UvA-DARE (Digital Academic Repository)

Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, rare perennial herb

Oostermeijer, J.G.B.; Brugman, M.L.; de Boer, E.R.; den Nijs, J.C.M.

Publication date
1996

Published in
Journal of Ecology

[Link to publication](#)

Citation for published version (APA):

Oostermeijer, J. G. B., Brugman, M. L., de Boer, E. R., & den Nijs, J. C. M. (1996). Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, rare perennial herb. *Journal of Ecology*, (84), 153-166.

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

Temporal and Spatial Variation in the Demography of *Gentiana Pneumonanthe*, a Rare Perennial Herb

J. Gerard B. Oostermeijer; Marc L. Brugman; Edwin R. De Boer; Hans C. M. Den Nijs

The Journal of Ecology, Vol. 84, No. 2. (Apr., 1996), pp. 153-166.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28199604%2984%3A2%3C153%3ATASVIT%3E2.0.CO%3B2-W>

The Journal of Ecology is currently published by British Ecological Society.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb

J. GERARD B. OOSTERMEIJER, MARC L. BRUGMAN,
EDWIN R. DE BOER and HANS C.M. DEN NIJS

*Hugo de Vries Laboratory, Institute for Systematics and Population Biology, University of Amsterdam,
Kruislaan 318, 1098 SM, Amsterdam, the Netherlands*

Summary

1 A total of 35 transition and elasticity matrices for the rare iteroparous herb *Gentiana pneumonanthe* was analysed for temporal and spatial variation. The data used were collected annually from 10 sites in six different populations on up to seven occasions in the period 1987–93.

2 In general, temporal variation was higher in transition matrices than in elasticities, while between-site variation was high for both transition and elasticity matrices.

3 The relative contributions of three life-history transitions, progression (or growth, G), recruitment from seed (fecundity, F) and survival (retrogression plus stasis, L) to the finite rate of increase, λ , were also highly variable, between years within as well as between sites. The observed variation is very large in comparison with that previously observed either between or within other iteroparous herbs from open habitats, even showing some overlap with demographic patterns normally characteristic of woody plants.

4 A G - L - F ordination shows a long, narrow band across the entire diagram from matrices with a low elasticity for L and high elasticities for G and F at one end to matrices which have an elasticity of 1.00 for L on the other.

5 Correlations between the G -, L - and F -elasticities, λ , and the vegetation cover suggest that the band in the ordination diagram represents a successional pathway in wet heathlands from invasive to regressive populations. Elasticity matrices from regularly mown hay meadows are characteristic of stable populations, but represent senile, regressive populations after mowing has ceased.

6 Relationships between λ and the elasticities of G , L and F show that in matrices of stable or declining populations ($\lambda \leq 1$) survival is most important. In growing populations ($\lambda > 1$) the contribution of progression and fecundity becomes larger.

7 Given their relatively large temporal and spatial variation, elasticities are useful in nature conservation and management only if the corresponding value of λ is taken into account.

8 Significant positive correlations between transition probabilities of different life stages were observed. This phenomenon may increase the risk of extinction by environmental stochasticity.

Keywords: conservation, elasticity analysis, life-history evolution, management, matrix analysis, succession

Journal of Ecology 1996, **84**, 153–166

Introduction

Demographic studies are essential for a better understanding of the relationships between individual plant

species and the vegetation of which they are part (Franco & Silvertown 1990; Silvertown & Franco 1993). They are especially useful when conducted in different habitat types and if demographic parameters are related to the temporal and spatial changes in the habitat that occur as a result of environmental stochasticity, succession or nature management.

Valuable new insights in the functioning of plant populations have been provided in this way (Keddy 1981; Franco & Silvertown 1990; Menges 1990; O'Connor 1993, 1994; Bengtsson 1993; Svensson *et al.* 1993; Bullock *et al.* 1994; Bastrenta *et al.* 1995; Boeken & Canham 1995; Økland 1995). Also, because most studies into the mechanisms of succession are on the level of the vegetation, long-term demographic studies are needed to gain more detailed knowledge of the ways in which species establish populations at a certain stage of succession and disappear again in a later stage (Gray *et al.* 1987; Pickett *et al.* 1987; Gleeson & Tilman 1990; Olff *et al.* 1994; Boeken & Canham 1995).

Gentiana pneumonanthe is a long-lived, iteroparous perennial occurring in open, successional habitats. Various (nature) management practices, such as mowing, grazing and sod-cutting, strongly affect the vegetation succession in the heathlands and grasslands where this species occurs (Oostermeijer *et al.* 1994a). Our demographic censuses of this species cover a wide range of such successional stages, both in time (within populations) and space (between and within populations). They are therefore very well suited to investigate the changes in demographic parameters that may occur during habitat succession.

