

Changes in rosette size distribution of *Saxifraga mutata* in a successional sere

Autor(en): **Holderegger, Rolf**

Objektyp: **Article**

Zeitschrift: **Bulletin of the Geobotanical Institute ETH**

Band (Jahr): **66 (2000)**

PDF erstellt am: **27.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-377828>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.

Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.

Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

Changes in rosette size distribution of *Saxifraga mutata* in a successional sere

ROLF HOLDEREGGER

Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland;
holder@systbot.unizh.ch

Summary

1 In the northern European Prealps, the regionally endangered *Saxifraga mutata* grows at sites frequently disturbed by erosion. With progressing succession, rosette size and abundance of flowering individuals increase while recruitment decreases. Because of this lack of rejuvenation, rosette size distributions should change from right-skewed to more symmetrical ones in later successional stages. The present study on the population structure of *S. mutata* tested this hypothesis.

2 Rosette diameter was positively correlated with measurements of vegetative vigour and sexual reproduction, but no correlation was found with asexual production of daughter ramets. Annual increment in rosette diameter was size-dependent and could not be used as (an easily applicable) measurement of individual age. Rosette size distributions became indeed less right-skewed during seral change, but there was substantial variation in mean rosette size among sampling plots even within successional stages.

3 The shape of rosette size distributions, not the number of large individuals or seedlings, reflects the overall vigour of populations of *S. mutata*. The evaluation of rosette size distributions may thus be a valuable tool in the conservation management of this species.

Keywords: conservation biology, Prealps, rosette size distribution, *Saxifraga mutata*, succession

Bulletin of the Geobotanical Institute ETH (2000), **66**, 3–10

Introduction

Landscape dynamics is an important ecological factor shaping population structure in plant species (Eriksson 1996). Population structure is often described in terms of recruitment rate and/or the distribution of age classes, life stages or genotypes. All these parameters have some potential to predict the future fate of a population (Harper 1977). Oostermeijer *et al.* (1996) showed that recruit-

ment and the distribution of life stage classes in ten populations of the rare *Gentiana pneumonanthe* strongly change with succession. Recruitment rate is highest in earlier stages and absent in later stages of wet heathland succession in The Netherlands. Small scale disturbances of the vegetation cover provide suitable safe sites for recruitment in *G. pneumonanthe*. If no open gaps are

created, survival of established individuals is the only factor influencing local population size in this species. Valverde & Silvertown (1997), in a survey of eight populations of *Primula vulgaris* in England, found that populations in closed coppice woodland mainly consist of old individuals and show no rejuvenation. Colonisation or significant recruitment only occurs in woodland gaps or in recently coppiced areas. A similar decrease of recruitment during succession has been shown in Swiss populations of the prealpine *Saxifraga mutata* (Holderegger 1997). Natural erosion creates new open habitat patches suitable for colonisation by *S. mutata*. Populations in early successional stages show high recruitment, but most individuals have only small rosettes and are in vegetative life stage. In closed vegetation, recruitment of *S. mutata* is almost absent, even though individuals are larger, and the probability of flowering is higher. Since individuals of *S. mutata* sometimes form daughter ramets, some asexual recruitment can occur even in successional stages with closed vegetation. Nevertheless, succession finally excludes *S. mutata* from a habitat patch (Holderegger 1997).

The above studies underline the value of demographic investigations in conservation biology. There are two principal types of demographic methods: dynamic and static ones. Dynamic methods are more time- and labour-intensive than static methods and can usually be applied to only a few populations. In combination with spatial environmental changes, e.g. along successional seres, static demographic studies have the potential to reveal general patterns of population dynamics of a species, since they allow the survey of a large number of populations.

Holderegger (1997) showed in a detailed study on three populations of *S. mutata* that flowering individuals have larger rosettes than

vegetative individuals. This study suggested that rosette sizes of *S. mutata* along a successional sere change from right-skewed distributions (*sensu* Sokal & Rohlf 1995), i.e. many small and few large plants indicating active recruitment, in early successional stages to more symmetrical distributions in later stages, pointing to strongly decreased sexual rejuvenation. The aim of the present study was to test whether this shift in rosette size distribution of *S. mutata* is a general feature of this species' biology by investigating sampling plots in 32 populations of north-eastern Switzerland using a static demographic approach. Correlations of rosette size with annual growth, vegetative vigour and measurements of sexual and asexual reproduction were additionally determined.

