Dispersal Can Limit Local Plant Distribution

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Abstract: The ability of species to establish new populations at unoccupied sites is a critical feature in the maintenance of biological diversity, and it has taken on new importance as a result of global climate change and expected changes in species distribution. To examine the dispersal potential of plant species, seeds of four annual plant species were experimentally dispersed 40 to 600 m from existing populations in Massachusetts (U.S.A.) to 34 nearby unoccupied but apparently suitable sites. At three of these sites, new populations were established that persisted for four generations and expanded slowly in area. At seven sites, a small initial population eventually died out. At the 24 other sites, new populations did not become established, indicating that the sites were in some way unsuitable, that not enough seeds arrived, or that conditions suitable for seed germination do not occur every year. These results suggest that some species may be unable to disperse naturally out of their existing ranges in response to global climate change, particularly if habitat fragmentation creates barriers to dispersal. These species may have to be assisted to reach suitable sites nearby to prevent their extinction in the wild.

La dispersión puede limitar la distribución local de las plantas

Resumen: La habilidad de las especies para establecer nuevas poblaciones en sitios desocupados, es un rasgo crítico en el mantenimiento de la diversidad biológica, pero ha adquirido nueva importancia como resultado de cambios climáticos globales y el esperado cambio en la distribución de especies. A los efectos de examinar el potencial de dispersión de especies vegetales, semillas de cuatro especies de plantas anuales fueron experimentalmente dispersadas, a distancias que oscilaron entre 40 y 600 m de sus poblaciones existentes en Massachusetts (Estados Unidos), hacia 34 sitios cercanos y desocupados, pero aparentemente apropiados. En tres de estos sitios, nuevas poblaciones fueron establecidas, las cuales persistieron por cuatro generaciones y se expandieron lentamente en superficie. En otros siete sitios, una pequeña población inicial eventualmente murió. En los 24 sitios restantes, no se establecieron nuevas poblaciones, indicando que los sitios fueron no aptos en cierta medida, no llegaron suficientes semillas, o que las condiciones convenientes para la germinación de las semillas no se dan todos los años. Estos resultados sugieren que algunas especies no serían capaces de dispersarse naturalmente fuera de sus rangos existentes en respuesta a cambios climáticos globales, particularmente si la fragmentación del hábitat crea barreas para la dispersión. Estas especies tendrían que ser asistidas para llegar a los sitios apropiados más cercanos a los efectos de prevenir su extinción en estado salvaje.
Introduction

The protection of rare and endangered species and the conservation of biological diversity have emerged as key concerns of modern biology (Syng 1981; Reid & Miller 1989; Soulé & Kohm 1989, McNeely et al. 1990). In addition to maintaining animals in zoos and plants in botanical gardens (Ashston 1988), conservation efforts have typically emphasized habitat protection as the crucial means for maintaining biological diversity (Reid & Miller 1989). However, as the surface of the Earth is altered by global warming, changing rainfall patterns, acid rain, and habitat destruction, species will go extinct locally unless they are able to migrate to new, suitable habitats (Davis 1989; Graham et al. 1990). To keep pace with global warming over the next hundred years, it is estimated that temperate-zone species with narrow latitudinal ranges may have to migrate northward at a rate of 3000 m per year, which is 10 times faster than certain plant species migrated following the retreat of the last glaciers (Davis 1989; Graham et al. 1990). In addition, habitat fragmentation, human barriers to dispersal, and loss of animal dispersers may prevent many plant species from achieving even their previous rates of dispersal. Land managers responsible for protecting biological diversity cannot expect to maintain the status quo under these conditions but must deal inevitably with constant changes in local distribution and population numbers of these species (Peters & Darling 1985; Graham et al. 1990).