An important tool in demographic analyses is the construction of age- or stage-based matrix projection models, from which a host of valuable population parameters can be derived (Caswell 1989). Matrix projection models allow, for instance, the use of elasticity analysis to determine the sensitivity of the finite rate of population increase, λ , to small changes in the various transitions via elasticity analysis (de Kroon *et al.* 1986). Because the elasticities of the transitions between stages are expressed as proportions and sum to unity, different regions within the matrix, representing different life-history processes, such as survival, fecundity and growth, can be summed (Silvertown *et al.* 1993). The method has successfully been used for comparative demographic studies of plant species with different life-histories (Silvertown *et al.* 1993; Silvertown & Franco 1993) and has led to valuable new insights on the population dynamics of species in relation to changes in their habitat (Silvertown & Franco 1993; Bullock *et al.* 1994; O'Connor 1993, 1994). Hence, it may also be a useful tool for the conservation and management of rare and endangered plant species (Silvertown *et al.* 1993, in press).

In this paper on *Gentiana pneumonanthe*, we present demographic data from 10 different sites, monitored for a maximum of six years (1987–93), yielding a total of 35 transition matrices. The aims of this study are (1) to analyse the temporal and spatial (intra- and interpopulation) variation in transition and elasticity-matrices, (2) to study effects of changes in habitat characteristics on the relative contribution of fecundity (F), growth (G), and retrogression plus stasis

(L , survival without growth) to the finite rate of increase, (3) to compare the variation in the elasticities of G , L and F within this species with the variation observed among a series of other iteroparous perennials of open habitats, and (4) to investigate the existence of correlations between transition probabilities within the matrices, as these may have important consequences for the effects of environmental stochasticity on the chances of extinction (Menges 1992).

Methods

DESCRIPTION OF THE STUDY SPECIES AND DEFINITION OF LIFE STAGES

Gentiana pneumonanthe L., the marsh gentian, is a long-lived, iteroparous herb that was once a common and characteristic species of heathlands and hay meadows (Oostermeijer *et al.* 1994a). Its distribution area ranges from southern Scandinavia to Northern Spain and Portugal and from Great Britain into Siberia (Meusel *et al.* 1978). Throughout this range, the species has become increasingly rare the past decades, mostly as a result of land reclamation, lowering of the ground water level, extensive use of fertilizers and the cessation of formerly common, small-scale agricultural land-use, such as sod-cutting, mowing, and grazing (Oostermeijer *et al.* 1994a). Many populations in deteriorated habitats have become small and isolated. These probably have low viability, owing to reduced levels of genetic variation (Raijmann *et al.* 1994), poor seed production (Oostermeijer *et al.* 1992) and reduced offspring performance (Oostermeijer *et al.* 1994b). A single-census demographic survey has suggested that small populations are generally senile (i.e. they consist only of adult individuals and show no seedling recruitment, Oostermeijer *et al.* 1994a).

The following six life-history stages can be distinguished (see Oostermeijer *et al.* 1994a).

1 seeds, which are very small and light and are normally produced in large numbers from August to November. They either germinate the next spring to summer or die. Only a very small fraction (< 1%) survives to the second year (Oostermeijer, unpublished data). Therefore, there is no significant seed pool of importance. This differs from a previous model for this species (Chapman *et al.* 1989);

2 seedlings, which can be recognized by the presence of green cotyledons and a rosette of one to three leaf pairs. The diameter of this rosette can vary greatly, from c. 5–50 mm;

3 juveniles, which still have cotyledons, but also overwintering shoots (short shoots with tiny scale-like leaves) that will develop into the next years' stems. Juveniles may either have leaves in a rosette or on a short stem (or both). Their leaves are thinner, not

revolute and generally more ovate than the leaves of mature individuals;

4 vegetative adults, which no longer have cotyledons and bear one to several nonflowering stems and in late summer also over-wintering shoots. The leaves are mostly thick and revolute;

5 generative or reproductive adults, which have one or more flowering (and frequently also nonflowering) stems. Each flowering stem may bear from one up to 10 flowers. Leaves are identical to those of vegetative adults. In late summer they develop over-wintering shoots;

6 dormants, which remain inactive below ground for one up to (very rarely) three years. Since the dormant period rarely lasts more than one or two years (only two individuals remained below ground for three), plants that were absent for more than two years were considered dead in the calculations of the last matrices of a series.

