flowering plants appeared on any of the 10 quadrats of this site in 1995 or 1996. Two sites in the Middlesex Fells (#3 and #5) and one in the Hammond Woods (#4) showed no seedlings or flowering plants in any year.

2. Successful establishments. At site #3 in the Hammond Woods, individuals appeared on 7 out of the 10 quadrats. Flowering individuals were noted on 6 of these, and in 1996, the population mean per quadrat was 556 individuals; in 1996, all individuals occurred on the 5 quadrats 26-30. At site #5, individuals appeared on every quadrat in 1993, probability of transition to flowering stage approached 80%, and in 1996 there were at least 50 flowering individuals (often many times more) and 50 seedlings on each quadrat. Mean quadrat population went from

7.7 in 1994 (when the total population was constituted by germinations from the original seeds) to 1570 in 1995, and 1391 in 1996, with almost 5000 flowering plants and an enormous seed production.

3. Vulnerable establishments. Site #4 in the Middlesex Fells showed individuals on three quadrats. On quadrat 31, a flowering plant in 1995 led to no seedlings in 1996. On quadrat 33, three flowering plants in 1995 were succeeded by 12 seedlings in 1996. On quadrat 32, there was one flowering plant in 1996, the only flowering individual on the site. Site #1 in the Hammond Woods showed a similar pattern, with the mean quadrat population varying from 0.1 in 1994 to 1.0 in 1995, and 0.5 in 1996. The species is present, but vulnerable.

Germination rates

Of 4000 seeds sown, 256 seedlings were observed in the first two years (before any flowering plants could set seed). This yields an overall germination rate of 6.4%.

Of the 200 quadrats established, seedlings appeared at 95 (47.5%) of the quadrats (61 in HW (61%), 34 in MF (34%)). Reproductive individuals appeared on 44 (22%) quadrats, (39 (39%) in HW, 5 in MF (5%)).

The maximum success for a site was 39.5% germination, and all of these seedlings flowered the following year. The minimum success was 0 germinations, seen at 5 sites (all ten quadrats at each site had no seedlings). Success in the HW was markedly higher than in the MF, with HW quadrats showing 11.65% germination, and 7.45% fruiting, while the MF quadrats showed 1.6% germination, and 0.3% flowering.

Persistence to flowering

Persistence to flowering was calculated as the percentage of seedlings on a quadrat in one year that survived to reproduce in the next year. This percentage was significantly different between the two reserves, with the Hammond Woods sites always showing a much higher value than the Middlesex Fells sites. Within each reserve, the persistence value varied from year to year. The year-to-year variation in this value was small, and in fact not statistically significant in the Hammond Woods, but the Middlesex Fells populations showed a large and significant variation from year to year, never reaching as high as 25%, and in 1995 reaching only 9% (Table 2-2).

Population growth rates

The number of individuals at each quadrat were censused annually, and the percentage of population increase per year was calculated as the ratio of population in one year (N_{t+1})to the population in the previous year (N_t). Table 2-3 shows mean population sizes and rates of increase. In 1993, the population consisted only of first-year rosettes; beginning in 1994, there were usually both first-and second-year plants present. In both reserves, there was a small increase in population in 1994, since the number of individuals represented second-year (reproductive indivduals that had not yet set seed) and new seedlings by addition from the seed bank, that is, from the 20 seeds sown in 1992. In both reserves there was a marked increase in 1995 after the first year of flowering, representing the first dispersal of seeds, and in 1996 a smaller increase in the number of individuals. This pattern is another reflection of the strongly bimodal population structure of this species in new populations, since seed was set in 1994 for the first time. In 1995, the few individuals that had germinated in 1994 from the original planting flowered and set seed, but the majority of individuals present were first-year rosettes from 1994's seeds. The population in 1996 grew as a result of seed germinations from those few flowering plants, and from germinations from dormant seed.

Population structure

Alliaria in northeast North America behaves as an obligate biennial. Although some seeds remained dormant in our study sites past the first year, the populations show a rather strict alternation in the predominance of individuals of one or the other life-stage: the first year after planting of seeds, there are only seedlings present. In the second year, almost all individuals are the second-year flowering stage of the first year's seedlings. In the third year, first-year rosettes predominate, the only exceptions being those individuals whose seeds germinated after a year's dormancy. Second-year plants flower and fruit regardless of size, within a very wide range of size: the tallest flowering individual measured during our studies was 158cm, with approximately 250 fruits. The smallest individual measured was 5cm,with a single fruit.

The small percentage of dormant seeds, however, slowly contributes to a breakdown of this strict alternation of life stages, and as populations persist the bimodality breaks down. The proportion of flowering individuals as a proportion of the whole population in the "invading phase" thus will rise and fall alternately from the year of dispersal, during which there will be no flowering plants. The populations from the Hammond Woods demonstrate this early phase clearly (Figure 2-1 and Table 2-4). However, there is an interesting difference between the behavior of populations with regard to this characteristic. In the case of the Middlesex Fells sites, in which experimental introductions of this species were less successful, the alternation is much less dramatic. In the Fells, the proportion of flowering individuals per year remains between 40 and 60% beginning with the first year of flowering, in 1994. This is likely to be an artifact of the small mean population size in the Fells, where the input to the seedling population from the bank of dormant seeds (originally no more than 20 in 1992) even if it numbers only two or three new germinations per year is a proportionally large input. Hence, the small populations have the appearance of a more mature invasion than do larger populations.

Extinctions

Within the time limit of this study, it is not possible to certify that a population created in the study has gone extinct, since it has been shown that garlic mustard seeds may remain dormant for up to five years (Baskin and Baskin 1992). It is of interest, however, to note cases in which quadrats which once had reproductive individuals show no individuals of either life stage.

These cases we will term "extinctions," and given the low rates of germination, it is likely that these may in fact be local extinctions.

Reproductive individuals appeared at least once on 16 quadrats in the Middlesex Fells, thus on 16% of total quadrats, or 47% of the quadrats on which seedlings appeared. Of these 16 sites, 10 showed no seedlings or flowering individuals in the last year of the study. Seven of these had had no more than a single flowering plant on the quadrat, which seem thus to have died without issue. Of the other three quadrats, two quadrats had had 2 flowering plants each, and one had had 4, once.

Using these numbers then, one can posit an "extinction rate" for the Medford site of 62%. That is, out of the 16 quadrats on which populations were "established" by the presence of fruiting individuals, 10 showed no seedlings or flowering plants by the end of the study. Although causes for this high rate of extinction are not clear, many of these sites were in high-disturbance areas (maintenance roadways, for example).

In the Hammond Woods, the populations show a different pattern. There 38 quadrats had flowering plants at least once during the study period. Of these sites, only three sites had no seedlings or flowering plants present in 1996, thus showing an "extinction" within the time of this study; two of these quadrats had had only one flowering plant. The rate in HW is thus 7.9% (3/38).

Among all populations (Hammond Woods and Middlesex Fells) there was only one extinction of a population which had had flowering plants in more than one year. Thus populations in which there were several reproductive individuals per year, or reproductive individuals in successive years, persisted as successful colonists.

Performance by genotypes

With respect to performance by genotype, the quadrats are assorted in these three categories as follows (data summarized in Table 2-1). In the Hammond Woods, 57% of quadrats can be assigned to class 1 ("failures"), 35% to class 2 ("successful establishments) and 8% to class 3 ("vulnerable establishments"). Thus 43% of Hammond Woods sites show populations present in 1996, the fourth year of the study. In the Middlesex Fells, 92% of quadrats are classifiable as "failures," 8% as "vulnerable establishments," and none (0%) as "successful establishments." Thus, in the Middlesex Fells, the picture here is of widespread failure.

Some differences in performance among the various genotypes used are discernible. The three bulk sources, from the Hammond Woods, the Fells, and from both, showed very different success: in Hammond Woods, 9.75% germination, and 6.25% fruiting, but in MF 1.3% germination, and 0.42% fruiting. Further, the bulk samples from the Hammond Woods, or HW and MF mixed, showed better rates of success in the Fells (10% and 15% respectively) than seeds from the Fells (5%). The complementary picture is seen in the Hammond Woods, where seed gathered from the Fells, or from both sites, show marginally better performance than seeds from the Hammond Woods itself.

Genotypes ranged in success from 0 germinating and fruiting individuals to one genotype with 28.75% germination, and 27.5% fruiting. Table 2-5a shows the numbers of seedlings and flowering plants recorded by genotype for all years in Hammond Woods, and Table 2-5b shows the numbers of seedlings and flowering plants recorded by genotype for all years in Middlesex Fells.

If one collapses the data on number of seedlings, and number of flowering plants, reported from each site, comparing the performance of seeds from the bulk sources and from the individual genotypes, one can see some indication of site/genotype interaction, but the general picture is of site characteristics predominating. In Figures 2-2a (Fells) and 2-2b (Hammond Woods), the total number of seedlings per site are reported by seed-source; Figures 2-3a and 2-3b show site/source interactions for total flowering plants reported. In the Fells, site 7 is significantly more successful for all genotypes, with the seeds from bulk sources far more successful. In the Hammond Woods, again the patterns of success are very similar from site to site, regardless of genotype. Sites 5 and 9 show significantly more success than all others. On site 5, the "bulk" seeds are significantly more successful than the "monotype" seeds.

Discussion

Establishment of new populations of plant species is an ancient management practice which has taken on fresh interest with the urgent concern for the prevention of species extinction (Allen 1994). Many horticultural techniques, buttressed and extended by the insights of conservation biology practice and theory (Primack 1996) have been pressed into service, but seed dispersal seems the simplest and lowest cost, and in many ways mimics the natural processes of colonization. Yet many aspects of the colonization event, though understood to some degree in general, have been little explored empirically. The frequency of colonization success, the relative contribution of biotic and abiotic factors, and the criteria for "establishment" or "success" are little documented.

In these experiments, a highly aggressive weed was used to explore some of these questions. The planting method very closely simulated the natural dispersal of this species, so possible effects of horticultural practice were effectively eliminated. Seeds from 15 different maternal families were sown at 200 sites in two different parts of greater Boston, in areas known in general to be hospitable to the species.

The results of these experiments suggest that site characteristics were more important than any genetic differences in establishment characteristics. Such genetic differences might include growth rates of seedlings, quantity or quality of secondary compounds or other defenses, variations in nutrient or energy reserves, and other characteristics (Naylor 1985). The experiments demonstrate this in two ways: first, there is no detectible, significant difference among genotypes in success of germination, seedling establishment, or reproductive success as measured by number of flowering progeny. Second, sets of 10 quadrats, situated in homogenous habitat, often showed similar results, suggesting that the whole site chosen was relatively suitable or unsuitable to the species. Although this experiments by establishing many populations by artificial seed dispersal, confirm results such as those reported by Primack and Miao (1992) showing that dispersal can limit the local distribution of a species, they also confirm that site quality is the dominant factor in successful colonization.

Although this conclusion is plausible, one must acknowledge that the experimental design probably did not provide enough data on the performance of the individual genotypes to give confidence in the results. In effect, a large variation in site quality was sampled with too few replicates of each genotype. Chapter 3 reports on experiments designed to overcome the "noisyness" of the experimental design by reducing the environmental variability, while maintaining as many replicates per genotype as permitted by the seed source.

It is striking that even with such an aggressive and successful invader, the establishment of a population, which in this species can be a single reproductive individual, is quite a rare event. Of 4000 seeds sown, only about 6.4% appeared as seedlings, and of these perhaps only half persisted to reproductive status. The results are important for restoration ecology, since they imply that while seed dispersal may be an attractive method of species reintroduction, the inherent dangers of the establishment phase will require a very large amount of seed to be sown, or a high degree of maintenance effort during the vulnerable phases of the seedlings' lives. If, as part of a reintroduction program, a target population of 100 individuals of this species was seen as desirable, one would have to plan on sowing approx. 2500 seeds to ensure a reasonable likelihood of success — yet we know that for many species the estalishment rate must be much less than that of the garlic mustard (Primack and Miao 1992).

Further caution for reintroduction protocols comes from a consideration of the criteria for "success." A recent consideration of just this topic (Pavlik 1996) suggests several useful criteria. For example, for a successful reintroduction of a selfing, short-lived perennial, one would look for evidence that there is a rate of increase (l) of more than 1.00 in at least 1 year, and that a minimal viable population (MVP) is attained, that is, a persisting population that can serve as a source for pollen and seed in the establishment of new population. Moreover, this kind of success must be achieved multiple times, since it is in a metapopulation that maximal genetic diversity will be maintained for such an organism. As Pavlik (1996) and others have emphasized, long-term monitoring and perhaps horticulture will be required in any reintroduction experiment, but "long term" seems hard to define in any general way. Our finding that, even for a weedy species with great reproductive potential, apparent establishment over the course of a year or two may be followed by local extinction, at a rate as high as 62%, suggests that when the actual reintroduction goal is a metapopulation, the number of sites may need to be quite large indeed.

The great variability in site-specific performance makes clear the necessity of careful site selection (Fiedler 1996), and the comparative lack of genetic advantage in establishment characteristics suggests that reintroduced populations can be reconfigured for general genetic diversity without special regard to establishment characteristics of particular genotypes. On the other hand our results also suggest that as part of site selection a bioassay using seed may well provide important information for long-term success, for example identifying areas in which the species can establish, but only under certain horticultural conditions, such as density of competing vegetation or levels of disturbance.

In the case of a species that has relatively short survival in the seed bank, success in a reintroduction will include not only reaching a threshold population size, but also a stable population structure (Primack 1996). Other experiments with *Alliaria* (Chapter 4) suggest that repeated disturbance (*sensu* Grimes 1977) that affects one life stage more than another can significantly affect population viability, by increasing vulnerability to stochastic demographic or environmental catastrophes (Gilpin and Soulé 1986). Garlic mustard with its high rates of rapid germination clearly preserves its characteristic bimodal population profile (rosette vs flowering individuals) for several years after establishment. Our experiment demonstrates that extinction is most likely when there is a small and intermittent seed rain.

This raises a consideration relevant to an understanding of the progress and possible control of this species. It is well known that infestations once established are very difficult to eradicate, short of severe burning or poisoning regimes. What is the point at which a population becomes "established"? For this species, on can suggest that this is the point at which the strong alternation of life-stage, one year all rosettes, the following year all second-year plants, has broken down, owing to the cumulative effect of the growing seed bank, which makes a small but significant contribution to the seedling population each year once some individuals have reached flowering status. How long might that be for the populations in this study? What is the relative contribution of each component of the species' life history in this colonization process?

The life-history parameters for this species can be depicted in a simple transition model (Figure 2-2). The population can be represented by three stages: seed, rosette (year 1), and reproductive (year 2).

Based on this schema, garlic mustard population dynamics can be modelled with a Lefkowitz matrix representing a stage-structured population. In this case, age-structure and stage-structure are very similar, given the strict biennial habit of the organism. In only one life-stage, seed, can an individual transition to the same stage in a succeeding year. In no case can an individual make a transition to a previous stage (e.g. a reproductive individual cannot become a rosette again).

As in Caswell 1989, the model is of the form

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where the matrix $\mathbf{n}(t)$ is a vector which contains the numbers of individuals in the population in each life stage at time t. **A** is a projection matrix, whose cells contain the probablities of transition from each stage to the next stage. The projection matrix is thus of the structure:

	seed	rosette	flowering indiv
seed	seed-to-seed	rosette to seed (empty)	flowering to seed (fecundity)
rosette	seed-to-rosette	rosette-to-rosette (empty)	flowering to rosette
flowering indiv	seed-to-flowering (empty)	rosette to flowering	flowering to flowering (empty)

Values for the transition parameters can be chosen on the basis of observations of the populations discussed here. Seeds can remain in the seedbank for 3-5 years, with an exponential decay of viability,with something like 5-10% of ungerminated seeds remaining viable per year. Many will germinate the first year after dispersal, however. In populations we have started with known quantities of seed, the proportion of seed reaching rosette stage ranges from 0.1 to 0.39 (See also Chapter 3). Of these, a proportion will survive to reproduce in the second year, this proportion varying from 0.09 to 0.63. Flowering individuals vary in fecundity, of course, with some noted with only a single fruit bearing two or three seeds, and other large individuals bearing 300 fruits, each with 10-14 seeds, thus dispersing as many as 4200 seeds. Using values chosen from these data, we can parametrize the matrix as follows:

Seed-to-seed 0.1 * (1 - .065)	Rosette to seed (empty)	Flowering to seed (fecundity) 600 seeds/plant
Seed-to-rosette 0.065	Rosette-to-rosette (empty)	Flowering to rosette (empty)
Seed-to-flowering (empty)	Rosette to flowering 0.5	Flowering to flowering (empty)

Analysis of this matrix yields a rate of population growth $\lambda = 2.7231$.

Sensitivity of λ to small changes in the various elements of the matrix is given by the following sensitivity matrix (cells with **bold text** indicate stage transitions realized for this species):

Seed-to-seed **0.34**	Rosette to seed (empty) 0.0081	**Flowering to seed** **(fecundity)** **0.0015**

Seed-to-rosette **13.8**	Rosette-to-rosette (empty) 0.3294	Flowering to rosette (empty) 0.0605
Seed-to-flowering (empty) 75.16	**Rosette to flowering** **1.79**	Flowering to flowering (empty) 0.3294

Of the cells that are defined (not empty), a small change in the the probability of transition from seed-to rosette will have the largest effect on population growth rate. Next most important is the transition from seed-to-tseed, then from rosette to flowering. Surprisingly, fecundity (flowering to seed) seems relatively unimportant, implying that a small change in fecundity will have relatively little impact on λ. In passing, it is worth noting that the "seed-to-flowering" cell, empty for this model, nevertheless has a potentially large impact on the demography of the plant: if in some cases the plant acted as a annual, so that some individuals flowered in their first year, this would substantially affect the rate of seed production, and eliminate the second-year life-stage. This is of interest since the species in temperate North America seems to have evolved from a winter annual habit (as reported in Europe) to a biennial habit; it would be of interest to explore the evolutionary biology of this change, and its geographical distribution, especially if, as Kelly (1985) suggests, one can draw a distinction between strict and facultative biennial life-histories, which sometimes may co-occur in the same species and population.

Kelly adapts equations from Silvertown (1983) to explore the life history of strict versus facultative biennials. These equations derive lambda (λ) as a function of survival to end of first year and fecundity (for annuals) and survival to end of first year, survival to flower in second year, and fecundity (for biennials), and assume biennial availability of sites. With this model, we can examine conditions under which biennials would be advantaged over annuals in *Alliaria* populations, with reference to two critical parameters, that is fecundity, and survival from rosette to flowering, both of which may be enhanced by the extra year of growth provided by the biennial habit.

The equations for annuals are as follows:
If

S_1 = survival to end of first year
S_2 = survival to end of second year
F = fecundity, mean seeds produced per individual
x = time in number of years in which new colonizable sites are , available; in this case, we choose $x = 2$

Then

$$\lambda_{\text{annual}} = (S_1F)^{1/x}$$

and

$$\lambda_{\text{biennial}} = (S_1S_2F)^{1/x}$$

First, let us look at the case in which fecundities are the same, survival to the end of the first year is the same (0.1), and survival of rosettes to flower is 50% (0.5). As Figure 2-5 shows, at a very wide range of fecundities, the annual habit has an advantage as measured by λ, by virtue of the additional mortality incurred by the biennials, under these conditions.

Now, suppose that the extra year of growth provides the advantage that a higher proportion of the biennial forms reach flowering, but their fecundity remains the same as that of the annuals. As Figure 2-6 suggests, even with a higher survivorship to flowering, biennials still lag behind if λ is defined as a function of individual performance.

It is possible that the biennial habit enhances fecundity. If we assume as much as a 70% enhancement of fecundity for the biennials, but the same survivorships as in scenario 1 (0.1 to end of first year, and 0.5 of those to end of second year), the annual habit still outcompetes the biennials (Figure 2-7).

So far, within the limits of this simple system, there seems to be no real reproductive advantage to the biennial habit. However, there are still two interesting scenarios to examine. The first is an enhancement of fecundity, and also some enhanced survivorship of rosettes. This last is plausible, on the basis of field values in this study and others, in which survivorship of rosettes approaches 80% in some populations. Further mechanisms for this are suggested by the recent studys of *Alliaria* defensive compounds, which seem to have a higher concentration in rosettes than in the second-year, flowering forms of the same individuals. Under this scenario, biennials with a somewhat enhanced fecundity (50% more than annual individuals) and a higher survivorship (70%) surpass annuals in population performance, as sketched in Figure 2-8.

The final scenario, however, reflects the behavior of *Alliaria* populations in North America, in which the biennial habit plus short-lived seed dormancy result in alternating subpopulations, as described by Kelly (1985) for *Linum catharticum* and other strict biennials. The effect may then be to enhance fecundity, but also to produce annual seed inputs (Figure 2-9); under the assumptions sketched in Figure 2-9, annuals still might have an advantage, but a very slight one in terms of fecundity and hence of population performance.

But persistence in the rosette stage may also affect other factors by way of "material affects", such as survivorship of seeds in the soil. Thus a slight enhancement of seed-survivorship, added to the previous scenario, results in a strong advantage for the biennial forms, under the assumptions of this model, which are for this species actually realistic in biological terms (Figure 2-10).

The implications are that in populations with annual and biennial forms, the biennial forms might well have a reproductive advantage under realistic assumptions. Longitudinal study of populations containing both forms, if they exist in North America or Europe, would provide interesting insights into the evolution of life-history variation. Some scattered reports of plants surviving to a third year as a result of injury to the flowering plant raise the possibility that in some populations there might even be annual, biennial, and multi-year monocarpic forms.

To return to discussion of the matrix model proposed above, an analysis of elasticity, that is proportional change in λ resulting from a proportional change in the matrix elements, provides a result more in line with the behavior of the plant in North America, and in line as well with the reasoning about the advantages of the biennial habit:

seed-to-seed	rosette to seed (empty)	flowering to seed (fecundity)
0.0117	0	0.0056

seed-to-rosette 0.3294	rosette-to-rosette 0	flowering to rosette 0
seed-to-flowering 0	rosette to flowering 0.3294	flowering to flowering 0

The transitions from seed to rosette (0.33) and from rosette to flowering plant (0.33) are relatively more important than fecundity (0.006) in a stable population structure based on the assumptions we have used.

