

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Are plant populations seed-limited? A review of seed sowing experiments

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We define seed limitation to be an increase in population size following seed addition. Here, we briefly consider how theoretical models deal with seed limitation and how seed sowing experiments can be used to unravel the extent of seed limitation in natural systems. We review two types of seed addition experiments: seed augmentation studies where seeds are added to existing populations; and seed introductions where seeds are sown in unoccupied sites. Overall, approximately 50% of seed augmentation experiments show evidence of seed limitation. These studies show that seed limitation tends to occur more commonly in early successional habitats and in early successional species. Most of the studies have concentrated on simply categorising populations as seed- or microsite-limited, but we believe that seed sowing experiments could be used to reveal much more about community structure, and we discuss possible future directions.

In 53% of introduction studies (where seeds were sown at sites from which the species was known to be absent) the introduced species was recorded in at least one of the experimental sites following sowing. However, of the subset of studies where both seedlings and adult plants were recorded, 64% of sites contained seedlings while only 23% contained adults. This implies that, for many species, conditions for establishment are more stringent than conditions for germination. The successful establishment of plants in unoccupied patches indicates the potential for immigration to enhance local diversity (the spatial mass effect). Few studies continued monitoring for long enough to determine whether or not self-sustaining populations were successfully established, and no study attempted to link introduction sites to a putative natural source of propagules, or considered the dynamics of the metapopulation as a whole.

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Recently, studies in both temperate (Clark et al. 1998) and tropical (Hubbell et al. 1999) forests have demonstrated that the seeds and seedlings of many species are absent from apparently suitable sites, suggesting that seed limitation may be widespread. Theoretical models deal with seed limitation in two quite different ways. In lottery models (e.g. Chesson and Warner 1981, 1985), the individual that successfully obtains tenure over a plant-sized patch of ground is selected at random from a pool of propagules. The identity of the winner is a lottery, and the probability of a given species obtaining site tenure increases monotonically with seed input (so long as the input of seed of competing species is constant). In contrast, models based on the competition/colonisation trade-off (Armstrong 1976, Hastings 1980, Shmida and Ellner 1984, Tilman 1994) assume that the identity of the winning plant is deterministic. Species are ranked by competitive ability, and if a seed of the competitively superior species is present, then an individual of that species will gain site tenure, no matter how many seeds of the inferior competitors are present. Recruitment of the superior competitor occurs wherever seed is present, and competitive exclusion of the inferior competitors is only prevented if seed production by the superior competitor is too low, or seed dispersal too localised, for all sites to contain seeds. In this extreme case, seed limitation is binary rather than continuous. For the inferior competitors, seed production must be sufficiently high and seed dispersal sufficiently effective that the scarce recruitment opportunities open to them (i.e. absence of the superior competitor) are colonised with sufficient frequency to allow population persistence (Hastings 1980, Tilman 1994).

These two extreme theoretical models make rather different predictions about the outcome of experiments involving seed sowing. If recruitment is a lottery, then recruitment will increase with seed addition for all the species involved, poor competitors as well as dominant species. In contrast, if plant dynamics involve the competitive asymmetry of the colonisation/competition trade-off, then the dominant plant species is much more likely to be seed-limited.

There are two distinct kinds of experiment on seed limitation. In the first case, the sown species are residents of the target community; we call this 'seed augmentation'. In the second case, the sown species are not part of the target community; we call this 'seed introduction'. Studies on augmentation and introduction tend to be carried out for rather different purposes. With resident species, it can be safely assumed that their regeneration niche exists (or at least existed) within the target community, and that abiotic conditions of substrate, microclimate, etc., do not present a fundamental barrier to recruitment. For non-resident species, we typically do not know this; their absence may reflect the

absence of suitable regeneration conditions, so that no amount of seed addition will lead to recruitment.

Both kinds of sowing experiment allow a range of responses. If nothing happens, it may be because recruitment opportunities (e.g. suitable microsites) were absent at the time of seed sowing, or because seed-feeding animals consumed all of the sown seeds. In augmentation studies, seedlings may be present, but seedling densities may be no higher with seed addition than without, suggesting that recruitment opportunities are microsite-limited, and that background (pre-addition) levels of seed production and/or seed bank recruitment are sufficient to occupy all of the available microsites. If recruitment is increased by seed addition, it may be because more of the available microsites are occupied, or because of a reduction in density-dependent seed mortality (e.g. predator satiation). Recruitment following seed addition in introduction experiments indicates that the regeneration niche exists, and absence of the species from the community can be attributed to dispersal limitation (e.g. non-indigenous species which become naturalised following introduction).

Here we begin by briefly considering the major classes of models which incorporate seed limitation both at the local and regional scale, although it is not our intention to provide an exhaustive review (for more thorough reviews of selected topics see, for example, Tilman and Pacala 1993, Fagerström and Westoby 1997 and for regional scale models see Hanski 1997). Second, we review experimental studies of seed augmentation and introduction, in order to test whether there are general patterns in the frequency of seed limitation across plant life history types, plant communities or successional stages. This has a wider relevance, in that herbivores would be expected to influence plant population density in seed-limited species, but not in species where recruitment was microsite-limited (Andersen 1989, Crawley 1990, Louda and Potvin 1995, Maron and Simms 1997). Herbivores could have threshold effects on recruitment if reduced herbivory led to seed densities sufficiently high to satiate granivorous animals (Janzen 1976, Ashton 1979, Silvertown 1980, O'Dowd and Gill 1984, Crawley and Long 1995, Herrera et al. 1998).

Models of local scale dynamics

Competition experiments with subsets of coexisting species have frequently revealed the presence of fully transitive competitive dominance hierarchies (Miller and Werner 1987, Tilman and Wedin 1991, Tilman 1994, Goldberg 1996). This raises the question of how the competitively inferior species persist when classical competition theory predicts exclusion by the species at

the top of the hierarchy (the competitive dominant). However, if the dominant is recruitment-limited, it is unable to colonise all sites, and space remains for a second species to invade. The characteristics required for successful invasion have been explored in a number of models (Skellam 1951, Horn and MacArthur 1972, Armstrong 1976, Hastings 1980, Shmida and Ellner 1984, Crawley and May 1987, Tilman 1994).

If species form a strict dominance hierarchy the dominant competitor is unaffected by the presence of any number of inferior competitors, while the second species in the hierarchy can establish in any unoccupied cell. Clearly, far fewer cells are available for occupation by inferior competitors, and the colonisation rate required for persistence is correspondingly higher. In the model described by Tilman, the colonisation rate required by the n th species in the hierarchy increases with the inverse square of the unoccupied space (Tilman 1994). We therefore expect competitive ability to be inversely related to colonising ability, and the dominant competitors to be the most strongly seed-limited. Theoretically, increasing seed inputs of the dominant competitors to high enough levels should precipitate a collapse in diversity (Pacala and Rees 1998, Turnbull et al. 1999).

