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REVIEW

Criteria for the introduction of plant species

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INTRODUCTION

Plant biodiversity is currently declining swiftly in many European regions and ecosystems, as documented by the declining number of recorded populations and increasing number of plant species on Red Data Lists. An estimated 20–30% of the native flora of The Netherlands is now considered seriously at risk or actually has become extinct in recent years. This follows from an analysis of distribution maps over the period 1960–80 (Weeda *et al.* 1990). This figure corresponds well with similar data for Germany (Korneck & Sukopp 1988), Switzerland (Landolt 1991), the USA (Falk 1992) and even for the whole of the vascular plant flora of the world (Raven 1987).

There is strong concern about the loss of diversity because diversity is frequently regarded as a measure of ecosystem quality and there is growing evidence that biodiversity is important for maintaining ecosystem functions (Naeem *et al.* 1996; Tilman *et al.* 1996). Moreover, because there is a time-lag before the deterioration of conditions is expressed in the extinction of populations, the recorded decline in regional biodiversity may represent only the forerunner of future larger losses (Tilman *et al.* 1994). This time-lag may be especially large in long-lived plants.

Explanations for this rapid and unprecedented decline involve habitat deterioration and fragmentation due to ever-increasing human activities. As a result fewer, smaller and more isolated habitat patches carry correspondingly fewer, smaller and more isolated plant populations. Smaller populations run a larger risk of chance extinction and when isolated have a lower chance of colonizing a patch elsewhere. Genetically speaking, smaller and isolated populations run the risk of inbreeding affecting key fitness traits for sessile organisms such as longevity and dispersal capacity (Olivieri & Gouyon 1996). The demographic and genetic factors act in concert. Reduced individual longevity increases the local extinction risk and reduced dispersal capacity diminishes the number of new colonizations elsewhere that must balance local extinctions. This creates what has come to be known as the (hypothetical) extinction vortex (Gilpin & Soulé 1986; Lamont & Klinkhamer 1993).

The conservation measures taken to halt the increasing decline in plant biodiversity show a stepwise increase that match, to a large extent, the increased threats to plant biodiversity: after an initial effort to set aside valuable habitats in nature reserves at the beginning of this century, it became clear that the quality of these reserves could only be maintained by maintaining the former land use that created these semi-natural landscapes in the first place (Westhoff 1971). As the impact of environmental change became increasingly serious management efforts began focusing on efforts to control the detrimental impact of external factors such as air, water and soil pollution. Controlling for the effects of environmental change, however, in many cases does not halt the ongoing decline in plant species biodiversity and the need for additional measures at the species level is now apparent. The translocation of plant species which includes the re-introduction of species into habitats where they have disappeared, the introduction into restored habitats where they have yet not appeared or the restocking of individuals into dwindling populations (Given 1994), is now a much debated option for management.

In this review we will outline briefly the current criteria for the translocation of plant species as a measure to halt declining plant species diversity, mainly focusing on (re-) introduction. We will then offset these criteria against extinction risks run by specific plants with specific life histories based on demographic and genetic arguments that, in our opinion, are relevant to the issue and we will conclude with suggestions for useful further specifications to the criteria used when considering the (re-)introduction of plant species.

CURRENT CRITERIA FOR THE (RE-)INTRODUCTION OF PLANT SPECIES

With respect to the (re-)introduction of species there is a curious dichotomy between plants and animals. Whereas there are numerous examples of (re-)introducing mainly highly mobile animals, there are few examples of the (re-)introduction of plants (Hodder & Bullock 1997). This is the more astonishing given the long sessile part of the life-cycle of plants and the, in comparison, very short mobile dispersal phase. Such a distinct two-phase lifestyle would benefit far more from considered (re-)introduction programmes than those already in place for mobile animals as most (re-)introduction is motivated by the problem of getting to a target area.