Then for this population to "break" from the strongly bimodal structure, so that there is a large seed input every year, would take on the order of 7 years to reach a population of approx. 1820 rosettes, 500 flowering plants, and a seed bank of approx. 10,ooo seeds, with an annual input of seed at 10K or above. At some point (not presently identified for this species) density-dependent factors will damp this explosive growth (Baskin and Baskin 1992), but such a population is likely to remain stable, and act as a source for seed dispersal, for a long period of time.

To what extent do the various transition probabilities affect this scenario? Manipulating the values of the model's parameters suggests that persistence in the seed bank is in fact an important factor in the growth of the population, and in the development of the age structure of a population from an alternating seedling-flowering structure to a more stable structure in which each year there is a substantial input of seed. Figure 2-11 projects annual population growth when one takes the basic assumptions outlined above, with an original founding "population" of 20 seeds, a 10% survival of seeds in the soil, 6.5% transition from seed to seedling, and 50% survival from seedling to flowering, with a mean fecundity of 600 seeds/individual. Figure

2-12 shows the results of the same model, changing only the mean fecundity, to a lower figure of 100 seeds per flowering individual, as for example in a less favorable site. In this case, the exponential growth does not become apparent until after the seventh year. Figure 2-13 shows that a lower attrition rate of seeds in the soil (50% as opposed to 90%) will add significantly to the population size (roughly by a factor of 10).

The consideration of the population dynamics of this aggressive species suggest that monitoring for successful establishment of a species capable of rapid local growth might well be necessary for the better part of a decade, and one can perhaps take this as a conservative figure for longer-lived perennials, or those with a markedly lower potential for population growth.

This paper has provided information about the dynamics of newly established populations of *Alliaria petiolata,* garlic mustard. The experiments suggest that site characteristics for this species will be the primary factors in the success of new colonies of the species, even when established by a relatively large number of founders. Site characteristics will continue to influence the population dynamics of the individual populations, but for this species with a short-lived dormancy, a period of perhaps 5-7 years will suffice for populations to reach considerable stability in the face of disturbance; this is explored in more detail in Chapter 4.

If one takes garlic mustard as a model system for plant reintroductions, the results reported here have two direct implications. First, site characteristics will play a critical role in the establishment of new populations by seed. This reinforces results reported in Chapter 1 and elsewhere, e.g. Primack 1996, which suggest that although it has many points in its favor, reintroduction by seed is not likely to produce a high rate of establishment. This aggressive invader has substantially higher rates of success of establishment than do the perennials we have worked with, and can be seen as showing something like the maximum rate of establishment that can be expected.

The second implication of the experiments for plant reintroduction is for the question of the importance of genetic factors affecting the success of colonization by seed. Conservation biology suggests that when new populations are designed for reintroduction the genetic diversity of the introductions is an important consideration, and the queston arises, whether this design should include selection for "colonization ability," which would obviously be a composite of several primary characters that might include seed size, germination speed, drought-tolerance, resistence to herbivory, and so forth. This would require a stage of data collection or experimentation to establish that such differences exist in the population, and a sampling/collection plan for seeds that took the results into account, substantially adding to the time and complexity of the plan's design and implementation. The experiments reported here provide no evidence that colonization ability is strongly genetic in character at least in this species. In order to establish this with any certainty, however, one would need to conduct a series of experiments upon factors that might make a colonizer successful in a wide range of situations, as opposed to a genotype that may be successful under one set of conditions, and not in others.

Finally, however, it must be said that this experiment, while yielding much information of interest, was not in the end a very good test of the question of genetic effects vs site effects in colonization success. The scenario, in which multiple genotypes are scattered across multiple colonization sites, is biologically realistic: it is in fact what happens in nature. In order to demonstrate what are likely to be rather subtle effects, however, the number of replicates of individual genotypes should have been much higher, and the environmental variability should have been reduced to the extent possible in a field study. Chapter 3 reports on two experiments designed to overcome some of the experimental weaknesses of this design, and focus more specifically on the question of colonization success of different maternal genotypes.

Tables

Table 2-1. Distribution of quadrats by "success classes" as described in text. Quadrats arranged according to genotype and location (Hammond Woods or Middlesex Fells). Percentages show percentage of quadrats of each genotype assignable to the success class. H = bulk sample from Hammond Woods, M = bulk sample from Middlesex Fells, HM = bulk sample from both reserves.

Hammond Woods

Success Class

	Failure		**Success**		**Vulnerable**	
Genotype	**No. of quadrats**	**%of genotype**	**No. of quadrats**	**%of genotype**	**No. of quadrats**	**%of genotype**
H	11	55	6	30	3	15
M	12	60	7	35	1	0
HM	11	55	7	35	2	10
4	3	75	1	25	0	0
5	2	50	2	50	0	0
6	3	75	1	25	0	0
7	2	50	2	50	0	0
8	2	50	2	50	0	0
9	2	50	2	50	0	0
10	4	100	0	0	0	0
11	1	25	2	50	1	25
12	1	25	2	50	1	25
13	2	50	1	25	1	25
Total	**56**	**56%**	**35**	**35%**	**9**	**9%**

Middlesex Fells

	Failure		**Success**		**Vulnerable**	
Genotype	**No. of quadrats**	**%of genotype**	**No. of quadrats**	**%of genotype**	**No. of quadrats**	**%of genotype**
H	18	90	0	0	2	10
M	19	95	0	0	1	5
HM	17	85	0	0	3	15
4	4	100	0	0	0	0
5	4	100	0	0	0	0
6	4	100	0	0	0	0
7	4	100	0	0	0	0
8	4	100	0	0	0	0
9	4	100	0	0	0	0
10	3	75	0	0	1	25
11	4	100	0	0	0	0
12	4	100	0	0	0	0
13	3	75	0	0	1	25
total	**92**	**92%**	**0**	0	**8**	**8%**

Table 2-2. Persistence of seedlings to flowering stage by year in Hammond Woods (HW) and Middlesex Fells (MF) sites.

Year	**H W**	**MF**
1994	0.6	0.21
1995	0.4	0.09
1996	0.63	0.24
Mean overall	0.54	0.18

Table 2-3. Mean population, size of largest population, and mean annual rates of increase for populations in Hammond Woods and Middlesex Fells.

Year	Hammond Woods			Middlesex Fells		
	Mean #plants	Size of largest pop	Mean pop growth N_{t+1}/N_t	Mean #plants	Size of largest pop	Mean pop growth N_{t+1}/N_t
1993	1.75	11	—	0.23	3	—
1994	1.83	14	1.3	0.19	4	1.00
1995	269	5000	111.00	1.02	50	7.8
1996	317	6000	58.4	0.9	50	1.7

Table 2-4. Mean percentage of flowering individuals in experimental populations in Hammond Woods and Middlesex Fells.

	Hammond Woods	Middlesex Fells
1993	0	0
1994	65%	42%
1995	14%	59%
1996	52%	45%

Table 2-5a. Numbers of seedlings and flowering plants by genotype for HW sites. H= planted from bulk sample from HW, M = planted from bulk sample from MF, HM= planted from bulk sample from both

	Hammond Woods	
Genotype	#seedlings	#flowering individuals
H	3927	115
HM	4884	755
M	17658	6229
P1	2306	507
P2	404	245
P3	1510	2007
P5	1364	367
P6	344	19
P9	7160	1361
P10	0	0
P13	319	364
P15	4088	504
P16	710	422

Table 2-5b. Numbers of seedlings and flowering plants by genotype for MF sites. H= planted from bulk sample from HW, M = planted from bulk sample from MF, HM= planted from bulk sample from both.

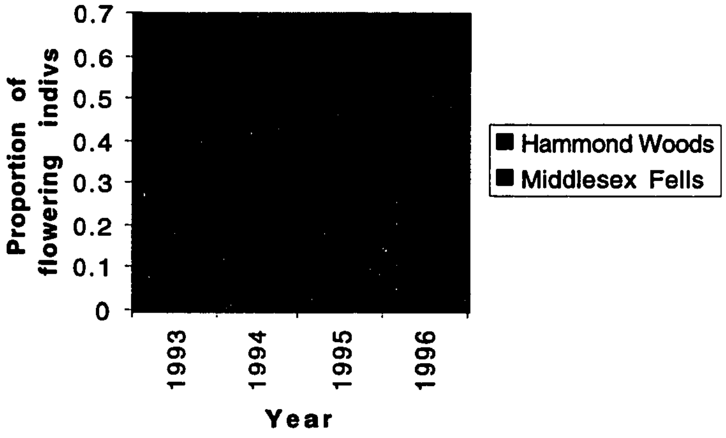
	Middlesex Fells	
Genotype	#seedlings	#flowering individuals
H	85	44
HM	4	0
M	11	8
P1	0	0
P3	0	0
P4	1	0
P5	12	1
P7	1	4
P8	0	0
P10	4	5
P12	0	1
P13	3	0
P15	9	4

Table 2-6. Results of one-way analysis of variance for significance of genotype for numbers of seedlings and flowering plants in Hammond Woods and Middlesex Fells

	Hammond Woods	Middlesex Fells	
Variable	p-level	Variable	p-level
SDLGS93	0.34	SDLGS93	0.896
SLDGS94	0.19	SDLGS94	0.692
SDLGS95	0.72	SDLGS95	0.989
SDLGS96	0.25	SDLGS96	0.878
FL94	0.40	FL94	0.887
FL95	0.71	FL95	0.473
FL96	0.58	FL96	0.993

Figures

Fig. 1. Mean proportion of flowering individuals in Hammond Woods and Middlesex Fells populations (1993 proportion is 0% for both)



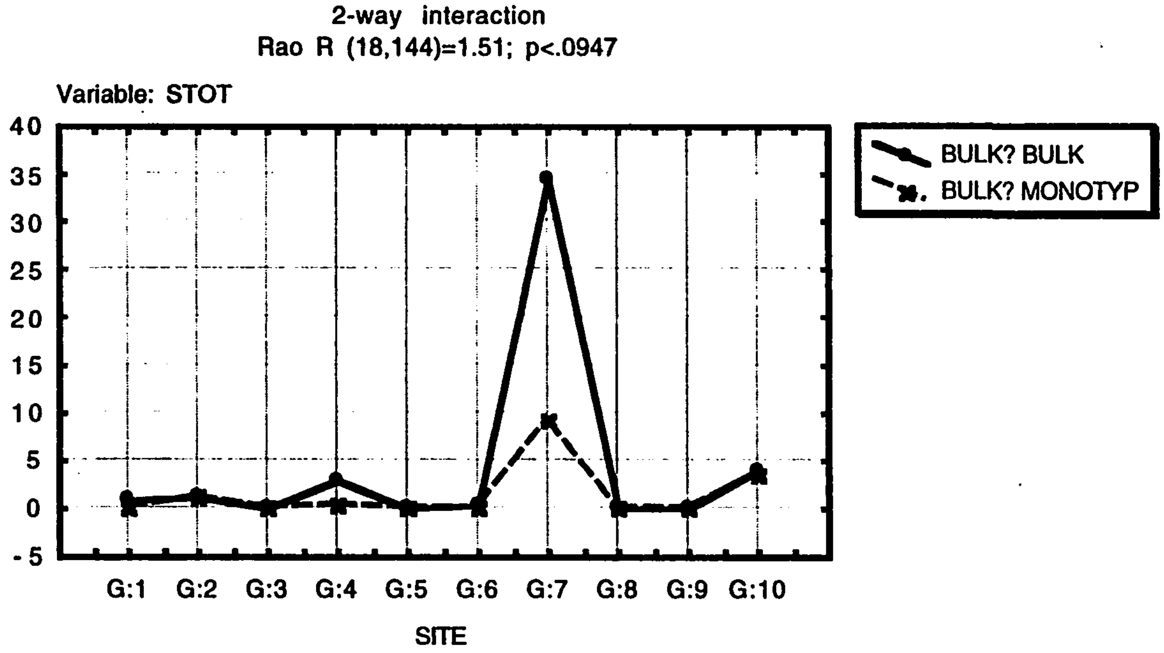


Figure 2-2a. Interaction plot of mean number of seedlings reported per site, by seed-source, for the Middlesex Fells. "Bulk" refers to seeds from bulk samples from the Fells, from the Hammond Woods, or both. "Monotype" refers to seeds from specific gentypes.

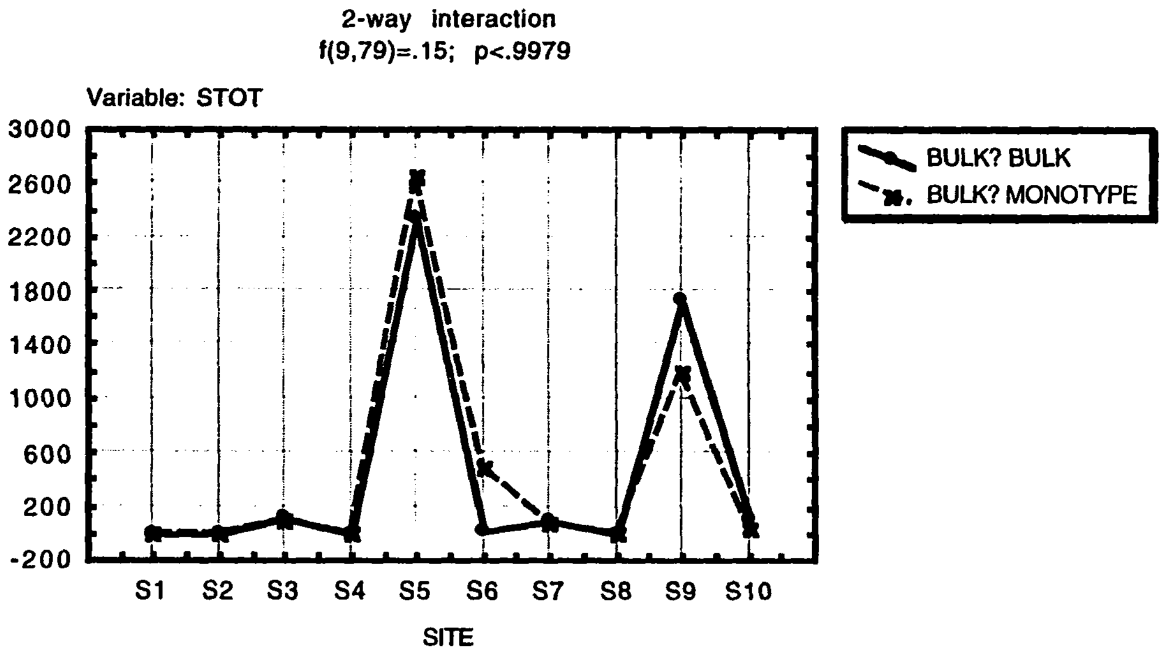


Figure 2-2b. Interaction plot of mean number of seedlings reported per site, by seed-source, for the Hammond Woods. "Bulk" refers to seeds from bulk samples from the Fells, from the Hammond Woods, or both. "Monotype" refers to seeds from specific gentypes.

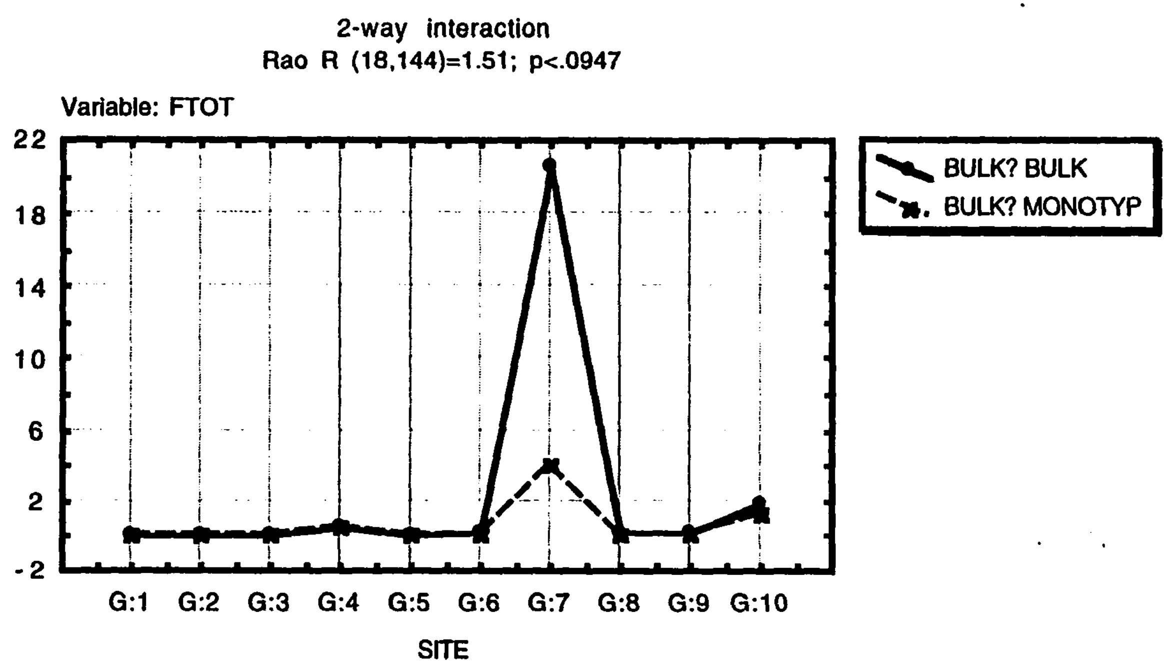


Figure 2-3a. Interaction plot of mean number of flowering individuals reported per site, by seed-source, for the Middlesex Fells. "Bulk" refers to seeds from bulk samples from the Fells, from the Hammond Woods, or both. "Monotype" refers to seeds from specific gentypes.

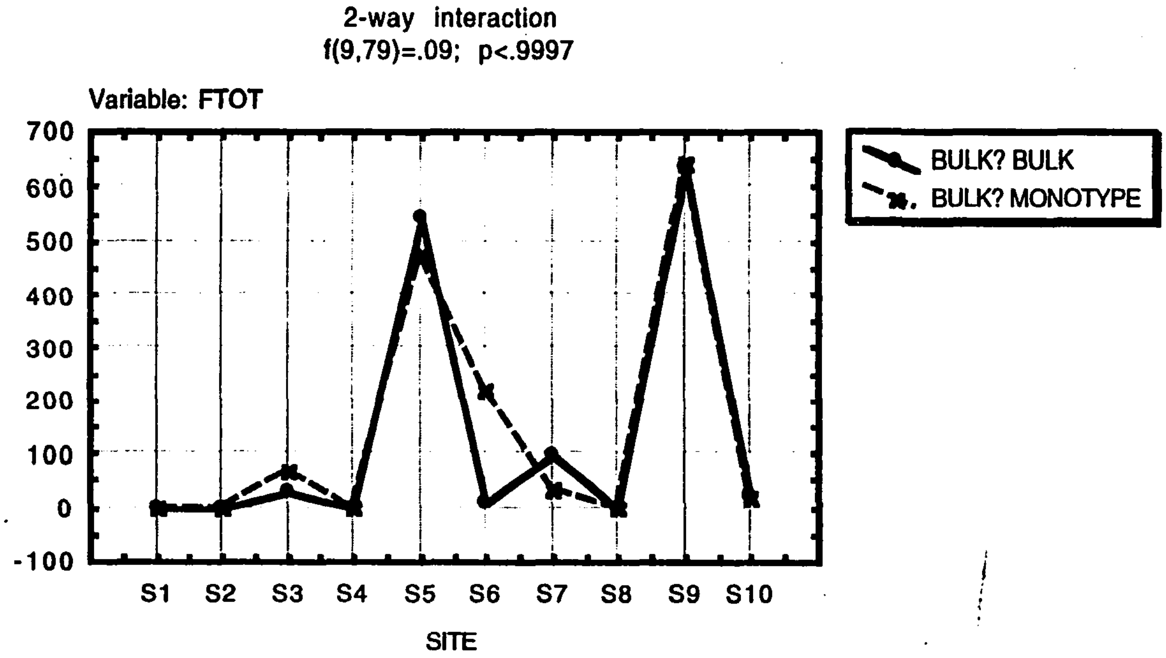
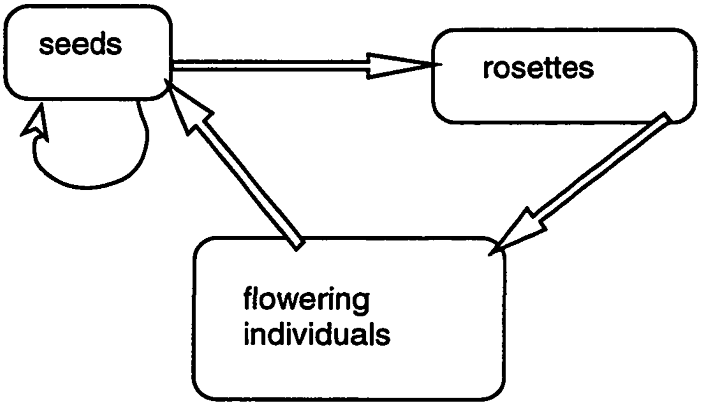


Figure 2-3b. Interaction plot of mean number of seedlings reported per site, by seed-source, for the Hammond Woods. "Bulk" refers to seeds from bulk samples from the Fells, from the Hammond Woods, or both. "Monotype" refers to seeds from specific gentypes.

Figure 2-4. Transition diagram for garlic mustard.