A crucial question that conservation biologists and plant ecologists must face is whether plant species are capable of dispersing to new, suitable sites before they go extinct on their original sites as a result of habitat alteration by such factors as climate change and habitat fragmentation. While there is a wealth of natural history data on seed dispersal (Howe & Smallwood 1982; Estrada & Fleming 1988) and many case studies of invasive, weedy species (Sauer 1988), there is surprisingly little information available on the degree to which seed dispersal limits the distribution of most plant species. The traditional view of plant distribution is that seeds of a species are dispersed widely over the landscape and that all suitable local habitats are eventually colonized by that species (Sauer 1988). An alternative hypothesis is that many species are much restricted in their distribution because they are unable to disperse to unoccupied sites that otherwise would be suitable for new populations. If this alternative hypothesis is true, it would have considerable practical implications for conservation biology, since new populations of rare species could potentially be established if seeds were introduced at the suitable unoccupied sites. It also would alter our understanding of community structure and dynamics, since dispersal would have to be recognized as a key factor along with substrate conditions in species distribution.

Despite the simplicity of this alternative hypothesis, it apparently has not been seriously advanced and rigorously tested as a theory to explain the distribution of plant species. Evidence for this hypothesis of dispersal limitation is indirect. For example, old forests often have plant species that are not found in adjacent younger forests (Peterkin & Game 1984; Whitney & Foster 1988). In general it is difficult to determine whether plant species have been unable to disperse to the younger forests or whether the younger forests have different and unsuitable environments for these plant species. The fact that more old forest species are found in young forests adjacent to old forests than in isolated young forests suggests that limited seed dispersal may be at least a partial explanation for the restricted distribution of many plant species (Peterkin & Game 1984). Experimental attempts to establish new populations of plant species beyond their natural range in experimental gardens have also met with some degree of success (Levin & Clay 1984; Carter & Prince 1988), suggesting that seed dispersal between suitable sites may be a limiting factor in plant distribution. On the other hand, attempts to add wildflower species to forest habitats and meadows by sowing seeds have typically been unsuccessful (Kenfield 1970; Heath & Primack 1991). This failure may be due primarily to the closed nature of the habitat, with establishment from seed normally occurring only after some disturbance that opens the vegetation, such as hurricanes and fire (Hobbs 1989), or when levels of seed and seedling predators are low (DeSteven 1991). It is this combination of seed dispersal occurring at a time suitable for establishment that may be crucial for new populations to become established.

Materials and Methods

In 1987 we decided to test experimentally the idea that dispersal is a limiting factor in the distribution of four annual plant species: bracted plantain (Plantago aristata: Plantaginaceae), velvet leaf (Abutilon theophrasti; Malvaceae), pinweed (Hypericum gentianoides; Hypericaceae), and jewelweed (Impatiens capensis; Balsaminaceae). All species grow in the Hammond Woods, a conservation area of approximately 80 ha in Newton, Massachusetts, containing a mixture of deciduous woods, swamps, meadows, roads, and parking lots (Primack 1972). The present vegetation seems quite stable, but rock walls are remaining evidence of farming activity in the area over a century ago. The advantage of using annuals as a bioassay of plant dispersal ability is that plants reproduce and die in one growing season, so that several generations can be studied quickly.

Each species occupies only a small percentage of the Hammond Woods but is locally abundant when it is found. Abutilon is introduced, while the other species
are native to the area. Plantago, a small rosette herb, first appeared in the Hammond Woods in the late 1970s and has become common in two sandy, disturbed vacant lots, each about 0.1 ha in area. Other similar and nearby sandy habitats are not occupied by this species. Abutilon is a tall, weedy species that occurs in one 10 m by 10 m section of a large, wet meadow. Abutilon plants appear at about five-year intervals at this one spot but never anywhere else in the Hammond Woods. Over 200 plants grew there in 1987, but no plants have occurred since that time. Why the species occurs only in one small area at irregular intervals is unknown, but it is possibly related to variation in soil moisture levels. Hypericum is a small annual with reduced leaves that grows each year only in one 20 m by 2 m area along the sandy edge of a parking lot. There are several hundred meters of similar edge habitat where this species does not occur. The species has been abundant and stable at this one locality for at least six years and occurs only in one other, tiny, isolated population on a mossy rock in the Hammond Woods. Impatiens is a tall plant of swamp and wet meadow habitats that occurs in several large, well-defined populations in the Hammond Woods.