The underlying reasons for this cautious attitude towards introducing plant species might be multiple. One argument at the community level could be that where plant ecology is concerned, there is a strong tradition for studying vegetation patterns. These plant assemblages are considered to reflect local abiotic and biotic conditions, and therefore altering the species composition is changing the indicator value of such a relationship. Paradigmatic to this idea is the assumption that local conditions select from the available species pool those species that are suited to live there, with the result that the species composition reflects the local conditions. In this view dispersal is rarely seen as a problem. The contrasting Gleasonian view of the plant community places more emphasis on the dispersal process, and within boundaries regards species assemblages as much more governed by chance processes. In such a view dispersal is a key process that determines species composition. However, this latter view is not widespread and consequently actively changing species composition is met with caution.

Another argument at the population level could be that the sum of all populations and their geographic distribution is seen as representative of the range of environmental conditions in which the species can be expected to live. In particular, the limits of distribution are considered sensitive indicators for the ecological amplitude of plant species and introductions might destroy the information contained in a species' area of distribution. In essence this is based on the same argument as given above and requires a relatively non-problematic dispersal so that the limits of distribution indeed reflect accurately the ecological possibilities. Related to this is the view that local populations are thought to be optimally adapted to their habitat and that the introduction of alien material could break down optimal trait complexes through outbreeding depression (e.g. Templeton 1991).

A third, more genetic, argument often used in the debate about (re-)introduction is the fact that there are a number of wilful introductions that had unexpected side-effects and the same applies for accidental introductions that became invasions. Of more than 12 000 alien species introduced to the British Isles mainly for horticultural reasons, more than 1500 have escaped from their original point of introduction and about 200 became established, 40 of which are considered pests (Williamson 1993). Introduced species also hybridize with native ones, thereby altering the original gene pool as demonstrated for the rare *Populus nigra* (Lauwaars *et al.* 1997). We have also, on a large scale, introduced native species from elsewhere for silvicultural or agricultural purposes, thereby altering the genetic make-up of local stock for species such as *Quercus robur*, *Pinus sylvestris* and *Poa pratensis*. This also shows a profound ambiguity with respect to introductions into so-called natural habitats compared to introductions into areas with a predominantly horticultural, silvicultural or agricultural function.

The sum of the above arguments has led to the following specific rules of thumb for the (re-)introduction of plant species (largely after Londo & Van der Meijden 1991; see also IUCN 1995 for more general guidelines and Hodder and Bullock 1997 for a recent review):

- Introduction is a last possible measure. First we need to improve habitat conditions and allow enough time for natural processes of dispersal and establishment including regeneration from an available seedbank to take place (Bekker *et al.* 1998, this issue). This strategy, however, may not be successful (Prins *et al.* 1998 this issue).
- The next step is to enhance natural dispersal. This could be achieved by creating seed sources next to protected target areas or to stimulate dispersal vectors such as grazing livestock. In this category man as a dispersal agent, through his use of land and machinery, has an important role (Strykstra & Verweij 1997).
- If introduction is to be considered then this should be achieved by using propagules from nearby sites to achieve maximum similarity between neighbouring populations. The propagules considered should preferably be seeds. Planting generally is not considered an option.
- (Re-)introductions once they have been done should be carefully monitored to measure the success and the possible impact on non-target species.

DETERMINANTS OF EXTINCTION RISKS

The rules of thumb concerning the (re-)introduction of plant species must be weighed against the risk run by plant species in a fragmenting and deteriorating landscape. When these risks are large, the general measures described above could be too conservative and there might arise the need for more directed species rescue programmes such as the ones developed for threatened animals (Hodder & Bullock 1997). Clearly, not all species

Table 1. The hypothetical sensitivity of species for habitat fragmentation following the classification of rarity after Rabinowitz (1981). An increasing number of + signs refers to increasing sensitivity to habitat fragmentation

Habitat preference	Natural population size	Geographic distribution: Large	Geographic distribution: Small
Wide	Large	+	+ + +
	Small	+/−	+
Small	Large	+ +	+ + + +
	Small	+	+ +

run the same risk and not all species will respond in the same way when rescue programmes are considered. What is needed is knowledge of which species will run larger risks than others and what life history traits they have in common so that we can, to a certain extent, predict the population responses to rescue management and amend the criteria for re-introduction in a species-specific way.