Material and methods

THE SPECIES

North of the Alps, *Saxifraga mutata* L. (Saxifragaceae) has a prealpine distribution (Kaplan 1995). Its often small and isolated populations are typically found between 800 and 1200 m a.s.l. The species' habitats are moist calcareous rocks of sandstone, marl or conglomerate, screes and steep slopes (Kaplan 1995). Erosion is a characteristic feature of these habitats. The species is listed as endangered in parts of its distribution area (Landolt 1991).

Saxifraga mutata produces basal rosettes with diameters of up to 24 cm (Holderegger 1997). The fleshy leaves are oblong to oblanceolate with acute tips and translucent leaf margins, which are sometimes jaggedly toothed (Webb & Gornall 1989). On average, thyrsoids bear 60 flowers with yellow to red, linear petals (Kaplan 1995). Individual rosettes are strictly monocarpic, but daughter ramets are sometimes formed, and genets

may then behave as perennials (Webb & Gornall 1989). *Saxifraga mutata* has a mixed breeding system; a trait thought to be important in a colonising species (Holderegger 1996).

SAMPLING PLOTS

The study was carried out in three regions of north-eastern Switzerland. (1) Küssnachtortobel; co-ordinates of the Swiss national grid: 687–689/241–244, 500–550 m a.s.l.; the three studied local populations of *S. mutata* (each with less than 100 rosettes) inhabited erosion slopes on marl and sandstone in a ravine (Holderegger 1994). (2) Zürcher Oberland; co-ordinates: 713–717/239–243, 800–1000 m a.s.l.; populations of *S. mutata* grew abundantly on cliffs of conglomerate, landslides and steep slopes in deep river valleys. Fourteen populations were studied. (3) Uetliberg; co-ordinates: 679–681/242–245; populations of *S. mutata* were found on erosion slopes of different sizes on marl and sandstone at elevations between 650 and 820 m (Landolt 1997). Here, 15 populations were studied. One sampling plot of 4 m² was investigated in each of the above 32 populations of *S. mutata*. Sampling plots were established in homogenous habitat patches of *S. mutata*. All studied populations were spatially isolated from each other by at least 30 m.

SUCCESSIONAL CHANGE, MORPHOLOGICAL MEASUREMENTS AND ANNUAL GROWTH

In static demographic studies, it is important to exclude the effects of yearly variation in germination and seedling recruitment, of intraspecific competition, which mainly acts in early life stages, and of high mortality of small and/or younger individuals (Harper 1977). Because of its slowly growing rosettes, it is difficult to define any early life stages in *S. mutata* apart from the seedling stage. The only

clear definition of a later life stage is when individuals reach the size of reproduction, i.e. rosette diameters larger than 39 mm (confidence limits: 28–50 mm; Holderegger 1997). Therefore, only rosettes with diameters larger than 30 mm, i.e. near the lower confidence limit of the reproductive threshold size, were investigated in the present study.

All sampling plots were ascribed to one of three successional stages, described in detail by Fabijanowski (1950). Successional stage I: almost bare rocks or slopes frequently disturbed by erosion; 20% vegetation cover. Stage II: slopes or rocks with a vegetation cover of 20–40%; vegetation similar to grassland fragments; less frequent natural disturbance. Stage III: slopes similar to stage II, but more stable; about 50% vegetation cover, giving the impression of steep meadows; first saplings of willows and pines. Natural disturbance can prevent the succession of habitat patches of *S. mutata* from one stage to the next.

The following six morphological characters related to vegetative vigour, sexual reproduction and asexual reproduction were measured on all plants of *S. mutata* within the sampling plots: leaf length, number of flowers, number of leaves, number of daughter ramets, rosette diameter and thyrsoid length. Because of variation in the number of suitable plants, sample sizes per plot varied strongly.

