

LIFE HISTORY TRAITS AS PREDICTORS OF PLANT RARITY, WITH PARTICULAR REFERENCE TO HEMIPARASITIC *OROBANCHACEAE*

Renie M. Bekker & Manja M. Kwak

Community and Conservation Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; fax +31 50 3632 273, e-mail R.M.Bekker@rug.nl, M.M.Kwak@rug.nl

Abstract: We made a comparison between life history and reproductive characteristics of a group of Dutch rare (30) and common (105) plant species, all dicotyledonous and insect-visited forbs. The traits life span, clonality, breeding system, seed production, seed dispersal, and soil seed bank longevity are considered. All trait values have been ranked according to their possible effect on the vulnerability of a species for extinction, where low values indicate a low risk and high values a high risk for a species. Rare and common plants differed significantly in four traits: seed production, breeding system, seed bank longevity and clonality. The discriminant analysis showed that 79% of the 135 species was correctly classified in the group they presently belong to. Especially species that are rare now but were much more common 50–100 years ago were classified as being common species, pointing at the detrimental effect of habitat loss these species encountered at which they have not yet been able to adapt to. The data set included eight hemiparasitic plant species (family *Orobanchaceae*), of which six are endangered in The Netherlands and two more common. Both rare and common hemiparasites scored high traits values, indicating that they are vulnerable for extinction. The hemiparasites had several characteristics in common: they are all annuals or biennials that have no means of clonal reproduction. They all have non-clustered, zygomorphic flowers that produce nectar and have a precise pollen presentation and are mainly visited by (bumble) bees. Mean life span was significantly shorter in the eight hemiparasitic *Orobanchaceae* than in the non-hemiparasitic *Scrophulariaceae* used for comparison (4 species). Overall, we concluded that hemiparasitic plants have a special combination of life history traits which makes them vulnerable for local and regional extinction.

Keywords: Breeding system, Clonality, Life span, Seed dispersal, Seed production, Soil seed bank

Nomenclature: VAN DER MEIJDEN (1996)

INTRODUCTION

Human demands and activities are responsible for the deterioration of the natural habitats of our wild flower populations (LANDE 1998). Numerous species are forced to live in small and isolated natural fragments either with or without formal protection. These “new” rare species are especially vulnerable to extinction, because their natural habitat and population size decline at a faster rate than they could adapt. In this respect, they differ from species that are naturally rare, such as endemics, which are often well adapted to small population size and low levels of genetic variation (HUENNEKE 1991).

Many characteristics of plant reproductive systems may be associated with rarity. However, after a study of 84 species, WELLER (1994) concluded that there is little compelling evidence that plant breeding systems or pollination biology alone have had a pervasive effect

in determining rarity. AIZEN et al. (2002) concluded that no overall conclusions can be drawn as to susceptibility to fragmentation based on compatibility systems and pollination generalization.

ŠERÁ & ŠERÝ (2004) found for nearly 500 Central European plant species various trade-offs but they did not relate them with rarity. We will explore a larger set of life history traits of common and rare species in the Netherlands, to determine which factors might account for the presently observed rarity or commonness of the species under study.

Rare and common plant species form a community in which flower-visiting insects forage, and may compete for visitation by the same insect species or even individual. Therefore, they may influence each other's pollination directly (by facilitation or competition, *sensu* RATHCKE 1983) or indirectly (by affecting fertilization and seed set after heterospecific pollen deposition). Pollination systems are under increasing threat from anthropogenic sources, including habitat fragmentation, changes in land use, modern agricultural practices, pesticides, and herbicides (RATHCKE & JULES 1993, ALLEN-WARDELL et al. 1998, KEARNS et al. 1998, KREMEN & RICKETTS 2000). OLESEN & JAIN (1994) described how fragmentation can harm both pollination and interactions that plants have with seed dispersers and other mutualists. Loss of these interactions could lead to an extinction vortex with negative consequences for biodiversity.

In this paper, we use the traits life span, clonality, breeding system, seed production, seed dispersal, and soil seed bank longevity to explain and possibly predict rarity or commonness of plant species. We pay special attention to the complex components of the breeding system of plants. We also focus on hemiparasitic *Orobanchaceae* and ask the question: are they special considering their reproductive traits with the exclusion of the hemiparasitic way of life?

The ability to disperse in space can be described by clonality (short distance) and by the dispersal of seeds (long distance); to disperse in time is described by the longevity of seeds in the soil (soil seed bank). A plant species' capability of vegetative expansion is often considered an escape strategy for survival if generative reproduction fails. DE KROON & VAN GROENENDAEL (1997) classified clonality types, but data on lateral spread are very scarce (KLIMEŠ & KLIMEŠOVÁ 1999). After seed production, seeds need to be dispersed to suitable habitats for establishment. Dispersal can take place along with different vectors such as wind, water, animals and man. Plant species adapted to long-distance dispersal have become less effective nowadays due to habitat fragmentation and different cultural practices (BONN & POSCHLOD 1998). Hemi-parasitic angiosperms need, after landing in a safe site, to find roots of hosts in the immediate vicinity of the site of germination or to get incorporated in the soil seed bank and wait for the germination trigger. Thus they make special demands to their environment in order to establish a population. Many plant species do not have any obvious adaptation to either long distance dispersal or seed longevity which makes them highly vulnerable for local extinction in the present dynamic and fragmented landscape (BAKKER et al. 1996, BEKKER et al. 1998b, BAKKER & BERENDSE 1999, TURNBULL et al. 1999, STRYKSTRA et al. 2002).