The risk of extinction of plant species is determined by the rate at which suitable habitat is lost through habitat deterioration and fragmentation. Both processes result in fewer, smaller and more isolated populations of (endangered) plant species and are defined at three hierarchically related levels: landscape, population and individual trait (Tilman 1994; Tilman *et al.* 1994; Schemske *et al.* 1994).

Landscape level

On the highest level there are the spatial dynamics of populations defined by colonization and extinction rates as originally formulated by Levin (1969); see also Gilpin & Hanski (1991). These rates determine the possibility for a species to maintain itself in a subdivided population and depend in the first place on the spatial configuration of the populations of the plant species involved. A given spatial configuration must be considered in the light of specific species traits such as dispersal capacity (see below), but will also depend on whether that configuration results from recent fragmentation processes or whether that configuration is close to normal. Species that used to occur in large, more or less continuous populations will be more sensitive to habitat fragmentation (Huenneke 1991) than species specialized to live in small numbers in rare habitats. The first to recognize the relationship between mean population size in the field, habitat preference and geographic distribution was Rabinowitz (1981). On these relationships she based her categorization of the rarity of species, which is relevant for understanding the sensitivity of species for habitat fragmentation (Table 1).

Population level

Apart from spatial configuration, colonization and extinction rates themselves depend on three important processes: the capacity to persist in a given site and prevent local extinction, the capacity to function as a seed source and to disperse away from that source and the capacity to colonize new sites or reinforce populations already existing in other sites. These rates define the second hierarchical level of the extinction risk of species: the demographic risks on the level of the population.

Table 2. Components of life-cycle traits that determine dispersal capacity, colonization and extinction rates

Traits associated with dispersal	Traits associated with colonization	Traits associated with extinction
Reproductive effort	Germination requirements	Competitive capacity
Seed number	Seedling vigour	Stress tolerance
Dispersal attributes	Seed dormancy	Disturbance resistance
		Seed/adult longevity
		Clonality/storage

Characteristic life-cycle traits that are important in this respect are adult lifespan, seed output, dispersal attributes, seed dormancy and, related to this, germination characteristics. Dispersal attributes determine the dispersal capacity and the ability to reach new sites (Van Dorp *et al.* 1997), seed dormancy and germination characteristics determine the capacity and timing to (re-)colonize a site (Olff *et al.* 1994) and adult lifespan determines the capacity to keep a site occupied and to function as a seed source. The most important components of life-cycle traits are listed in Table 2.

Between the traits of Table 2, several trade-offs are reported. Species that do disperse well do not show repeated recruitment mostly because of lack of dormancy mechanisms (Eriksson 1989). There is the well-known trade-off between adult longevity and reproductive effort (Fitter 1986), where a large reproductive effort is associated with greater numbers of seeds. For numerical reasons alone this increases the chance for dispersal. In successional series the well-dispersed species appear first, but have a restricted territory holding capacity, compared to the later successional ones (Grime *et al.* 1988). A trade-off has been postulated between competitive ability for nutrients, which enhances longevity, and reproductive effort (Gleeson & Tilman 1990). Between longevity and RGR of seedlings or seedling vigour a negative relation is found (Grime *et al.*, 1988). Stress tolerance, e.g. for water shortage and dispersal distance (Platt & Weiss 1977), and water shortage tolerance and seed number (Werner & Platt 1976) are traded off against each other. There is the widely recognized trade-off between seed size and dormancy (Rees 1993), between dormancy and dispersability (Rees 1993) and between longevity of the adult and dormancy (Rees 1993). Other authors report the trade-off between competitive ability for N as a proxy for longevity and time to colonization (Tilman 1990), between root allocation (storage) and reproductive effort (Tilman & Wedin 1991). An extremely relevant trade-off is the one between seed size (a measure of seedling and subsequent adult success) and dispersal distance (Rees 1993), based on the relation between seed size and seedling survival (Westoby *et al.* 1996). Finally, trade-offs between dormancy and dispersability (Willson 1993), between seed size and seed number (Wilson & Thompsson 1993; Roff 1992) have been reported. See also Bakker *et al.* (1996) and Strykstra *et al.* (this issue).