DEMOGRAPHIC CENSUSING

Demographic censuses were made in six different populations, four in heathlands and two in hay meadows (Table 1, Fig. 1). In each population, the corners of permanent plots were fixed by means of metal bars between which a aluminium frame of 1 m², divided into dm², could be mounted in exactly the same position every census. The number and location of these plots depended on the density and spatial structure of the particular population. Where clear distinctions existed within the boundaries of the population, a number of sites were selected per population and treated as separate units (hereafter referred to as 'sites'). These are indicated with the same population name but with a different number. Sites may reflect differences in hydrology (e.g. Dwingeloo-1 vs. Dwingeloo-2, two sod-cut sites in the same population, but site 1 was drier than site 2), or vegetation type (Texel-1 vs. Texel-2). In populations that occurred in a relatively homogeneous environment, sites may also represent different management regimes that either already existed (e.g. Dwingeloo-2 vs. Dwingeloo-3: sods cut vs. unmanaged) or were experimentally installed (e.g. De Deelen-2 vs. De Deelen-3: mowing ceased in 1988 vs. mowing changed from September to July).

Demographic data were obtained by mapping and describing all individual plants within the permanent plots at the end of each flowering season (September/October), when all flowers/fruits, stems and over-wintering shoots had been formed and could be counted. Early germinating seeds had by then usually developed into juveniles, while seeds germinating late were present as seedlings. In the first and second year of the study, two censuses (one in May/June and one in September/October) were made. Since this showed that most of the seedling and juvenile mortality occurred during their first over-wintering, one annual census was thereafter considered sufficient to describe

the population dynamics. Each census, also the total vegetation cover in the censusing plots was estimated on the following scale: 1 = total cover < 10%, 2 = cover 10–35%, 3 = cover 35–60%, 4 = cover 60–85% and 5 = cover 85–100%.

MATRIX CONSTRUCTION AND ANALYSIS

From the demographic data, matrices comprising a time interval of one year were constructed on the basis of a life-cycle diagram with five stages: seedlings, juveniles, vegetative adults, reproductive adults and dormants (Fig. 2a). Seeds were omitted, since we could not demonstrate a long-term seed pool in any of our study populations (but see Chapman *et al.* 1989). Also, including the seed stage in the matrix would have resulted in a one year delay in seedling and juvenile recruitment (Caswell 1989). Assuming that no net dispersal of seeds occurred into or out of the plots, fecundities (F_{sg} and F_{jg}) were calculated by dividing the number of seedlings or juveniles in year t by the number of reproductive adults in year $t-1$. In two cases where the number of reproductive adults in year $t-1$ was zero, the few observed seedlings must have germinated from the small, dormant seed pool, and in these cases, fecundity was calculated on the basis of the number of reproductive adults in year $t-2$.

Dominant eigenvalues and eigenvectors of the matrices were calculated by means of the power method (Caswell 1989) and elasticity matrices were derived from the formulae given by de Kroon *et al.* (1986) and Caswell (1989).

Following the approach of Silvertown *et al.* (1993), the elasticity matrices were also divided into regions describing different parts of the life-cycle (Fig. 2b). Four of the six regions described by these authors applied to our study populations: E_2 , seedling and juvenile recruitment; E_4 , retrogression of plants due to flowering plants becoming vegetative or to individuals entering the dormant stage; E_5 , stasis, in which plants remain in the same stage; and E_6 , progression to a more developed stage (e.g. seedling to juvenile, dormant to vegetative adult, vegetative to reproductive adult). E_1 (recruitment of seeds to the seed-pool, see above) and E_3 (clonal growth) were not observed in this species. The region elasticities were used to calculate the relative contribution of: F , fecundity ($= E_2$); L , survival (the sum of E_4 and E_5); G , growth ($= E_6$) to the finite rate of increase (i.e. the dominant eigenvalue of the matrix, λ).

Temporal variation (variation among years within separate sites and over all sites for a subset of years that was available for all sites) and spatial variation (variation among sites for the same subset of years) in both transition and elasticity matrices was analysed using log-linear analyses, following the methods described by Caswell (1989). In similar analyses, tem-

Table 1 Basic information on the populations/sites where demographic monitoring of *Gentiana pneumonanthe* was performed. HM = hay meadow, H = heathland. Plant nomenclature follows van der Meijden (1990) for vascular plants, and Margadant & During (1982) for bryophytes