Heterogeneous environments

Although many experiments have revealed that strict dominance hierarchies exist, it is entirely plausible that competitive rankings depend critically on the experimental conditions, for example, on the ratio of limiting resources (Tilman 1982). Coexistence may then depend on differences in the environmental conditions between sites that allow each species to be the best competitor in some fraction of the habitat, making local-scale habitat heterogeneity critical to coexistence (Pacala and Tilman 1994). Because the outcome of competition is deterministic we might expect seed limitation to have little effect. However, if the local environmental conditions vary independently in time and space, species need to disperse between 'good' patches (Comins and Noble 1985). Hurtt and Pacala (1996) explored the effect of recruitment limitation in such a habitat. Unless fecundity is infinite, no species reaches all the sites for which it is the best competitor, allowing inferior competitors to win sites 'by forfeit'. If inferior competitors are *not* allowed to win sites when the dominant competitor is absent, the number of species that can persist in the model is greatly reduced. In addition, as species richness increases and each species becomes proportionally more rare, the amount of winning-by-forfeit increases, which slows the rates of competitive exclusion. Increasing the seed inputs of any of the component species will reduce winning-by-forfeit and lead to a reduction in diversity. However, the underlying habitat heterogeneity prevents any one species from excluding all others.

Lottery models

In lottery models, juveniles are chosen at random from the pool of potential recruits (Sale 1977). The number of sites won by juveniles of the i th species in an n -species community is

$$N_i = \frac{X_i \beta_i c_i}{\sum_{j=1}^n X_j \beta_j c_j} \cdot K \quad (1)$$

where c_i is the relative competitive ability of the i th species, β_i is its per capita seed production and K is the number of available sites. Several empirical studies seem to support the idea that the recruitment process can be modelled as such a biased lottery (Lavelle and Lebreton 1992, Lamont and Witkowski 1995). Note, that all species are seed-limited, as increasing the seed production of any species will generally increase population size. However, as the number of sites won by a particular species also depends on the seed production of competing species, the relationship between seed output and number of recruits is likely to exhibit a great deal of scatter (Chesson 1986). This scatter is likely to be greatest for the poorest competitors where recruitment is strongly influenced by the reproductive output of superior competitors.

If there is a strict dominance hierarchy such that $c_1 = 1$ and $c_{j \neq 1} = 0$, species 1 wins every site which becomes available and other species are immediately excluded. As all sites draw from the same pool of recruits, there is no opportunity for inferior competitors to establish in sites where the dominant competitor is absent. In fact, inferior competitors can only win sites if the competitive dominant entirely fails to produce viable juveniles in some rounds of recruitment ($\beta_1 = 0$) providing other species do not suffer the same fate ($\beta_{j \neq 1} \neq 0$).

Where the outcome of competition is less deterministic, inferior competitors can win sites in each recruitment round. If the environment varies between recruitment rounds, and this variation affects birth rates, an inferior competitor can potentially persist through episodic recruitment, if the survival of adults or dormant seeds buffers the population between favourable recruitment episodes. We would expect the inferior competitor to have superior temporal dispersal abilities, perhaps by having fewer episodes of reproductive failure (Rabinowitz et al. 1989) and longer-lived seeds. Clearly, the species must also respond differently to the environmental variation, otherwise episodes of poor seed production coincide and other species are unable to exploit the poor recruitment episodes of the dominant. As we move toward the limit, $c_1 = c_i = 1$, relative birth rates are all-important in determining recruitment success and much smaller fluctuations in the environment are required for coexistence (Chesson and Warner 1981).

In summary, low seed production in space or time can promote coexistence, by preventing species from exploiting all the sites that they could otherwise win. If there is a single, deterministic hierarchy, the dominant species should be the most strongly seed-limited, and the addition of its seeds should have the greatest effect on diversity. If the environment is heterogeneous, the removal of seed limitation should not lead to a total collapse of diversity, but can still lead to reduced diversity as a result of the loss of winning-by-forfeit. In lottery models the outcome of competition is generally assumed to be less deterministic and relative numbers of recruits influence the probability of winning sites. That is, all populations are implicitly assumed to be seed-limited. In this case, much smaller fluctuations in reproductive outputs caused by changes in the environment can allow inferior competitors to exploit years in which the reproductive output of the dominant competitor is poor.

Regional scale dynamics

Metapopulation theory predicts that there should be suitable, but unoccupied, patches at the regional as well as at the local scale (Levins 1969, Levins and Culver 1971, Hanski 1997). In the classic formulation, populations are lost from suitable patches via stochastic processes, but are subsequently re-established by immigration. However, some authors maintain that the empirical evidence for stochastic causes of population extinction is weak (Harrison 1991, Thomas 1994). In this view it is accepted that small populations face a high risk of extinction, but such populations are either considered to play a relatively minor role in the dynamics of the region, or are considered to have declined for deterministic reasons (Caughley 1994). In this case, there are unlikely to be many substantial but unoccupied sites.

Plant populations may be particularly well buffered against extinction because of the presence of persistent seed banks (Eriksson 1996, Husband and Barrett 1996). For example, in a sand dune annual community, populations of *Cerastium semidecandrum* are observed to crash regularly but immediate recovery usually ensues (Rees et al. 1996). Such an event is probably a result of environmental fluctuations and recovery is almost certainly due to the persistence of seeds in the soil seed bank. The widespread occurrence of seed banks in many plant species may ensure that a single successful colonisation event is sufficient to ensure long-term population persistence in the face of short-term environmental fluctuations (unless the patch only supports a very small population when demographic and genetic stochasticity may also pose a serious threat). In this case, it is feasible that all suitable patches above some

minimum size could be permanently occupied and regional recruitment limitation would be rare.

If regional sites become unsuitable for prolonged periods, colonisation limitation is likely to become a more potent force. In the classic metapopulation model with a fixed set of suitable sites, regional persistence only requires that the colonisation rate (c) exceed the extinction rate (m). However, in a set of dynamic sites, even when patches are being re-created as fast as they are being lost (for example at some rate v), the colonisation rate required for regional persistence is higher because of the extra mortality inflicted by the loss of patches ($c > m + v$; from Hanski and Ranta 1983). Many plant species occur in such temporary habitats, for example, many biennial species (reviewed in van der Meijden et al. 1992), and forest herbs and pioneer tree species which rely on canopy gaps (van Baalen and Prins 1983, Valverde and Silvertown 1995).

Finally there may be sites suitable for the germination and establishment of a few individuals, which are incapable of supporting self-sustaining populations (Shmida and Ellner 1984, Pulliam 1988). For example, the flux of propagules from self-sustaining populations is known to support satellite populations of the sand dune annual *Cakile edentula* (Keddy 1982, Watkinson 1985). However, a recent study showed that such spatial 'mass effects', while present, may be weak for many species (Kunin 1998).

Clearly, seed introductions offer a direct way of identifying if suitable unoccupied patches exist at the regional scale. However, such patches may, or may not, form part of a metapopulation depending on their connections to other sites in the region. We also need to distinguish between putative source populations ($\lambda > 1$) and those which are putative sinks ($\lambda < 1$). The successful establishment of a few individuals, but not of a self-sustaining population, indicates the potential for mass effects to enhance local diversity (Shmida and Ellner 1984, Kunin 1998).

Seed addition experiments

Seed augmentation

Augmentation studies are often carried out for purposes other than to assess the extent of seed limitation, and for this reason were only included if sowing was carried out within a natural or semi-natural community, *with unsown control plots established and monitored*. Studies were also excluded if an unequivocal result was not presented for each of the augmented species. A total of 27 studies incorporating some 90 species were found to fulfil these criteria. In order to facilitate comparisons between future studies a guide to a simple single-species addition experiment is given in Table 1. The augmentation studies included here were

carried out within a limited range of ecosystems, and have therefore been placed in one of six habitat categories: newly ploughed fields; early or mid-successional fields (unploughed for 2–30 yr before sowing); intact arid grassland (unploughed for > 30 yr before sowing); intact mesic grassland (unploughed for > 30 yr before sowing); temperate woodland; and coastal shingle or sand dunes. Only one study, conducted in sub-tropical forest, could not be placed into one of these categories.