The trade-off relationships that exist between life history traits indicate that the trait space for these traits is not evenly filled but that certain combinations or strategies have a greater prevalence. From Table 2 three main traits are selected: adult longevity, seed longevity which results from dormancy mechanism and germination characteristics and the capacity to disperse. Their hypothetical trade-off relations are mapped in a triangular diagram (Fig. 1), indicating that species with persistent seeds are supposed

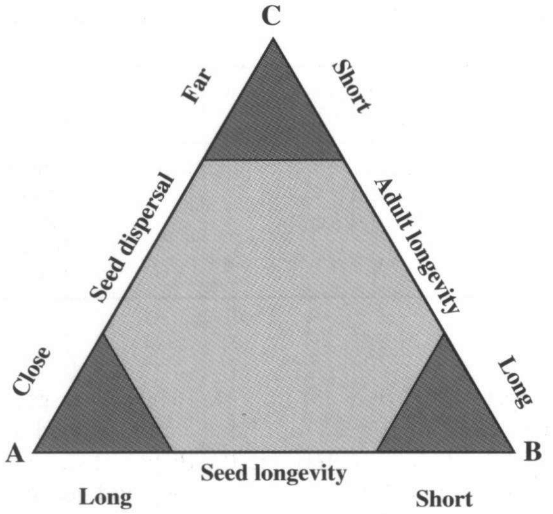

Fig. 1. Hypothetical trade-offs between seed longevity, dispersal capacity and adult longevity. Letters refer to the combinations of life-cycle traits as presented in Table 3.

Table 3. Three hypothetical combinations of life-cycle traits. Each combination represents one corner of the triangular diagram of Fig. 1, by reading this diagram counter-clockwise. As the value of one of three traits is determined by the way the diagram is read these values are placed between brackets

Trait	A	B	C
Seed longevity	Long >5 years	Short <5 years	(Short <5 years)
Adult (genet) longevity	(Short <5 years)	Long >5 years	Short <5 years
Distance of dispersal	Close to adult	(Close to adult)	Far from adult
Breeding system	Selfing	Outcrossing (wind)	Outcrossing (insect)

to have limited capacity to spread (A; lower left-hand corner), that adult longevity is important because of the negative relationship with seed survival (B; lower right-hand corner) and that short-lived species tend to disperse far (C; top corner). By reading the triangular diagram from the lower left-hand corner, counter-clockwise towards the top corner, three hypothetical combinations of life-cycle traits are formed. Each hypothetical combination of life-cycle traits can be attributed a different sensitivity for the effects of landscape fragmentation (Table 3). Combination C is most vulnerable while A is least vulnerable. A can be seen as the typical species that depends on repeated local disturbance, independent of spatial configuration, whereas species C needs enough colonizable sites in large uninterupted stretches of habitat. This strategy is most affected by habitat fragmentation.

Individual trait level

The individual traits that make up the persistence and dispersal attributes of a species are subject to continuous change as a result of selection processes, the third level in the hierarchical determination of species extinction risks: the genetic risks. Selection itself depends on heritable genetic variation which is dependent not only on the size but also on the spatial configuration of the populations involved (Bijlsma *et al.* 1994; Young 1995). Therefore, fragmentation does not only cause demographic problems. There are also clear genetic effects that impact on the capacity of plant species to survive in fragmented habitats. The (positive) relationship between population size and genetic marker variation and the (negative) relation between this genetic variation and isolation have been shown in a number of studies (Van Treuren *et al.* 1991; Raijmann *et al.* 1994). The next step, however, the relation between genetic marker variation and better individual survival probabilities, has never been shown unambiguously: in some studies it could be shown (Oostermeijer *et al.* 1995), in others it could not (Van Treuren *et al.* 1993; Ouborg & Van Treuren 1994). Although the relation between genetic marker variation and quantitative genetic variation is disputed, the role of genetic variation for the capacity to adapt to a changing environment is undisputed.