Data were log-transformed before analysis, except the number of daughter ramets, which was log ($x + 0.01$)-transformed. Pearson correlation coefficients between all morphological characters were calculated in order to evaluate whether high vegetative vigour leads to high sexual and asexual reproduction. Probability values were adjusted for table-wide significance using sequential Bonferroni adjustments (Rice 1989). The skewness (*sensu* Sokal & Rohlf 1995) of the rosette diameters

Table 1. Pearson correlation coefficients¹ of morphological traits² of *Saxifraga mutata*

	Number of flowers	Number of leaves	Number of daughter ramets	Rosette diameter	Thyrsoid length
Leaf length	0.69**	0.67**	0.14 ^{ns}	0.92**	0.73**
Number of flowers ³		0.44**	0.07 ^{ns}	0.73**	0.86**
Number of leaves			- 0.01 ^{ns}	0.72**	0.41**
Number of daughter ramets ⁴				0.08 ^{ns}	0.10 ^{ns}
Rosette diameter					0.79**

¹ Table-wide significance after sequential Bonferroni adjustment; **, $P < 0.01$; ^{ns}, $P > 0.05$.

² Vegetative traits, $n = 796$ individuals; reproductive traits, $n = 174$ individuals.

³ Number of open flowers and flower buds on the single flowering stalk of an individual rosette.

⁴ Number of vegetative offspring rosettes (daughters) produced per (mother) rosette.

was calculated per sampling plot, and the effects of region (random factor) and successional stage (fixed factor) on these skewness values were analysed in a two-way ANOVA.

Fifteen individuals of *S. mutata* were marked in each of four sampling plots of successional stage II (Küsnachtertobel: one plot; Zürcher Oberland: one plot; Uetliberg: two plots). Rosette diameters were measured in spring and fall during two years, starting in spring 1991. A linear regression between annual increment in rosette diameter and initial rosette diameter was calculated (data not transformed). Differences in growth rate among sampling plots were analysed with an ANOVA, using annual increment values relative to initial rosette diameter.

All analyses were performed on SYSTAT, Version 5 (Wilkinson *et al.* 1992). Normal distribution of data or of residuals, in the case of ANOVAs, was verified by Kolmogorov-Smirnov tests with Lilliefors correction.

Results

Morphological characters related to vegetative vigour (leaf length, number of leaves, rosette diameter) or sexual reproduction

(number of flowers, thyrsoid length) were positively correlated with each other in *Saxifraga mutata* ($r \geq 0.41$ with $P < 0.01$ in all cases; Table 1). Rosette diameter showed high correlations with most characters. However, the number of daughter ramets was not significantly correlated with any other character. Of the 796 investigated individuals, 21.9%

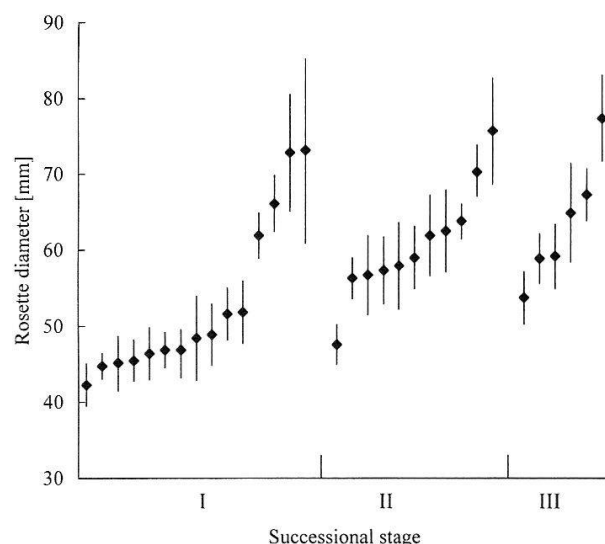


Fig. 1. Mean rosette diameter (rhomboids) and standard error (\pm SE; vertical lines) per sampling plot ($n = 32$) within consecutive successional stages I–III of *Saxifraga mutata*. Means are given in the order of increasing values within each successional stage, respectively.