In the Netherlands, in total 11 species of hemiparasitic *Orobanchaceae* do occur, belonging to the genera *Melampyrum* (2 species), *Euphrasia* (2 species), *Odontites*

Table 1. Traits, number of classes and possible values of the traits. A value of 0.1 indicates vulnerability and 0.9 highest vulnerability.

Trait	Number of classes	Values of trait
1. life span	3	long-lived – 0.1, biennial – 0.5, annual – 0.9
2. clonality (> 10 cm per year)	2	yes – 0.1, no – 0.9
3. breeding system	12	range 0.16–0.9; value composed out of $3a-3f: (4(a+b+c+d)+2(e+f))/6$
3a. flower unit visited by insect visitor	2	umbel or cluster – 0.1 single flower – 0.9
3b. flower morphology	2	actinomorph – 0.1, zygomorph – 0.9
3c. pollen deposition on insect body	2	diffusely – 0.1, precise – 0.9
3d. nectar presentation	2	no – 0.1, yes – 0.9
3e. pollen deposition on stigma	3	autodeposition – 0.1 autodeposition but reduced seed set – 0.5 no autodeposition – 0.9
3f. purity of pollen deposition by insects as a function of specialization of insect visitor	3	high purity – 0.9 (specialist insect) medium – 0.5 (generalist and specialist) low purity – 0.1 (generalist visitors)
4. seed production	6	0–250 seeds – 0.96 251–500 seeds – 0.80 501–1000 seeds – 0.64 1001–2500 seeds – 0.48 2501–5000 seeds – 0.32 > 5001 seeds – 0.16
5. seed dispersal > 100 m	5	All four vectors for long distance (wind, water, epi- and endo-zoochory) possible – 0.1; three vectors – 0.3; two vectors – 0.5; only one vector – 0.7; no adaptations for any of the vectors present – 0.9
6. soil seed bank longevity	9	seeds do not persist longer than 1 year – 0.1 seeds persistent at least 5 years – 0.9

(1 species), *Parentucellia* (1 species), *Pedicularis* (2 species), and *Rhinanthus* (3 species). Most of them are considered being rare or decreasing in numbers (VAN DER MEIJDEN et al. 2000). The Dutch situation can have a signal function for other countries. Plant species, rare in the Netherlands, may still be common in neighbouring countries but may become locally rare in the future, as the “new rare species”.

MATERIALS AND METHODS

Our analysis is inspired by the results of BOND (1994) who presented a vulnerability index for plant species. He ranked each plant trait according to high (1) or low risk (0) for the plant's extinction. We choose not to include zeroes in the scores. Our trait rankings range from 0.1 to 0.9, with 0.1 indicating a low vulnerability and 0.9 indicating a high vulnerability for the plant's extinction. For each trait the classification is explained in Table 1. The assignment of two or more (if possible) levels of specialization of each trait was derived from many data sources.

DATA SET AND TRAIT DATA COLLECTION

In the Netherlands, plant species are recorded intensively and a data set of the Dutch flora containing the distribution and rarity (VAN DER MEIJDEN et al. 2000) is available. Rarity in this study is used only for plants that are listed on the Red List of endangered plants species of the Netherlands which is composed according to the IUCN (1994) criteria. The data set used here, is restricted to insect-visited herb species and bushes, in total 135 species (30 rare species and 105 common species) from 31 families, excluding plantains (*Plantago* species). From this set of species flower visitation and extensive breeding system data were available from a study performed by F. HOFFMANN & M.M. KWAK (unpubl. data). They monitored the plants and insects in a large landscape survey in the Netherlands in 2000 and 2001. Most of the species of our set occur in road and railway verges and along ditches. We added observational and measured data of plant species studied by Dutch colleagues including data of a few rare plants occurring in nature reserves. The hemiparasitic species included in this data set are: *Euphrasia stricta*, *Melampyrum arvense* and *M. pratense*, *Pedicularis palustris* and *P. sylvatica*, *Rhinanthus alectorolophus*, *R. angustifolius* and *R. minor*. Three locally present hemiparasitic *Orobanchaceae*, were not included in the analysis (*Euphrasia rostkoviana*, *Odontites verna* and *Parentucellia viscosa*).

The life span data are derived from the Dutch Botanical Database (CBS 1987). The classification for clonality is derived from KLIMEŠ & KLIMEŠOVÁ (1999) and completed with data from flora's and observations from the field survey. Seed production was mainly taken from the field survey, own measurements and completed by additional data from literature.

Their main source for the seed dispersal and seed longevity data were STRYKSTRA et al. (2002) and TAMIS et al. (2004), completed with data from various authors (SALISBURY 1942, FENNER 1992, PROCTOR et al. 1996, THOMPSON et al. 1997, BEKKER et al. 1998a,b, BOUMAN et al. 2000).

STATISTICS

We used discriminant analysis (DA) to test whether the two groups of plants, rare and common, could be differentiated based on specific trait value combinations of the six traits life span, clonality, breeding system, seed production, seed dispersal, and soil seed bank longevity.