The consequence of the above is that habitat fragmentation leads to reduced geneflow and increased risk of inbreeding as a result of restricted seed and pollen dispersal. This means that to fully understand the consequences of habitat fragmentation, geneflow through seed and pollen has to be brought into the equation (for an excellent short recent review, see Den Nijs & Oostermeijer 1997). In addition to seed and adult longevity and dispersal capacity, reproductive biology is therefore an important factor determining the sensitivity to fragmentation (Table 3). Specifically cross-pollinating species are vulnerable because of the neccessity to exchange between genetically distinct individuals. Absence of non-related partners can lead to a decreasing seed set and to an increase of inbreeding (Lamont *et al.* 1993) that by itself might add to the problems, because it can lead to reduced persistence, lower reproductive output and possibly to reduced dispersal capacity. Moreover, fragmentation may negatively influence the pollinating vector such as insects (Bronstein 1995; Kwak 1988).

The problems with maintaining genetic variation in fragmented and isolated populations of plants show that extinction risks based solely on demographic characteristics might be too optimistic. In the long term a larger number of individuals is required to maintain a genetically viable population, compared to strict demographic arguments. The reason is that the effective population size always is much smaller than the actual population size (Wright 1938) because not all individuals are involved in breeding, sex ratios may not be equal, matings occur between neighbours who presumably are also relatives and incompatability or pollinator limitation may reduce seed set. This all leads to the fact that there is an unequal contribution of individuals to the next generation and this requires a larger number of individuals than would be apparent from strict demographic reasoning.

Another genetic effect is the fact that the good dispersers who found new populations over successional time will be replaced by individuals who are better at competing rather than at dispersing (Olivieri & Gouyon 1996; Cody & Overton 1996). Fragmentation will enhance this effect as good dispersers, when isolated in a fragmented habitat, lose a disproportionate fraction of their seeds to a hostile environment. This results in selection pressure on the non-dispersing genotypes and to loss of dispersal capacity and possibilities to colonize new sites. When there is a general decline in the number of sites occupied, there will also be less opportunity to test new genotypes over a wide range of available conditions, thus reducing the number of genes from the gene pool that get expressed. This is especially true for marginal habitats and for sites at the edges of distribution that are supposed to have a crucial role in adapting a species to its habitat (Holt & Gaines 1992). More generally, local specialization following colonization and isolation may render the offspring incapable of colonizing sites slightly different from the source site.

Based on genetic arguments one can expect that fragmentation will enhance the extinction risks of outbreeding, insect-pollinated plant species over outbreeding species that are wind-pollinated and certainly over strict selfing species. As the breeding system is related to the longevity of plants, with short-lived plants being predominantly selfing and long-lived plants being predominantly outbreeding, this ties the breeding system into the trait space depicted above (Table 3). Another link is the fact that good dispersers, as in category C, will suffer even more from fragmentation when this results in selection pressure against dispersal capacity, an interaction also known as the extinction vortex (Gilpin & Soulé 1986).

FURTHER CRITERIA FOR (RE-)INTRODUCTION

From the above it can be concluded that well-dispersing plant species with short generation times, both in the adult and seed stages, will be affected more by fragmentation and isolation than species with either long seed survival or a long adult life and short dispersal distances. This contrast will be most pronounced when the former group of species shows insect pollination and when the latter consists of selfers. Therefore the first group is hypothesized to show stronger effects of habitat fragmentation in terms of increased extinction rates and increased inbreeding. When such sensitive species used to occupy formerly common and widespread habitats then they most probably will have lost many habitats to grow in and have already suffered from habitat fragmentation, the so-called ‘new rares’ (Huenneke 1991). These species therefore are the most logical targets for (re-)introduction programmes.

The arguments raised above not only lead to a choice of species but also to suggestions of where best to introduce. It is common practice nowadays to select those sites that best match the optimum habitat of the species and/or sites from which the species have only recently disappeared. However, the (re-)introduction of species preferably should be done not only into what we perceive to be the optimal conditions for a species. First, we may be wrong about what is optimal. Secondly, we might restrict unnecessarily the expression of the potential of a species to grow over a range of habitats. Especially marginal habitats might have a clear function in the dynamic process of selection and adaptation. Here new genotypes are tested and new ecotypes might be the result, capable of surviving under different environmental conditions and thereby better preparing a species to live in a rapidly changing world.