Table 2. Two-way ANOVA of the skewness of rosette diameters of *Saxifraga mutata* within 32 sampling plots from three regions and three consecutive successional stages

Source	SS	df	F ^l
Region	0.73	2	1.43 ^{ns}
Successional stage	3.39	2	5.99**
Region x Successional stage	1.13	4	1.11 ^{ns}
Error	5.86	23	

^l**, $P < 0.01$, ^{ns}, $P > 0.05$

flowered, but only 6.3% produced at least one daughter ramet. In summary, individuals of *S. mutata* with larger rosettes had more and longer leaves, taller thyrsoïds and more flowers, but did not produce more daughter ramets than individuals with smaller rosettes.

Mean rosette diameter increased from 52.8 ± 2.7 mm ($\pm SE$; $n = 15$ plots) in successional stage I and 60.8 ± 2.3 mm ($n = 11$) in stage II, to 63.6 ± 3.4 mm ($n = 6$) in stage III. Mean rosette diameters per sampling plot largely overlapped among successional stages (Fig. 1). Distributions of rosette diameters became more symmetrical in the course of succession, as indicated by a mean skewness of 1.33 ± 0.14 ($\pm SE$) in stage I, 0.78 ± 0.15 in stage II and 0.01 ± 0.26 in stage III. Thus, there were fewer small individuals in successional stage III than in the stages I and II. Two-way ANOVA revealed that only successional stage had a significant effect on the skewness of rosette diameters per plot ($P < 0.01$; Table 2). There was no significant effect of the regions where the samples had been taken (Table 2).

Mean annual increment in rosette diameter of *S. mutata* was 8.2 ± 1.2 mm ($\pm SE$). Linear regression showed that annual increment values were dependent on initial rosette sizes ($F_{1,37} = 11.2$, $P < 0.01$, $r^2 = 0.23$). Annual growth was thus size-dependent. Relative annual increment in rosette diameter showed no

differences among the sampling plots investigated (ANOVA, $F_{2,36} = 0.02$, $P > 0.05$). No marked individual flowered or produced a daughter ramet during the census.

Discussion

There was a distinct relationship between mean rosette size per sampling plot and successional habitat change in *Saxifraga mutata*. On average, rosettes were larger in diameter and their distributions less right-skewed in later successional stages. Holderegger (1997) showed that the frequency of flowering individuals increases while sexual recruitment decreases with succession. Nevertheless, many rosettes which had reached the reproductive threshold size in rosette diameter did not flower in the present study. Physiological mechanisms that lead to large vegetative rosettes have been investigated in some plant species (Tissue & Nobel 1990; Worley & Harder 1996). Above the threshold size of reproduction, the amount of nutrient and carbon resources necessary to form sexual reproductive organs increases, because the larger the plant size, the larger is also the flowering stalk and the number of flowers. If this critical amount of resources is not gained in a particular year, annual net production is allocated to vegetative growth. Several subsequent years in which this resource level is not

met can lead to exceptionally large vegetative rosettes. This phenomenon is known as “accumulation of lag times” (Boucher 1997). Succession influences the probability of individuals to reach the reproductive threshold size and to allocate enough resources to the production of reproductive organs (Gross & Werner 1982).

In contrast to other plant species (see references in Molau 1997), which exhibit a linear relation between individual size and age, annual increase in rosette size in *S. mutata* was size-dependent, but not affected by the sampling plots. Boucher (1997) showed that age-stage distributions within plant populations become flatter and more symmetrical with progressing successional change. More symmetrical size distributions in later successional stages were also found in the present study on *S. mutata*.

Morphological characters related to vegetative vigour and sexual reproduction were positively correlated with rosette size, but there was no significant relationship with the number of daughter ramets. Ramets were seldom formed in *S. mutata*, and larger rosettes did not have any enhanced ability of asexual reproduction. Remembering that recruitment of *S. mutata* in late successional stages is almost absent (Holderegger 1997), the larger rosette sizes found in these stages having taller flowering stalks and more flowers did not point to especially viable populations, but to populations lacking active rejuvenation and having increased numbers of old individuals. Larger rosettes could not escape from this reproductive dilemma by the production of more daughter ramets. Daughter ramets were usually formed when the apical meristem of the mother plant was damaged by herbivores, rockfall or erosion, and ramet production was rare in all successional stages. If semelparity and iteroparity are viewed as the extreme

ends of a continuum, *S. mutata* has to be placed at the semelparous side, at least in the northern Prealps.