Discriminant analysis (SPSS 2003) creates a linear combination of variables, in this case our traits, that maximizes the separation of cases (species) assigned to different groups. The success of the analysis is, among other things, assessed by how well the species are re-classified into their pre-determined groups. Stepwise entering/removal of traits was applied to determine which traits were significantly reducing the residual variance ($F < 0.05$ for entering, $F > 0.01$ for removal) and therefore contributed to the differentiation between the two groups. The total number of step was set to 12. Prior to analysis the within groups variance and covariance matrix (Box's *M* test) was checked to ensure equal magnitudes of variation and covariance within the population as a prerequisite for DA. Likewise, equitability of groups means was tested using the Wilk's Lambda.

The same procedure was performed on the subset of species of families *Scrophulariaceae* and *Orobanchaceae*. The groups to be determined by the traits were now the hemiparasitic

Table 2a. ANOVA table of Wilks Lambda test of equality of group means of traits between rare and common plants, the ratio of the within-groups sum of squares to the total set of variables (n.s. means not significant).

	Wilks Lambda	F statistic	d.f.	Sig. (=P)	P < 0.05
Life span	1.00	0.37	1, 133	0.545	n.s.
Clonality	0.95	6.95	1, 133	0.009	**
Breeding system	0.92	12.36	1, 133	0.001	***
Seed production	0.87	20.27	1, 133	0.000	***
Seed dispersal	0.97	3.81	1, 133	0.053	n.s.
Seed bank longevity	0.935	10.75	1, 133	0.001	***

Table 2b. Results of the discriminant analysis of rare and common plant species, only the significant traits listed are entered in the analysis, in sequence of importance.

Step	Entered	Wilks Lambda		Statistic	Exact F		Sig.
		Statistic	d.f.		d.f.		
1	Seed production	0.87	1, 1, 133	20.27	1, 133	.000	
2	Breeding system	0.83	2, 1, 133	13.31	2, 132	.000	
3	Seed bank longevity	0.80	3, 1, 133	11.13	3, 131	.000	
4	Clonality	0.77	4, 1, 133	9.99	4, 130	.000	

Table 2c. Classification results of the discriminant analysis of rare and common plant species. Overall 79.3% of original grouped species was correctly classified. In bold numbers and percentages of wrongly classified species are indicated.

Classification of occurrence		Predicted group membership		Total number
		Common	Rare	
Count	Common	95	10	105
	Rare	18	12	30
Percentage	Common	90.5	9.5	100.0
	Rare	60.0	40.0	100.0

($n = 8$) versus the non-hemiparasitic members ($n = 4$, *Digitalis purpurea*, *Linaria vulgaris*, *Scrophularia nodosa* and *Veronica chamaedrys*) of the formerly combined family included in this data set.

RESULTS

The results of the discriminant analysis differentiating the rare and common plant species by means of six life-history and reproductive traits are given in Table 2. The two groups are significantly separated by a combination of four out of six traits, in order of decreasing importance seed production, breeding system, soil seed bank longevity and clonality. They all point in the direction that rare plants have higher scores for the risk of extinction for each of these four traits than common plants, indicating that rare plant species are more vulnerable for extinction than the group of common plants. In the discriminant analysis 79.3% of all species were correctly classified into the group that they belong. The set of 28 wrongly classified

species can be subdivided into 18 presently rare species that have a trait combination that predicts them to be common. Among those species such as *Pedicularis palustris*, *Scabiosa columbaria* and *Succisa pratensis* (see Appendix). It is striking that 60% of the presently rare species was wrongly classified. These species are nearly all perennials that have only intermediate scores of at least 2 or more of the other five traits tested. Ten presently common species have been predicted to be rare (only 10.5% of this group). Among these *Rhinanthus angustifolius*, *Melampyrum pratense* and *Galeopsis speciosa*. These species all are short-lived, non-clonal species that have a complex breeding system and only a low or medium seed production, seed longevity and dispersal capacity.

The hemiparasitic plant species (all belonging to the family of *Orobanchaceae*) differed significantly from the non-hemiparasitic species of *Scrophulariaceae* in three traits: life span, seed production and soil seed bank longevity. All hemiparasites are short-lived (annual or biannual) and have both a lower seed production and lower seed bank longevity than the non-hemiparasites (Table 3a). In the stepwise entering procedure of the discriminant analysis only lifespan is entered, leaving on 29% of the variance explained. Seed production is just left out ($F = 0.089$) due to too low power of significance (Table 3b).

The DA predicted 91.7% of the species to belong to the proper group. Only one non-parasitic species was wrongly classified as a hemiparasite (*Digitalis purpurea*). When we look into more detail to the distribution of high and low trait values of individual species we summed the individual trait values into a cumulative trait value for the ease of ordering the list. It appears the rare species *Rhinanthus alectorolophus* and *R. angustifolius* received the highest cumulative value of this data set, the highest possible value (5.46) was not found (see Appendix). The lowest cumulative value was found in *Hypericum perforatum* (1.26). The lowest possible value (0.66) was also not found, probably due to the fact that no wind-pollinated species were involved in our set. All hemiparasites were found in the top 15 of both rare and common species. In the top ten of the common species we found species such as *Cynoglossum officinale* and *Symphytum officinale* that are not rare but have a trait combination that might bring them to rarity if their abundance drops drastically due to e.g. loss of habitat. *Impatiens glandulifera* has high values for the traits tested here as well, although this species is spreading in the Netherlands.