A similar argument applies to the source material: when (re-)introduction is considered, it is usually advisable to use local or regional seed material. First of all, if we restrict ourselves to using local material because it might best fit the local conditions in the introduction site, we again restrict the potential for selection and adaptation. A neighbouring population that serves as a seed source, especially when already from a fragmented population and from an isolated habitat, might have lost the genetic diversity required for successful establishment elsewhere. Genetically diverse material from large core populations might be a better option and provide the right genotypes that can found new populations elsewhere. Secondly, using seeds for (re-)introduction also does not necessarily represent the best option. One of the arguments for the use of seeds as the source material is that this way only those individuals will be selected and establish that can complete the whole life-cycle from germination until successful seed production. However, this requires large numbers of seeds and frequent repeats, comparable to what plant species normally do: flower repeatedly and produce large numbers of offspring. For this, seeds have to be collected in large numbers from elsewhere and this could represent a substantial drain on the local seed rain in the source population. This can easily be avoided by introducing a restricted number of carefully selected adults that will subsequently do the seed production and seeding in the required numbers and with the natural timing and frequency. In this way it is also possible to avoid founder effects that can result from too small a number of individuals that establish a new population when using seed and to control the number of individuals necessary to form a minimum viable population size (Gilpin & Soulé 1986; Van Groenendael 1995).

The above is summarized in the following rules of thumb that can be used when considering species introductions:

Which species to select?

- Species from formerly common widespread habitats;
- species with clear long-distance dispersal;
- species that are short-lived without clear dormancy; and
- species that are outcrossing and insect pollinated.

Where to introduce?

- In existing populations that have become small;
- in existing but non-occupied habitat;
- in marginal habitat to bring to expression as much from the gene pool as possible.

What source material to use?

- Adult transplants to avoid the large demographic risks run bysowing seeds and that can serve as repeated seed and pollen source; and
- transplant material from more than one regional source to avoid possible local inbreeding.

How many?

- Around 50 or more adults to create an effective population size and to reduce chance extinction risks.

REFERENCES

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. (1996): Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl.* 45: 461–490.

Bekker, R.M., Schaminée, J.H.J. & Bakker, J.P. (1998): Seed bank characteristics of Dutch plant communities. *Acta Bot. Neerl.* 47: 15–26.

Bijlsma, R., Ouborg, N.J. & Van Treuren, R. (1994): On genetic erosion and population extinction in plants: a case study in *Scabiosa columbaria* and *Salvia pratensis*. In: Loeschcke, V., Tomiuk, J. & Jain, S. (eds.): *Conservation Genetics*, pp. 255–271, Birkhauser Verlag, Basel.

Bronstein, J.L. (1995): The plant-pollinator landscape. In: Hansson, L., Fahrig, L. & Merriam, G. (eds.): *Mosaic Landscapes and Ecological Processes*, pp. 256–288, Chapman and Hall, London.

Cody, M. & Overton, J.McC. (1996): Short-term evolution of reduced dispersal in island plant populations. *J. Ecol.* 84: 53–61

Den Nijs, J.C.M. & Oostermeijer, G.B. (1997): Reproductive biology and gene flow in a fragmented landscape. *Bocconea* 7: 153–165.

Eriksson, O. (1989): Seedling dynamics and life histories in clonal plants. *Oikos* 55: 231–266.

Fitter, A.H. (1986): Acquisition and utilization of resources. In: Crawley, M.J. (ed.): *Plant Ecology*, pp. 375–405, Blackwell Scientific Publications, Oxford.

Falk, D.A. (1992): From conservation biology to conservation practice: strategies for protecting plant diversity. In: Fiedler, P.L. & Jain, S.K. (eds): *Conservation Biology: the theory and practice of nature conservation*, pp. 397–431, Chapman & Hall, New York.

Gilpin, M.E. & Soulé, M.E. (1986): Minimum viable populations: processes of species extintion. In: Soulé, M.E. (ed.): *Conservation Biology: The Science of Scarcity and Diversity*, pp. 19–34, Sinauer Associates, Sunderland, MA.

Gilpin, M.E. & Hanski, I. (1991): *Metapopulation Dynamics: empirical and theoretical investigations*, Academic Press, London.