While Impatiens has an explosive capsule that can disperse seeds over several meters, the seeds of the other three species simply fall out of their capsules onto the ground around the parent plant. Seeds of Impatiens all germinate in the spring following dispersal (Leck 1979; Primack & Levy 1988); seeds of Abutilon apparently have the ability to remain dormant in the soil and form seed banks, as shown by the irregular appearance of the population. The seeds of Hypericum and Plantago are hard and dry and probably also have prolonged dormancy.

For each target species we located sites in the Hammond Woods that appeared to be suitable but where the species had not been observed to grow for at least 20 years. Site selection was based on the presence of associated “indicator” species that occur with the target species elsewhere and on local environmental characteristics, including soil texture, soil moisture, light availability, and plant cover. No quantification of site characteristics was made. Sites also were selected to be mostly free of plant cover, so that seed germination would not be inhibited by competition with other plants. The Plantago and Hypericum sites were sunny, dry, open areas with sandy soil; the Abutilon sites were fields with some level of disturbance; and the Impatiens sites were both open and shaded wetland areas. For Hypericum, Impatiens, and Plantago seven sites each were selected, while for Abutilon six sites were used. Each of these unoccupied sites were within 40–600 m of an existing population of the target species (Table 1).

In Fall 1987 a sample of mature, fully formed seeds was collected from one Hammond Woods population of each target species at the time of seed dispersal. Both visual examination and subsequent germination in the field confirmed that seeds of all four species were viable at the time of dispersal. At each site selected, in Fall 1987, seeds were scattered evenly on the ground around a stake at a distance equal to the height of the plants: 30 cm from the stake for Hypericum and Plantago, 60 cm for Abutilon, and 100 cm for Impatiens. The ground was then lightly raked to cover the seeds. The weather from seed sowing until the following spring of 1988 was normal. The sites were examined in Spring and Summer 1988 for the presence of seedlings, and adult plants were mapped. Seed production was estimated by counting the number of fruits per plant and the number of seeds in a sample of fruit. Adult plants were allowed to disperse their seeds. The sites were checked again in 1989, 1990, and early 1991 for population size, seed production, and plant distribution. An additional seven unoccupied wetland sites were selected and planted with Impatiens in Fall 1988.

Results

For Plantago, five of the sites had seedlings and adults in 1988, four sites were occupied in 1989, and only two sites maintained populations in 1990 and 1991 (Table 1). At all five sites with plants in 1988, all seedlings appeared within 30 cm of the stake, where they were scattered six months earlier. For site 21, the seedlings recruited in this same area in 1989 and again in 1990 and 1991, indicating a complete lack of subsequent dispersal. For site 20, however, the seeds dispersed downslope after Summer 1988, establishing seedlings as far as 18 m away from the release point in 1989 and 1990 (Fig. 1). In 1991, the large numbers of plants were all found within 6 m of the marker.

For Impatiens, seedlings were present at all seven experimental sites in 1988, but in varying numbers (Table 1). At sites 1–6, the seedlings all emerged within 1 m of the stake. By 1990, Impatiens was no longer present at any of these sites. At site 7, while most seedlings established near the stake in 1988, a clump of three seedlings recruited 3.5 m away from the release point (Fig. 1). In 1988, the Impatiens plants grew to a large size at site 7 and produced about 1500 seeds, with large numbers of plants also found in 1989 and 1990. In 1991, the plants grew vigorously, with 750 plants producing an estimated 56,000 seeds. The area of the population has increased each year, spreading about 2 m per year beyond the original site (Fig. 1). Of the seven new, unoccupied sites selected and sown with Impatiens seeds in Fall 1988, no site had a permanent population as of 1991, even though Site 11 had plants in 1989 and 1990 (Table 1).

For Abutilon, five of the six sites had no seedlings in any year. At the sixth site, a disturbed field that was unexpectedly tilled by tractor in the spring for a garden and then abandoned, seven seedlings were present on
Table 1. Success of establishment of *Impatiens* and *Plantago* at experimental sites; for each site the distance to the nearest natural population of the species is given as well as a brief site description.