If we compare sand dunes, temperate woodlands and intact grasslands, we see that the extent of seed limitation is highest in sand dunes and lowest in grasslands (Fig. 1a). Within grasslands, the prevalence of seed limitation declines in the order newly ploughed fields \cong early/mid-successional fields > arid grasslands > mesic grasslands (Fig. 1b). This progression implies that community composition is likely to be less influenced by the nature of the colonising pool as succession proceeds. For example, Gross and Werner (1982) showed that mid-successional species were only absent from newly ploughed sites because of a lack of seeds, but that early successional species could not persist in mid-successional fields. This is consistent with

Table 1. A suggested protocol for seed addition experiments.

● *Estimation of the natural population seed output*

Comparisons between studies would be facilitated if the experimental seed input were some specified multiple of the natural population seed output (for example two, three and ten times the natural seed output during the year the study is undertaken, or two, three and ten times the maximum known natural seed output).

● *Manipulation of seed outputs over a sufficient range of densities*

If possible both reductions and additions should be attempted. Reductions in seed output could be achieved by removing inflorescences prior to seed set. The highest sowing rate used should be sufficiently high to give unequivocal results, should there be no significant increase in recruitment (for example, at least ten times the natural seed output).

● *Duration of monitoring*

Existing studies vary greatly in their duration, some stopping at the seedling emergence stage, whilst others continue for several years. As a rule of thumb, monitoring should continue at least until the plants reach reproductive age.

● *Seed-feeding herbivores*

Herbivore enclosures should be considered in most habitats as losses of sown seed to generalist seed predators can be substantial. If possible, seed addition experiments should be performed both with and without predator exclusion.

● *Spatial and temporal scale*

Most existing studies have augmented seed inputs in a single pulse, but if recruitment is highly episodic in time, the results may be highly year dependent. Ideally the experiment should be repeated in a number of years, particularly if temporal variability in seed outputs is suspected to be a potential mechanism of coexistence. The appropriate spatial scale of seed addition experiments depends on the nature of the question, for example, whether interest centres on local abundance or on regional distribution.

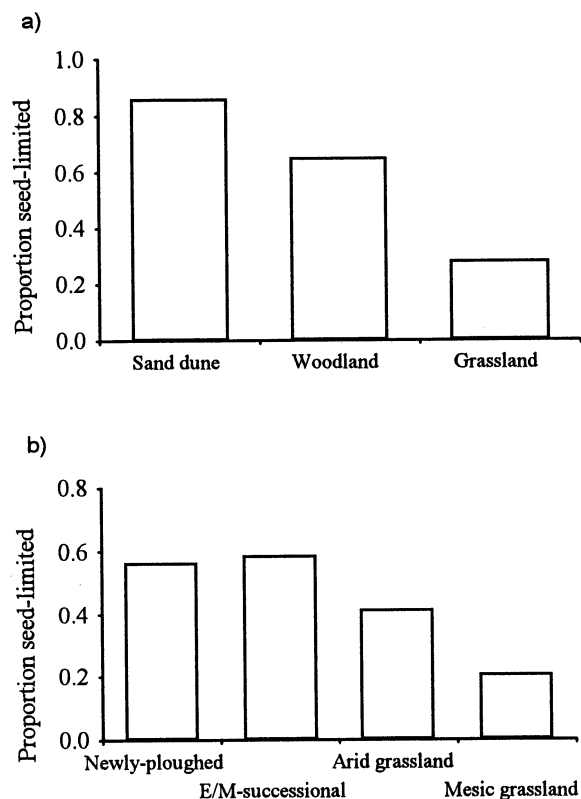


Fig. 1. The incidence of seed limitation (proportion of cases) in different habitats. (a) The three major intact habitat types in which there was a reasonable number of studies. Grassland includes both mesic and arid grasslands unploughed within 30 yr prior to study. (b) The incidence of seed limitation in recently disturbed and intact grasslands. Early/Mid (E/M)-successional grasslands are those ploughed within 30 yr prior to study.

the idea that recruitment limitation is likely to be more prevalent in transient habitats. The particularly low incidence of seed limitation in mesic grassland is consistent with more general reports of low seedling numbers in this ecosystem (Cavers and Harper 1967, Turkington et al. 1979, Barrett and Silander 1992, Johnston 1992).

These patterns across habitats appear to be correlated with the availability of bare earth (for example, higher in sand dunes than in grasslands) and hence the number of competition-free microsites. If seed limitation becomes more prevalent as the availability of bare earth increases, we might expect a disturbance treatment, such as the removal of adult plants or soil disruption, to enhance the extent of seed limitation. In 20 out of the 29 cases where a disturbance treatment was applied, a statistical interaction between seed sowing and disturbance was detected. In 19 of these, recruitment in disturbed + sown treatments was higher than in plots receiving either seed additions or disturbance alone. This implies that the removal of adults often provides additional microsites, but that seeds are

not always present to take advantage of such events. In the case of *Carlina vulgaris*, there was actually substantially lower recruitment in disturbed + sown plots than in undisturbed + sown plots (Greig-Smith and Sagar 1981). This was thought by the authors to be due to the greater visibility of seeds in plots where the vegetation had been removed, leading to higher rates of seed predation. The presence of such interactions indicates that populations cannot easily be characterised as either seed- or microsite-limited.

To a lesser extent, life form also influences the probability of a species being seed-limited. The likelihood of seed limitation declines in the order annuals/biennials > perennial non-woody species > perennial woody species (Fig. 2a). The higher incidence of seed limitation among short-lived species is partly confounded with their association with early successional habitats (they constitute most of the species found in sand dunes and newly ploughed fields). However, the higher incidence of seed limitation in ruderal species is not consistent with the competitive dominants being the most strongly recruitment-limited, as required by competition/colonisation trade-off models. Within perennial non-woody species, legumes showed a particularly high incidence of seed limitation compared with grasses and non-leguminous

forbs (Fig. 2b). This is perhaps due to the unusually high seed weights of leguminous species which may constrain their fecundity (the seed size/seed number trade-off) and their high palatability, often leading to high levels of herbivore attack, and consequently to reduced seed output (see for example Ehrlén 1995, Harrison and Maron 1995). The low incidence of seed limitation in woody species may be due to the removal of seeds by generalist herbivores prior to germination (Borchert and Jain 1978, Hulme 1994, Maron and Simms 1997). For example, seed burial was essential for successful recruitment in *Quercus robur* due to the rapid removal of unburied acorns by seed-feeding animals (Crawley and Long 1995).

Seed introductions

Whether or not the current regional distribution of a species is limited by seed availability can be investigated by sowing seed in sites where the species is known to be absent. Thirteen studies were found incorporating some 100 species (Appendix 2). In nearly all cases, the introduced species naturally occurred in habitats similar to that at the introduction site, and all studies were carried out within natural or semi-natural communities within the native range of the species. Introductions were deemed successful if at least one adult plant was present at the time of the census; it does not necessarily indicate the presence of a self-sustaining population.