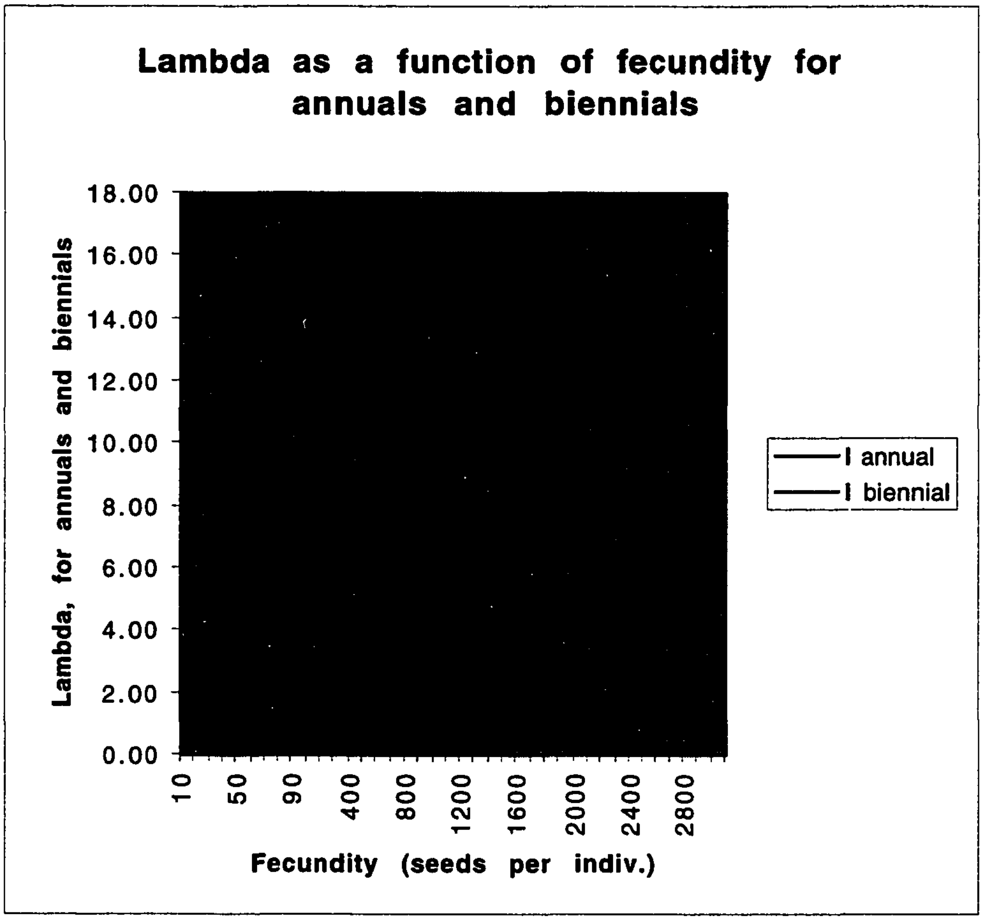


Figure 2-5. λ for annual and biennial forms, assuming survival to the end of the first year 0.1, and survival of rosettes to flower is 50% (0.5).

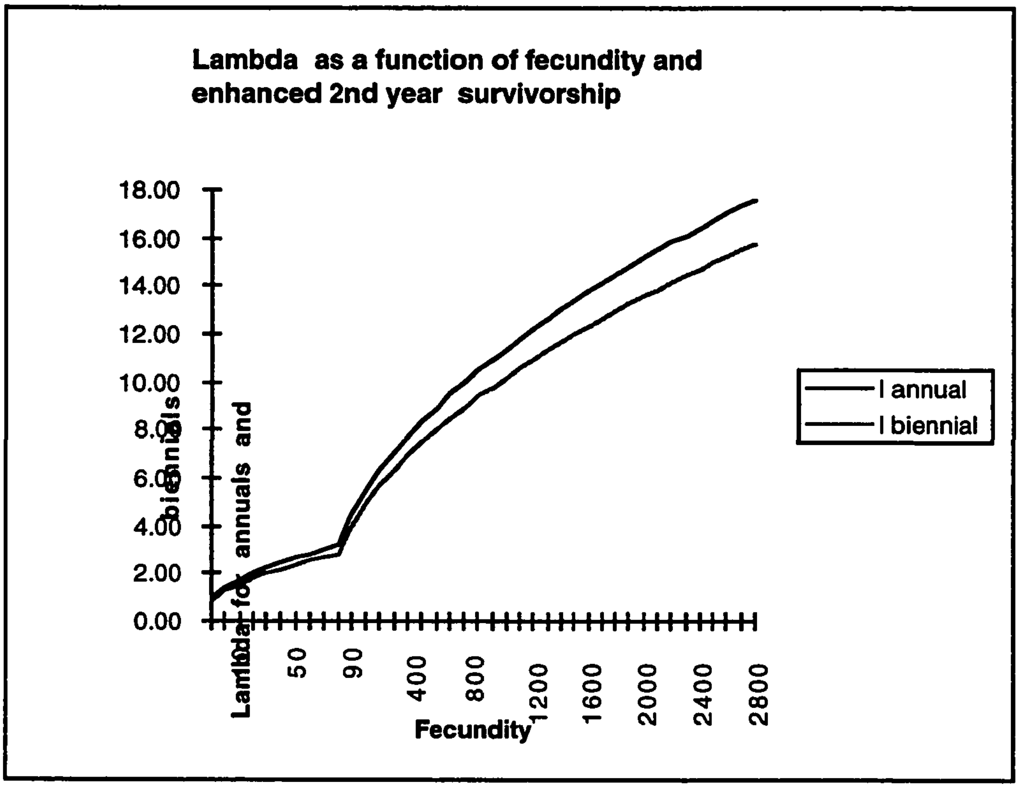


Figure 2-6. λ for annual and biennial forms, assuming survival to the end of the first year 0.1, and survival of rosettes to flower is 80% (0.8).

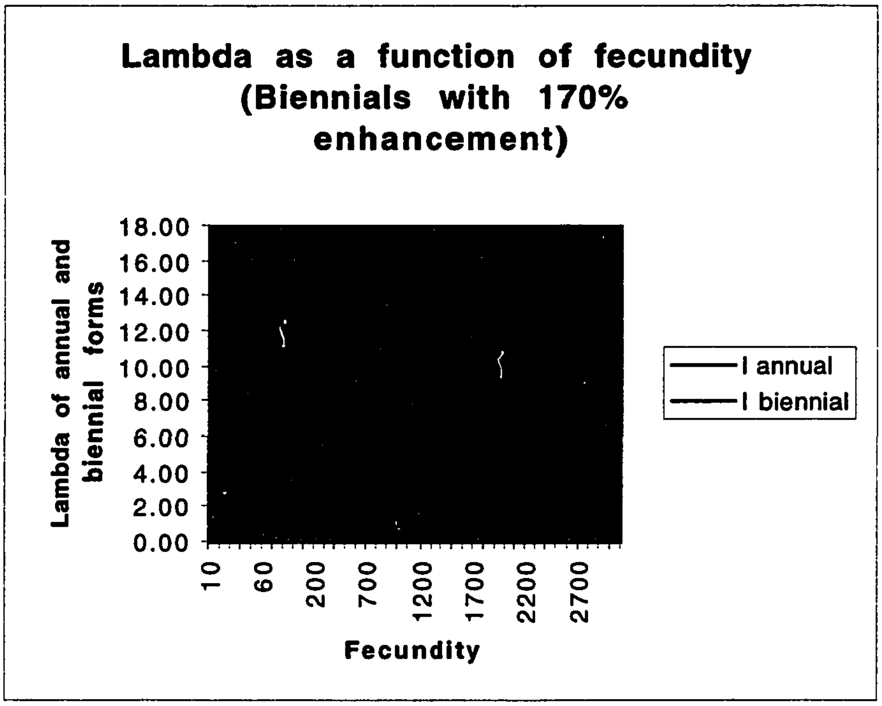


Figure 7-7. λ for annual and biennial forms, assuming survival to the end of the first year 0.1, and survival of rosettes to flower is 50% (0.5). Fecundity for biennials is 1.7 * the value for annuals.

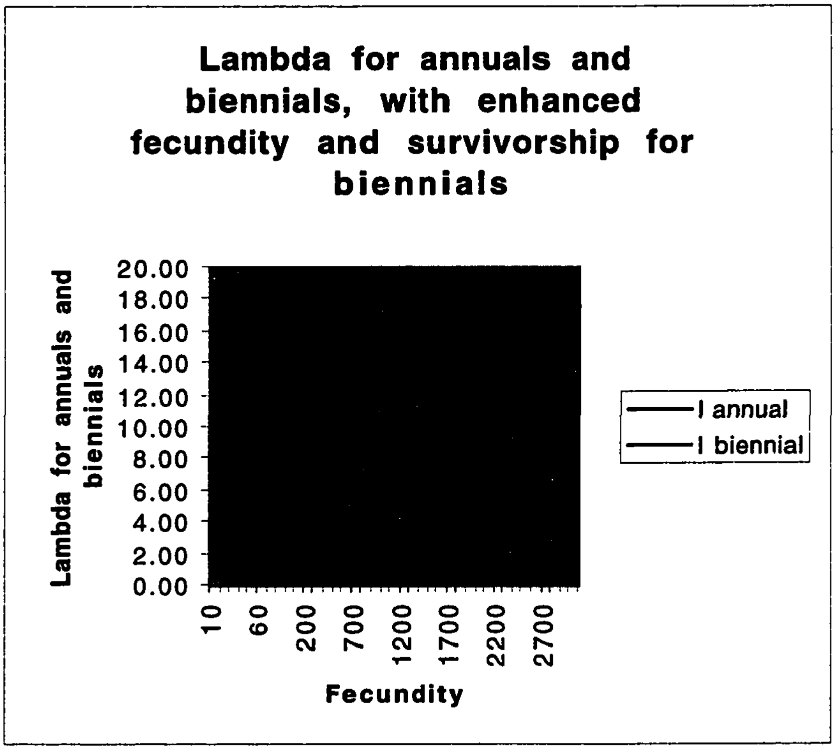


Figure 2-8. l for annual and biennial forms, assuming survival to the end of the first year 0.1, and survival of rosettes to flower is 70% (0.7). Fecundity for biennials is 1.5 * the value for annuals.

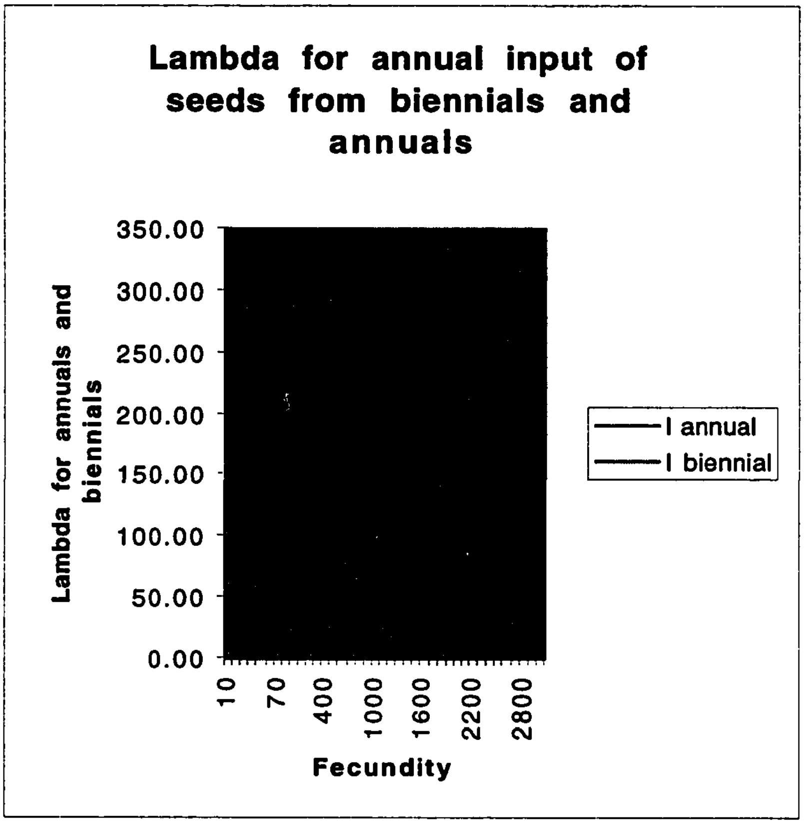


Figure 2-9. λ for annual and biennial forms, assuming survival to the end of the first year 0.1, and survival of rosettes to flower is 50% (0.5).

Fecundity for biennials is 1.8 * the value for annuals.

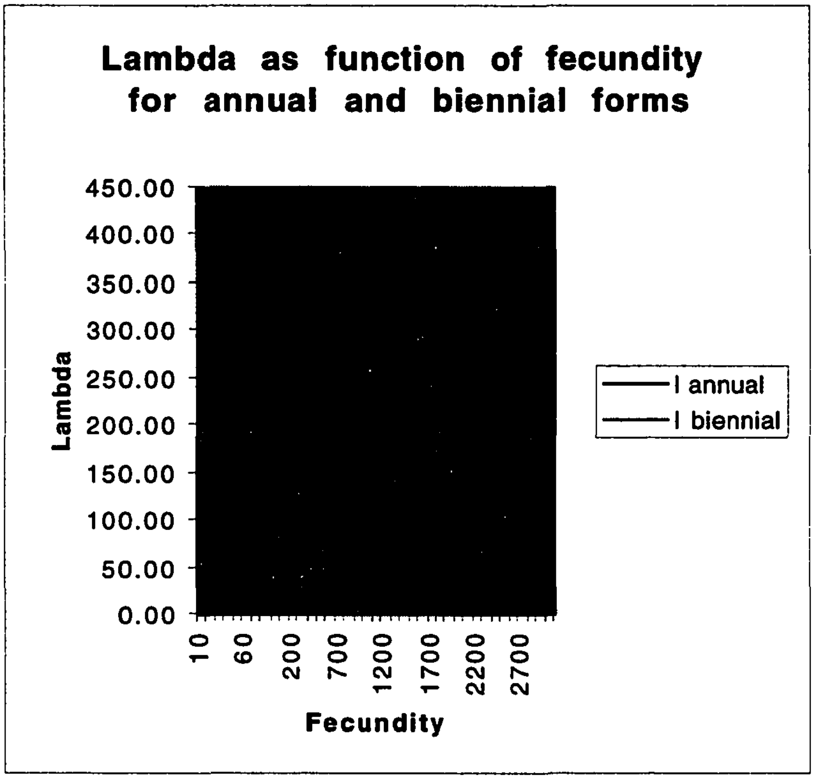


Figure 2-10. λ for annual and biennial forms, assuming survival to the end of the first year 0.1 for annuals, but for biennials of 0.15, and survival of rosettes to flower is 50% (0.5). Fecundity for biennials is 1.8 * value for annuals.

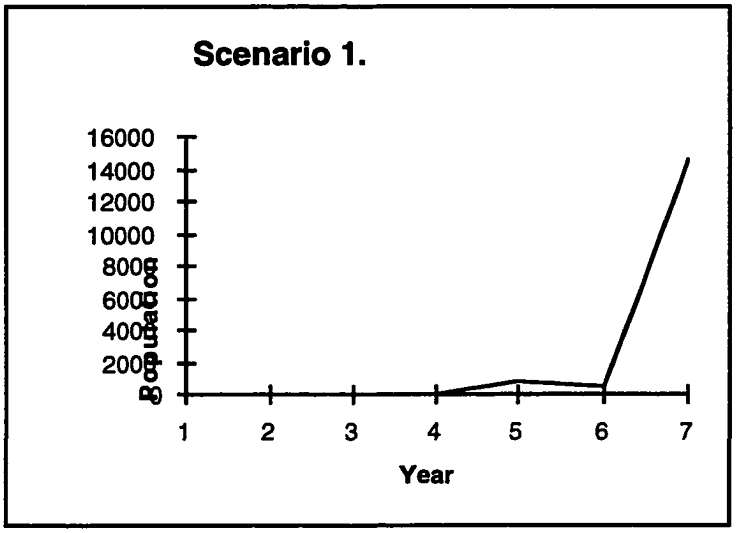


Figure 2-11. Annual population growth, assuming 20 seeds arriving at the site, 90% attrition of seeds in soil per year after year 1, a germination rate of 6.5%, transition rate of rosettes to flowering stage 50%, and an average fecundity of 600 seeds per flowering individual.

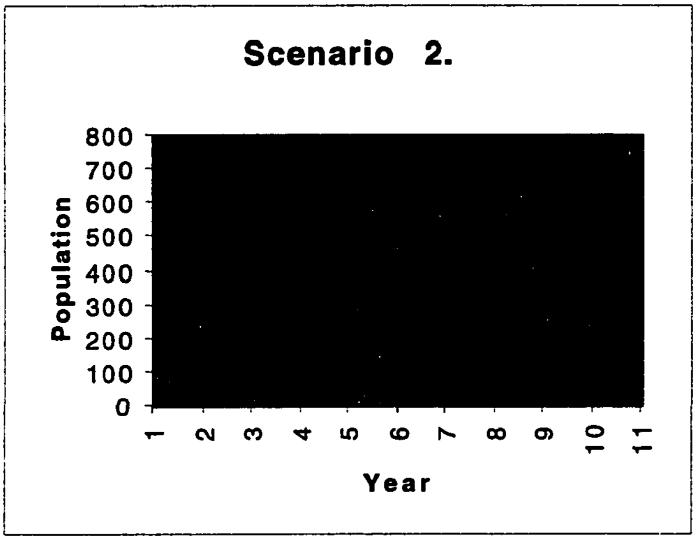


Figure 2-12. Annual population growth, assuming 20 seeds arriving at the site, 90% attrition of seeds in soil per year after year 1, a germination rate of 6.5%, transition rate of rosettes to flowering stage 50%, and an average fecundity of 100 seeds per flowering individual.

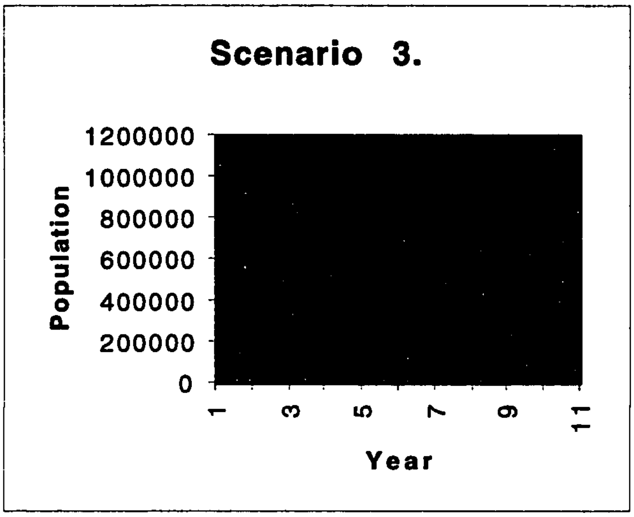


Figure 2-13. Annual population growth, assuming 20 seeds arriving at the site, 50% attrition of seeds in soil per year after year 1, a germination rate of 6.5%, transition rate of rosettes to flowering stage 50%, and an average fecundity of 600 seeds per flowering individual.

Chapter 3.

Genetic and site influences on establishment success in experimental populations of Garlic Mustard (*Alliaria petiolata*)

The colonization of new habitat sites is a critical element in the persistence of species in a particular location. Colonization rates, the analogue for metapopulations of birth rates for populations, are one of the fundamental terms in models of species' persistence in the landscape over time (Hanski 1991). Colonization rates are calculated in many such models as a function of immigration rate, or perhaps better the rate of establishment on a site of reproducing individuals. The relation of genetic variation to colonization success is an important consideration in plant conservation, especially in reclamation or reintroduction efforts, in which the genetic make-up of the artificially created population(s) may be an important, perhaps decisive element of the design (Guerrant 1996). Usually, the genetic make-up of the design of such introduced material is aimed at preserving maximum genetic diversity, which may well increase the likelihood of the population's viability once established. It is not at all clear, however, how the variability which makes for colonization success is related to the variability that makes for longer-term population viability (Parsons and Zedler 1997), and it may be that some genotypes will be more successful colonizers (under particular conditions) than others.

The "fit" between a site and a potential colonist is usually discussed in terms of the site characteristics, but suitability of a site is not an absolute, rather there are a range of values of suitability, depending on the colonizer's characteristics, and indeed weather conditions during the colonization period, as well as intrinsic characteristics of the site such as soil, compass orientation, or slope (Harper 1977, Bazzaz 1996). In plants, the hereditary make-up of the colonizer (including both genome and maternal effects) plays an important but poorly understood role in the interaction between colonizer and potential site. Characteristics that might affect colonization success include: dispersal abilities, germination rates, rates of shoot- or root-elongation, competitive advantages of other types (e.g. for nutrients) and resistance to drought or herbivores (Naylor 1985, Cavers and Harper 1967).

Although there have been many studies of population genetic structure as a result of founding effects and dispersal syndromes (e.g. Hamrick and Nason 1996), there has been little examination of genetic effects on founding or colonization events themselves, and in general the dynamics of species establishment are not widely investigated.

In this paper, I report on two experiments to explore factors affecting rates of success in the establishment of populations of Garlic Mustard (*Alliaria petiolata*) in a conservation area in Greater Boston, using seeds of different maternal genotypes and with different numbers of seeds used to establish the populations. The experiments were designed to address the questions:

Is there a difference in colonization success of different genotypes of a species in a relatively homogeneous microsite?

Does larger number of seeds input increase the likelihood of population establishment?

How likely is the founding of a new population of this species?

The use of a weedy species as a model raises important biological and methodological issues (Peters 1991, Mack 1985). The success of a species introduction cannot be measured only in terms of germination rates, or presence of individuals on the experimental site. The metric has to include successful reproduction, and ideally reproduction by a second generation (Pavlik 1996). The aim of this experiment was to explore possible differences in establishment in the field by genotype, and therefore a rapidly cycling species is desirable. A species such as *Alliaria petiolata* will provide more rapid response in experiments than would polycarpic perennials, whose establishment and population dynamics require quite long-term studies. Furthermore, the strict biennial life-cycle of the species (in North America) means that the age structure of populations will be quite simple, facilitating the exploration of the factors regulating demographic variables.

Experimental organism, study site, and methods

Experimental organism

Garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande, Brassicaceae) is a European native, first recorded in North America in 1868, and in New England in the 1890s (Nuzzo 1993a). A biennial in North America, though a "winter annual" in Europe, adapted to wide range of conditions (Cavers *et al.*

1979, Anderson & Dhillion 1991) in some areas of North America it is displacing native vegetation (Nuzzo 1993b, White *et al.* 1993, Cavers *et al.* 1979). *Alliaria* outcrosses, but is self-compatible, and in fact may usually be selfing. In an experiment conducted in 1993 (Drayton, unpublished data), rate of fruit-formation per flower was essentially identical among (hand-pollinated) out-crossed, selfed, and non-pollinated plants, above 80%, and observations suggested that most flowers were self-pollinated before anthesis. Anderson *et al.* (1996) present evidence of pre-anthesis autogamy. They also report that the result of emasculation experiments exclude apomyxis; these observations are supported by the extensive studies of Cruden *et al.* (1996).