Given, D.R. (1994): *Principles and Practice of Plant Conservation*, Chapman & Hall, London.

Gleeson, S. & Tilman, D. (1990): Allocation and the transient dynamics of competition during succession on poor soils. *Ecology* **71**: 1144–1155.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988): *Comparative Plant Ecology.*Unwin Hyman, London.

Hodder, K.H. & Bullock, J.M. (1997): Translocations of native species in the UK: implications for biodiversity. *J.Appl.Ecol.* **34**: 547–565.

Holt, R.D. & Gaines, M.S. (1992): Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.* **6**: 433–447.

Huenneke, L.F. (1991): Ecological implications of genetic variation in plant populations. In: Falk, D.A. & Holsinger, K.E. (eds.): *Genetics and Conservation in Rare Plants*, pp.75–86, Oxford University Press, Oxford

IUCN (1995): *Guidelines for Reintroductions.* IUCN/SSC Reintroduction Specialist Group, Gland, Switzerland.

Korneck, D. & Sukopp, H. (1988): Rote Liste der in der Bundesrepublik Deutschland ausgestorbenen, verschollenen und gefaehrdeten Farn- und Blutenpflanzen und ihre Auswertung fuer den Arten- und Biotopschutz. *Schriftenr. Vegetat.* **19**: 1–210.

Kwak, M.M. (1988): Pollination ecology and seed set in the rare annual species *Melampyrum pratense* L. *(Scrophulariaceae). Acta Bot. Neerl.* **27**: 153–168.

Lamont, B.B. & Klinkhamer, P.G.L. (1993): Population size and viability. *Nature* **362**: 211.

Lamont, B.B., Klinkhamer, P.G.L. & Witkowski, E.T.F. (1993): Population fragmentation may reduce fertility to zero in *Banksia Goodii*—a demonstration of the Allee-effect. *Oecologia* **94**: 446–450.

Landolt, E. (1991). *Gefaehrdung der Farn- und Blutenpflanzen in der Schweiz.* Bundesamt fuer Umwelt, Wald und Landschaft, Bern.

Lauwaars, S.G., Arens, P., Willink, G., Coops, H. & Vosman, B. (1997): *Populaties van Zwarte Populier langs de Rijn in Nederland: is herstel mogelijk?* EHR publication 68–1997. RIZA, Lelystad.

Levins, R. (1969): Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Ent. Soc. Am.* **15**: 237–240.

Londo, G. & Van der Meijden, R. (1991): (Her-) introductie van plantesoorten: floravervalsing of natuurbehoud. *De Lev. Nat.* **92**: 176–182.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994): Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734–737.

Olivieri, I. & Gouyon, P.-H. (1996). Evolution of migration and other traits: the metapopulation effect. In: Hanski, I. & Gilpin, M.E. (eds.): *Metapopulation Dynamics: ecology, genetics and evolution*, Academic Press, San Diego.

Olff, H., Pegtel, D., Van Groenendael, J.M. & Bakker, J.P. (1994): Germination strategies during grassland succession. *J. Ecol.* **82**: 69–78.

Oostermeijer, J.G.B., Van Eijck, M.W. & Den Nijs, J.C.M. (1995): Analysis of the relationship between allozyme heterozygosity and fitness in the rare *Gentiana pneumonanthe* L. *J. Evol. Biol.* **8**: 739–757.

Ouborg, N.J. & Van Treuren, R. (1994): The significance of genetic erosion in the proces of extinction. IV. Inbreeding load and heterosis in relation to population size in the mint *Salvia pratensis. Evolution* **48**: 996–1008.

Platt, W.J. & Weiss, I.M. (1977): Resource partitioning and competition within a guild of fugitive prairie plants. *Am. Nat.* **111**: 479–513.

Prins, A.H., Dijkstra, G.A. & Bekker, R.M. (1998): Feasibility of target communities in a Dutch brook valley system. *Acta Bot. Neerl.* **47**: 71–88.

Rabinowitz, D. (1981): Seven forms of rarity. In: Synge, H. (ed.): *The Biological Aspects of Rare Plant Conservation*, pp. 205–217, John Wiley and Sons, New York.