The tendency towards higher sexual reproduction in populations as succession progresses is sometimes seen as an adaptive response in metapopulations, caused by selection for low dispersability in early successional stages and high dispersability in later stages (Brachet *et al.* 1999). In a metapopulation context, the increase in sexual reproduction that was observed in populations of *S. mutata* in later successional stages might thus increase the probability of such populations to escape from their site, since the latter no longer provides any opportunities for population growth and survival, and local extinction is inevitable.

Rare plants with naturally isolated and/or small populations like *S. mutata* may not be endangered by negative genetic impacts of small population size (Young *et al.* 1996). Therefore, maintenance of their populations may mainly depend on demographic and stochastic environmental factors. Successful recruitment is mostly restricted to open ground and pioneer situations in *S. mutata* (Holderegger 1997), a fact reflected by the asymmetry of rosette size distributions found in early successional stages. Protective measures against floods nowadays prevent erosion in prealpine river valleys or ravines. Thus, the formation of new open habitat patches, which are suitable for intrapopulation rejuvenation or colonisation, is often prohibited. This can lead to the local extinction of *S. mutata* (Holderegger 1997).

Dispersal is a critical factor in the dynamics of patchy populations or metapopulations (Ouborg 1993). In the ravine at Küssnachtobel, only three small local populations of *S. mutata* are left. Several other local populations disappeared during this century (Hol-

deregger 1994). Although there were unoccupied habitat patches suitable for *S. mutata* at distances of less than 100 m, no (re-)colonisation occurred. Seeds of *Saxifraga* species are small (0.8 mm in length in *S. mutata*; Holderegger 1996) and easily dispersed by wind and water (Bonn & Poschlod 1998). Nevertheless, the limited number of individuals in the three small populations remaining at Künsnachtertobel produced so few seeds that dispersal between habitat patches had become a very improbable event. The number of sexual reproductive organs produced in *S. mutata* is size-dependent, as it is in most plant species (Rees & Crawley 1989; Thompson *et al.* 1991; Worley & Harder 1996). Most individuals found at Künsnachtertobel were large, but their few inflorescences were not large enough to compensate for the reduced seed production of the populations. Hence, the extinction of *S. mutata* in the whole Künsnachtertobel region may only be a matter of time. In fact, one of the populations at Künsnachtertobel vanished since the present study was carried out in 1991, despite appropriate nature conservation management, and no colonisation of new sites occurred (R. Holderegger, pers. observ.).

In summary, rosette diameter in *S. mutata* was correlated with several measurements of plant vigour and sexual reproduction, but not with asexual reproduction. Though variable, mean rosette size per sampling plot increased with progressing successional change, and rosette size distribution became less right-skewed, reflecting a decrease in recruitment in later succession. Germination, seedling mortality and recruitment can strongly vary among years (Harper 1977). Because the early-successional habitats of *S. mutata* are subjected to irregular erosion, the occurrence of many seedlings in a population of *S. mutata* does not necessarily point to successful rejuve-

nation. For instance, high numbers of seedlings are usually found in populations of *S. mutata* growing in open gullies. However, almost all seedlings are washed off during heavy summer thunderstorms, while larger established rosettes survive (R. Holderegger, pers. observ.). In static demographic studies on *S. mutata*, it is neither the number of large rosettes exhibiting high sexual reproduction nor the occurrence of many seedlings, but the right-skewed shape of rosette diameter distribution which points to high population vigour. Therefore, the determination of local rosette size distribution may be a valuable tool in conservation management of this species.

Acknowledgements

I thank Robert M.M. Crawford, Felix Gugerli and J. Jakob Schneller for reading earlier drafts of the manuscript. Critical comments by Johannes Kollmann, Sabine Güsewell, Ivana Stehlik and two anonymous reviewers greatly improved its final version. Financial support by the Splinter Fonds and by the Swiss National Science foundation while writing this paper is acknowledged.