The species has no known dispersal vector (Cavers *et al.* 1979), which is a common characteristic of plants in deciduous forests and margins where this plant is largely found (Hughes et al. 1994; Chambers and MacMahon 1994; Willson et al. 1990). The seeds fall to the ground upon the dehiscence of the siliques, and the majority of seed fall no further off than the height of the mother plant. Dispersal in the study areas was largely down slopes and along paths and roadways, suggesting that long-distance secondary dispersal occurs by tracking of fallen seeds by human and animal feet and vehicle tires, and occasionally by surface water run-off and similar agencies. This dispersal can in fact be very long-distance, as exemplified by the existence of isolated populations in southern New Hampshire (Hillsborough Co.) and central Maine (Kennebec Co.) with no discovered seed source nearby (Drayton, pers. obs.).

Seeds dispersed in late summer overwinter, and germinate early in the following spring, forming a rosette of two or three leaves which persist through the winter. In the second spring following dispersal, rosettes bolt regardless of size, and produce racemes of small white flowers on one or more leafy stems.

Recently established garlic mustard populations show a marked "dimorphism" in their population structure noted in other strict biennial species (Kelly 1985). Thus, the first year after seeds arrive on a site, only seedlings (first-year rosettes) will be visible. The following year, only reproductive individuals will be visible. The third year, again only rosettes from seeds dispersed in Year 2, and so on. This alternation continues for several generations.

Methods and experimental sites

Both these experiments were located in the Hammond Woods in Newton. The Hammond Woods is a conservation area approximately 80 hectares in area. It comprises a mixture of deciduous woods, swamps, parking areas, meadows, ledges, and roads. Many parts of the Woods were already subject to invasion by garlic mustard during the previous five years. Sites for experimentation were chosen in advance of the invading fronts of the plant, on the basis of visual inspection of the sites for suitability, mesic areas along the edges of paths and roadways or forest edges, with partial shade to full sun, and the presence of species usually co-occurring with garlic mustard in the area. Such species included poison-ivy (*Toxicodendron radicans*), jewelweed (*Impatiens capensis*), and wild-geranium (*Geranium maculatum*). Sites were situated at sufficient distance from naturally occurring *Alliaria* populations to make dispersal from those populations unlikely. The lack of appearance of garlic mustard on control quadrats, or on the ground surrounding the experimental sites, suggests that there was little if any migration by seed into the experimental areas, though the invasion of the sites within 5 to 10 years is a virtual certainty.

Methods

Experiment 1.

In 1993, we created experimental populations of garlic mustard by sowing seed on 200 quadrats at a site in the Hammond Woods approximately 15 by 25 meters in extent. The site was a level area of secondary woods, near a commonly used path, but the site was not itself frequently crossed, as far as was known. Quadrats were located at 1m intervals, and marked with numbered wooden stakes in a rectangular grid.

Seeds were collected from 10 large mother plants (referred to hereafter as genotypes) in several populations in Newton, and sown within a few weeks of collection. Seeds were sown directly onto the ground, with no site preparation, within a 25 cm radius of each stake. Treatments consisted of sowing 5, 10, or 30 seeds of one of ten genotypes assigned to quadrats at random, totalling as follows:

10 genotypes
3 numbers of seeds (5, 10, 30)
6 replicates

Thus, for each genotype a total of 270 seeds were sown on 18 quadrats. Seeds were sown on 180 of the 200 marked quadrats, with the 20 remaining quadrats being controls. Also, there were 20 control quadrats on which no seeds were sown.

In 1994, 1995, and 1996, the site was visited several times during the growing seasons. Data were taken on number of seedlings emerging per quadrat, number of flowering plants per quadrat, and number of fruits per flowering plant. In 1995, the first year flowering plants were present, two fruits were taken from each of up to three flowering plants per quadrat, and five seeds were weighed from each sample thus obtained, and mean weight of seeds calculated. Germination rates per genotype were calculated from these data, as well as survival from year 1 to year 2. Statistical analyses were performed using the Statsoft Statistica™ (Release 4.1) program, and Microsoft Excel™ versions 4 and 5.

Experiment 2.

In 1994 we created another grid experiment with a different 10 genotypes at a distance of 20 meters from Experiment 1. There were trees on the site, but it was not completely shaded. In addition to the presence of some indicator species, the site was discovered to be thickly populated with *Urtica dioica,* which provided much more competition for *Alliaria* seedlings, and impeded field work significantly.

Seeds were obtained from 10 large mother plants in the Hammond Woods. In this case, we planted the same number of seeds (10) at each quadrat. The quadrats, one meter apart, were laid out in a Latin Square design as follows:

The overall plot was 12 x 12 quadrats, and the quadrats were assigned to one of four blocks. There were 36 quadrats per block; in each block there were three replicates of the basic unit, which consisted of one site for each genotype (ten seeds of a genotype on a quadrat), plus 6 controls. Thus, each genotype was planted in 12 quadrats, and there were 24 control quadrats with no seeds. Treatments (genotype or control) were assigned randomly within blocks. Seeds were sown directly onto the ground, with no site preparation, within a 25cm radius of each stake. The experiment ran from 1994 through the growing season of 1996, when the plants grown from seed sown in 1994 flowered and set fruit.

The site was visited several times during during the growing season. Data were taken on number of seedlings and number of flowering individuals per quadrat. When flowering plants were present, the number of fruits present on each plant was counted. Germination rates per genotype were calculated from these data, as well as persistence, that is, the proportion of flowering (second year) individuals to rosette (first-year) individuals. Statistical analyses were performed using the Statsoft Statistica™ (Release 4.1) program, and Microsoft Excel™ versions 4 and 5.

Results

A. Number of seeds sown

In Experiment 1, seeds were sown at three different densities, as described above. Fifty out of the 200 (25%) quadrats had no seedlings present in either the first or second year. There was a significant difference in the likelihood of seedlings being present among the three size treatements (5, 10, and 30 seeds), with quadrats sown with 30 seeds far more likely to be occupied than quadrats sown with fewer seeds (Tukey's HSD p = .0001). Quadrats on which 5 seeds had been sown accounted for more than half of the unoccupied quadrats, while only 4 quadrats on which 30 seeds had been sown were unoccupied during the study. Table 3-1 shows the number of quadrats occupied for each treatment by size.

B. Genotype and germination rate

Germination rates for genotypes, that is, the appearance of seedlings aboveground, in these two experiments ranged from a high of 33% to a low of 9%; even the highest value is significantly lower than that obtained in the laboratory, which approached 90%. The seeds of all genotypes showed some germinations, that is, none failed to germinate and achieve rosette status.

Experiment 1 provided evidence consistent with the hypothesis that genetic variation would be discernible at the establishment stage, while Experiment 2 showed no statistical difference among genotypes. In addition, there was no statistically significant difference among the four replicate blocks of the experiment.

Detailed results for each experiment:

Experiment 1

All genotypes were represented by at least some occupied quadrats. Unoccupied quadrats pre genotype ranged from 2 (1.11% for genotype A) to 9 (50%, for genotype B) (Table 3-2), with an overall mean of 14.8%. No seedlings occured on any control quadrat. A one-way analysis of variance of mean germinations by genotype is statistically significant (p = .02). Tukey's HSD test shows genotype A to differ significantly from genotypes D, G, and J. (Table 3-2).

Experiment 2

The germination rates for the genotypes planted in Experiment 2 range from 17.5% to 28.3% (Table 3-3), with an overall mean of 22%. The mean values do not differ from each other significantly, on the basis of a one-way analysis of variance. Twenty nine quadrats (24.2% of planted quadrats) showed no seedlings at all. Occupied quadrats were distributed by genotype as shown in Table 3-3.

The mean germination rates by replicate block are shown in Table3- 4. These show no significant difference, and range from about 19% to about 28%.

C. Genotype and Number of flowering plants

Again, Experiment 1 shows a difference among the genotypes with respect to mean number of flowering plants, with genotype A showing a higher mean. Genotype A also had a significantly higher ratio of flowering individuals to seeds sown overall. Experiment 2, however, did not show any differences by genotype, but there were significant differences by replicate block, thus suggesting that the location had a significant influence on the ability of a plant to reach the reproductive stage.

Experiment 1

Seventy eight quadrats (39% of the total) had no flowering plants during the study. These included quadrats planted with all genotypes, as seen in Table 5. An analysis of variance by ranks showed that the number of flowering plants of genotype A was higher than all other genotypes, with the difference being significant ($p < .05$) in comparison with three other genotypes (Table 3-5), but the number or percentage of unoccupied (or occupied) quadrats did not differ significantly among the genotypes (Table 3-5). Genotype A also had the highest ratio of flowering individuals to seeds planted of any genotype; an analysis of variance and Tukey's HSD test for significant differences showed a significant difference between A and G,I, and J, which did not differ from each other at a significant level.

Experiment 2

No flowering individuals appeared on 60 of the 120 quadrats on which seeds were planted. Mean flowering individuals per quadrat by genotype ranged from 0.17 for genotype J to 1.5 for genotype A (Table 3-6). A two-way analysis of variance shows that there are significant differences ($p = .02$) among the mean values, depending not on genotype but on which square the quadrats are drawn from. Squares 1 and 4 differ significantly from each other and square 4 from the from the overall mean (Tukey's HSD). Table 3-7 shows mean number of flowering individuals by square.

D. Persistence

The persistence of first-year individuals to the flowering stage was calculated as a simple ratio of the number of flowering individuals in year 2 to the number of seedlings in year 1 on each quadrat. The mean for all quadrats in Experiment 1 was 0.73 (Table 3-8), with values ranging from 0.86 (Genotype H) to 0.63 (G,I, J). There was no correlation between germination percentage and persistence values (Spearman's Rank r = 0.011), suggesting that performance in the transition from seed to rosette is not correlated with the transition from rosette to flowering. The mean for Experiment 2 was 0.89.

Experiment 1

Table 3-8 shows the mean persistence by genotype. These values range from 0.67 to 0.83, but the differences are not statistically significant (as tested by one-way analysis of variance).

Experiment 2

The overall mean persistence by genotype for Experiment 2 was 0.82 (± 0.69). The means for the four blocks of the experiment are shown in Table 3-9, and the means for the genotypes in Table 3-10. In neither case was there statistical significance among the values, though the values for blocks 3 and 4 are higher than the values for blocks 1 and 2. This is of interest since in other variables, blocks 3 and 4 do show significant differences from 1 and 2.

E. Number of fruits

The number of fruits per plant probably reflects both heredity and environmental conditions. In Experiment 1, the data suggest that one genotype has a significantly higher value than the other genotypes in the experiment, but in Experiment 2 the significant difference is seen not among genotypes but among replicate blocks.

Experiment 1

The number of fruits were counted; the number per plant ranged from a high of 315 to a low of 1. The mean number per individual was calculated, for the individuals of each genotype. Table 3-11 shows the means for each genotype, which range from 55.7 for genotype A to 95.8 for genotype H. A one-way ANOVA for mean fruit number is significant (p= .05); Tukey's HSD test shows a significant difference between A and H.

Experiment 2

Mean values for fruit number by genotype range from 12 (genotype J) to 59.3 (B). Table 3-11 shows the mean number per plant by genotype. An ANOVA shows no significant difference among the genotypes with respect to number of fruits per plant.

The mean number of fruits per plant, by square was also calculated (Table 3-12). The differences here were significant, as indicated on the basis of a Tukey HSD. Square 4 in particular showed a significantly higher mean number of fruits per plant than other squares.

F. Seed weight

In Experiment 1, samples of five seeds from up to three fruiting plants per quadrat were weighed, and their means compared. Table 3-13 shows mean seed weight by genotype; an analysis of variance showed no significant differences among these values, and this value was not calculated for Experiment 2.

Discussion

These experiments were designed to explore the relation between number of seeds sown and the probability of the establishment of a population, and the relationship between genotype and site in the establishment of new populations. The variables on which data were taken are relevant to the establishment of populations. Germination rates, rates of persistence to flowering, and rates of fruit set are the most important characteristics involved in the establishment of populations, indeed until the first reproduction a population cannot be said to be established. Other experiments with the same species (see Ch. 2) have shown that even with this aggressive invasive species the probability of establishment of a population is rather low: in those experiments, in one set of 100 quadrats reproductive individuals appeared on only 39% of the sites, and in another set of 100 quadrats, reproductive individuals appeared on only 4% of quadrats.

The rate of population establishment, defined as the presence of fruiting individuals, was higher in the present experiments than in the experiment reported in Chapter 2. In the experiments reported here, Experiment 1 showed flowering individuals on 61% of the quadrats, while Experiment 2 shows flowering individuals on 50% of the quadrats.

Within this overall picture, though, these experiments show some of the factors at work in the establishment of populations. First, dispersal can be a limiting factor on the distribution of the species (Primack and Miao 1992): at the majority of sites in both experiments, unoccupied by the species but apparently suitable for it, seedlings emerged, and flowering plants were observed. Second, the rate of dispersal into an area can be an important factor in the probability of success of establishment. In the first experiment reported here, there is a clear relation between the number of seeds sown on a quadrat and the success of establishment of the species on that quadrat: the more seeds arriving at the quadrat, the higher the likelihood that seedlings and flowering plants would be found there in subsequent years. Rosette establishment is a critical threshold event in this species with respect to colonization success, since persistence to flowering can be as high as 86% (as in experiment 1).

The present experiment varied the number of seeds arriving simultaneously on a site, producing the very strong effects reported above. It is worth considering how this relates to natural dispersal events for this or another species. There is no well-established dispersal vector for this species beyond gravity, though circumstantial evidence indicates strongly that secondary dispersal by foot traffic is common in the study areas. It is not established, nor determinable at present, how often aggregations of *Alliaria* seed arrive at potential habitat sites. Informal observation in the field suggests that very many populations begin with the arrival of a small number of seeds, leading to the presence of one or two flowering individuals. Given the relatively high germination and persistence rates for the species, in many cases a colonization event of this size may represent the simultaneous arrival of more than one, but still few seeds, perhaps no more than 10.

On the other hand, the presence of seed dormancy in this species means that in an area of active infestation there may be a succession of small dispersal events, leading over the course of 3-5 years to the accumulation of a seed bank whose persistence increases the effective number of seeds germinating. Thus it is likely that the simultaneous dispersals of this experiment do provide information about the effects of short-term serial dispersals to a particular site in proximity to a consistent seed source.

The experiments cast some light on the "filter" effect of the environment, as it interacts with the genotype of the putative colonizer. Seeds of a particular mother may be better suited to colonize a particular site — during a particular year — than other genotypes. This may be due to maternal effects not related to the genome per se, or may be due to some encoded trait(s). A maternal advantage might result in a seed that performs better at the initial stages of establishment (Naylor 1985), or it might affect the offspring's later growth and reproductive performance (Miao et al. 1991). In the first experiment reported here, one genotype (Genotype A) showed a significantly higher rate of seedling establishment and germination rate than the other nine. Given persistence rates that did not differ significantly from one genotype to another, it is not surprising that this genotype had a higher number of flowering plants overall, but the number of populations established (that is, in the terms of this experiment, the number of quadrats occupied by reproducitive individuals) was not significantly different.

In considering the dynamics of colonization, what long-term consequences for the genetic structure of a population will differential success at seedling-establishment have? If "colonization" means the establishment of a population that will maintain or increase its numbers, then the genetic structure established by initial seedling success will be modified by the differential contributions of the constituent genotypes to the next generation. In the first experiment reported here, the genotype that showed the most success at germination and in terms of number of flowering individuals was not the most successful in terms of average contribution to the next generation (by seed set), and in fact showed a somewhat lower (though not statistically significant) rate of persistence. An experiment of this duration can only raise the question, whether these rates of performance would be a consistent characteristic of the genotypes, but if they were these trends would result in the shifting of relative proportions of representation of the genotypes in the population.

An experiment of this duration also cannot answer for this population other questions about the relation between intial and long-term genetic structure, because it was designed to minimize environmental heterogeneity, both in space and in time. Thus we took data on one generation. If it were possible to follow this population over time, keeping track of the family lines, one could explore whether other characteristics, specifically responses to environmental stresses not encountered during the years 1993-5, altered the population structure and in what ways. It is generally considered that weedy species have a large ecological amplitude (Cousens and Mortimer 1996), but it does not follow that the characteristics which make for successful seedlings are the same as those that make for resilience in reproduction in the face of the same kinds of stress or disturbance as endured by the earlier life stage.

For example, it is well established that in a genetically heterogeneous population of plants some genotypes will show more resistance to pathogens or herbivores than others. The work of Berenbaum and others on the relationship between wild parsnip and its moth herbivore (Berenbaum and Zangerl 1988) demonstrate the differences within and across populations with respect to resistence to herbivory. Recent work by Chew and others on the secondary compounds of *Alliaria* show that they can inhibit oviposition by *Pieris* butterflies whose caterpillars would use the plant as host (Huang *et al*. 1995), and further work has shown that *Alliaria* produces feeding inhibitors against its herbivores. In addition, these compounds seem to be present in much higher concentrations in rosettes than in flowering plants (F. Chew, personal communication). Since the concentration of such compounds is often a function both of nutrient availability and genotype, the differential resiliance to herbivory or some other large-scale disturbance of different genotypes may well mean that an intial genetic structure produced by differential seedling establishment will be altered by subsequent selection pressures on the populations.

One aspect of the design of this study which the experimental data cannot address directly is the value of using a species such as *Alliaria* as a model species for the study of population or ecological processes with implications for other species. The process of choosing a model species for the exploration of biological processes is well-established, of course, as the dependence of much modern biology on work done on *Escherichia coli, Gallus domestica,* *Arabidopsis thaliana, Lactuca sativa,* and *Coenorhabditis elegans* attests. Yet for the most part the value of these "models" lies in the assumption (and subsequent establishment) of some identity of mechanisms for, e.g. genetic transcription or embryological development. In the choice of a species as an ecological model, the great variety of life-history strategies would suggest that the kind of anchor of identity of mechanism that "validates" and qualifies molecular models may not be possible, or even make sense, for ecological processes. Henry Horn once pointed out (Horn 1971, pg.41) that experiments on the effects of allelopathic chemicals in *Sassafras* on lettuce germination only really proved why we don't find more lettuces under sassafras trees. Peters (1991) argues categorically against the value of "model system" in ecological research. Yet we do in fact make provisional generalizations on the basis of such experiments, which are taken as an approximate model applicable more widely. Such an approach opens a new line of research to establish as precisely as possible the value and limits of the model's components. A fundamental question remains, how concrete must the identity (as opposed to the analogy) between the model and the modelled be in order for the model to be useful?

In the case of garlic mustard, the long-term demographic behavior of a population may not be sufficiently useful model for, e.g. polycarpic perennial herbs such as *Sanguinaria canadensis.* Assumptions about ecological amplitude, genetic flexibility, and similar traits in which invasive weeds may differ from such perennials, however, remain to be established in the general case, and in fact are not necessarily relevant in any event to the processes studied in experiments such as those reported in this paper, which explores the interaction of genotype, size of dispersal event, and site characteristics -- factors which are decisive in the life of any plant, annual or perennial. This logic would suggest that within the time frame set by the life-cycle of this species, *Alliaria* can provide a useful model for the exploration of colonization factors common to very many species of varied life-history.

Tables

Table 3-1. Sites occupied in relation to number of seeds sown, Experiment 1.

Number of seeds sown	Number of occupied quadrats	% of quadrats of that size class
5	33	55
10	41	68
30	56	93.3

Table 3-2. Germination success by genotype, Experiment 1. Superscripts mark values that differ significantly.

Genotype	#seedlings	Mean # seedlings per quadrat	Germi nation %	% of genotype quadrats occupied
A	88	4.9^a	33	88.9
B	38	2.1	14	50
C	51	2.8	19	83.3
D	30	1.7^a	11	61.1
E	52	2.9	19	77.8
F	42	2.3	16	77.8
G	27	1.5^a	10	72.2
H	47	2.6	17	72.2
I	39	2.2	14	66.7
J	24	1.0^a	9	72.2

Table 3-3. Germination percentage, and percentage of genotype quadrats occupied for Experiment 2

Genotype	Germination %	% genotype quadrats occupied
A	28.3	10
B	17.5	9
C	18.3	9
D	15.8	9
E	26.7	10
F	19.2	10
G	21.7	9
H	25.8	9
I	20.0	7
J	28.3	9

Table 3 4. Mean germination % by square, Experiment 2

Square	Germination percentage
1	22.0
2	19.0
3	19.0
4	28.7

Table 3-5. Experiment 1: Number of flowering individuals per genotype, number of flowering individuals as a proportion of seeds planted, and percentage of quadrats per genotype on which flowering individuals were found. Significant differences marked by superscript ^{a}.

Genotype	No. of flowering individuals	flowering indivs/seeds planted	Percentage of genotype quadrats
A	61	22.6^a	72.2
B	22	8.1	50
C	30	11.1	55.6
D	23	8.5	61
E	39	14.4	72.2
F	26	9.6	55.6
G	18	6.7^a	50
H	30	11.1	61
I	17	6.3^a	55.6
J	6	2.2^a	38.9

Table 3-6. Flowering individuals per genotype, Experiment 2

Genotype	Seedlings per quadrat	Flowering plants per quadrat
A	2.83	1.5
B	1.75	1.33
C	1.83	0.92
D	1.58	0.833
E	2.67	1.3
F	1.92	1.08
G	2.17	1.00
H	2.58	0.92
I	2.00	1.25
J	2.83	0.167

Table 3-7. Mean number flowering individuals per quadrat, by replicate block, for Experiment 2. Superscript indicates values that differ significantly.

Replicate block	Mean # flowering individuals per quadrat
1	0.6^a
2	0.9
3	1.2
4	1.5^a

Table 3-8. Mean persistence values by genotype, Experiment 1.

Genotype	Persistence
A	0.67
B	0.74
C	0.68
D	0.81
E	0.78
F	0.83
G	0.63
H	0.86
I	0.63
J	0.63

Table 3-9. Proportion of rosette survival to flowering, by replicate block, Experiment 2.

Replicate Block	Persistence
1	0.44
2	0.59
3	0.71
4	0.89

Table 3-10. Proportion of rosettes persisting to flower, by genotype, Experiment 2.