In 53% of cases, the species was present in at least one of the introduction sites at the end of the monitoring period. Nine studies, involving 16 species at 90 sites, recorded establishment at both the seedling and adult stage. Of these, seedlings were present at 64% of sites while adult plants were only present at 23% of sites. This suggests that many apparently suitable sites cannot support adult plants although the species may germinate successfully. The small number of studies and the wide range of habitats make between-habitat comparisons difficult. However, two studies carried out in intact grasslands reveal a similar degree of seed limitation in both intact arid (55%) and mesic (59%) grassland (Burke and Grime 1996, Tilman 1997). These figures seem surprisingly high, but in both cases species presence was based on percentage cover and biomass scores and we cannot be sure that adult plants were always present. Indeed, at least for the mesic grassland study, it is stated that many species were only represented as seedlings and juvenile plants (Burke and Grime 1996). Once again disturbance increased the probability of successful establishment in 9 out of the 10 studies where a disturbance treatment was incorporated. It therefore seems that established adults form a considerable barrier to successful seedling establishment.

None of the studies attempted to link the chosen introduction sites with other occupied sites within dis-

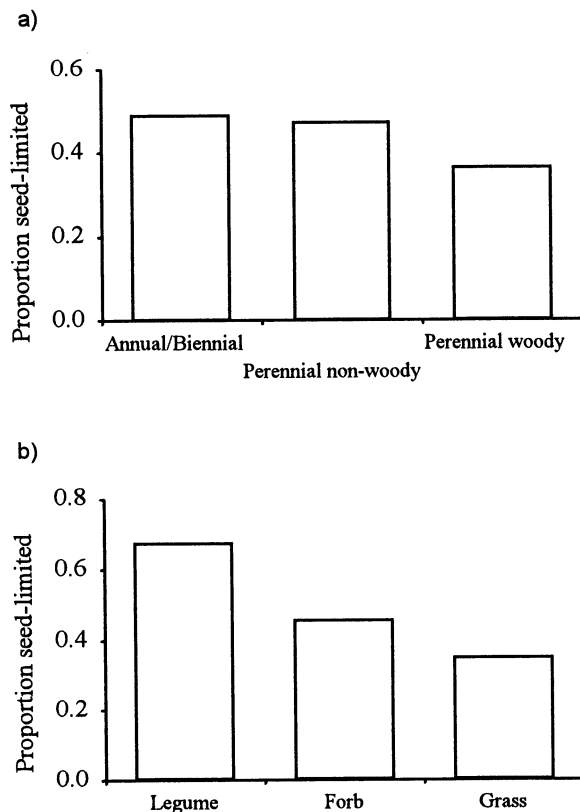


Fig. 2. The incidence of seed limitation in different life-form categories. (a) Differences between major life-form groups. (b) Differences within perennial non-woody categories.

persal range. As such it is impossible to know whether or not such sites form part of a metapopulation. The lack of long-term monitoring in many cases does not allow us to deduce whether successful introductions might lead to self-sustaining populations which could in turn act as new source populations.

Discussion

The issue of seed limitation is clearly an important one in plant ecology: in several of the best known models of multi-species dynamics, local scale coexistence can only be achieved when the component species suffer from seed limitation in either space or time. Seed addition studies have revealed that seed limitation often occurs within established populations, but that the prevalence of seed limitation varies greatly between habitats (for example, it is much more common in early successional habitats than in grasslands, and some kinds of communities (e.g. mesic grasslands) show extremely low rates of seed limitation). This variation may have important consequences for other ecological processes. For example, seed predators are more likely to have substantial effects on recruitment in arid grassland where seed limitation is particularly common. Similarly, models of coexistence which assume that the competitive dominants are recruitment-limited might be less relevant in mesic grassland communities where the incidence of seed limitation is known to be particularly low.

To date, seed addition studies have focused simply on whether or not seed limitation occurs, which, while important, does not allow several alternative models of coexistence to be distinguished. However, we believe that seed addition studies do have the potential to provide powerful insights into community structure (see also Pacala and Rees 1998). For example, the addition of seeds of all species at high density will ensure that all species reach all microsites (providing that there is little post-dispersal seed predation). If there is a high degree of competitive asymmetry, the competitive dominant should exclude other species in all sown areas (Turnbull et al. 1999). In this case, recruitment limitation in either space or time must be critical to coexistence, although further work would be required to demonstrate the proximate causes of this recruitment limitation. If, however, the identity of the dominant species varies from place to place, it seems likely that underlying spatial heterogeneity is more important in maintaining diversity. If recruitment is a lottery, and species have similar competitive abilities, attention should focus on the magnitude of between-year variability in relative seed outputs and/or germination fractions (Chesson and Huntly 1989).

We have seen that seed introduction commonly leads to the successful establishment of plants in sites where the species was formerly absent, supporting the idea that

local diversity can be enhanced through immigration (Cornell and Lawton 1992). It is worth noting, however, that many studies did not identify adult plants, and in those that did, the incidence of species presence dropped dramatically between the seedling and adult stages. Sowing experiments can be particularly useful in the study of mass effects by revealing the level of immigration required to supply a given density of new recruits. It might then be possible to determine the likelihood of substantial mass effects given the level of seed export from established populations, and the distance to putative sites. Disturbance enhanced the probability of successful establishment which supports the idea that equilibrium communities might be much more resistant to mass effects (Kunin 1998). The increasingly disturbed nature of the landscape is likely to mean that recruitment limitation will become more prevalent: the importance of introducing the seeds of desirable species into newly created, or restored, sites is being increasingly appreciated in the conservation literature (Buckley and Knight 1989, Francis and Morton 1995).

Longer-term monitoring is clearly required if we wish to establish whether or not the introduced plants form self-sustaining populations. This involves recording the seed output from sown recruits and would clearly be difficult for some long-lived species. If self-sustaining populations are successfully established, they have the potential to act as new source populations and this might allow the species to colonise a new region formerly out of reach (Pysek and Prach 1993, Thomson et al. 1993). The unequivocal identification of self-sustaining populations might also be difficult for species where suitable sites are transient, and population life time is inevitably short (Gross 1980, van der Meijden et al. 1992). However, it is in such populations that recruitment limitation is most likely to play a major role in regional dynamics.

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References

- Ackerman, J., Sabat, A. and Zimmerman, J. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. – *Oecologia* 106: 192–198.
- Andersen, A. N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? – *Oecologia* 81: 310–315.
- Armstrong, R. A. 1976. Fugitive species: experiments with fungi and some theoretical considerations. – *Ecology* 57: 953–963.
- Ashton, D. H. 1979. Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. – *Aust. J. Ecol.* 4: 265–277.
- Barrett, J. P. and Silander, J. A. 1992. Seedling recruitment limitation in white clover (*Trifolium repens*; Leguminosae). – *Am. J. Bot.* 79: 643–649.
- Borchert, M. I. and Jain, S. K. 1978. The effect of rodent seed predation on four species of Californian annual grasses. – *Oecologia* 33: 101–113.