References

- Bonn, S. & Poschlod, P. (1998) *Ausbreitungsbiologie der Pflanzen Mitteleuropas*. Quelle & Meyer, Wiesbaden.
- Boucher, D.H. (1997) General patterns of age-by-stage distributions. *Journal of Ecology*, **85**, 235–240.
- Brachet, S., Olivieri, I., Godelle, B., Klein, E., Frascaria-Lacoste, N. & Gouyon, P.-H. (1999) Dispersal and metapopulation viability in a heterogeneous landscape. *Journal of Theoretical Biology*, **198**, 479–495.
- Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.
- Fabijanowski, J. (1950) Untersuchungen über die Zusammenhänge zwischen Exposition, Relief,

- Mikroklima und Vegetation in der Fallätsche. *Beiträge zur Geobotanischen Landesaufnahme der Schweiz*, **29**, 1–104.
- Gross, K.L. & Werner, P.A. (1982) Colonising abilities of “biennial” plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology*, **63**, 921–931.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Holderegger, R. (1994) Zur Flora und Vegetation des Küsnachtertobels: Veränderungen innerhalb der letzten 50 Jahre. *Botanica Helvetica*, **104**, 55–68.
- Holderegger, R. (1996) Reproduction of the rare monocarpic species *Saxifraga mutata* L. *Botanical Journal of the Linnean Society*, **122**, 301–313.
- Holderegger, R. (1997) Intrapopulational size structure of the monocarpic species *Saxifraga mutata* and its relationship to succession. *Flora*, **192**, 151–156.
- Kaplan, K. (1995) Saxifragaceae. *Hegi G., Illustrierte Flora von Mitteleuropa IV2A* (ed. H.E. Weber), pp. 130–229. Blackwell, Berlin.
- Landolt, E. (1991) *Gefährdung der Farn- und Blütenpflanzen in der Schweiz mit gesamtschweizerischen und regionalen roten Listen*. BUWAL, Bern.
- Landolt, E. (1997) Beiträge zur Flora der Stadt Zürich. IV Dicotyledonen 2 (Berberidaceae bis Rosaceae). *Botanica Helvetica*, **107**, 29–50.
- Molau, U. (1997) Age-related growth and reproduction in *Diapensia lapponica*, an arctic-alpine cushion plant. *Nordic Journal of Botany*, **17**, 225–234.
- Oostermeijer, J.G.B., Brugman, M.L., de Boer, E.R. & den Nijs, H.C.M. (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology*, **84**, 153–166.
- Ouborg, N.J. (1993) Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine system. *Oikos*, **66**, 298–308.
- Rees, M. & Crawley, M.J. (1989) Growth, reproduction and population dynamics. *Functional Ecology*, **3**, 645–653.
- Rice, W.R. (1989) Analysing tables of statistical tests. *Evolution*, **43**, 223–225.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry. The Principles and Practice of Statistics in Biological Research*. Freeman, New York.
- Thompson, B.K., Weiner, J. & Warwick, S.I. (1991) Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany*, **69**, 442–446.
- Tissue, D.T. & Nobel, P.S. (1990) Carbon relations of flowering in a semelparous clonal desert perennial. *Ecology*, **71**, 273–281.
- Valverde, T. & Silvertown, J. (1997) A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *Journal of Ecology*, **85**, 193–210.
- Webb, D.A. & Gornall, R.J. (1989) *Saxifragas of Europe*. Christopher Helm, London.
- Wilkinson L., Hill, M.-A., Welna, J.P. & Birkenbeuel, G.K. (1992) *SYSTAT for Windows: Statistics, Version 5*. SYSTAT Inc., Evanston.
- Worley, A.C. & Harder, L.D. (1996) Size-dependent resource allocation and costs of reproduction in *Pinguicula vulgaris* (Lentibulariaceae). *Journal of Ecology*, **84**, 195–206.
- Young, A., Boyle, T. & Brown, T. (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution*, **11**, 413–418.

Received 7 June 1999

revised version accepted 15 November 1999