Genotype	Persistence
A	0.64
B	0.83
C	0.72
D	0.67
E	0.81
F	0.66
G	0.70
H	0.48
I	0.68
J	0.21

Table 3-11. Mean number of fruits per plant by genotype for Experiments 1 and 2. Superscripts denote genotypes whose values differ significantly.

Experiment 1		**Experiment 2**	
Genotype	#fruits	Genotype	#fruits
A^a	55.66	A	39.2
B	84.95	B	59.3
C	54.62	C	58.1
D	81.26	D	29.9
E	69.5	E	49.5
F	66.63	F	50.1
G	82.28	G	37.5
H^a	95.8	H	46.0
I	66.65	I	34.3
J	87	J	12.0

Table 3-12 Mean # fruits per plant
Experiment 2, by replicate block (st. dev).

Replicate block	Fruits
1	18.8^{ac} (12.6)
2	27.2^{bc} (19.15)
3	49.6^{abc} (45.7)
4	59.8^{ab} (37.4)
All groups	44.4 (37.9)

Table 3-13. Mean seed weights by genotype, Experiment 1 (st. dev.).

Genotype	Mean seed weight (mg) (standard deviation)
A	2.37mg (1.0)
B	2.5 mg (1.0)
C	1.9 mg (0.1)
D	2.4 mg (0.9)
E	2.3 mg (1.2)
F	2.2mg (0.6)
G	2.4 mg (1.2)
H	2.5 mg (0.3)
I	2.2 mg (1.3)
J	2.8 mg (1.3)

Chapter 4.

Experimental eradications of Garlic Mustard (*Alliaria petiolata*)

The dynamics of extinction are pivotal to many aspects of population ecology, and it is therefore surprising that few experimental studies of extinctions exist. From the point of view of conservation biology, the effects of disturbance or stress on particular life stages, and their influence on population behavior, are a critical element in the analysis of a population's viability (Gilpin and Soulé 1986). Both in predicting a population's future behavior, and in designing a conservation strategy that includes plant reintroductions, it is necessary to understand what are the vulnerable points in the plant's life history (Schemske et al. 1994), and to understand how long a population can endure particular levels of stress or disturbance before extinction becomes inevitable. From the point of view of weed science, it is useful to understand what can drive a pest population to extinction or at least to acceptable levels, when designing a control program for an invasive species. In a reserve area, such control programs must often be designed to take into account both the biology of the pest and the conservation requirements of the reserve (White et al. 1993).

Models or metaphors for the dynamics of a species distributed across the landscape give different emphases to the role of extinctions. In the model discussed in Moody and Mack (1988), a species that is on the increase in an area will be represented by a few large population foci and many "nascent foci," small local invasions which result from long-distance dispersal from a large source population. The total area occupied by these satellites can quickly exceed that of the large, well-established foci, even though they are small enough to escape notice from land managers; their "latent" period of increase and establishment, before these populations are detectible, can be decisive in the rate and irreversibility of the invasion of the pre-existing flora. In this model, rates of extinction of the nascent foci are implicit, but not directly addressed; nor are patterns of dispersal, which will vary with the species, but in general are likely to show a decline in density of propagules as the inverse of distance from the source population.

Metapopulation theory explicitly incorporates rates of extinction into its model of species persistence. Frequent extinctions are taken to be a basic feature of metapopulations (Hanski 1991). In models of metapopulations, a species is assumed to exist in a space consisting of occupied and unoccupied habitat patches. Its viability in that space is regulated by the relative rates of occupancy of new patches and of extinctions at occupied sites. Furthermore, rates of immigration between patches occupied by the species will affect the population dynamics in those patches (Hanski and Simberloff 1997). Thus a basic metapopulation model posits that the fraction of habitat patches occupied at any one time **t** is a function of the local extinction rate (**e**) and the colonization rate (**m**). The values of these parameters are to be determined empirically, case by case, and the determination of each of them presents special problems. For example, except for species with highly specialized habitat requirements, how does one quantify unoccupied habitat patches (Wiens 1997), distinguishing them from unoccupiable sites?

The extinction parameter for populations of a species in a landscape is hard to quantify. Most studies of extinctions are before-and-after comparisons at a landscape scale and period of many years (e.g. Drayton and Primack 1996, Kattan et al. 1994, Norton 1991, Holland and Sorrie 1989), noting presence and absence of species, but such studies give little information about the dynamics of the species' disappearance. Some few studies of plant population viability have monitored extinction rates (e.g. Menges 1990) in species of concern, or as part of a reintroduction effort, in which the area or time of monitoring is relatively small and with a restricted variation of habitat type (DeMauro 1994). Many demographic studies of importance to the understanding of extinctions in face are concerned with mortality rates within experimental populations, rather than extinction rates of whole (sub)populations (e.g. Putwain et al. 1968, Cavers and Harper 1967).

Now, we know in general terms about mechanisms of extinction and about extinction rates on a large scale of time or space. Such extinctions can be due to many causes, but an important class of them involves an increased vulerability to demographic or environmental stochastic events. This increased vulnerability is owing to a disturbance of some aspect of the population structure which affects population growth rates or the rates of colonization relative to that of extinction (Carter and Prince 1988).

Modelling studies (e.g. Foley 1997, Menges 1992) consider that the parameter values in their models can be related to various characteristics of life-history strategies or demographies. For example, it is assumed that larger populations will be more resiliant under disturbance at least for the short term. Again, species with low population growth rates are conjectured to have evolved under conditions of low disturbance (low environmental stochasticity), thus rendering them vulnerable in a changing disturbance regime, less resilient in the face of perturbation. Finally, most models assume an extinction rate that is in a sense independent of population history, for example, age of population. This is significant, since the seed dormancy present in many plant species results in a population of seeds in the soil, which is a source of recruits in addition to the propagules produced in the current year, and to the propagules dispersed into the population from others nearby. The seed-bank enables a kind of immigration from the past (or into the future), whose size will vary with the size of the seedbank itself, and with the physiological regulators of dormancy and germination for each species. This seed-bank population may in fact be an important component of the genetic diversity of the species at that site.

For a new colony, the sensitive parameters will include the rate and density of seed dispersal onto appropriate sites, the rate of propagule establishment, and the mortality rates of seeds and seedlings. Disturbances of established colonies will affect other parameters, however, regulating population growth-rate and leading in the extreme case to local extinction.

A decrease in population size has positive feedback effects, intensifying the "extinction vortex" leading to increasing demographic stochasticity and vulnerability to environmental variation (Gilpin and Soulé 1986). Very often, such interactions are related to a species' breeding system. For example, smaller populations of some species are known to be less successful in attracting pollinators, thus decreasing pollination rates and thus seed set. Smaller populations may become subject to genetic impoverishment. If the species outcrosses, nearer neighbors are more likely to provide pollen than individuals further away; if the local population shrinks in size, genetic variability is thus reduced, which is hypothesized to contribute to increased vulnerability to adverse environmental change, and has been demonstrated to result in reduced seed quality in some species.

On the other hand, there are factors in many populations which result in resilience in the face of severe disturbance. Asexual reproduction is one; seed dormancy is another, as is high reproductive rate (high fecundity and high seed viability). Regeneration of individuals from perennating parts, e.g. sprouting from root or stump after fire or drought, also can contribute to the persistence of a population.

The processes of extinction are thus of interest to evolutionary and conservation biology, and especially in the latter science the focus is on understanding the dynamics that lead to extinction in order to prevent extinctions, or to predict what populations or species are vulnerable to extinction. From a very different point of view, it may be desirable to create extinctions: most obviously in the control of pest organisms, considerable science and technology is directed at the most effective eradication of undesirables. In addition to preventing new incursions of propagules, the prevention of reproduction is a primary focus for weed control. ()

Both from the point of view of exinction prevention and extinction creation, empirical studies of the population dynamics of extinction and resiliance are therefore of interest. There are, however, relatively few experimental studies that document the effects on populations of attempted extinctions. Is it in fact the case that extinctions are common occurances on the metapopulation, or at least landscape, scale? Are newer colonies more vulnerable to extinction than older populations, which thus serve as a persistent source of propagules? What kinds of disturbance might be expected to lead to an extinction, and is one kind of disturbance enough?

We report here an experiment in which we attempted to cause extinctions of wild populations of an actively colonizing plant species, *Alliaria petiolata,* the garlic mustard, an alien bienniel herb currently invading eastern MA and elsewhere in the continental United States (Nuzzo 1991, Cavers *et al.* 1979). Garlic mustard is problematic as a pest species because it can invade woodland areas, and in fact is among the minority of invaders of the flora of eastern North America which prefer more mesic, shaded sites (Brothers 1992). From the point of view of weed control, this characteristic can be problematic, since it may invade conserved forest areas whose composition may preclude very drastic elimination methods such as regular burning or herbicides, owing to possible damage to the conserved flora or fauna in the same location (Nuzzo 1996). Cutting or eradication may be the best alternative (Nuzzo 1991), but what intensity and duration are necessary to eliminate or control an invasion, and how long will monitoring and repeated removals be necessary to ensure permanent success?

In studying the response of experimentally disturbed populations of garlic mustard, we were able to compare characteristics of the wild populations with those of populations experimentally created in the same general locale in which the extinctions were studied. Although the establishment experiments provide information about new colonies rather than established ones, their behavior since establishment provided initial hypotheses about the response of wild populations to experimental disturbance.

In these experiments, we compared 61 experimental populations from which all flowering individuals had been removed for three successive years with 56 control populations. This paper explores the following questions:

- What were the extinction rates for the populations under study?
- What were the population growth rates, area growth rates, and density growth rates for the populations under study?
- Do the extinction rates for control and experimental populations differ?
- Is there a difference in these rates according to size of original population?
- What is the effect of the removal of flowering individuals on age structure in the populations (in this case, the relative proportion of first year and second year plants)?
- How do these characteristics compare with those of experimental populations whose demography and history we know (See chapter 2)?

Methods, site description, and experimental organism

Site description

We conducted the experiments in two forested parks in the greater Boston area. Cold Springs Park in Newton, Ma. has an area of approximately 20 hectares. It includes mixed deciduous woods, trails, wetlands, and maintained and abandoned fields including athletic fields, parking lots, and an aqueduct right of way. It is used extensively for recreations such as hiking and running. Garlic mustard populations are widely distributed along paths and at the edges of parking areas, and extending into adjoining wooded areas. The Middlesex Fells Reservation is approximately 800 hectares 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. Garlic mustard occurs on both halves of the reserve, in three principal areas of infestation, plus a few smaller stands at some distance from these. Although these sites are centered on areas of public access such as parking areas and hiking trails, the populations are expanding into adjacent wooded areas.

Experimental organism

Garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande, Brassicaceae) is a European native, first recorded in North America in 1868, and in New

England in the 1890s (Nuzzo 1993a). A biennial in North America, though a "winter annual" in Europe, adapted to wide range of conditions (Cavers *et al.* 1979, Anderson & Dhillion 1991) in some areas of North America it is displacing native vegetation (Nuzzo 1993b, White *et al.* 1993, Cavers *et al.* 1979). *Alliaria* outcrosses, but is self compatible, and in fact may usually be selfing. In an experiment conducted in 1993 (Drayton, unpublished data), rate of fruit-formation per flower was essentially identical among (hand-pollinated) out-crossed, selfed, and non-pollinated plants, above 80%, and observations suggested that most flowers were self-pollinated before anthesis. Anderson *et al.* (1996) present evidence of pre-anthesis autogamy. They also report that the result of emasculation experiments exclude apomyxis; these observations are supported by the extensive studies of Cruden et al. (1996).

The species has no known dispersal vector (Cavers *et al.* 1979), which is a common characteristic of plants in deciduous forests and margins where this plant is largely found (Hughes et al. 1994; Chambers and MacMahon 1994; Willson et al. 1990). The seeds fall to the ground upon the dehiscence of the siliques, and the majority of seed fall no further off than the height of the mother plant. Dispersal in the study areas was largely down slopes and along paths and roadways, suggesting that long-distance secondary dispersal occurs by tracking of fallen seeds by human and animal feet and vehicle tires, and occasionally by surface water run-off and similar agencies. This dispersal can in fact be very long-distance, as exemplified by the existence of isolated populations in southern New Hampshire (Hillsborough Co.) and central Maine (Kennebec Co.) with no discovered seed source nearby (Drayton, pers. obs.).

Seeds disperse in late summer overwinter, and germinate early in the following spring (Baskin and Baskin 1992). A rosette of two or more leaves forms in the summer and fall and persists through the winter. In the second spring following dispersal, rosettes bolt regardless of size, and produce racemes of small white flowers on one or more leafy stems.

Recently established garlic mustard populations show a marked "dimorphism" in their population structure noted in other strict biennial species (Kelly 1985). Thus, the first year after seeds arrive on a site, only seedlings (first-year rosettes) will be visible. The following year, only reproductive individuals will be visible. The third year, again only rosettes from seeds dispersed in Year 2 will be present, and so on. This alternation continues for several generations. (Figure 1).

Methods

In 1993, we identified 117 naturally occurring populations of garlic mustard in Newton and Medford (MA). In our experiment, we treated as "populations" stands of the plant that included at least one flowering individual and that represent at least one colonization event, at least 2 meters distant from the next stand. We did not consider the issue of gene flow by pollen; as described above, the pollination biology of the plant suggests a low rate of cross-pollination. We also ignored the issue of immigration/emigration as a significant factor in the dynamics of these local stands since this plant is a poor disperser, and the distances between patches were sufficient to preclude significant inputs of seeds, in the absence of human intervention. The likelihood of this had been established in our earlier studies of population establishment, which suggest that the plant spreads slowly and radially from fruiting individuals, with rare long-distance travel.

For each population we recorded the number of flowering individuals and seedlings and the area occupied by each population. Populations were assigned randomly to control or experimental groups. The numbers of control and experimental populations are shown in Table 4-1. The populations in 1993 ranged in size from 1 to over 2000 individuals, with the populations in Medford larger on average than those in Newton, as seen in Table 4-2.

Treatment of the experimental populations consisted of eradication of all flowering individuals (before seed-set): these individuals were pulled up by the roots, with care taken not to break stems off at ground level, which might make regrowth possible. First-year plants ("seedlings") were left undisturbed. In the control populations, we made small holes in the ground the groundin and around the population, without damaging plants, to create the same level of soil disturbance as in comparable experimental populations. We repeated these treatments in 1994 and 1995, taking data on number of first-year and second-year (reproductive) individuals, area of population, and height of largest plant in each population. Statistical analyses were performed using the Statsoft Statistica™ (Release 4.1) program, and Microsoft Excel™ versions 4 and 5.

Results

After a general discussion of types of response noted in several populations, we examine effects on population size, changes in population density and area, and population structure.

A. Trends

The response to the experimental intervention was complex. We can divide the populations according to their response into four categories:

a. Populations that continued to grow vigorously, increasing exponentially each year, with both first- and second-year individuals present each year

b. Populations that stayed at approximately the same size,

c. Populations whose size declined

d. Populations that went extinct (these treated in §B below).

The percentages of populations assigned to each category in the two reserves are shown in Table 4-3.

The populations in the Middlesex Fells and in Cold Springs Park showed significant differences in the incidence of each category. For example, in Newton, extinctions occurred only among experimental populations, and many experimental populations declined. In the Middlesex Fells, there were extinctions among both experimental and control populations, but many experimental populations increased significantly in numbers.

The range of behavior in these populations can be illustrated by some comparisons between control and experimental populations from the two locations.

1. Examples of experimental populations that have continued rapid growth.

Cases 5 and 6 are from the Middlesex Fells. Case 5 was a control population, and Case 6 was an experimental population. Their behavior over the course of the experiment is summarized in the following table. For each year, the number of flowering individuals ("flwer") and first-year rosettes ("Sdlgs") is given. The control population shows rapid annual increase in numbers. The experimental population, though it starts out slightly larger than Case 5, increases almost three-fold over the same period. (See Chapter 2.)

Case	Treatment	Flwr 1993	Sdlgs 1993	Flwr 1994	Sdlgs 1994	Flwr 1995	Sdlgs 1995	Flwr 1996	Sdlgs 1996
5	C	170	1000	500	1000	550	5000	700	2000
6	E	200	500	200	1000	175	200	250	1500

These two populations are similar in initial size, although #5 has a lower ratio of flowering plants in the 1993 population (14.5%) than #6 (28.5%). The proportion of flowering plants in the control population grows until in 1996 it is about 26%. Meanwhile, the experimental population continues to grow, more than doubling in size, and tripling the number of seedlings present, while the proportion of flowering individuals declines to 14.3%. In 1995, there is a considerable reduction in the number of seedlings present, presumably owing to the removal of fruiting adults on the site. Yet in 1996 there is a large number of new seedlings. Although this could be a result of a late flush of germinations from seeds dispersed before 1993, it is likely that this population was augmented by seeds dispersed from nearby sites by human activity, since during these years there was an increase in human traffic. Other possible agencies are transport over the ground surface by runoff water, or the persistence of very small reproductive individuals.

2. Experimental treatment sends population into decline

Case	Treat men	Flwr 1993	Sdlgs 1993	Flwr 1994	Sdlgs 1994	Flwr 1995	Sdlgs 1995	Flwr 1996	Sdlgs 1996
5	C	133	0	2	100	35	40	35	800
7	E	118	10	14	70	58	28	11	0

These two sites, which differ from those just discussed in their strong bimodal population structure, show clearly the effect of experimental treatment. The two flowering individuals on Site #5 (C) must have arisen from seedlings overlooked in 1993. Judging by the simultaneous presence of both seedlings and flowering plants starting in 1993, this population has been present for at least two years. The presence of seedlings on #5 in 1993, and on #7 in 1994 suggests at least one flowering generation before. Seeds from that earlier event persist on Site #7 for two more years, but by 1996 seedlings do not appear. This population is thus in serious decline, and may go extinct with one more year's disturbance. Site #5, however, shows a population distribution that is likely to lead to vigorous increase in the following years.

3. A small control population increases slowly, a small experimental population is remains very small.

Case	Treat ment	Flwr 1993	Sdlgs 1993	Flwr 1994	Sdlgs 1994	Flwr 1995	Sdlgs 1995	Flwr 1996	Sdlgs 1996
6	E	2	0	0	1	0	1	0	1
24	C	2	0	0	0	3	4	5	250

These sites are both likely to be new colonies, as suggested by the small number of seedlings emerging each year. On site #24 (C), the flowering individuals of 1993 and 1995 produce relatively few seedlings. Given this pattern of low seed production and survival, this population is probably at risk if the transition rate from rosette to reproductive individual is low. Nevertheless, the experimental population is clearly marginal, and likely will be exterminated in one more year, either by natural attrition of the (single) rosette plant, or by the exhaustion of the seed bank.

B. Extinctions

For the purposes of this study, we define a population as extinct if there were no individuals, either flowering or rosette, present in 1996. There were 16 extinctions out of the 117 populations used in the study, for an overall rate of 13.6%. Of these, 13 were of experimental populations (21.3%), and 3 were of control populations (5.4%). Excluding two very large and anomalous sites, mean population size for the extinction sites was 6.4. Results for extinctions were somewhat different between the two study sites.

In the Cold Springs Park sites, there were 6 extinctions, all of experimental populations (Table 4-4), thus 8.8% of all populations, or 6/35 experimental populations (17.1%) . The original population sizes at the extinction sites were all less than 5. There were no extinctions among control populations in Cold Springs Park during the study period.

In the Middlesex Fells (Table 4-5), 7 experimental populations and three control populations went extinct during the course of the study, thus 20.4% of the total populations, 26.9% of experimental populations,and 13.04% of controls. The original population sizes at these sites varied from 1 to 1100. In sites #23 (E), #37(E), and #48(C) remarkably few rosettes survived to flower from 1993 to 1994. Other work would suggest a survival rate from rosette to flowering of about 40-50%; in these three populations, the transition rates were in the range of 0.1-0.4%. One possible explanation is an increase in disturbance, owing to park maintenance work in the immediate area.

C. Effects on surviving experimental populations

Effects of the intervention were examined with regard to changes in population size for experimental vs control populations, and for populations on the basis of their original size. Effects were examined for the experimental vs control groups as a whole, and also with reference to the populations' original sizes in 1993, by the size classes described below:

a. <10
b. > 10 but < 50
c. >50 but < 500
d. > 500.

From the basic data on population number, numbers of seedlings and flowering plants per population, and population length and width, several derived measures of population performance were calculated, as follows:

a. Population growth, calculated as N_{t+1}/N_t

b. Population area calculated as length x width
c. Population density, calculated as number of inviduals per unit area(m^2)
d. Proportion of flowering plants in each population, a simple descriptor of population structure.

1. Effects on population sizes

The populations designated as experimental (E) and control (C) were not statistically different in size in 1993 at the commencement of the experiment (Mann-Whitney U-test). In 1994, the differences between E and C groups widened to statistical significance, and it remained true through the final two years (1995-6) that the experimental populations were significantly smaller than the control populations (Table 4-6, Figure 4-2). The two study sites show some differences in the details of their response to the experimental treatment.

In Cold Springs Park starting in 1994, control populations were significantly larger than experimental populations (Table 4-7, Figure 4-3). This relationship is consistent for every size class, though the differences do not reach statistical significance in every case.

The mean population sizes for the Middlesex Fells (Table 4-8, Figure 4-4) are larger at the beginning of the study than in Cold Springs Park. The mean population size for the experimental populations is slightly larger than for the controls in 1993, before experimental treatment. In each successive year the mean population sizes for experimental popuations are smaller than for the controls, but in no year is the difference significant at the 0.05 level.

2. Population growth rates

Overall, the experimental populations show a significantly lower rate of growth than the control populations in the three years of the experimental intervention, where this rate is calculated as N_{t+1}/N_t (Table 4-9). It is of interest that the means for the experimental populations are larger than 1, so that even with the removal of the annual crop of seeds, many of the experimental populations are growing. However, among the control populations, fewer than 3% have growth rates for 1995-6 that are smaller than 1.0, while 52% of the experimental populations have growth rates below 1.0.

As with other categories, the two study areas showed different behaviors. In Cold Springs Park, the experimental groups had a consistently lower growth rate than the control groups (Table 4-10). This difference is seen both for all populations and for all size classes.