- Buckley, G. P. and Knight, D. G. 1989. The feasibility of woodland reconstruction. – In: Buckley, G. P. (ed.), Biological habitat reconstruction. Belhaven Press, London, pp. 171–188.
- Burke, M. J. W. and Grime, J. P. 1996. An experimental study of plant community invasibility. – *Ecology* 77: 776–790.
- Caughley, G. 1994. Directions in conservation biology. – *J. Anim. Ecol.* 63: 215–244.
- Cavers, P. B. and Harper, J. L. 1967. Studies in the dynamics of plant populations. I. The fate of seed and transplants into various habitats. – *J. Ecol.* 55: 59–71.
- Chesson, P. L. 1986. Environmental variation and the coexistence of species. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper & Row, New York, pp. 240–256.
- Chesson, P. L. and Warner, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems. – *Am. Nat.* 117: 923–943.
- Chesson, P. L. and Warner, R. R. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. – *Am. Nat.* 125: 769–787.
- Chesson, P. L. and Huntly, N. 1989. Short-term instabilities and long-term community dynamics. – *Trends. Ecol. Evol.* 4: 293–298.
- Clark, J. S., Macklin, E. and Wood, L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. – *Ecol. Monogr.* 68: 213–235.
- Comins, H. N. and Noble, I. R. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. – *Am. Nat.* 126: 706–723.
- Cornell, H. V. and Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. – *J. Anim. Ecol.* 61: 1–12.
- Crawley, M. J. 1990. The population dynamics of plants. – In: Hassell, M. P. and May, R. M. (eds), Population regulation and dynamics. Royal Society, London, pp. 3–18.
- Crawley, M. J. and Nachapong, M. 1985. The establishment of seedlings from primary and regrowth seeds of ragwort (*Senecio jacobaea*). – *J. Ecol.* 73: 255–261.
- Crawley, M. J. and May, R. M. 1987. Population dynamics and plant community structure: competition between annuals and perennials. – *J. Theor. Biol.* 125: 475–489.
- Crawley, M. J. and Long, C. R. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. – *J. Ecol.* 83: 683–696.
- Duggan, A. E. 1989. Population ecology of *Cardamine pratensis* L and *Antocaris cardamines* L. – Ph.D. thesis, Imperial College of Science and Technology, UK.
- Ehrlén, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. – *J. Ecol.* 83: 297–308.
- Ehrlén, J. and Eriksson, O. 1996. Seedling recruitment in the perennial herb *Lathyrus vernus*. – *Flora* 191: 377–383.
- Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. – *Oikos* 77: 248–258.
- Eriksson, O. and Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. – *Oecologia* 91: 360–364.
- Fagerström, T. and Westoby, M. 1997. Population dynamics in sessile organisms: some general results from three seemingly different theory-lineages. – *Oikos* 80: 588–594.
- Fowler, N. L. 1986. Density dependent population regulation in a Texas grassland. – *Ecology* 67: 545–554.
- Francis, J. L. and Morton, A. J. 1995. Restoring the woodland field layer in young plantations and new woodlands. – In: Urbanska, K. M. and Grodinsha, K. (eds), Restoration ecology in Europe. Geobot. Inst. SFIT, Zurich, pp. 1–13.
- Goldberg, D. J. 1996. Competitive ability: definitions, contingency and correlated traits. – In: Silvertown, J. W., Franco, M. and Harper, J. L. (eds), Plant life histories: ecological correlates and phylogenetic constraints. *Philos. Trans. R. Soc. Lond. B*, pp. 1377–1385.
- Greig-Smith, J. and Sagar, G. R. 1981. Biological causes of local rarity in *Carlina vulgaris*. – In: Syngé, H. (ed.), The biological aspects of rare plant conservation. John Wiley, Chichester, pp. 389–400.
- Gross, K. L. 1980. Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. – *J. Ecol.* 68: 919–927.
- Gross, K. L. and Werner, P. A. 1982. Colonizing abilities of “biennial” plant species in relation to ground cover: implications for their distributions in a successional sere. – *Ecology* 63: 921–931.
- Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. – In: Hanski, I. and Gilpin, M. E. (eds), Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA, pp. 69–91.
- Hanski, I. and Ranta, E. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. – *J. Anim. Ecol.* 52: 263–279.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. – *Biol. J. Linn. Soc.* 42: 73–88.
- Harrison, S. and Maron, J. L. 1995. Impacts of defoliation by tussock moths (*Orgyia vestusta*) on the growth and reproduction of bush lupine (*Lupinus arboreus*). – *Ecol. Entomol.* 20: 223–229.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. – *Theor. Popul. Biol.* 18: 363–373.
- Hawthorn, W. R. and Cavers, P. B. 1976. Population dynamics of the perennial herbs *Plantago major* L. and *P. rugelii*. – *J. Ecol.* 64: 511–527.
- Herrera, C. M., Jordano, P., Guitián, J. and Traveset, A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. – *Am. Nat.* 152: 576–594.
- Horn, H. S. and MacArthur, R. H. 1972. Competition among fugitive species in a harlequin environment. – *Ecology* 53: 749–752.
- Hubbell, S. P., Foster, R. B., O'Brien, S. T. et al. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. – *Science* 283: 554–557.
- Hulme, P. E. 1994. Postdispersal seed predation in grassland – its magnitude and sources of variation. – *J. Ecol.* 82: 645–652.
- Hurt, G. C. and Pacala, S. W. 1996. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. – *J. Theor. Biol.* 176: 1–12.
- Husband, B. C. and Barrett, S. C. H. 1996. A metapopulation perspective in plant population biology. – *J. Ecol.* 84: 461–469.
- Janzen, D. H. 1976. Why bamboos wait so long to flower. – *Annu. Rev. Ecol. Syst.* 7: 347–391.
- Johnston, M. A. 1992. Rabbit grazing and the dynamics of plant communities. – Ph.D. thesis, Imperial College of Science and Technology, UK.
- Keddy, P. A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. – *J. Ecol.* 69: 615–630.
- Keddy, P. A. 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. – *Oecologia* 52: 348–355.
- Kelly, D. 1989. Demography of short-lived plants in chalk grassland. II. Control of mortality and fecundity. – *J. Ecol.* 77: 770–784.
- Klinkhamer, P. G. L. and de Jong, T. J. 1988. The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale*. – *J. Ecol.* 76: 383–392.
- Kunin, W. E. 1998. Biodiversity at the edge: a test of the importance of spatial “mass effects” in the Rothamsted Park Grass experiments. – *Proc. Natl. Acad. Sci. USA* 95: 207–212.