DISCUSSION

This study presents a significant differentiation between rare and common plants species composed of four out of six life history and reproductive traits. Species were characterized by classified trait values ranging from a low to a high risk of extinction seen from the plant's point of view. In the discriminant analysis 79.3% of the species was correctly classified into the group they belong to, rare or common species. We know of no other study that succeeded to explain differences between rare and common plants from a set of traits, except for BOND (1994) who only gave a few examples of individual species. Moreover, to our knowledge it is the first time that for a large set of species a combined value for a plant's breeding system, including the flowering unit visited, the flower morphology, pollen deposition onto the insect body, nectar presentation, pollen deposition on the stigma, and the purity of pollen deposition by insects as a function of specialization of insect visitor, was taken into account and proven to

Table 3a. ANOVA table of Wilks Lambda test of equality of group means of traits between hemi- and non-hemiparasitic *Scrophulariaceae*, the ratio of the within-groups sum of squares to the total set of variables (n.s. means not significant).

	Wilk' Lambda	F	d.f.	Sig. (= P)	P < 0.05
Life span	0.27	26.67	1, 10	0.000	***
Clonality	0.82	2.22	1, 10	0.167	n.s.
Breeding system	0.70	4.40	1, 10	0.062	n.s.
Seed production	0.40	14.78	1, 10	0.003	**
Seed dispersal	0.98	0.25	1, 10	0.630	n.s.
Seed bank longevity	0.66	5.11	1, 10	0.047	*

Table 3b. Results of the discriminant analysis of hemi- and non-hemiparasitic *Scrophulariaceae*, only the significant trait Life span is entered in the analysis.

Step	Entered	Statistic	Wilks' Lambda d.f.	Statistic	Exact F d.f.	Sig.
1	Life span	0.27	1, 1, 10	26.67	1, 10	.000

be significantly discriminative. Separate variables of the breeding system appeared to be insufficient to predict rarity (WELLER 1994, AIZEN et al. 2002). In general, rare plants in the Netherlands do not differ in breeding system compared to common ones. We are not aware of plant species that are decreasing due to poor pollination as a consequence of missing the right pollinator, however, we will discuss this in more detail for the group of hemiparasites below.

We have shown that a subset of presently common plant species were predicted to be rare plants from the combination of trait values. These plant species may turn out to be the species that will become rare in the near future. They have a trait combination resembling the presently rare plants, indicating a high risk for extinction when further habitat deterioration takes place and when habitat fragmentation increases such as *Cynoglossum officinale*, *Anchusa officinalis* and *Lathyrus pratensis*. This, however, does not apply to *Impatiens glandulifera* (Jewelweed); it has occurred in Europe since 1839, hailing from the Himalayas and India and introduced as a garden plant (COOMBE 1956). It is found in the Netherlands along rivers and disturbed areas but it is also a garden escaper. The species has seeds with a short longevity, and, despite ballistic seed dispersal, the range of dispersal does not exceed 100 m. It has a complex flower morphology with bumblebees as the main pollinators. CHITTKA & SCHÜRKEN (2001) stated that this successful invader tempts bee pollinators away from native flowers, reducing the seed set of local plants in the vicinity (*Stachys palustris*, in their example). This might enable *I. glandulifera* to take over, its spread facilitated by insect pollination, reducing the fitness of native flora. In addition, PERRINS et al. (1993) estimated the actual spread of this species in Britain at 38 km yr⁻¹ mainly due to occasionally long-distance dispersal by human activity. Moreover, they found that its frost tolerance, high seed production and competitive ability, especially its high relative growth rate enabling it to establish monospecific stands, adds to the species conversion it into a pest plant out competing all surrounding species.

The set of rare species which were predicted to be common might indicate the presently “new rare” species. Their trait combination still represents the historic distribution in a more natural landscape and they have not yet adapted to the actual, highly fragmented landscape. Species that were much more abundant 50–100 years ago are e.g. *Euphrasia stricta*, *Gentiana pneumonanthe*, *Knautia arvensis*, *Scabiosa columbaria*, and *Arnica montana*.

We expect that the importance of the seed dispersal by human activities such as hemerochory (dispersal through vehicles and agricultural machines, tires, trains, boots etc.) will increase in future. Most diverse grassland communities, which may contain hemiparasitic *Orobanchaceae* species such as *Pedicularis palustris* and three *Rhinanthus* species, nowadays are situated in nature reserves, and are cut for hay by machinery instead of by scythe. This has proved to increase dispersal distances considerably for some species (STRYKSTRA et al. 1997), for instance *R. angustifolius*. However, data on the impact of local connecting effects are still not available for many other plant species.

Hemiparasitic *Orobanchaceae* (8 species) differ from the non-parasitic *Scrophulariaceae* in such a way that the hemiparasites have significantly higher values for three traits, i.e. they are more vulnerable (life span, seed production and seed bank longevity). All hemiparasitic *Orobanchaceae* in our set have no capability of clonal growth. This striking result is in coherence with the fact that STRYKSTRA et al. (2002) already argued that hemiparasites, as short-lived species, are the only species that are able to coexist in a system of perennials by the fact that they act like perennials. They parasitize on the perennial root system of surrounding perennials, thus not having to built an extensive root system themselves.