In the Middlesex Fells (Table 4-11) it is also true that experimental populations grow more slowly than control populations, but the picture is more complex than in Cold Springs Park. While the experimental populations as a whole show a lower rate of annual increase for 1995 and 1996, these differences are never statistically significant. For the smallest populations, in 1994, after the first eradications, the experimental populations show a larger increase than the control populations do. For populations between 10 and 50, control populations show a slightly higher rate than experimental populations in 1994, but a lower rate in 1995. In the larger size classes (>50), the first year's intervention is followed by a smaller growth rate among the experimental populations, but by 1996 the experimental populations were growing faster than the controls.

3. Changes in population area

A common measure of the rate of spread of weedy species is the area of the populations (Cousens and Mortimer 1996). Using measurements of patch length and width (at the broadest point), garlic mustard patch areas were estimated, in square meters (m^2). As Table 4-12 shows, the experimental and control populations began with similar areas, but after the inception of the experimental treatment, the control populations increased at a much greater rate than the experimental populations, such that significant differences between the two treatments resulted in each of the three treatment years. Again, there were differences between the Cold Springs Park and Middlesex Fells populations.

For Cold Springs Park, experimental and control populations overall are significantly different in area and in growth of area in 1995 and 1996, after two years of the experimental treatment (Table 4-13). These differences are seen in the smallest size class in 1996, and in the second grouping (10-50) in 1995 and 1996 as well. In the third size class (50-500), there is no trend discernible. In the largest class of populations (>500) the means show a wide disparity in size, with the experimental populations much smaller in area, on average, but so few populations are represented that statistical significance cannot be established.

In the Middlesex Fells populations (Table 4-14), the overall mean areas for experimental populations are smaller than for control populations each year after the experimental eradications began. These differences do not , however, approach statistical significance. From the point of original population size, again the picture is complex. In the smallest size class, the mean area of experimental populations started out slightly smaller than that of control populations in 1993, and continued smaller in 1994 and 1995. In 1996, however, the experimental population mean was higher than the mean for control populations. The same pattern appears for the populations originally between 50 and 500 individuals in size. The populations in the 10-50 size class started with a smaller mean population size (owing to our choice by number of flowering individuals, not total number), and this difference persists.

4. Changes in population density.

Change in population density, though derivative from population size and population area, can reflect an "intensification" after the initial phases of a colonization, as population densities build towards their limits. It is of interest that both the experimental populations and the controls showed a marked decline in density, suggesting that the population growth was accompanied by a strong expansion of occupied area. In many cases, this was visible as an attenuating band of rosettes stretching beyond the body of the population. As Table 4-15 shows, the experimental populations showed a greater reduction in density than the controls, and in 1996 experimental mean density was significantly different from that of control populations. Table 4-16 shows the differences by size-class for Cold Springs Park; by 1996, the experimental populations showed a lower mean density than control populations, in all size classes except the smallest. In the Middlesex Fells populations, these differences do not become significant (Table 4-17).

5. Changes in population structure

One might predict that in control populations, as individuals flower and set seed, the proportion of flowering individuals would fall, by comparison with experimental populations, in which recruits to the rosette stage, limited to seeds from the seed bank, would be steadily declining. The data in fact bear this out, as depicted in Table 4-18 and Figure 4-1.

In Cold Springs Park, a differentiation between the experimental and control populations begins in the second year of the experiment (Table 4-19). In the Middlesex Fells populations (Table 4-20), experimental populations overall show a lower proportion of flowering plants in 1994 and 1996. This difference is not statistically significant in any year. When original population size is considered, only in the smallest populations do the experimental populations show a consistent (lower) difference from controls.

Discussion

Most models of metapopulation dynamics assume a relatively high frequency of extinction of local populations. Yet there have been few studies of rates of population extinction over short time periods (Husband and Barrett 1996).

In this study populations of different size were subjected to repeated disturbance whose effect was to interrupt seed production in a strict biennial plant. *Alliaria petiolata* in North America has a simple life-history, with three stages: seed, first-year rosette, and reproductive second-year plant. Individuals surviving to the second year flower and set seed regardless of size. The experiment examines the relative contribution of repeated reproduction in the persistence of populations. It could be conjectured that, given the vulnerability of an individual's transition between the first two stages, from seed to rosette and from rosette to flowering, that removal of the seed rain might substantially increase extinction rates, owing to demographic or environmental variability. This experiment confirms that this is the case.

With respect to extinctions, it is clear that at the Cold Springs Park sites the experimental intervention had a significant impact on the fate of garlic mustard populations. Chapter 2 reported on experiments in which garlic mustard populations were created experimentally. In that study, Newton and Medford populations showed strongly different rates of establishment and population increase, and they also showed rather large differences in extinctions of these new populations, which were in no case older than four years (counting the year of dispersal, in which the populations all started as 20 seeds). The Newton populations in that study showed an extinction rate of 7.9% and the Medford populations a much higher rate of 62%. The general pattern in both studies is that smaller populations are more vulnerable.

The results reported here for Cold Springs Park, with extinction rates of experimental populations at about 17%, are much higher than the "natural" rates of extinction in the new populations created in 1992. In all cases in Cold Springs Park the populations going extinct were quite small, none larger than 6 individuals.

This is in contrast to the populations in the Middlesex Fells, where about 27% of experimental populations went extinct. This is much higher than the rate for control populations,13%, but both rates are much lower than in the new populations created in the Fells in 1992.

Events that have demographic impact on a population often do not extinguish the population immediately, but rather render it more vulnerable to further disturbance and damage. Demographic stochasticity can render a population more vulnerable to environmental effects, or an environmental event can reduce or fragment a population so as to make demographic stochasticity more of a problem for long-term viability. Both these trajectories will have population-genetic effects which may have positive or negative feedback effects. The complex interactions have been called "extinction vortices" (Gilpin and Soulé 1986) , and it is of interest to understand something of the dynamics of these vortices on organisms of different life-history and ecological characteristics.

The very different results for the Middlesex Fells and Cold Springs Park suggest that environmental (site) factors are important to the resiliance of populations under disturbance. As seen in Chapter 2, site conditions are likely to control the establishment of new populations at the germination and establishment phase. In the experimental populations in the present case, recruitment from the seedbank is likely to be the principal mechanism for persistence.

In both cases, the losses are concentrated in small populations. The differences between the two sites are of unclear cause, though the Fells populations were on average larger than the Cold Springs park populations at the beginning of the experiment. Thus the expected result, that smaller populations are more vulnerable than large, is borne out on at least two counts, the vulnerablity to disturbance of small populations, and the resilience of large populations. Yet in fact many smaller populations did survive, and this suggests that the seed bank has played a role in the persistence of these populations. The seed bank can be conjectured to have a "rescue effect" (Hanski 1996) analogous to that provided to animal populations by immigration from source to sink populations, with the result of buffering populations against adverse conditions of relatively short duration. The continue emergence of seedlings in experimental plots shows that the input of seeds from previous flowering seasons was substantial, and the dormancy of 3-5 years noted for the seeds of this species (Baskin and Baskin 1992). Continuation of the experimental treatment for another two or three years might in fact result in the extirpation of more of these populations.

Thus another variable in the dynamics of this invasion is time: older populations, even of relatively small size, can be more resilient to disturbance than more recent ones. One can infer from the data here that, in species with even short seed dormancy, populations that are relatively recently established are more vulnerable to disturbance than are populations that are longer established. As described in Chapter 2, *Alliaria* shows a strong bimodality with respect to the relative proportion of first and second year plants, in new populations. Even with an input of 20 seeds in the first colonization event, it might take 7 years to reach a point of stability, in which there is a substantial proportion of both life-stages present in the population, with a flowering-to-total population of approx 30%.

Moody and Mack (1988) describe weed invasions as becoming established through "nucleating satellite" populations, a variant of the "mainland-island" metapopulation model. These satellite populations are the result of relatively long-distance dispersal events from a source population. They would be more vulnerable to extinction, but those that survive will begin a process of exponential growth perhaps not evident to observation for a few years, until the satellites reach a point of stability and size at which they are resiliant to disturbance. Mody and Mack suggest that the way to prevent the occupation of new sites is to prevent the intiation of satellites. Their model assumed that [a] new foci are only detected and controlled when they reached a critical detectable size; [b] allowed large and small satellites to expand at different rates, and [c] allowed the rate of satellite initiation to increase in a logistic relationship with total area occupied by the species.

On a landscape scale, an invader's spread is limited by the availability of colonizable sites and dispersal limitations. At a particular site, "spread" will continue until the colony reaches the boundaries of the suitable site, and also reach the limits of population density within the site.

Our data on *Alliaria* illustrate many aspects of this general model. There is a growth in density and in area for populations of all sizes. The experiments show also that once an invasion has reached a certain size, definable in terms of number of populations, size of populations, and age of each population, its eradication in practical terms becomes extremely difficult. With a species such as garlic mustard, the relative slowness of dispersal may limit the rate of establishment of new populations, but as Mack and Moody suggest, for such a species the "latent period" in which the metapopulation is becoming established unnoticed may ensure that the the species is resilient to many kinds of dsiturbance, as involved in eradication attempts.

Nuzzo (1991) suggests that fire may be the most effective control method for this species. The drawback is that repeated burnings will be necessary in an area in which the plant has become well established (perhaps within 5 years of arrival), and the effects on co-exising vegetation may be severe enough that the treatment will in the short term at least be undesirable in its effects. Eradication, that is the removal of the flowering plants before seed set, would be effective early on in an infestation, with much less impact on the coöcurring species. However, if eradication is not complete, or if the treatment ends while a substantial seed bank population persists, the species can maintain itself on a site for long periods of time, or resume explosive growth.

Therefore a disturbance that prevents seed production or dispersal will have different effects depending on when it occurs in the life of the population, the intensity of the disturbance, and its duration. There are thus interactions both with the plant's life history, and with the history of a particular population.

At first, the population shows a strict alternation between first-year rosettes and second-year flowering individuals. Kelly (1985) posits a "strict biennial" life-history pattern for a small number of species, for example *Linum catharticum*. These species, if their seeds exhibit any dormancy or survival in the seedbank, characteristically show two subpopulations; as garlic mustard illustrates, in the first few years of a population, there is a "seedling year" and a "flowering year." At least with garlic mustard, however, this is not a permanent feature of a population. The length of time that this striking pattern persists will vary, depending on the reproductive output of flowering individuals, and on the rate of rosette establishment. If relatively few seeds survive as rosettes, then until seed output is large relatively few seeds will germinate from the seed bank during years in which flowering plants predominate. Over time, however, the population structure will change, including both first and second-year plants simultaneously. Therefore there comes to be an annual rather than a biennial seed input, and population growth can become explosive. In addition, the enhanced and annually renewed seedback provides a measure of resilience to disturbance. How much resilience? By building on the population model sketched in Chapter 2, we can explore this first by setting the stage for a population with stable age distribution, and then examining the effects on population growth of the experimental eradications reported in this chapter.

To recapitulate from Chapter 2, garlic mustard population dynamics can be modelled with a Lefkowitz matrix representing a stage-structured population. (In this case, age-structure and stage-structure are very similar, given the strict biennial habit of the organism.) In only one life-stage, seed, can an individual transition to the same stage in a succeeding year. In no case can an individual make a transition to a previous stage (e.g. a reproductive individual cannot become a rosette again).

As in Caswell 1989, the model is of the form

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where the matrix **n**(t) is a vector which contains the numbers of individuals in the population in each life stage at time t. **A** is a projection matrix, whose cells contain the probablities of transition from each stage to the next stage. The projection matrix is thus of the structure:

	seed	rosette	flowering indiv
seed	seed-to-seed	rosette to seed (empty)	flowering to seed (fecundity)
rosette	seed-to-rosette	rosette-to-rosette (empty)	flowering to rosette
flowering indiv	seed-to-flowering (empty)	rosette to flowering	flowering to flowering (empty)

Values for the transition parameters can be chosen on the basis of observations of the populations discussed in Chapters 2 & 3. Seeds can remain in the seedbank for 3-5 years, with an exponential decay of viability,with something like 5-10% of ungerminated seeds remaining viable per year. Many will germinate the first year after dispersal, however. In populations we have started with known quantities of seed, the proportion of seed reaching rosette stage ranges from 0.1 to 0.39 (See Chapters 2 & 3). Of these, a proportion will survive to reproduce in the second year, this proportion varying from 0.09 to 0.63. Flowering individuals vary in fecundity, of course, with some noted with only a single fruit bearing two or three seeds, and other large individuals bearing 300 fruits, each with 10-14 seeds, thus dispersing as many as 4200 seeds. Using values chosen from these data, we can parametrize the matrix as follows:

Seed-to-seed 0.1 * (1 - .065)	Rosette to seed (empty)	Flowering to seed (fecundity) 600 seeds/plant
Seed-to-rosette 0.065	Rosette-to-rosette (empty)	Flowering to rosette (empty)
Seed-to-flowering (empty)	Rosette to flowering 0.5	Flowering to flowering (empty)

Given these assumptions, a rate of population growth, λ, can be calculated as

$$\lambda = 2.7231.$$

Sensitivity of λ to small changes in the various elements of the matrix is given by the following sensitivity matrix:

Seed-to-seed **0.34**	Rosette to seed (empty) 0.0081	**Flowering to seed** **(fecundity)** **0.0015**
Seed-to-rosette **13.8**	Rosette-to-rosette (empty) 0.3294	Flowering to rosette (empty) 0.0605
Seed-to-flowering (empty) 75.16	**Rosette to flowering** **1.79**	Flowering to flowering (empty) 0.3294

Of the cells that are defined (not empty), a small change in the the probability of transition from seed-to rosette will have the largest effect on population growth rate. Next most important is the transition from seed-to-tseed, then from rosette to flowering. Surprisingly, fecundity (flowering to seed) seems relatively unimportant, implying that a small change in fecundity will have relatively little impact on λ. However, given the high rate of seed set, and especially the very large range of variability in potential seed set (from approx. 10 to approx. 3200), this makes sense. In passing, it is worth noting that the "seed-to-flowering" cell, empty for this model, nevertheless has a potentially large impact on the demography of the plant: if in some cases the plant acted as a annual, so that some individuals flowered in their first year, this would substantially affect the rate of seed production, and eliminate the second-year life-stage. This is of interest since the species in temperate North America seems to have evolved from a winter annual habit (as reported in Europe) to a biennial habit; it would be of interest to explore the evolutionary biology of this change, especially if, as Kelly (1985) suggests, one can draw a distinction between strict and facultative biennial life-histories.

An analysis of elasticity, that is proportional change in λ resulting from a proportional change in the matrix elements, provides a result more in line with the behavior of the plant in North America:

seed-to-seed 0.0117	rosette to seed (empty) 0	flowering to seed (fecundity) 0.0056
seed-to-rosette 0.3294	rosette-to-rosette 0	flowering to rosette 0
seed-to-flowering 0	rosette to flowering 0.3294	flowering to flowering 0

The transitions from seed to rosette and from rosette to flowering plant are relatively more important than fecundity in a stable population structure based on the assumptions we have used.

Using the model sketched above, we can first examine the effects on λ of variation in the fecundity parameter. Table 4-21 shows a comparison of the value of λ derived above with the values resulting from the substitution of other fecundity values in the projection matrix. The values are derived from the data presented in Chapters 2 & 3, and represent maximum, minimum, and mean values for fecundity, based on numbers of fruits reported on individual plants and assuming a mean of 12 seeds per fruit.

Thus it can be seen that a six-fold increase in average seed production is calculated to result in an 83% increase in growth rate. At the other extreme, a 98% decrease in mean seeds per individual results in a rate of population growth considerably below 1, thus a rate of decrease. A value of about 30 seeds per individual will result in a λ of about 1 (1.0238).

However, what kind of population trajectory does this model imply for a population which experiences a repeated perturbation whose effect is to reduce seed production? What effect does the perturbation have when applied at various points in the history of a population, and for varying lengths of time? These questions are of interest from the point of view of control of an infestation, since they bear directly on the intensity and duration of intervention necessary to reverse or extirpate a garlic mustard invasion.

The following scenarios suggest the resiliance of the population to an interruption of seed-set. With one exception, all assume that when the intervention begins, it is 100% effective in preventing the dispersal of seeds.

The following model cases all start with an initial 40 seeds arriving at the site. The models assume the following, derived from observed values: a transition probability from seed to first year rosette of 0.065; a transition probability from rosette to flowering stage of 0.5; mean fecundity (number of seeds produced) per individual of 600; a survival in the seed bank of 0.1, and arbitrary initial number of seeds, 40. In addition, the annual population is calculated, and also the proportion of flowering individuals in the population, and the annual rate of increase, λ, calculated as the ratio of population in a given year (N_{t+1}) to the population of the previous year (N_t), thus N_{t+1}/N_t). Case 1 shows the population growing without intervention. Case 2 shows the population growing for five years, with flowering individuals removed each year thereafter. Case 3 shows the trajectory with eradication of seed-bearing individuals beginning in the 7th year. the same intervention, but with a resumption of seed dispersal after two years of removal of flowering individuals. Case 4 shows the eradications beginning at at age 11. Case 5 shows 100% interdiction of seed production beginning in year 5, with dispersal resuming after 3 years. Finally, Case 6 shows 95% removal of seed-producers beginning in year 3.

Case 1: Population grows undisturbed (Figure 4-7)

In this case, the effects of increasing density are not included as the population grows very large, that being immaterial to the point, which is to demonstrate the explosive growth often seen in *Alliaria* populations, and also the unusual population structure at the early stages of an infestation. Note that the proportion of flowering individuals in the population vacillates between 1 and 0 for the first few years; as as result, λ alternates strongly as well, which continues for some years.

Case 2. Population is strongly perturbed starting in the fifth year. (Figure 4-8)

In this scenario, seed dispersal is prevented (as by our experimental eradications) starting in year 4, and continuing each year thereafter. All other population parameter values remain the same. With intervention at this early stage in the population's existence, extinction happens within two years.

Case 3. Eradication begins at year 7 (Figure 4-9).

This scenario shares the same assumptions as the previous ones, with respect to transition probabilities. The only difference is the time of first intervention, after 6 years of undisturbed growth. The alternation between dominance by seedlings and dominance by flowering individuals continues until the seventh year; with the removal of seed source, the seed bank is depleted, and the proportion of flowering individuals approaches 1 rapidly. Extinction is delayed for four or five years

Case 4. Disturbance begins in the 11th year (Figure 4-10). In this scenario, the population declines slowly, but the seedbank provides a continuing source of new recruitment for some years -- the actual length depending on the longevity of the seeds in the soil. Given the large number of seeds produced up until the point that eradication efforts begin, even a low proportion of surviving seeds can extend the potential life of the population for some years.

Case 5. Disturbance lasts three years, then undisturbed growth resumes (Figure 4-11).

In this case, the population suffers a clear decline, reflected in the higher proportion of reproductive individuals and in the values for λ. Nevertheless, with the resumption of seed production, the population recovers rapidly, as does the rate of growth in "seeding years."

Case 6. Eradication prevents 95% of seeds from dispersing (Figure 4-12).

It can be seen that the population levels off, but even with almost complete interdiction of seeds, the population (still showing the residual oscillation of the two "subpopulations" characteristic of earlier stages of establishment) shows a slow mean increase in size. This in fact corresponds to the value calculated above (Table 4-21) assuming a fecundity of 30 seeds/plant, which yields a value for λ of 1.024, thus roughly a 2% annual increase in population. At this level of reproductive output, the population essentially remains stable in numbers, and always with the potential of explosive growth if fecundity should increase.

Alliaria petiolata is in many ways a typical invasive species, self-compatible, with a short generation time, and a high potential rate of increase. Yet its strict biennial habit in North America renders it vulnerable to disturbance in the first few years of a population's existence, if that disturbance interdicts the seed rain. The short seed dormancy can provide some resilience in the face of such disturbances, so that if seeds are dispersed at all the population can survive and resume its rapid expansion.

If the population is well-established, perhaps 5-7 years old, however, the seed bank is not the only source of resilience: seedlings appear each year, from seeds that are one season old, plus those surviving from previous seasons. As this contribution from the seedbank continues, the population moves from an alternation between all first-year and all second-year plants, achieving more stability with the presence of both life-stages simultaneously.

From the point of view of weed control, these findings are of interest because *Alliaria* can be a pest in areas that are sensitive to some control methods. Since the species is not resistant to fire, burning can be used to eradicate invading populations in areas in which the native species are not adversely affected by fire. In mesic woods and margins where some species are not fire-resistant, however, fire is not desirable as a control method. In this case, eradication may be the method of choice, as causing the least amount of damage to the area. Our results show, however, that this approach must begin rather early in the life of an infestation, must continue for some time until the seed bank is exhausted, and must be thorough enough to prevent seed dispersal from a few individuals that may not be noticed in the surrounding undergrowth, given *Alliaria*'s high reproductive potential.

Having studied the behavior of a weedy species such as *Alliaria*, can one make any generalization from this behavior to that of other species with other life history patterns? Although *Alliaria* shows a high rate of germination in the laboratory, the probability of reaching the rosette stage is rather low in many field situations. Yet the mean values found in one study, used here in our models, are comparable to those achieved in many cases with perennials (less than 10%). Once a seedling has lived through its first growing season, it has a 20-50% chance of reaching reproductive age. Again, this shows relatively low mortality by comparison with some other species, but again mortality of new recruits tends to drop significantly in other spcies that have been studied, once the seedling stage has been passed; indeed, that is why so many plant reintroduction efforts have used transplants propagated until they have passed that vulnerable stage.

The two parameters that seem to contribute most to the resilience of populations of *Alliaria* are fecundity and age of the population. It is obvious that a population producing higher number of seeds will be more likely to persist than other populations. It is that many other species are quite vulnerable, since in many species reproductive adults produce relatively few viable seeds. Population age is important, and of course interacts with other factors, since time allows for the differentiation of population structure, which may render the population less vulnerable to some kinds of disturbance that might target one life-stage more than another, as seen even with the relatively simple population structure of *Alliaria,* in which apparently older populations are more resistant to disturbance than newer ones.