- Lamont, B. B. and Witkowski, E. T. F. 1995. A test for lottery recruitment among four *Banksia* species based on their demography and biological attributes. – *Oecologia* 101: 299–308.
- Lavorel, S. and Lebreton, J. D. 1992. Evidence for lottery recruitment in Mediterranean old fields. – *J. Veg. Sci.* 3: 91–100.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Bull. Entomol. Soc. Am.* 15: 237–240.
- Levins, R. and Culver, D. 1971. Regional coexistence of species and competition between rare species. – *Proc. Natl. Acad. Sci. USA* 68: 1246–1248.
- Louda, S. M. and Potvin, M. A. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. – *Ecology* 76: 229–245.
- Maron, J. L. and Simms, E. L. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). – *Oecologia* 111: 76–83.
- Miller, T. E. and Werner, P. A. 1987. Competitive effects and responses between plants species in a first-year old-field community. – *Ecology* 68: 1201–1210.
- O'Dowd, D. J. and Gill, A. M. 1984. Predator satiation and site alteration: mass reproduction of alpine ash (*Eucalyptus delegatensis*) following fire in southeastern Australia. – *Ecology* 65: 1052–1066.
- Orth, R. J., Luckenbach, M. and Moore, K. A. 1994. Limited dispersal of *Zostera marina* seed in shallow coastal waters. – *Ecology* 75: 1927–1939.
- Pacala, S. W. and Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. – *Am. Nat.* 143: 222–257.
- Pacala, S. W. and Rees, M. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. – *Am. Nat.* 152: 729–737.
- Peart, D. R. 1989. Species interactions in a successional grassland. II. Colonization of vegetated sites. – *J. Ecol.* 77: 252–266.
- Primack, R. B. and Miao, S. L. 1992. Dispersal can limit local plant distribution. – *Conserv. Biol.* 6: 513–519.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. – *Am. Nat.* 132: 652–661.
- Putwain, P. D., Machin, D. and Harper, J. L. 1968. Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella*. – *J. Ecol.* 56: 421–431.
- Pysek, P. and Prach, K. 1993. Plant invasions and the role of riparian habitats – a comparison of 4 species alien to central Europe. – *J. Biogeogr.* 20: 413–420.
- Rabinowitz, D., Rapp, J. K., Cairns, S. and Mayer, M. 1989. The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. – *Am. Nat.* 134: 525–544.
- Reader, R. J. and Buck, J. 1986. Topographic variation in the abundance of *Hieracium floribundum*: relative importance of differential seed dispersal, seedling establishment, plant survival and reproduction. – *J. Ecol.* 74: 815–822.
- Rees, M. 1989. The population ecology of annual crucifers. – Ph.D. thesis, Imperial College of Science and Technology, UK.
- Rees, M., Grubb, P. J. and Kelly, D. 1996. Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. – *Am. Nat.* 147: 1–32.
- Ribbens, E., Silander, J. A. and Pacala, S. W. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. – *Ecology* 75: 1794–1806.
- Robinson, G. R., Quinn, J. F. and Stanton, M. L. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. – *Ecology* 76: 786–794.
- Sagar, G. R. and Harper, J. L. 1960. Factors affecting the germination and early establishment of plantains (*Plantago lanceolata*, *P. media* and *P. major*). – In: Harper, J. L. (ed.), *The biology of weeds*. Blackwell, Oxford, pp. 236–245.
- Sagar, G. R. and Harper, J. L. 1961. Controlled interference with natural populations of *Plantago lanceolata*, *P. major* and *P. media*. – *Weed Res.* 1: 163–176.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. – *Am. Nat.* 111: 337–359.
- Shaw, R. G. and Antonovics, J. 1986. Density-dependence in *Salvia lyrata*, a herbaceous perennial: the effects of experimental alteration of seed densities. – *J. Ecol.* 74: 797–813.
- Shea, K. 1994. Matrix models in population ecology. – Ph.D. thesis, Imperial College of Science and Technology, UK.
- Sheppard, A. W. 1987. Insect herbivore competition and the population dynamics of *Heracleum sphondylium* L. (Umbelliferae). – Ph.D. thesis, Imperial College of Science and Technology, UK.
- Shmida, A. and Ellner, S. 1984. Coexistence of plants species with similar niches. – *Vegetatio* 58: 29–55.
- Silvertown, J. and Tremlett, M. 1989. Interactive effects of disturbance and shade upon colonization. – *Funct. Ecol.* 3: 229–235.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. – *Biol. J. Linn. Soc.* 14: 235–250.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. – *Biometrika* 38: 196–218.
- Smith, B. H. 1983. Demography of *Floerkea prosepinaoides*, a forest-floor annual. III. Dynamics of seed and seedling populations. – *J. Ecol.* 71: 413–425.
- Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. – *Conserv. Biol.* 8: 373–378.
- Thompson, K. and Baster, K. 1992. Establishment from seed of selected Umbelliferae in unmanaged grassland. – *Funct. Ecol.* 6: 346–352.
- Thomson, A. G., Radford, G. L., Norris, D. A. and Good, J. E. G. 1993. Factors affecting the distribution and spread of rhododendron in North Wales. – *J. Environ. Manage.* 39: 199–212.
- Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press, Princeton, NJ.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. – *Ecology* 78: 81–92.
- Tilman, D. and Wedin, D. 1991. Dynamics of nitrogen competition between successional grasses. – *Ecology* 72: 1038–1049.
- Tilman, D. and Pacala, S. W. 1993. The maintenance of species richness in plant communities. – In: Ricklefs, R. E. and Schluter, D. (eds), *Species diversity in ecological communities*. Univ. of Chicago Press, Chicago, pp. 13–25.
- Turkington, R., Cahn, M. A., Vardy, A. and Harper, J. L. 1979. The growth, distribution and neighbor relationships of *Trifolium repens* in a permanent pasture. III. The establishment and growth of *Trifolium repens* in natural and perturbed sites. – *J. Ecol.* 67: 231–243.
- Turnbull, L. A., Rees, M. and Crawley, M. J. 1999. Seed mass and the competition/colonisation trade-off: a sowing experiment. – *J. Ecol.* 87: 899–912.
- Valverde, T. and Silvertown, J. 1995. Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment. – *Funct. Ecol.* 9: 942–950.
- van Baalen, J. and Prins, E. G. M. 1983. Growth and reproduction of *Digitalis purpurea* in different stages of succession. – *Oecologia* 58: 84–91.
- van der Meijden, E., Klinkhamer, P. G. L., de Jong, T. J. and Vanwijk, C. A. M. 1992. Meta-population dynamics of biennial plants – how to exploit temporary habitats. – *Acta Bot. Neerl.* 41: 249–270.
- Waite, S. and Hutchings, M. J. 1979. A comparative study of establishment of *Plantago coronopus* L. from seeds sown randomly and in clumps. – *New Phytol.* 82: 575–583.
- Watkinson, A. R. 1985. On the abundance of plants along an environmental gradient. – *J. Ecol.* 73: 569–578.
- Werner, P. A. 1977. Colonization success of a biennial plant species: experimental field studies of species co-habitation and replacement. – *Ecology* 58: 840–849.

Appendix 1. Studies augmenting seed inputs to existing populations in natural or semi-natural vegetation.