Hemiparasitic *Orobanchaceae* in the Netherlands have single, zygomorphic, nectar containing flowers. They are pollinated by bees, resulting in an expected high purity of the pollen deposition. In most species the stigma is protruding which makes auto deposition of self pollen nearly impossible. *Odontites verna* is, except by bumblebees, visited by honeybees and to a small extent by syrphids. *Euphrasia* species have flowers with a remarkable nectar guide; however, in most cases the flowers received very few insect visits (see also GOMEZ 2002). *Pedicularis* species all over the world are very dependent on bumblebee-pollination to set seed; a few species receive visits of hummingbirds or other insects (HARTL 1974, MACIOR 1982, 1993, 1995, ERIKSEN et al. 1993, KWAK & BERGMAN 1996). However, various bumblebee species are in decline in Europe, especially long-tongued species like *Bombus hortorum* (RASMONT 1988, WILLIAMS 1989, KWAK & TIELEMAN 2000). Also short-tongued bumblebees perform a pollen-collecting behaviour resulting in pollination on certain plant species including hemiparasitic *Orobanchaceae*. However, they only perform this pollen-collecting behaviour if the number of flowers is large enough to trigger this behaviour (KWAK 1977, 1979, 1988). Honeybees are rarely observed as pollinators of species of hemiparasitic *Orobanchaceae* in the Netherlands, except for *Odontites* and to a low extent for *Euphrasia*. The presence of honeybees on *Rhinanthus angustifolius* is unpredictable; even if hives are placed besides large fields of flowering *Rhinanthus*, honeybees made their own choice and that was not always *Rhinanthus* (KWAK 1980). FOSSEL (1974, 1977) mentioned honeybees as visitors of *Rhinanthus* species in the Alps.

Many hemiparasitic *Orobanchaceae* show a decreased seed set in the absence of pollinators (*Pedicularis palustris*: KWAK 1979, ERIKSEN et al. 1993, ROSENTHAL & FINK

1996, KARRENBERG & JENSEN 2000; arctic *Pedicularis* species: PHILIPP et al. 1996, American *Pedicularis* species: MACIOR 1982, 1986, 1995; *Pedicularis sylvatica*, *Rhinanthus angustifolius*, *R. minor* and *Melampyrum pratense*: KWAK 1979; *R. alectorolophus*: KWAK, unpubl. data). The number of seeds produced per capsule in hemiparasitic plant species is not extremely high, always below 100 (KWAK 1979). For several species (*R. angustifolius*: KWAK & JENNERSTEN 1986; *M. pratense*: KWAK & JENNERSTEN 1991) we found that they need multiple pollination events in order to reach maximum seed set. At least three hemiparasitic species show myrmecochory as mode of seed dispersal (two *Melampyrum* species and *Pedicularis sylvatica*; see for *P. sylvatica*: ROCIO et al. 1996). *Rhinanthus* species have seeds with small or large wings, but dispersal by wind of the heavy seeds is very restricted. *Rhinanthus* and *Pedicularis palustris* seeds can float on water. Soil seed bank longevity of all hemiparasitic *Orobanchaceae* is very restricted.

Summarizing, we can say that hemiparasitic *Orobanchaceae* combine the often more vulnerable form of each of the traits studied here. A combination that makes them special.

Acknowledgements: Many thanks to Frank Hoffmann, Wim Ozinga, Ger Boedeltje, Jelte van Anandel, Jan Bakker, Roel Strykstra, Els Boerrigter, Odilia Velterop, Martina Stang, Theodora Petanidou, Gerard Oostermeijer and Michiel Wallis de Vries for collecting data, ideas, discussions and comments on the manuscript. The students Alie Hagedoorn, Cees van der Brandt, Alex Witte, Stefan te Velde, Alje Zandt, Hans Imberg, Theo Boudewijn, Maaïke de Vlas, Maaïke Smelter, Carola van der Muren and Henk Hunneman collected a part of the data.

REFERENCES

- AIZEN M., L. ASHWORTH L. & GALETTO L. (2002): Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *J. Veg. Sci.* 13: 885–892.
- ALLEN-WARDELL G., BERNHARDT P., BITNER R., BURQUEZ A., BUCHMANN S., CANE J., COX P.A., DALTON V., FEISINGER P., INGRAM M., INOUE D., JONES C.E., KENNEDY K., KEVAN P., KOPOWITZ H., MEDELLIN R., MEDELLIN-MORALES S., NABHAN G.P., KAVLIK B., TEPEDINO V., TORCHIO P. & WALKER S. (1998): The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biol.* 12: 8–17.
- BAKKER J. P., POSCHLOD P., STRIJKSTRA R.J., BEKKER R.M. & THOMPSON K. (1996): Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl.* 45: 461–490.
- BAKKER J. P. & BERENDSE F. (1999): Constraints in the restoration of ecological diversity in grassland and heath land communities. *Trends Ecol. Evol.* 14: 63–67.
- BEKKER R. M., BAKKER J. P., GRANDIN U., KALAMEES R., MILBERG P., POSCHLOD P., THOMPSON K. & WILLEMS J. H. (1998a): Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. *Funct. Ecol.* 12: 834–842.
- BEKKER R. M., SCHAMINÉE J.H.J., BAKKER J. P. & THOMPSON K. (1998b): Seed bank characteristics of Dutch plant communities. *Acta Bot. Neerl.* 47: 15–26.
- BOND W. (1994): Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philos. Trans., Ser. B* 344: 83–90.
- BONN S. & POSCHLOD P. (1998): *Ausbreitungsbiologie der Pflanzen Mitteleuropas*. Quelle und Meyer Verlag, Wiesbaden.
- BOUMAN F., BOESEWINKEL D., BREGMAN R., DEVENTE N. & OOSTERMEIJER G. (2000): *Verspreiding van zaden (Seed dispersal)*. KNNV Uitgeverij, Utrecht.
- CBS (1987): *Botanisch basisregister (Botanical statistics)*. Centraal Bureau voor de Statistiek. Leiden.
- CHITTKA L. & SCHÜRKENS S. (2001): Successful invasion of a floral market. *Nature* 411: 653.
- COOMBE D.E. (1956): Biological flora of the British Isles: *Impatiens parviflora* DC. *J. Ecol.* 44: 701–713.