<table>
<thead>
<tr>
<th>Site #</th>
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<th>Site characteristics</th>
<th>Seedlings</th>
<th>Adults</th>
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<th>Seedlings</th>
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Initially, 100 seeds were scattered at these unoccupied sites. *Impatiens* sites 1–7 and *Plantago* sites 15–21 were established in Fall 1987; *Impatiens* sites 8–14 were established in Fall 1988. The data are the number of seedlings and adults at each site and an estimate of the total number of seeds produced.

June 7, 1988. Five seedlings remained by August 9, the furthest being 104 cm from the stake. Eventually, two plants produced mature fruit, one producing 40 seeds and the other 30 seeds. No seedlings appeared in 1989 or 1990 at the site, even though the ground was again lightly tilled.

For *Hypericum*, no plants occurred on any of the unoccupied sites in 1988 or 1989. In 1990, however, 38 plants grew up within 50 cm of the stake at one experimental site. The plants had about 50 fruits per plant and produced an estimated 19,000 seeds.

**Discussion**

Our results demonstrate that dispersal can limit the distribution of annual plant species on a local scale. Even those species that produce abundant seeds were apparently unable to reach potentially suitable sites less than 100 m away from large natural populations over 20 years of observation. This lack of dispersal ability is particularly surprising for *Impatiens*, since ducks and other bird species frequently move among the wetland sites of Hammond Woods and would presumably be carrying mud and seeds on their feet. The lack of mobility of seeds once they arrive at a site is demonstrated by the appearance of seedlings exactly where seeds had been planted months or even years before and by the lack of areal expansion or the slow expansion of many new populations. At its original site, *Plantago* has been expanding in area by several meters per year, while the other species are apparently stable at their original sites. Animals walking and digging through the soil, plus the action of wind and water flow, apparently do not move seeds any significant distance once they have landed on the soil surface. At one site, four generations of *Plantago* have remained almost exactly in the same place. At
Figure 1. The expansion of two annual species at previously unoccupied sites. In 1987, 100 seeds were scattered within 1 m of the stake for Impatiens and within 0.3 m of the stake for Plantago. (A) Impatiens: The limits of the population at site 7 are shown based on adult distribution in 1988 and seedling distribution in 1989 and 1990. (B) Plantago: The limits of the population at site 20 are based on the distribution of adults in 1988 and 1989. Adult distributions in 1989 and 1990 were very similar.

the extreme is the Hypericum site, where the seeds germinated precisely where they had been scattered 2.5 years earlier. At the Abutilon site, the seedlings came up within 1 m of the stake even after the site had been lightly tilled by a tractor. At one Plantago site and one Impatiens site, however, populations were able to expand at the rate of several meters per year.

Many perennial plant species with more limited seed production may be far more restricted in their ability to disperse to new sites than these annual species, as suggested by the inability of many old-growth woodland species to disperse into adjacent younger forest over a period of hundreds of years (Peterkin & Game 1984; Whitney & Foster 1988). Such species may become established in nearby sites only under specialized environmental conditions, such as following a fire or a hurricane, which creates additional temporal restrictions on the ability of species to form new populations (Hobbs 1989). We are currently investigating these possibilities in our studies of perennial plant species in forests affected by simulated hurricane damage.

These results indicate that many plant species with restricted local distributions may be unable to migrate northward hundreds of kilometers at a rate sufficient to keep pace with climate changes associated with global warming (Davis 1989). Certain species also may be unable to disperse to newly available microsites that are only hundreds or thousands of meters away, which would be necessary as climatic zones shift higher on mountain slopes. Such restrictions on dispersal ability also would apply to certain animals that occupy isolated habitats, such as aquatic species of isolated ponds, vertebrates on isolated mountain peaks, and ground-inhabiting, flightless invertebrates. As a result, many of these plant and animal species will undoubtedly go extinct. Therefore, plant conservation biologists should at least consider trying to assist rare species to shift their ranges slightly northward, to somewhat higher elevations or to more suitable local environments, in response to global climate change—while at the same time recognizing the potential for unanticipated ecological and evolutionary consequences (Conant 1988; Wikramanayake 1990). The advantage of using the seed dispersal techniques described here rather than transplanting wild or artificially propagated adults, which is a technique commonly used in attempts to establish new populations, is that experimental seed dispersal mimics the natural dispersal process and allows large numbers of genotypes to be utilized.