Species	Life form	Habitat	Number of sowing densities	Range of densities (/m ²)	Disturbance treatment	Increased establishment following sowing			Interaction with disturbance	Reference
						<6 months	6-12 months	>12 months		
<i>Plantago lanceolata</i>	PF	MG	1	5511	-	Y	N	-	-	Sagar and Harper 1960
		MG	1	5511	-	N	N	-	-	
		MG	1	5511	-	N	N	-	-	
<i>Plantago major</i>	PF	MG	1	5511	-	N	N	-	-	Sagar and Harper 1961
<i>Plantago media</i>	PF	MG	1	5511	-	Y	N	-	-	
		MG	1	5511	-	N	N	-	-	
<i>Plantago lanceolata</i>	PF	MG	3	689 to 2756	RV	N	N	Y	Y	
		MG	3	689 to 2756	RV	N	N	Y	Y	
<i>Plantago major</i>	PF	MG	3	689 to 2756	RV	Y	N	-	N	
<i>Plantago media</i>	PF	MG	3	689 to 2756	RV	Y	Y	-	Y	
<i>Rumex obtusifolius</i>	PF	S	1	8888	-	Y	-	Y	-	Cavers and Harper 1967
		D	1	8888	-	Y	-	Y	-	
		W	1	8888	-	Y	-	Y	-	
		MG	1	8888	-	N	-	N	-	
<i>Rumex crispus</i> var. <i>littoreus</i>	PF	S	1	8888	-	Y	-	Y	-	
		D	1	8888	-	Y	-	Y	-	
		W	1	8888	-	Y	-	Y	-	
		MG	1	8888	-	Y	-	Y	-	
<i>Rumex crispus</i> var. <i>trigranulatus</i>	PF	S	1	8888	-	Y	-	Y	-	
		D	1	8888	-	Y	-	Y	-	
		W	1	8888	-	Y	-	Y	-	
		MG	1	8888	-	N	-	N	-	
<i>Rumex acetosella</i>	PF	S	5	555 to 55 555	-	-	N	-	-	Putwain et al. 1968
<i>Plantago major</i>	PF	S	1	625	-	Y	N	-	-	Hawthorn and Cavers 1976
<i>Plantago rugelii</i>	PF	S	1	625	-	Y	Y	Y	-	
<i>Plantago coronopus</i>	PF	D	3	1250 to 5000	-	Y	N	-	-	Waite and Hutchings 1979
<i>Verbascum thapsus</i>	BF	D	1	10 000	-	N	N	-	-	Gross 1980
<i>Carlina vulgaris</i>	BF	D	1	3200	-	Y	Y	Y	-	Greig-Smith and Sagar 1981
<i>Daucus carota</i>	BF	N	1	1000	-	Y	Y	Y	-	Gross and Werner 1982
		S	1	1000	-	Y	Y	Y	-	
<i>Oenothera biennis</i>	BF	N	1	10 000	-	Y	Y	Y	-	
		S	1	10 000	-	N	N	N	-	
<i>Tragopogon dubium</i>	BF	N	1	120	-	Y	Y	Y	-	
		S	1	120	-	Y	Y	Y	-	
<i>Verbascum thapsus</i>	BF	N	1	10 000	-	Y	Y	Y	-	
		S	1	10 000	-	Y	Y	Y	-	
<i>Senecio jacobaea</i>	BF	N	1	1000	-	-	N	-	-	Crawley and Nachapong 1985
<i>Bouteloua rigidiseta</i>	PG	AG	1	4469	RV	-	Y	-	N	Fowler 1986
<i>Hieracium floribundum</i>	PF	MG ¹	1	47 000	RV+SD	Y	N	-	Y	Reader and Buck 1986
		MG ²	1	47 000	RV+SD	Y	N	-	Y	
<i>Salvia lyrata</i>	PF	MG	8	300 to 14 400	RV	Y	Y	Y	Y	Shaw and Antonovics 1986
<i>Cirsium vulgare</i>	BF	D	1	1110	RV+SD	Y	Y	Y	Y	Klinkhamer and de Jong 1988
<i>Cynoglossum officinale</i>	BF	D	1	1110	RV+SD	Y	Y	Y	Y	

Appendix 1. (Continued)

Species	Life form	Habitat	Number of sowing densities	Range of densities (/m ²)	Disturbance treatment	Increased establishment following sowing			Interaction with disturbance	Reference
						<6 months	6-12 months	>12 months		
<i>Cardamine pratensis</i>	PF	N	1	2200	-	Y	-	-	-	
<i>Festuca rubra</i>	PG	N	1	1000	-	Y	-	-	-	
<i>Papaver dubium</i>	AF	N	1	1000	-	N	-	-	-	
<i>Rumex acetosella</i>	PF	N	1	1000	-	N	-	-	-	
<i>Tripleurospermum inodorum</i>	BF	N	1	1000	-	N	-	-	-	
<i>Betula allegheniensis</i>	PW	W	1	300	-	-	Y	-	-	Ribbens et al. 1994
<i>Tsuga canadensis</i>	PW	W	1	300	-	-	Y	-	-	
<i>Cirsium palustre</i>	BF	MG	1	250	C	N	N	-	N	Shea 1994
<i>Quercus robur</i>	PW	N	8	1 to 1000	-	N	N	-	-	Crawley and Long 1995
<i>Tolamnia variegata</i>	PE	SF	1	-	-	Y	-	-	-	Aekerman et al. 1996
<i>Lathyrus vernus</i>	PL	W	5	140 to 36 000	-	Y	Y	-	-	Ehrlén and Eriksson 1996
<i>Ambrosia artemisiifolia</i>	AF	AG	1	1119	-	-	-	-	-	Tilman 1997
<i>Amorpha canescens</i>	PL	AG	1	1991	-	-	-	-	-	
<i>Andropogon gerardi</i>	PG	AG	1	1557	-	-	-	-	-	
<i>Asclepias syriaca</i>	PF	AG	1	941	-	-	-	-	-	
<i>Asclepias tuberosa</i>	PF	AG	1	854	-	-	-	-	-	
<i>Aster azureus</i>	PF	AG	1	26 470	-	-	-	-	-	
<i>Aster ericoides</i>	PF	AG	1	75 000	-	-	-	-	-	
<i>Bouteloua curtipendula</i>	PG	AG	1	1077	-	-	-	-	-	
<i>Desmodium canadense</i>	PL	AG	1	955	-	-	-	-	-	
<i>Lespedeza capitata</i>	PL	AG	1	1860	-	-	-	-	-	
<i>Liatris aspera</i>	PF	AG	1	1875	-	-	-	-	-	
<i>Monarda fistulosa</i>	PF	AG	1	13 636	-	-	-	-	-	
<i>Oenothera biennis</i>	BF	AG	1	10 976	-	-	-	-	-	
<i>Panicum capillare</i>	AG	AG	1	22 500	-	-	-	-	-	
<i>Polygonum convolvulus</i>	AF	AG	1	888	-	-	-	-	-	
<i>Potentilla arguta</i>	PF	AG	1	37 500	-	-	-	-	-	
<i>Rosa arkansana</i>	PW	AG	1	308	-	-	-	-	-	
<i>Rudbeckia serotina</i>	PF	AG	1	30 000	-	-	-	-	-	
<i>Schizachyrium Scoparium</i>	PG	AG	1	2500	-	-	-	-	-	
<i>Setaria lutescens</i>	AG	AG	1	987	-	-	-	-	-	
<i>Solidago nemoralis</i>	PG	AG	1	75 000	-	-	-	-	-	
<i>Sorghastrum nutans</i>	PG	AG	1	1974	-	-	-	-	-	
<i>Stipa spartea</i>	PG	AG	1	304	-	-	-	-	-	

Life form A = annual, B = biennial or monocarpic perennial, P = polycarpic perennial, F = non-leguminous forb, L = leguminous forb, G = grass, W = woody, E = epiphyte. Habitat D = sand dune or beach, N = newly ploughed field, S = early/mid-successional field (unploughed within 2-30 yr), AG = intact arid grassland (unploughed for at least 30 yr), MG = intact mesic grassland (unploughed for at least 30 yr), W = temperate woodland, SF = subtropical forest, (1 = bottom of depression, 2 = top of depression, 3 = pasture site, 4 = lawn site).

Range of densities minimum and maximum sowing densities.