- DE KROON H. & VAN GROENENDAEL J. M. (1997): *The ecology and evolution of clonal plants*. Backhuys Publishers, Leiden.
- ERIKSEN B., MOLAU U. & SVENSSON M. (1993): Reproductive strategies in two arctic *Pedicularis* species (*Scrophulariaceae*). *Ecography* 16: 154–166.
- FENNER M. (1992): *Seeds. The ecology of regeneration in plant communities*. CAB International, Wallingford.
- FOSEL A. (1974): Die Bienenweide der Ostalpen, dargestellt am Beispiel des steirischen Ennstales. *Mitt. Naturwiss. Vereins Steiermark* 104: 87–118.
- FOSEL A. (1977): Raffinierter Nektarraub beim klappertopf (*Rhinanthus* sp.). *Bienenvater* 1: 1–4.
- GOMEZ J.M. (2002): Self-pollination in *Euphrasia wilkommii* FREYN (*Scrophulariaceae*), an endemic species from the alpine of the Sierra Nevada (Spain). *Pl. Syst. Evol.* 232: 63–71.
- HARTL D. (1974): *Scrophulariaceae*. In: HEGI G., *Illustrierte Flora von Mittel-Europa* 6. Carl Hanser Verlag, München, pp. 451–469.
- HUENNEKE L.F. (1991): Ecological implications of genetic variation in plant populations. In: FALK D.A. & HOLSINGER K.E. (eds.), *Genetics and conservation of rare plants*, Oxford University Press, New York, pp. 31–44.
- IUCN (1994). *IUCN Red List Categories. Prepared by the IUCN Species Survival Commission*. IUCN, Gland.
- KARRENBERG S. & JENSEN K. (2000): Effects of pollination and pollen source on the seed set of *Pedicularis palustris*. *Folia Geobot.* 35: 191–202.
- KEARNS C.A., INOUE D.W. & WASER N. M. (1998): Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Rev. Ecol. Syst.* 29: 83–112.
- KLIMES L. & KLIMEŠOVÁ J. (1999): CLO-PLA 2 – A database of clonal plants in central Europe. *Pl. Ecol.* 141: 9–19.
- KREMEN C. & RICKETTS T. (2000): Global perspectives on pollination disruption. *Conservation Biol.* 14: 1226–1228.
- KWAK M.M. (1977): Pollination ecology of five hemiparasitic, large-flowered *Rhinanthoideae* with special reference to the pollination behaviour of nectar-thieving, short-tongued bumblebees. *Acta Bot. Neerl.* 26: 97–017.
- KWAK M.M. (1979): Effects of bumblebee visits on the seed set of *Pedicularis*, *Rhinanthus* and *Melampyrum* (*Scrophulariaceae*) in the Netherlands. *Acta Bot. Neerl.* 28: 177–195.
- KWAK M.M. (1980). The pollination value of honeybees to the bumblebee plant *Rhinanthus*. *Acta Bot. Neerl.* 29: 597–603.
- KWAK M.M. (1988): Pollination ecology and seedset in the rare annual species *Melampyrum arvense* L. (*Scrophulariaceae*). *Acta Bot. Neerl.* 37: 153–163.
- KWAK M.M. & JENNERSTEN O. (1986): The significance of pollination time and frequency and of purity of pollen loads for the seed set in *Rhinanthus angustifolius* (*Scrophulariaceae*) and *Viscaria vulgaris* (*Caryophyllaceae*). *Oecologia (Berlin)* 70: 502–507.
- KWAK M.M. & JENNERSTEN O. (1991): Bumblebee visitation and seed set in *Melampyrum pratense* and *Viscaria vulgaris*: heterospecific pollen and pollen limitation. *Oecologia (Berlin)* 86: 99–104.
- KWAK M.M. & BERGMAN P. (1996): Early flowers of *Bartsia alpina* (*Scrophulariaceae*) and the visitation by bumblebees. *Acta Bot. Neerl.* 45: 355–366.
- KWAK M.M. & TIELEMAN I. (2000): *Het Hommelleven (The life of bumblebees)*. KNNV uitgeverij, Utrecht.
- LANDE R. (1998): Anthropogenic, ecological and genetic factors in extinction and conservation. *Res. Populat. Ecol.* 40: 259–269.
- MACIOR L.W. (1982): Plant community and pollinator dynamics in the evolution of pollination mechanisms in *Pedicularis* (*Scrophulariaceae*). In: AMSTRONG J.A., POWELL J.M. & RICHARDS A.J. (eds.), *Pollination and evolution*, Royal Botanic Gardens, Sydney.
- MACIOR L.W. (1986): Floral resource sharing by bumblebees and hummingbirds in *Pedicularis* (*Scrophulariaceae*) pollination. *Bull. Torrey Bot. Club* 113: 101–109.
- MACIOR L.W. (1993): Pollination ecology of *Pedicularis palustris* L. (*Scrophulariaceae*) in North America. *Pl. Spec. Biol.* 8: 35–44.
- MACIOR L.W. (1995): Pollination ecology of *Pedicularis* in the Teton Mountain Region. *Pl. Spec. Biol.* 10: 77–82.