The fact that no new populations arose at most of our sites suggests that the great majority of nearby, apparently suitable but unoccupied sites, are actually not suitable or are only infrequently suitable for colonization of the species. This conforms with the observations that most attempts to establish new populations using transplantation of either adult plants or seeds end in failure (Hall 1987) and that many species have specialized habitat and germination requirements (Krucekberg 1954; Baskin & Baskin 1985; DeSteven 1991; Facelli & Pickett 1991). Even when the transplanted adults survive, they typically do not sustain viable new populations. As a result, seeds or other propagules must be dispersed to many potential sites over several seasons to ensure that at least a few sites are successfully colonized. It may be that only the fortuitous combination of a particular genotype in a suitable microsite in a particular year will result in a successful adult plant. This combination is unlikely to occur if only a relatively few adult plants are used or if seeding occurs in only one year. The strategy of many years of releases at many sites has been found to be the most successful in establishing populations of weed control species (Crawley 1989).

Certain cautionary notes should be considered before
the experimental seed dispersal program advocated in this paper is implemented. First, universities, museums, government agencies, and nongovernment conservation groups are accumulating exact locality data for rare and endangered plant species. Anyone seriously attempting to increase the range of these rare species should provide project proposals, progress reports, and final reports to one or more of these groups. Second, there is an increasing awareness and interest in the genetic variability of natural populations. Wherever possible, seeds used in these experiments should come from the nearest possible wild populations and the seed source should be noted. Using such appropriate seed sources will certainly increase the chance of success of the experiments. Third, research involving rare species is usually covered to some extent by government regulations (Rails & Brownell 1989). In the United States, establishment of an experimental population of a species legally listed as rare and endangered is controlled to some extent by the Endangered Species Act and may require permits. Similar laws apply in other countries and will affect where and how the research is carried out. For each species, it must also be determined that seeds can be collected in the wild without violating the law. Finally, the ecological and evolutionary consequences of expanding the range of a species need to be carefully considered. In particular, it must be determined if there are other rare and vulnerable species at that site. In general, however, this should not be too serious a problem, as rare species of restricted distribution generally do not have the characteristic profile of weedy, invasive species (Ehrlich 1989; Noble 1989). These characteristics include early and abundant reproduction, ability to self-fertilize, strong competitive ability, and abundance within the original range.

It is our opinion that conservation biology should develop methods not only to understand and preserve existing populations of rare species, as has been described by Simberloff (1988) and Brussard et al. (1992), but also to provide techniques for making rare species more common and creating new populations. Such a positive goal of establishing new populations is necessary to reverse the alarming trend of species extinction, which is occurring throughout the world as a result of habitat destruction. The situation for many species will certainly get worse due to human impact on the environment, resulting in changing weather patterns, acid rain, habitat destruction, and extinction of natural seed dispersers. In the face of such changes, species will have to migrate out of existing nature reserves or face extinction (Peters & Darling 1985; McDonald & Brown 1992). In this situation rare plant species are particularly vulnerable, since they generally have fewer initial populations to serve as focal points for dispersal and may be poor dispersers in any case (Rabinowitz & Rapp 1981; Rabinowitz et al. 1986). Due to small population size, they may also be producing fewer seeds for dispersal. As a result, many rare plant species may be unable to migrate north of their current range or to higher elevations as their present localities become unsuitable. The experimental dispersal approach we describe here for establishing new populations provides a potential method for preventing extinction of many such plant species and comparable sedentary animal species.

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Literature Cited