Raijmann, L.E.L., Van Leeuwen, N.C., Kersten, R., Oostermeijer, J.G.B., Den Nijs, J.C.M. & Menken, S.B.J. (1994): Genetic variation and outcrossing rate in relation to population size in *Gentiana pneumonanthe* L. *Cons. Biol.* **8**:1014–1026.

Raven, P.H. (1987). The scope of the plant conservation problem world wide. In: Bramwell, D., Hamann, O., Heywood, V. & Synge, H. (eds.): *Botanic Gardens and the World Conservation Strategy*, pp. 19–20, Academic Press, London,

Rees, M. (1993): Trade-offs among dispersal strategies in British plants. *Nature* **366**: 150–152.

Roff, D.A. (1992): *The Evolution of Life Histories: theory and analysis.* Chapman & Hall, New York

Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M. & Bishop, J.G.

(1994): Evaluating approaches to the conservation of rare and endangered plant species. *Ecology* **75**: 584–606.

Strykstra, R.J., Verweij, G.L. & Bakker, J.P. (1997): Seed dispersal by mowing machinery in a Dutch brook valley system. *Acta Bot. Neerl.* **46**: 387–401.

Templeton, A.R. (1991): Off-site breeding of animals and implications for plant conservation strategies. In: Falk, D.A. & Holsinger, K.E. (eds.): *Genetics and Conservation of Rare Plants*, pp.182–194, Oxford University Press, Oxford.

Tilman, D. (1990): Constraints and trade-offs: toward a predictive theory of competition and succession. *Oikos* **58**: 3–15.

Tilman, D. (1994): Competition and biodiversity in spatially structured habitats. *Ecology* **75**: 2–16.

Tilman, D. & Wedin, D. (1991): Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* **72**: 685–700.

Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. (1994): Habitat destruction and the extinction debt. *Nature* **371**: 65–66.

Tilman, D., Wedin, D. & Knops, J. (1996): Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718–720.

Van Dorp, D., Schippers, P. & Van Groenendael, J.M. (1997): Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automaton model. *Landscape Ecol.* **12**: 39–50

Van Groenendael, J.M. (1995): Hoe klein mogen kleine populaties worden? *Lev. Nat.* **96**: 35–39.

Van Treuren, R., Bijlsma, R., Van Delden, W. & Ouborg, N.J. (1991): Genetic differentiation in *Salvia pratenis* and *Scabiosa columbaria* in relation to population size. *Heredity* **66**: 181–189.

Van Treuren, R., Bijlsma, R., Ouborg, N.J. & Van Delden, W. (1993): Inbreeding depression and heterosis effects caused by selfing and outcrossing in *Scambiosa columbaria. Evolution* **47**: 1669–1680.

Weeda, E.J., Van der Meijden, R. & Bakker, P.A. (1990): Rode lijst van de in Nederland verdwenen en bedreigde vaatplanten (*Pteridophyta* en *Spermatophyta*) over de periode 1980–1990. *Gorteria* **16**: 2–26.

Werner, P.A. & Platt, W.J. (1976): Ecological relationship of co-occurring goldenrods (*Solidago: Compositae*). *Am. Nat.* **110**: 959–971.

Westhoff, V. (1971): Nature management in coastal areas of Western Europe. *Vegetatio* **62**: 523–532.

Westoby, M., Leishman, M. & Lord, J. (1996): Comparative ecology of seed size and dispersal. *Phil. Trans. R. Soc. Lond. B* **351**: 1309–1318.

Williamson, M. (1993): *Biological Invasions*. Chapman & Hall, London.

Willson, M.F. (1993): Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* **107/108**: 261–280.

Wilson, A.M. & Thompsson, K. (1989): A comparative study of reproductive allocation in 40 British grasses. *Funct. Ecol.* **3**: 297–302.

Wright, S. (1938): Size of populations and breeding structure in relation to evolution. *Science* **87**: 430–431.

Young, A. (1995): Landscape structure and genetic variation in plants: empirical evidence. In: Hansson, L., Fahrig, L. & Merriam, G. (eds.): *Mosaic Landscapes and Ecological Processes*, pp. 153–177, Chapman & Hall, London.