- OLESEN J.M. & JAIN S.K. (1994): Fragmented populations and their lost interactions. In: LOESCHCKE V., TOMIUK J. & JAIN S.K. (eds.), *Conservation genetics*, Birkhäuser Verlag, Basel, pp. 417–426.
- PERRINS J., FITTER A. & WILLIAMSON M. (1993): Population biology and rates of invasion of 3 introduced *Impatiens* species in the British-isles. *J. Biogeogr.* 20: 33–44.
- PHILIPP M., WOODDELL S.R.J., BOCHER J. & MATTESSON O. (1996): Reproductive biology of four species of *Pedicularis* (*Scrophulariaceae*) in West Greenland. *Arctic Alpine Res.* 28: 403–413.
- PROCTOR M., YEO P. & LACK A. (1996): *The natural history of pollination*. Harper Collins Publishers, London.
- RASMONT P. (1988): *Monographie ecologique et zoogeographique des bourdons de France et de Belgique* (Hymenoptera, Apidae, Bombinae). PhD. Thesis, University of Gembloux, Gembloux.
- RATHCKE B. (1983): Competition and facilitation among plants for pollination. In: REAL L. (ed.), *Pollination biology*, Academic Press, New York, pp. 305–329.
- RATHCKE B.J. & JULES E.S. (1993): Habitat fragmentation and plant-pollinator interactions. *Curr. Sci.* 65: 273–277.
- ROCIO J., PASTOR J. & IMMACULADA F. (1996): Studies of fruits, seeds and pollen morphology of *Pedicularis sylvatica* L. subsp. *lusitanica* (HOFFMANNS and LINK) COUT. (*Scrophulariaceae*). *Anales Jard. Bot. Madrid* 54: 312–318.
- ROSENTHAL G. & FINK S. (1996): *Pedicularis palustris* L. in the Bremen area: Distribution, ecology, and causes of its decline. *Abh. Naturwiss. Vereine Bremen* 43: 429–447.
- SALISBURY E. J. (1942): *The reproductive capacity of plants. Studies in quantitative biology*. G. Bells and Son, Ltd, London.
- ŠERÁ B. & ŠERÝ M. (2004): Number and weight of seeds and reproductive strategies of herbaceous plants. *Folia Geobot.* 39: 27–40.
- SPSS (2003): *SPSS Base 12.0 user's guide*. SPSS Inc. Chicago.
- 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.
- STRYKSTRA R.J., BEKKER R.M. & VAN ANDEL J. (2002): Dispersal and life span spectra in plant communities: a key to safe site dynamics, species coexistence and conservation. *Ecography* 25: 145–160.
- TAMIS W.L.M., VAN DER MEIJDEN R., RUNHAAR J, BEKKER R.M., OZINGA W., ODI B. & HOSTE I. (2004): Standaardlijst van de Nederlandse flora 2003 (Standard list of the flora of the Netherlands 2003). *Gorteria* 30: 101–195.
- THOMPSON K., BAKKER J.P. & BEKKER R.M. (1997): *Soil seed banks of NW Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.
- TURNBULL L.A., CRAWLEY M.J. & REES M. (1999): Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225–238.
- VAN DER MEIJDEN R., ODI B., GROEN C.L.G., WITTE J.P.M. & BAL D. (2000): Bedreigde en kwetsbare vaatplanten in Nederland, Basisrapport met voorstel voor de Rode Lijst (Endangered vascular plants in The Netherlands, with proposal for the Red List). *Gorteria* 26: 85–208.
- WELLER S.G. (1994): The relationship of rarity to plant reproductive biology. In: BOWLES M.L. & WHELAN C.J. (eds.), *Restoration of endangered species: conceptual issues, planning, and implementation*, Cambridge University Press, Cambridge, pp. 90–117.
- WILLIAMS P.H. (1989): Why are there so many bumble bees at Dungeness? *Bot. J. Linn. Soc.* 101: 31–44.

Received 25 May 2004, revision received and accepted 25 January 2005

Encl. Appendix p. 242

APPENDIX

Values for the six traits of all rare species, top 10 and bottom 10 common species, ordered from highest cumulative risk value (= sum of the six traits) to lowest value. Species in bold are hemiparasitic *Orobanchaceae*, * – indicates species wrongly classified in the DA analysis (see text).