A final consideration for conservation biology is related to the resiliance of an introduced or protected population to disturbance. For example, the low rates of success for reintroductions of perennial species reported in Chapter 1 and references there are due in part to herbivory or other damage to seedlings or adult plants. In those cases, the colonies were all of quite recent age, so that even for species that exhibit seed dormancy (e.g. *Sanguinaria canadensis* or *Osmorhiza claytoni*) a destructive event early in the colony's life will be fatal, as the seed bank either is very small, or has not yet begun, because the new plants have not yet begun reproducing. In addition, for most of those species, there is a pre-reproductive period sometimes lasting years, during which time the population is vulnerable because there is no local source of recruits. In a setting in which there is likely to be intense herbivory or other disturbance, the new colony will require protection, and monitoring even post-protection for several years, before its establishment can be considered successful; and for each species, the characteristics contributing to population resiliance must be characterized and incorporated in a reintroduction or recovery plan.

Tables

Table 4-1. Numbers of control vs. experimental populations in the study sites

Site	Control	Experimental
Cold Springs Park	33	35
Middlesex Fells	23	26
Total	56	61

Table 4-2.
Size distribution of study populations in
Cold Springs Park (Newton, MA) and
Middlesex Fells Reservation (Medford, MA)

	Cold Springs Park			Middlesex Fells		
Size	**Total**	**Control**	**Experi-mental**	**Total**	**Control**	**Experi-mental**
≤ 10	26	11	15	15	7	8
> 10, <50	17	10	7	8	4	4
> 50, <500	18	7	11	14	7	7
>500	7	5	2	12	5	7
Total	68	33	35	49	23	25
mean	151.62	212.15	94.54	339.57	342.26	350.7
(st. dev)	321.5	426.2	160.53	533.8	552.9	533.6

Table 4-3. Percentages of populations showing each of four types of response to treatment in Cold Springs Park and the Middlesex Fells

	Cold Springs Park		Middlesex Fells	
Response class	Control %	Experimental %	Control %	Experimental %
1 steep growth	84.4	30.6	61.9	21.7
2 Flat population	15.6		23.8	34.8
3 Population declines	0.0	27.8	0.0	13.0
4 Population goes extinct	0.0	16.7	14.3	30.4

Table 4-4. Populations going extinct in Cold Springs Park. Numbers in parentheses show numbers of flowering (f) and seedling (s) individuals. E = experimental treatment.

Site	Treatment	Year			
		1993	1994	1995	1996
18	E	3 (2 f, 1s)	3 (1f, 2s)	2 (1f, 1s)	0
25	E	1 (1f)	0	0	0
27	E	2 (1f,1s)	1 (1f)	1 (1f)	0
37	E	1 (1f)	0	0	0
50	E	3 (1f,2s)	2 (2f)	0	0
68	E	6 (1f, 5s)	5 (5f)	0	0

Table 4-5. Populations going extinct in Middlesex Fells. Numbers in parentheses show numbers of flowering (f) and seedling (s) individuals. C= control, E = experimental treatment.

Site	Treat-ment	Year			
		1993	1994	1995	1996
4	E	22 (2f, 20s)	0	0	0
7	E	3 (3f, 0s)	5 (1f, 4s)	4 (1f, 3s)	0
12	E	1 (1f)	0	0	0
16	E	1 (1f)	0	0	0
23	E	1120 (120f, 1000s)	1 (1f)	0	0
37	E	1000 (1f, 1000s)	4 (0f, 4 s)	0	0
50	E	1 (1f)	0	0	0
9	C	2 (2f)	0	0	0
11	C	1 (1f)	0	0	0
48	C	43 (23f, 20s)	0	0	0

Table 4-6. Population Means (Standard Deviations) and Medians by treatment. An * marks years in which Control differs significantly (p < .05) from Experimental.

Year	Mean (st.dev.)		Median	
	Controls	Experimental	Control	Experimental
1993	260 (478)	197 (381)	38	27
1994*	299. (445)	128 (265)	101	28
1995*	596 (1241)	160.81 (490)	75	22
1996*	2140.29 (3308)	367 (715)	917	28

Table 4-7. Mean population sizes (with st. dev), for control (C) and experimental (E) populations in Cold Springs Park. When control and experimental values for a particular year differ significantly (p ≤ .05), they are marked with *

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total population	215. (439)	99. (167)	245* (406.)	57.* (99)	448* (958)	65* (94)	2318* (3569.	328* (694) 4 2)
By size class								
≤ 10	2. (1.8)	2 (1.2)	19 (18)	4.42 (6)	34 (44)	12 (22)	696* (996)	2289* (718)
10-50	28 (11)	28 (89)	157* (112)	18* (22)	504 (1200)	20* (27)	2050* (3290)	74* (19)
50-500	252 (152)	167 (112)	551* (738)	123* (134)	199 (255)	102 (59)	1460* (1119)	469. (692)
> 500	977 (694)	605 (144.)	534 (359)	180 (120)	1569* (1329)	349 (38)	7397 (5360)	1275 (1308)

Table 4-8. Mean population sizes (with st. dev), for control (C) and experimental (E) populations in Middlesex Fells.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total pops	342.26 (553)	350.68 (534)	402.67 (515)	238.13 (387)	993.13 (1744.)	332.05 (823)	1354 (1697)	503.78 (811)
By size class								
≤ 10	2.86 (3)	1.71 (1)	20.33 (28)	16.67 (24)	67.67 (113)	21.67 (33)	176 (2912)	131.75 (264)
10-50	33.5 (12	20.00 (7)	194.75 (251.95)	33.25 (48)	40.00 (38)	13.67 (14)	2237.5 (1810)	801.4 (1007)
50-500	209.71 (109)	129.14 (59)	225.83 (231.51)	191.86 (186)	125.5 (856)	67.75 (97)	875 (884)	752.33 (1120)
> 500	1250.00 (553)	1110.14 (436)	1240.00 (163.55)	650.17 (562)	3530 (1571)	1107 (1351.48)	3600 (1273)	1750 (0)

Table 4-9. Mean growth rates for all populations. An * marks years in which the differences are significant.

Year	Control	Experimental
1993-4*	5.1	3.3
1994-5*	3.3	1.4
1995-6*	11.9	6.4

Table 4-10. Mean growth rates of populations in Cold Springs Park (Standard deviations in parens)
C = control populations, E = experimental populations.
* Marks groups significantly different within each year.

	1993-4		1994-5		1995-6	
	C	E	C	E	C	E
Total population	6.11* (11)	2.22* (5)	3.21 (9)	1.51 (2)	13.21* (13)	6.87* (21)
By size class						
≤ 10	11.36 (18)	4.33 (7)	2.68 (4.)	1.63 (2.)	18.67* (17)	15.67* (39)
10-50	5.9* (5)	0.56* (0.59)	5.42 (15)	0.7 (0.62)	11.17* (13)	1.14* (1)
50-500	2.06 (2)	0.76 (0.37)	0.64 (10)	1.64 (2.)	13.82* (8)	4.25* (6.)
> 500	0.64 (0.36)	0.28 (0.13)	3.13 (2)	2.58 (2)	5.25 (2)	3.48 (3)

Table 4-11. Mean Population growth rates,
Middlesex Fells., by year (standard deviations in parens).
C = control populations, E = experimental populations.
Differences are not statistically significant at $p \leq 0.05$.

	1994		1995		1996	
	C	E	C	E	C	E
Total pops	3.45 (5.0)	5.01 (13.48)	3.4 (5.91)	1.23 (1.14)	4.58 (6.26)	4.34 (93.8)
By size class						
≤10	5.46 (6.87)	16.11 (24.37)	7.39 (11.66)	1.16 (0.43)	8.31 (10.23)	3.56 (5.04)
11	6.35 (7.05)	1.56 (2.42)	0.56 (0.17)	0.9 (.00)	---	----
50-500	1.35 (0.95)	1.24 (1.07)	2.21 (1.46)	1.05 (1.18)	3.85 (0)	4.76 (4.74)
> 500	1.22 (0.68)	0.6 (0.63)	2.73 (1.00)	1.54 (1.75)	1.12 (1.03)	4.67 (0)

Table 4-12. Areas (in m^2) by treatment.
Years in which differences are significant ($p \leq 0.05$) are marked by *.

Year	Control	Experimental
1993	14.7	16.04
1994*	19.5	11.8
1995*	37.7	25.04
1996*	60.1	18.5

Table 4-13. Mean areas of Cold Springs Park populations in m^2. (Standard deviations in parens)

* Marks groups significantly different within each year.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total Pops	6.45 (14.54)	4.68 (10.84)	5.61 (12.45)	4.7 (8.72)	25.27* (43.5)	10.89* (17.51)	46.47* (74.84)	16.91* (29.37)
By size class								
≤ 10	0.13 (0.23)	0.44 (1.19)	0.03 (0.1)	0.21 (0.55)	3.21 (4.3)	3.53 (6.72)	20.48* (12.16)	4.5* (8.45)
10-50	2.44 (1.93)	2.57 (1.41)	2.47 (4.46)	0.58 (0.86)	14.43* (4.67)	2.9* (3.65)	24.6* (12.16)	3.21* (3.95)
50-500	7.36 (11.01)	11.19 (17.46)	5.18 (5.3)	9.84 (9.68)	18.31 (14.44)	22.18 (23.5)	30.13 (14.4)	32.73 (40.77
>500	27.08 (28.58)	8.06 (11.23)	24.8 (24.18)	24.47 (12.16)	105.2 (70.9)	31.88 (25.63)	162.64 (138.79)	60.2 (25.17)

C = control populations, E = experimental populations.

Table 4-14. Mean areas of Middlesex Fells populations

C = control populations, E = experimental populations.
Differences are not significant ($p \leq 0.05$) in any category.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total Pops	26.56 (39)	31.34 (78)	41.32 (68.58)	22.06 (52)	63.48 (125)	51.17 (136)	120.57 (196)	21.41 (46)
By size class								
≤ 10	1.06 (3)	0.39 (0.58)	1.87 (3)	0.37 (0.62)	7.6 (11)	0.99 (2)	1.5 (2.)	2.0 (4.)
10-50	10.3 (13)	1.0 (2)	12.00 (13)	1.00 (2)	2.67 (4)	0.88 (0.78)	---	---
50-500	20.52 (23)	20.26 (30)	17.79 (20)	12.56 (20)	64.75 (105)	16.63 (22)	40.00 (11)	58.04 (81)
>500	92.2 (30)	90.71 (131)	137.00 (87)	69.00 (89)	231.00 (167)	169.2 (231)	---	---

in m^2. (Standard deviations in parens)

Table 4-15. Densities in 1993 and 1996, in indivs/m^2. Differences between Control and Experimental populations are significant in 1996 ($p = 0.5$)

Year	Control	Experimental
1993	176	321.6
1996	38.01	27.6

Table 4-16. Mean population densities in Cold Springs Park. C = control E = Experimental.
(Standard deviations in parens)
* marks where C and E values differ significantly.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total Pop.	93838 (523,537)	174,735 (748,581)	295312* (605,036)	3627.12* (112,669)	336.48 (17645)	727.62 (2619)	707.92* (2489)	4021.54* (14,135)
By size class								
≤ 10	7458.8 (8895.93)	6069.27 (6256.25)	243186 (190362)	99095.94 (176940)	4012.02 (3158)	2008 (4212)	1844.47 (4032)	14036.17 (25058)
10-50	29.66 (27)	14.3 (9)	683104* (911678)	4853.27* (7554)	47.47 (127)	16.52 (16)	123.56* (227)	17.36* (22)
50-500	430562 (1137420)	547305 (1297121)	4371.17 (10926)	21.67 (19)	11.78 (8)	16.35 (28)	48.58* (28)	25.46* (37)
>500	94.25 (103)	2117.93 (2933)	25.59* (13)	7.00* (1)	18.02 (15)	15.45 (11)	50.56* (25)	18.23* (14)

Table 4-17. Population density
in Middlesex Fells. C= control, E= experimental.
(Standard deviations in parens).
C and E values do not differ significantly in any year.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total Pops	8740 (33333)	402333 (2001601)	84.96 (275.4)	696.79 (2573)	17.67 (13.98)	43.24 (112.57)	13.754 (11.47)	35.94 (28.52)
By size class								
≤ 10	5810 (7789)	5716 (5343)	11.1 (2.51)	53.33 (25.17)	13.37 (8.65)	147.49 (218.43)	--	---
10-50	40010 (79993)	1924.46 (1398.31)	---	---	27.86 (24.24)	15.11 (5.03)	---	---
50-500	34.66 (33.45)	69.54 (150.47)	28.25 (36.75)	38.69 (42.12)	7.99 (7.48)	6.09 (4.33)	19.53 (16.57)	15.51 (17.72)
>500	12.24 (3.33)	1430018 (3783416)	236.15 (510.86)	2009.19 (4466.6)	21.75 (15.77)	6.76 (4.69)	---	----

Table 4-18. Proportion of flowering individuals, by year and treatment

Year	Control	Experimental
1993	0.65	0.61
1994	0.16	0.28
1995	0.44	0.51
1996	0.047	0.16

Table 4-19. Proportion of flowering individuals in study populations, in Cold Springs Park. (Standard deviations in parens)
C = control populations, E = experimental populations.
* Marks groups significantly different within each year.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total popss	0.64 (0.37)	0.59 (0.42)	0.1* (0.2)	0.26* (0.31)	0.52 (0.27)	0.68 (0.32)	0.02 (0.02)	0.17 (0.29)
By size class								
≤ 10	0.94 (0.25)	0.84 (0.31)	0.153 (0.37)	0.23 (0.4)	0.63 (0.35)	0.54 (0.36)	0.01 (0.02)	0.02 (0.04)
10-50	0.77 (0.28)	0.85 (0.27)	0.03* (0.04)	0.43* (0.41)	0.53 (0.29)	0.70 (0.41)	0.02 (0.03)	0.10 (0.22)
50-500	0.44 (0.39)	0.37 (0.41)	0.11* (0.13)	0.36* (0.26)	0.39 (0.25)	0.60 (0.3)	0.026 (0.013)	0.32 (0.37)
> 500`	0.23 (0.26	0.15 (0.2)	0.18 (0.08)	0.57 (0.46)	0.41 (0.14)	0.21 (0.02)	0.027* (0.022)	0.012* (0.04)

Table 4-20. Proportion of flowering plants to total population, Middlesex Fells populations (Standard deviations in parens)
C = control populations, E = experimental populations.
Differences between Control and Experimental populations are not significant (p ≤ 0.05) for any category.

	1993		1994		1995		1996	
	C	E	C	E	C	E	C	E
Total pops	0.62 (0.36)	0.54 (0.4)	0.27 (0.35)	0.18 (0.25)	0.25 (0.12)	0.37 (0.28)	0.19 (0.15)	0.12 (0.13)
By size class								
≤ 10	0.93 (0.19)	1 (0.00)	0.43 (0.44)	0.07 (0.12)	0.25 (0.12)	0.25 (0.21)	0.18 (0.28)	0.05 (0.00)
10-50	0.58 (0.38)	0.38 (0.42)	0.08 (0.04)	0.03 (0.008)	0.33 (0.0)	0.37 (0.12)	--	--
50-500	0.55 (0.38)	0.51 (0.34)	0.36 (0.5)	0.12 (0.18)	0.21 (0.03)	0.69 (0.32)	0.1 (0.14)	0.14 (0.17)
> 500	0.33 (0.22)	0.2 (0.17)	0.18 (0.1)	0.39 (0.34)	0.21 (0.19)	0.22 (0.19)	0.3 (0.05)	0.14 (0.0)

Table 4-21. Effects on λ of different values for fecundity in the projection matrix

Fecundity (seeds/indiv)	λ	% change from model λ, 2.732
3750	4.989	+83%
852	3.057	+12%
30	1.024	- 62%
12	0.763	- 72%

Figures

Figure 4-1. Proportion of flowering individuals in the population, by year and treatment.

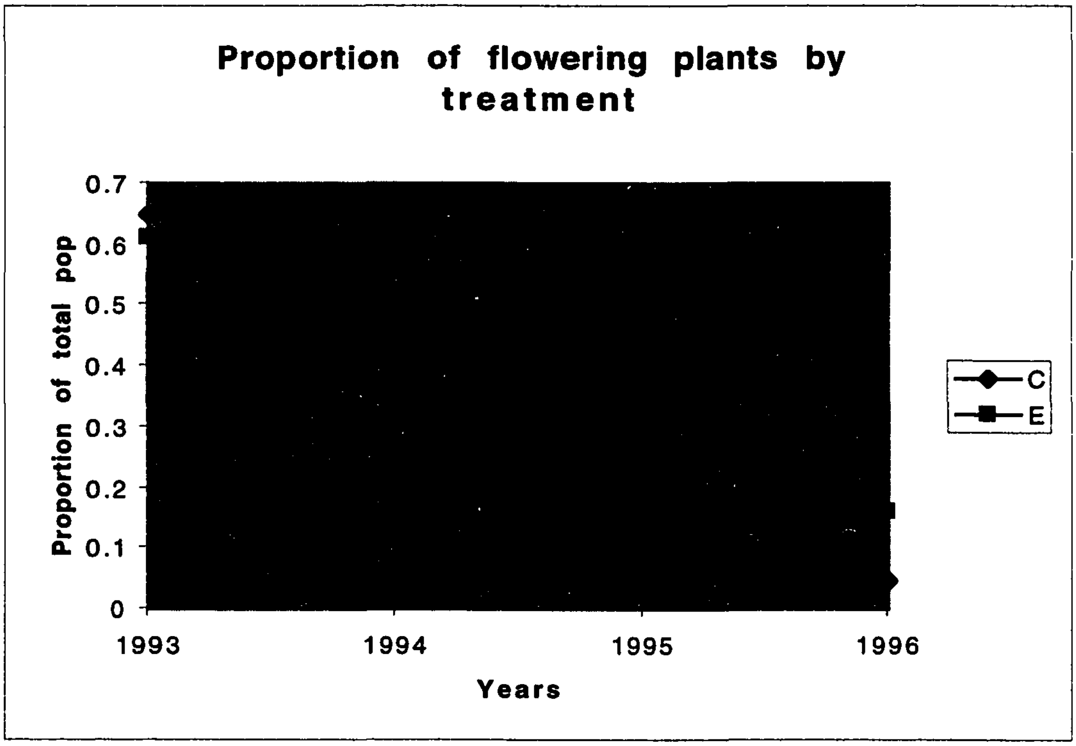


Figure 4-2. Mean population sizes for control and experimental populations

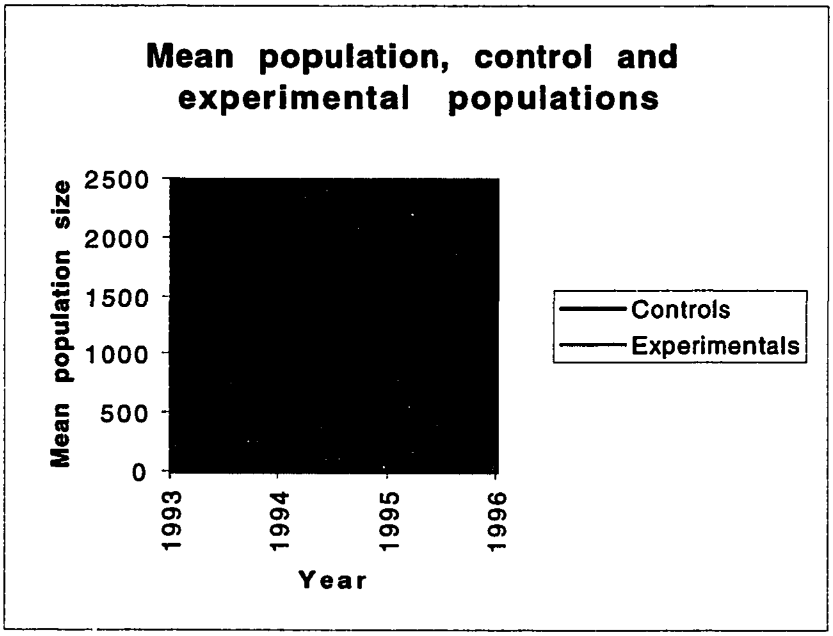


Figure 4-3. Cold Springs Park:
Mean population sizes for control and experimental populations, by year.

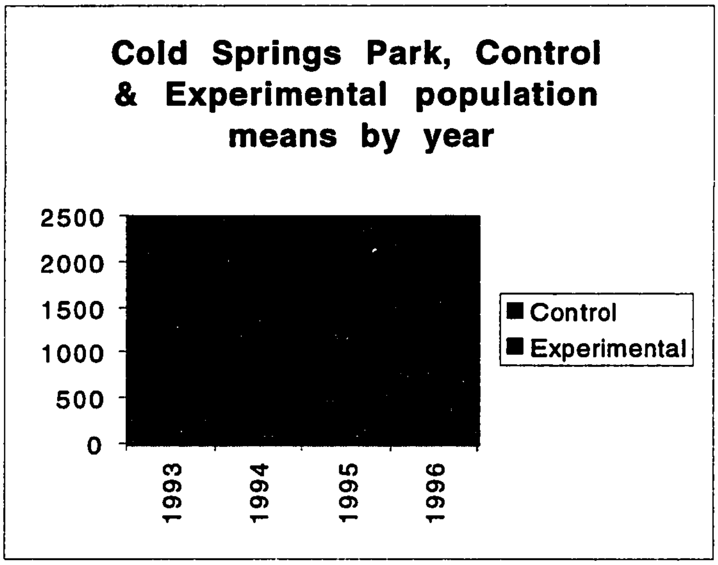


Figure 4-4. Middlesex Fells:
Mean population sizes for control and experimental populations, by year

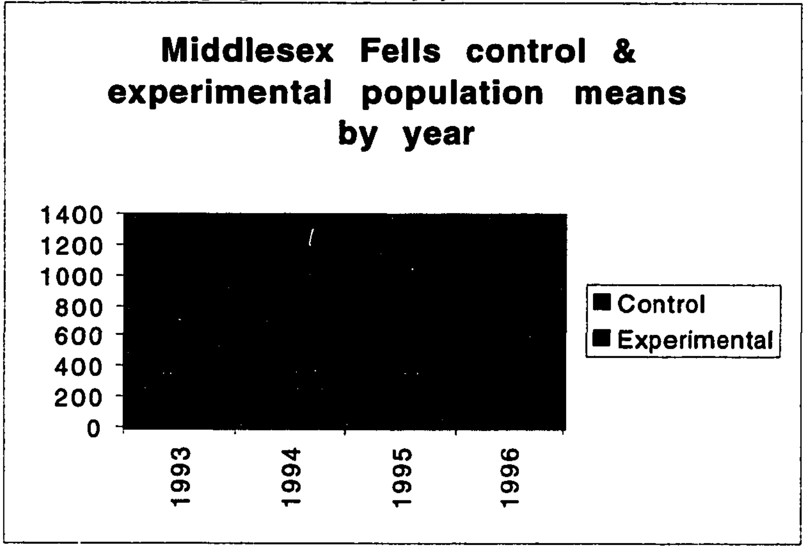


Figure 4-5. Life-stage diagram for *Alliaria*.