Disturbance treatment RV = Removal of above-ground vegetation, SD = Soil disturbance.

Increased establishment following sowing more plants in sown plots compared with unsown control plots (Y/N).

Interaction with disturbance a statistical interaction between sowing density and the disturbance treatment (Y/N).

Appendix 2. Studies in which seed introductions were attempted.

Species	Life form	Habitat	No. of sites	No. of sowing densities (/m ²)	Range of densities (/m ²)	DT	Number of sites with established plants			ID	Reference
							<6 months	6-12 months	>12 months		
<i>Plantago lanceolata</i>	PF	heath/bog	3	1	5511	-	0	0	-	-	Sagar and Harper 1960
		W	2	1	5511	-	2	0	-	-	
		N	1	1	5511	-	1	1	-	-	
<i>Plantago major</i>	PF	MG	3	1	5511	-	1	1	0	-	
		heath/bog	3	1	5511	-	0	0	-	-	
		W	2	1	5511	-	2	0	-	-	
		N	1	1	5511	-	1	1	-	-	
		MG	6	1	5511	-	3	1	0	-	
<i>Plantago media</i>	PF	heath/bog	3	1	5511	-	0	0	-	-	
		W	2	1	5511	-	2	0	-	-	
		N	1	1	5511	-	1	1	-	-	
		MG	5	1	5511	-	4	1	0	-	
		MG	1	3	689 to 2756	RV	1	1	-	Y	Sagar and Harper 1961
		MG	2	3	689 to 2756	RV	2	0	-	Y	
		MG	2	3	689 to 2756	RV	2	0	-	Y	
		S	8	1	600	-	8	7	7	-	Werner 1977
		D	3	7	25 to 5000	-	3	3	-	-	Keddy 1981
		W	2	4	1111 to 6666	-	2	-	-	-	Smith 1983
		MG	2	1	600	RV+SD	2	2	1	N	Sheppard 1987
<i>Plantago aristata</i>	BF	MG	2	1	4000	RV+SD	1	-	0	Y	Silvertown and Tremlett 1989
	BF	N	1	1	4000	RV+SD	1	-	0	Y	
	BF		1	1	4000	-	1	-	0	Y	
	BF		1	1	4000	-	1	-	0	Y	
	BF		1	1	4000	-	1	-	0	Y	
	BF		1	1	4000	-	1	-	0	Y	
	BF		1	1	88	-	1	-	0	-	Primack and Miao 1992
	AF	S	6	1	354	-	1	1	0	-	
	AF	open, sandy wetland	7	1	32	-	0	0	0	-	
	AF	Open, sandy	14	1	32	-	11	3	1	-	
	AF		7	1	354	-	5	4	2	-	Thompson and Baster 1992
	BF	S	1	1	160	-	-	-	0	-	
	BF		1	1	600	-	-	-	0	-	
	BF		1	1	320	-	-	-	0	-	
	BF		1	1	880	-	-	-	0	-	
BF		1	1	160	-	-	-	0	-		
BF		1	1	240	-	-	-	0	-		
BF		1	1	400	-	-	-	0	-		
BF		1	1	80	-	-	-	0	-		
AF		1	1	400	-	-	-	0	-		
PF	Estuary		1	255	-	-	1	0	-	-	Orth et al. 1994
BF	AG		1	500	G+M	1	1	1	Y	Robinson et al. 1995	
BF	MG		1	55 to 550 ¹	RV+SD	-	-	32 spp ²	Y	Burke and Grime 1996	
54 spp	AG		1	90 000	-	-	-	1 ³	-	Tilman 1997	
<i>Achillea millefolium</i>	PF		1	19 565	-	-	-	1	-	-	
<i>Agastache foeniculum</i>	PF		1	2133	-	-	-	1	-	-	
<i>Allium stellatum</i>	PF		1	4167	-	-	-	1	-	-	
<i>Anemone cylindrica</i>	PF		1		-	-	-	1	-	-	

Appendix 2. (Continued)

Species	Life form	Habitat	No. of sites	No. of sowing densities	Range of densities (/m ²)	DT	Number of sites with established plants			ID	Reference
							<6 months	6–12 months	>12 months		
<i>Asclepias verticillata</i>	PF		1	1	2000	–	–	–	1	–	–
<i>Aster novae-angliae</i>	PF		1	1	16 667	–	–	–	0	–	–
<i>Astragalus canadensis</i>	PL		1	1	2813	–	–	–	1	–	–
<i>Baptisia leucantha</i>	PL		1	1	304	–	–	–	1	–	–
<i>Celastrus scandens</i>	PW		1	1	287	–	–	–	0	–	–
<i>Coreopsis palmata</i>	PF		1	1	3191	–	–	–	1	–	–
<i>Delphinium virescens</i>	PF		1	1	8654	–	–	–	0	–	–
<i>Elymus canadensis</i>	PG		1	1	824	–	–	–	0	–	–
<i>Gentiana andrewsii</i>	PF		1	1	90 000	–	–	–	0	–	–
<i>Heuchera richardsonii</i>	PF		1	1	90 000	–	–	–	0	–	–
<i>Heuchera cristata</i>	PG		1	1	50 000	–	–	–	1	–	–
<i>Lupinus perennis</i>	PL		1	1	183	–	–	–	1	–	–
<i>Minutus ringens</i>	PF		1	1	450 000	–	–	–	0	–	–
<i>Nepeta cataria</i>	PF		1	1	7759	–	–	–	1	–	–
<i>Panicum virgatum</i>	PG		1	1	5000	–	–	–	1	–	–
<i>Paspalum ciliatifolium</i>	PG		1	1	4737	–	–	–	0	–	–
<i>Penstemon grandiflorus</i>	PF		1	1	2273	–	–	–	0	–	–
<i>Petalostemum candidum</i>	PF		1	1	3041	–	–	–	1	–	–
<i>Petalostemum purpureum</i>	PF		1	1	2941	–	–	–	1	–	–
<i>Petalostemum villosum</i>	PL		1	1	2459	–	–	–	1	–	–
<i>Solidago rigida</i>	PF		1	1	9184	–	–	–	1	–	–
<i>Solidago speciosa</i>	PF		1	1	225 000	–	–	–	0	–	–
<i>Sporobolus heterolepis</i>	PG		1	1	2922	–	–	–	0	–	–
<i>Verbena stricta</i>	PF		1	1	4787	–	–	–	0	–	–
<i>Veronicastrum virginicum</i>	PF		1	1	112 500	–	–	–	0	–	–
<i>Vicia villosa</i>	AL		1	1	186	–	–	–	0	–	–
<i>Zizia aptera</i>	PF		1	1	2228	–	–	–	1	–	–

Life form as described in Appendix 1.

Habitat as described in Appendix 1 except where full details given.

Number of sites the number of distinctly different sites used for the introductions (i.e. not experimental plots within a single habitat patch).

Range of densities minimum and maximum sowing densities (1 = sowing densities differed between species depending on seed mass).

DT (Disturbance treatment) RV = removal of vegetation, SD = soil disturbance, G = grazing, M = mowing.

Number of sites with established plants number of sites with at least one seedling (<6 months) or at least one adult (6–12 or >12 months) present at the time of census except 2 (biomass >0) and 3 (percentage cover >0).

ID Interaction with disturbance Y = a statistical interaction between sowing density and the disturbance treatment.