Species	Family	Life span	Clonality	Breeding system	Seed production	Seed dispersal	Seed bank	Cumulative risk value
All rare species								
Rhinanthus alectorolophus	Scrophulariaceae	0.9	0.9	0.9	0.8	0.7	0.8	5
Rhinanthus minor	Scrophulariaceae	0.9	0.9	0.77	0.8	0.7	0.8	4.87
Melampyrum arvense	Scrophulariaceae	0.9	0.9	0.9	0.96	0.5	0.7	4.86
Gentianella amarella	Gentianaceae	0.9	0.9	0.9	0.64	0.7	0.8	4.84
Pedicularis sylvatica	Scrophulariaceae	0.5	0.9	0.9	0.96	0.9	0.6	4.76
Fritillaria meleagris	Liliaceae	0.1	0.9	0.9	0.96	0.7	0.9	4.46
Gentianopsis ciliata	Gentianaceae	0.1	0.9	0.9	0.96	0.7	0.8	4.36
Salvia pratensis	Lamiaceae	0.1	0.9	0.9	0.96	0.7	0.8	4.36
Gentianella germanica*	Gentianaceae	0.5	0.9	0.9	0.48	0.7	0.8	4.28
Genista anglica	Fabaceae	0.1	0.9	0.77	0.64	0.9	0.9	4.21
Euphrasia stricta*	Scrophulariaceae	0.9	0.9	0.7	0.48	0.9	0.3	4.18
Dianthus deltooides	Caryophyllaceae	0.1	0.9	0.5	0.96	0.9	0.8	4.16
Pinguicula vulgaris	Lentibulariaceae	0.1	0.9	0.9	0.64	0.7	0.8	4.04
Anthyllis vulneraria	Fabaceae	0.1	0.5	0.83	0.96	0.7	0.9	3.99
Pedicularis palustris*	Scrophulariaceae	0.5	0.9	0.9	0.48	0.7	0.5	3.98
Gentiana pneumonanthe*	Gentianaceae	0.1	0.9	0.9	0.32	0.7	0.8	3.72
Knautia arvensis*	Dipsacaceae	0.1	0.9	0.43	0.64	0.7	0.9	3.67
Cirsium dissectum	Asteraceae	0.1	0.9	0.37	0.96	0.5	0.8	3.63
Phyteuma spicatum subsp. nigrum*	Lamiaceae	0.1	0.5	0.57	0.64	0.9	0.9	3.61
Valeriana dioica*	Valerianaceae	0.1	0.5	0.37	0.96	0.7	0.9	3.53
Dactylorhiza incarnata*	Orchidaceae	0.1	0.9	0.9	0.16	0.5	0.9	3.46
Phyteuma spicatum subsp. spicatum*	Campanulaceae	0.1	0.5	0.57	0.48	0.9	0.9	3.45
Scabiosa columbaria*	Dipsacaceae	0.1	0.9	0.43	0.8	0.5	0.7	3.43
Arnica montana*	Asteraceae	0.1	0.5	0.37	0.64	0.9	0.9	3.41
Parnassia palustris*	Saxifragaceae	0.1	0.5	0.57	0.64	0.5	0.9	3.21
Succisa pratensis*	Dipsacaceae	0.1	0.9	0.43	0.64	0.3	0.8	3.17
Gentiana cruciata*	Gentianaceae	0.1	0.5	0.9	0.16	0.7	0.8	3.16
Primula vulgaris*	Primulaceae	0.1	0.5	0.77	0.48	0.9	0.4	3.15
Viola canina*	Violaceae	0.1	0.5	0.9	0.64	0.7	0.3	3.14
Geum rivale*	Rosaceae	0.1	0.1	0.57	0.8	0.5	0.9	2.97
Top 10 of common species								
Rhinanthus angustifolius*	Scrophulariaceae	0.9	0.9	0.9	0.8	0.7	0.8	5
Impatiens glandulifera*	Balsaminaceae	0.9	0.9	0.9	0.8	0.7	0.8	5
Melampyrum pratense*	Scrophulariaceae	0.9	0.9	0.83	0.96	0.5	0.7	4.79
Raphanus raphanistrum	Brassicaceae	0.9	0.9	0.83	0.64	0.9	0.6	4.77
Cynoglossum officinale*	Boraginaceae	0.5	0.9	0.9	0.96	0.7	0.8	4.76
Lamium purpureum	Lamiaceae	0.9	0.9	0.83	0.96	0.9	0.2	4.69
Symphytum officinale*	Boraginaceae	0.1	0.9	0.9	0.8	0.9	0.9	4.5
Galeopsis tetrahit	Lamiaceae	0.9	0.9	0.83	0.8	0.5	0.5	4.43
Anchusa officinalis	Boraginaceae	0.5	0.9	0.9	0.96	0.7	0.4	4.36
Lathyrus pratensis*	Fabaceae	0.1	0.9	0.83	0.64	0.9	0.9	4.27
Bottom 10 of common species								
Leucanthemum vulgare	Asteraceae	0.1	0.1	0.3	0.32	0.7	0.6	2.12
Rubus idaeus	Rosaceae	0.1	0.1	0.57	0.32	0.7	0.3	2.09
Rubus fruticosus	Rosaceae	0.1	0.1	0.5	0.16	0.7	0.5	2.06
Hieracium pilosella	Asteraceae	0.1	0.1	0.37	0.16	0.5	0.8	2.03
Eupatorium cannabinum	Asteraceae	0.1	0.1	0.3	0.48	0.3	0.7	1.98
Ranunculus sceleratus	Ranunculaceae	0.1	0.9	0.37	0.16	0.3	0.1	1.93
Hypericum dubium	Hypericaceae	0.1	0.5	0.3	0.16	0.5	0.3	1.86
Chamerion angustifolium	Onagraceae	0.1	0.1	0.57	0.16	0.5	0.4	1.83
Ranunculus repens	Ranunculaceae	0.1	0.1	0.37	0.48	0.3	0.3	1.65
Hypericum perforatum	Hypericaceae	0.1	0.1	0.3	0.16	0.5	0.1	1.26