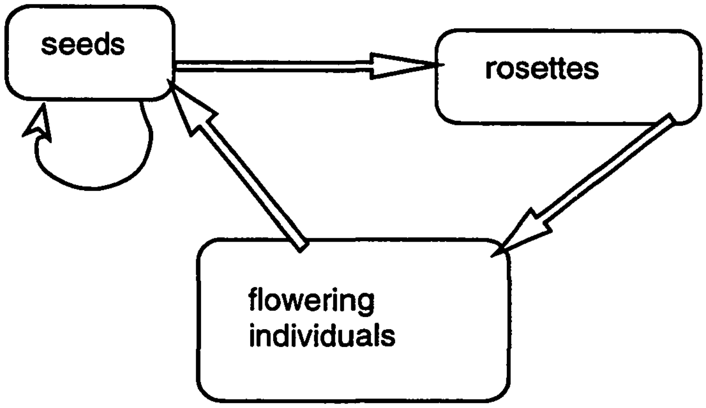


Figure 4-6.

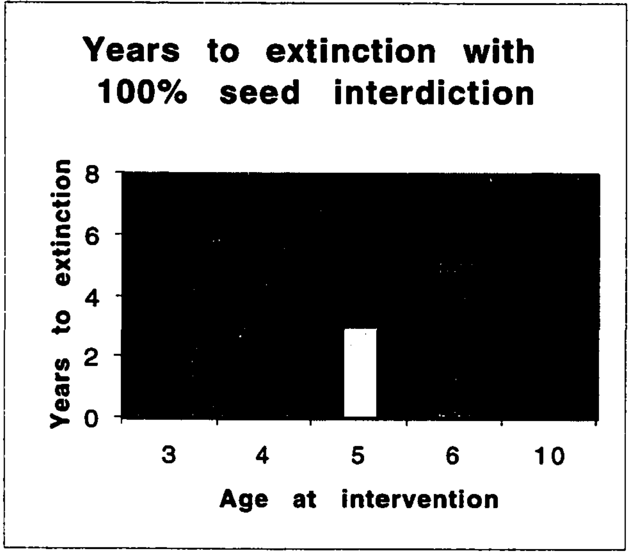

Years to extinction with 100% seed interdiction
Years to extinction
8
6
4
2
0
3
4
5
6
10
Age at intervention

Figure 4-7. Case 1, population growth without disturbance

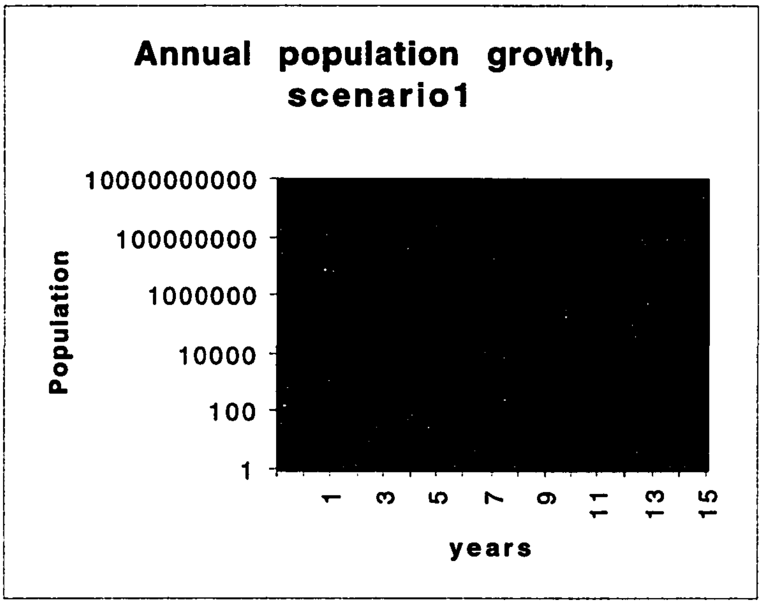


Figure 4-8. Case 2. 100% seed removal starts Year 5.

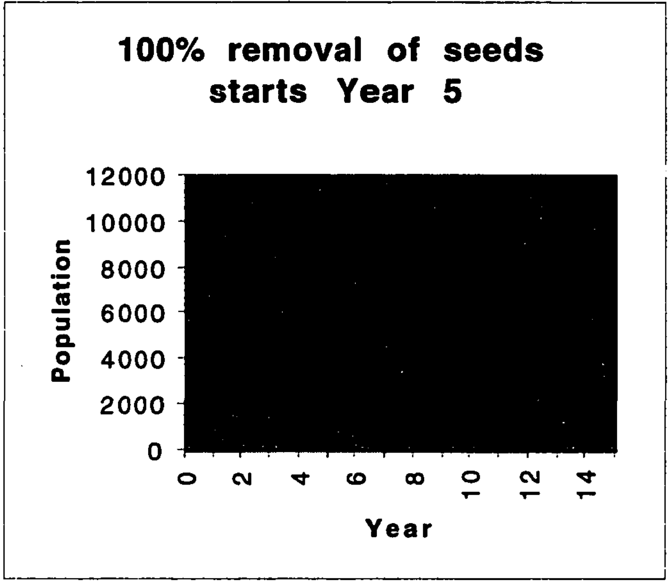


Figure 4-9. Case 3. 100% seed removal begins in the 7th year

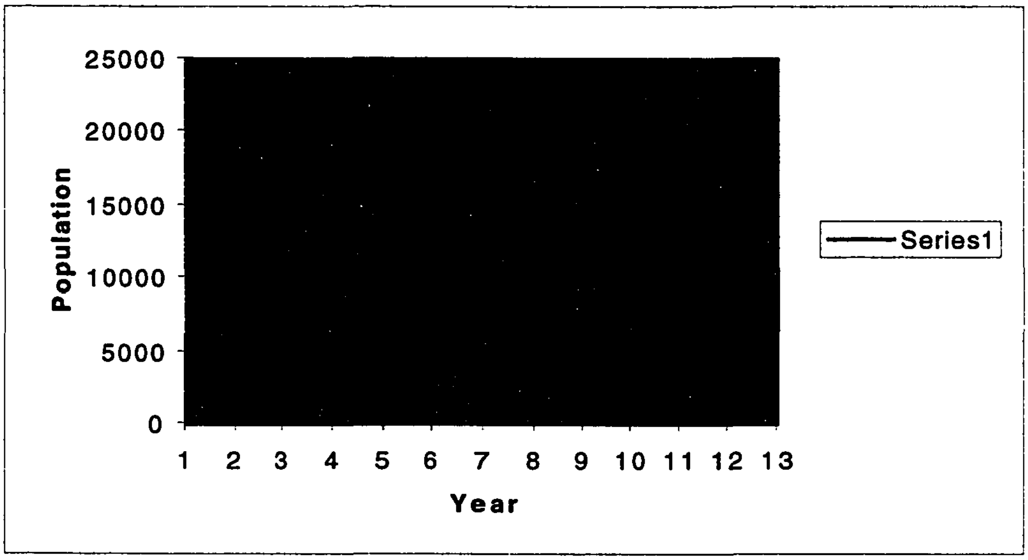


Figure 4-10. Case 4, 100% seed removal begins 11th year (Logarithmic plot)

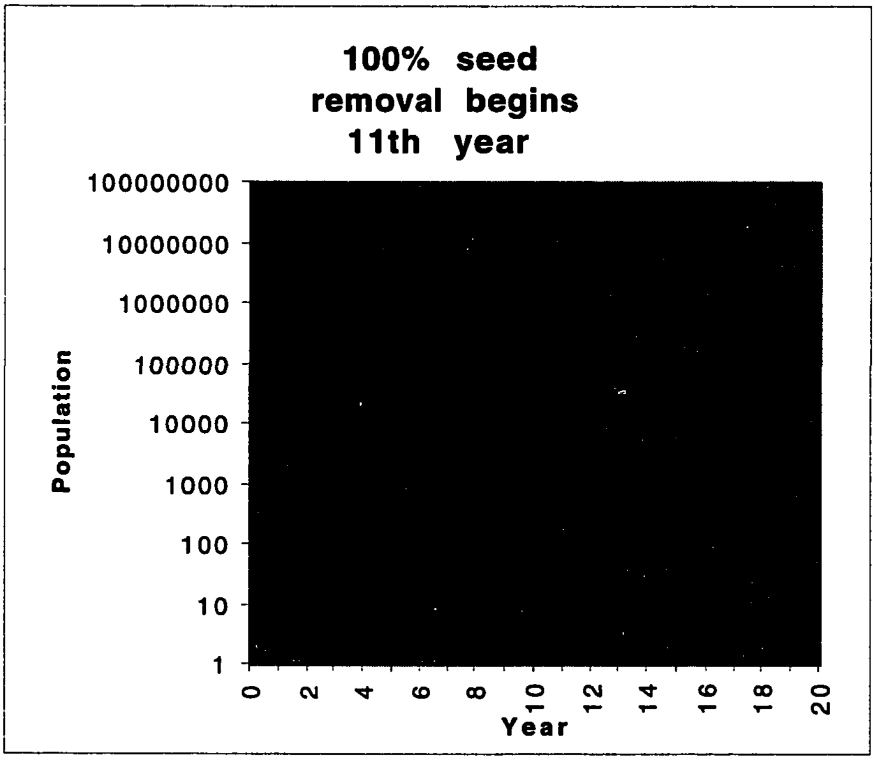


Figure 4-11. Disturbance begins in 5th year, lasts for 3 years, then undisturbed growth resumes.

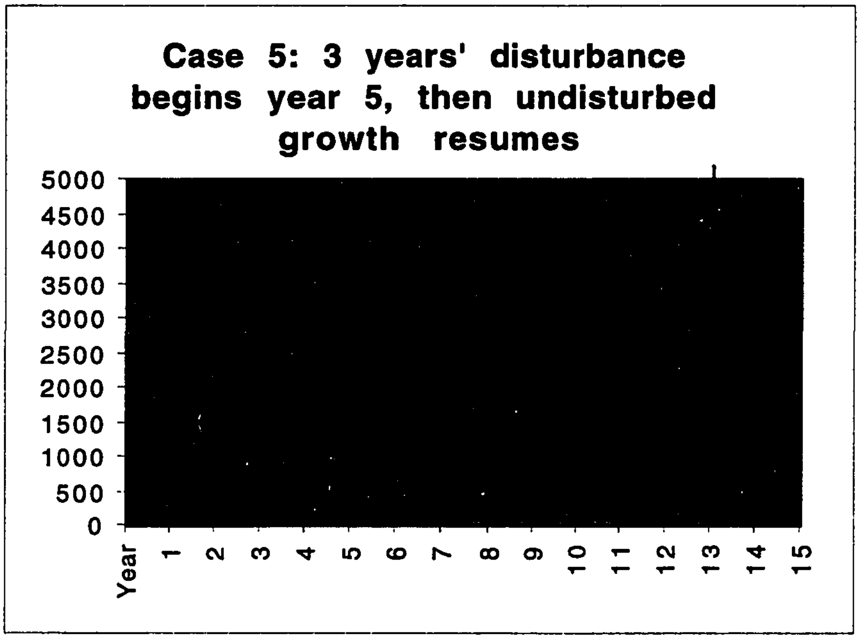
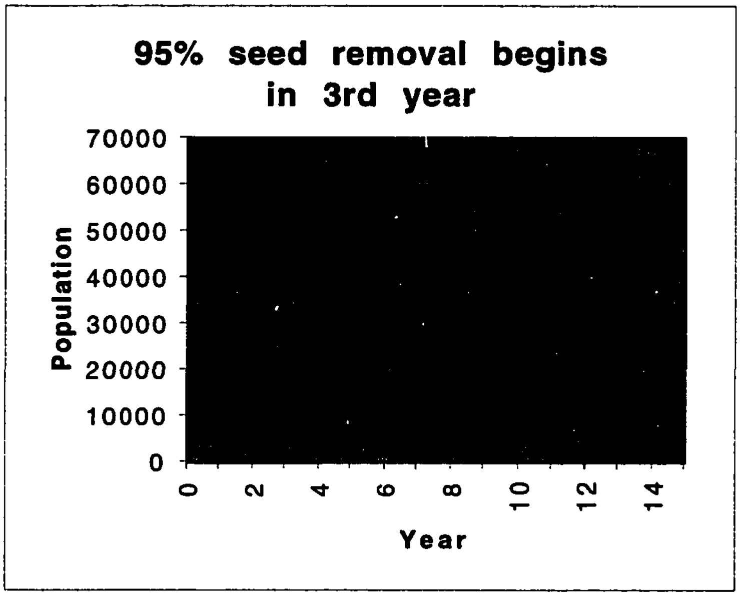


Figure 4-12. 95% removal of seeds begins at year 3 and continues each year.



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Work Experience

TERC, Cambridge, MA

Project Director/Scientist/Senior Research Associate, 1986 – Present

Project director, researcher, curriculum developer, and proposal writer for a variety of experimental projects, with an emphasis on curriculum and teacher change towards a constructivist classroom, and the use of telecommunications in support of educational reform.

Astrobiology (NSF/IMD).

Project director for a four-year project to develop an innovative, integrated high-school science curriculum, based on the search for life on other planets.

Teacher Enhancement Electronic Communications Hall

Researcher on NSF project linking principal investigators of teacher enhancement and systemic reform projects in an electronic community.

Eyes to the Future: Middle school girls envisioning math science and technology in high school and beyond

Co-PI for pilot project linking middle-school girls with high-school girls and women mentors in math, science, and technology. Funded by Arthur D. Little.

Teacher Enhancement in Pedagogy and Ecology

Project Director from 8/95 to end (7/97). (NSF-TE) on project that linked high school science teachers in an innovative year-long mentorship program with working ecologists.

Ecology Curriculum

Project Director. Co-wrote proposal for this project, and, along with PI, shaped, developed, and led others in developing a high-school ecosystems curriculum, now published by Kendall/Hunt. (NSF-IMD)

Hands-On Elementary Science

Project Director. Designed and developed teacher-enhancement workshops for elementary science teachers, under grant from Department of Education (FIE). Wrote successful continuation proposal.

LabNet Project

Network Manager. Co-developed and delivered teacher workshops. Co-author of successful three-year continuation grant. (NSF-TPE)

Global Laboratory Project

Director of Curriculum Development. (NSF-AAT)

Star Schools Project

Assistant Director of Curriculum Development. (Department of Education)

Microcomputer-based Laboratory

Curriculum Developer. (NSF-AAT)

Lesley College, Cambridge, MA

Lecturer, 1988 – 1993

Faculty for an adult-degree program, including study-planning and supervision. Studies supervised were in cognitive science and linguistics (including language history, social applications, and propaganda), life and physical sciences, religious studies and church history.

New England Friends Home

Director, 1981 - 1984

Director for small, Level IV rest home on Boston's South Shore. I was responsible for all aspects of the Home's operation: financial management and fund raising, community relations, personnel, medical oversight, licensing, maintenance, and so forth.

Selected Publications and presentations

Drayton, B. (1997) Review of Falk, Donald A., Constance J. Millar, and Margaret Olwell (Eds).*Restoring Diversity: Strategies for reintroduction of endangered plantss* Island Press. *Plant Science Bulletin*.43(2):33.

Drayton, B. 1996. "Floristic change and conservation in the Middlesex Fells Reservation." Presentation to the Friends of the Fells annual meeting.

Drayton, B. (1996) Review of D. R. Given. 1995. *Principles and practice of plant conservation.* Portland OR: Timber Press and Frankel, Otto et al. 1995. *The conservation of plant biodiversity.* Cambridge: at the University Press. *Conservation Biology* 10(2): 690.

Drayton, B. and R. B. Primack. 1996. "Garlic mustard as a model system for the study of issues in plant reintroductions." Paper presented at annual meeting of Ecological Society of America, August 12, 1996, at Providence, RI.

Drayton, B . and R.B. Primack. (1996) Plant species lost in an isolated conservation area in Metropolitan Boston from 1894 to 1993.*Conservation Biology* 11(1):30-39.

Drayton, B. and J.K. Falk , 1997. What do the ecologists get from an innovative mentoring program with high school teachers? *Bulletin of the Ecological Society of America* 78(4):256-260

Falk, J.K. and B. Drayton (1998) Before the innovation hits the classroom: teachers' self-image as an element of teacher enhancement. Paper presented to American Educational Research Assoc. annual meeting 1998.

Falk, J. K. & B. Drayton. (1997). Dynamics of the relationships between teachers and scientists in an innovative mentorship collaboration. Paper presented to American Educational Rresearch Assoc March, 1997.

Primack, R.B. and B. Drayton (1998). *Reintroduction as a conservation tool.* In: J. Gibbs, M. Hunter, and E. Sterling. Problem-solving in conservation biology and wildlife management. Blackwell Science: Boston.

Primack, Richard B. and Brian Drayton(to appear). Monitoring and Restoring Biological Diversity: Case Studies from Eastern United States in *Sibthorp Papers.*

Primack, Richard B. and Brian Drayton, 1997. The experimental ecology of reintroduction. *Plant Talk,* 11:25-8.

Primack, R. B., B. Drayton, and J. Walker. 1996. "The experimental ecology of plant reintroductions." Paper presented at annual meeting of Ecological Society of America, August 12, 1996, at Providence, RI.

Research summarized in several popular publications, including Science section of the *New York Times* (Feb 13, 1996) and the *Boston Globe* (June 16, 1996).

Professional Memberships

American Botanical Society
American Educational Research Association
British Ecological Society
Ecological Society of America
Linguistic Society of America
New England Botanical Club
Society for Conservation Biology

Education

Ph.D. candidate, Plant Ecology, Boston University
M.A., Plant Ecology, Boston University, 1993
A.M., Linguistics, Harvard University, 1978
Summer Program, Dublin Institute for Advanced Studies, 1975
A.B., Linguistics and Celtic (cum laude), Harvard College, 1975

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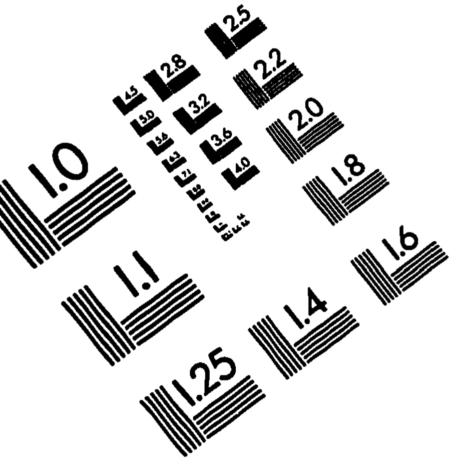
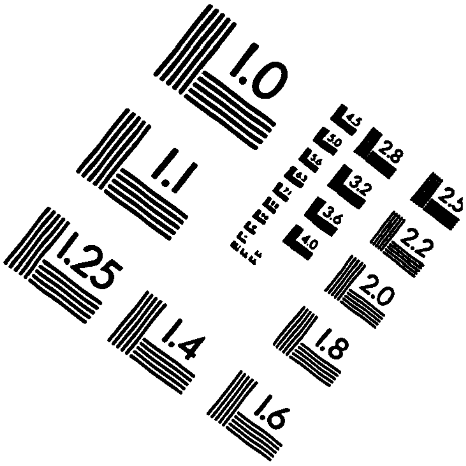

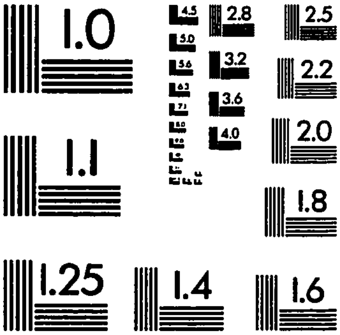

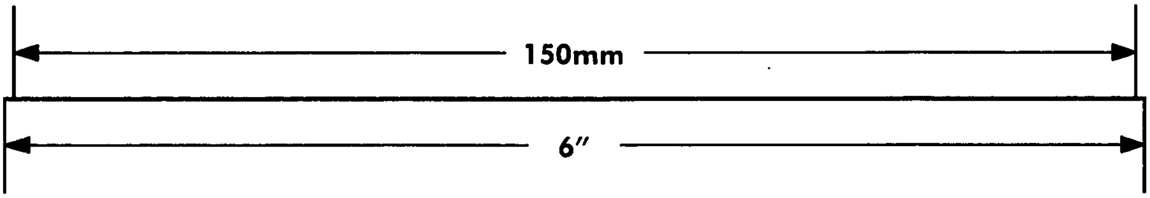

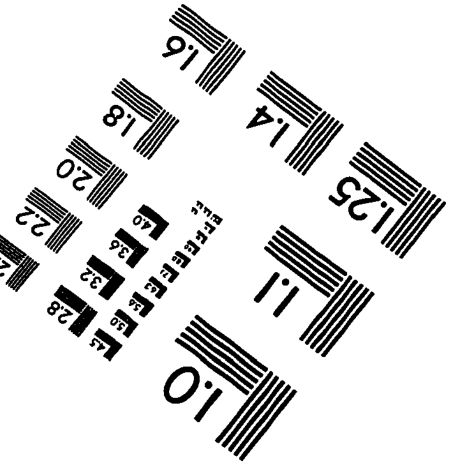
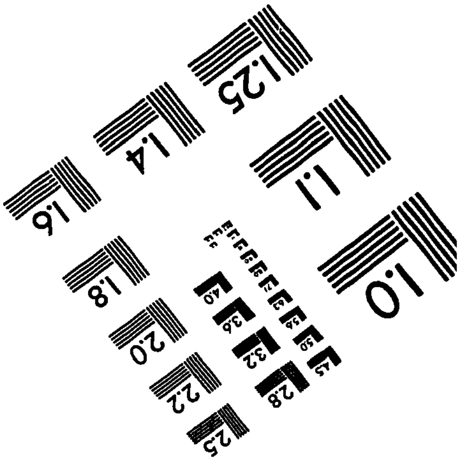

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