Population/ site	Habitat type	Dominant species in vegetation	Management/ groundwater regime	1-m ² plots censused	Number of plants per plot (yearly in chronological order)	Censusing years
Kooilust	HM	<i>Molinia caerulea</i> , <i>Cirsium dissectum</i> , <i>Leucobryum glaucum</i>	Yearly mowing (July) Wet or inundated in winter.	40	46, 49, 55, 79, 75	1988–91
De Deelen-2	HM	<i>Nardus stricta</i> , <i>Festuca</i> <i>ovina</i> , <i>M. caerulea</i> , <i>Galium saxatile</i>	Yearly mowing (Sept.), ceased in 1988. Wet or inundated in winter.	4	262, 226, 94, 62	1988–91
De Deelen-3	HM	<i>Nardus stricta</i> , <i>Festuca</i> <i>ovina</i> , <i>M. caerulea</i> , <i>Galium saxatile</i>	Yearly mowing (Sept.), changed to July in 1988. Wet or inundated in winter.	4	203, 214, 183, 177	1988–91
Lochem	H	<i>M. caerulea</i> , <i>Erica</i> <i>tetralix</i> , <i>Hypnum</i> <i>cupressiforme</i> var. <i>ericetorum</i>	Litter removed in winter by raking. Wet or inundated in winter.	10	55, 69, 78, 121	1988–91
Dwingeloo-1	H	<i>M. caerulea</i> , <i>Drosera</i> <i>intermedia</i> , <i>E. tetralix</i> , <i>Calluna</i> <i>vulgaris</i>	Sods cut in 1986. Drier elevated site, occasionally inundated.	3	157, 343, 144, 174, 360	1987–90
Dwingeloo-2	H	<i>D. intermedia</i> , <i>Rhynchospora</i> spp., <i>E. tetralix</i> , <i>M. caerulea</i>	Sods cut in 1986. Wet depression, inundated in winter.	15	109, 89, 105, 402, 411	1987–90
Dwingeloo-3	H	<i>E. tetralix</i> , <i>M. caerulea</i> , <i>Scirpus cespitosus</i> , <i>Sphagnum</i> spp.	Unmanaged border of heathland pool. Inundated in winter.	3	86, 276, 72, 67, 109	1987–90
Texel-1	H	<i>E. tetralix</i> , <i>Empetrum</i> <i>nigrum</i> , <i>Carex trinervis</i> , <i>D. rotundifolia</i>	Sods cut in 1984, mown in 1988 & 1990. Inundated in winter.	10	49, 36, 46, 60, 89	1987–91
Texel-2	H	<i>E. tetralix</i> , <i>Empetrum</i> <i>nigrum</i> , <i>M. caerulea</i> , <i>Sphagnum</i> spp.	Sods cut in 1984, mown in 1988 & 1990. Inundated in winter.	12	42, 60, 90, 108, 265	1987–91
Terschelling	H	<i>E. tetralix</i> , <i>Empetrum</i> <i>nigrum</i> , <i>Oxycoccus macrocarpos</i>	Sods cut in 1981. Inundated in winter.	8	335, 626, 762, 582, 415, 251, 267	1987–93

poral and spatial variation in the relative contribution of the *G*, *L* and *F* matrix regions to the finite rate of increase was investigated.

Correlation coefficients were calculated between all nonzero matrix entries. With this analysis, it is possible to investigate whether the matrix elements varied independently of each other or if (some of the) entries were positively or negatively correlated. Significance levels for the correlation coefficients were determined by means of a randomization test (Manly 1991). Two frequency distributions (with a class interval of 0.100) were calculated: one for the correlation coefficients between the observed matrix elements (the observed distribution) and one for the correlation coefficients between the randomized matrix elements (the

expected distribution). A χ^2 -test was used to test if the observed frequency distribution differed significantly from the expected distribution.

Regression analysis was performed to analyse the association between vegetation cover, and population growth rate, λ . Second, multiple regression was used to detect the independent effects of vegetation cover and λ on the elasticities of the *G*, *L* and *F* regions within the matrix. No correlations were determined between the different regions in the elasticity matrix, since the fact that these sum to one may produce spurious correlations, which are difficult to interpret in the sense of trade-offs between life-history traits, especially when $\lambda \neq 1$ (see Silvertown *et al.* 1993; Shea *et al.* 1994; and Franco & Silvertown 1994).

Fig. 1 Map of The Netherlands showing the location of the six populations and 10 sites censused demographically. See Table 1 for a description of the study sites.

Results

TEMPORAL AND SPATIAL VARIATION IN
TRANSITION PROBABILITIES AND
ELASTICITIES

Variation between transition matrices within sites (i.e. temporal variation, since there were no differences in treatments within sites) was significant for all sites (Table 2a). The same was true for the elasticity

matrices, except for the sites Deelen-3 and Dwingeloo-3 (Table 2a). When the matrices were decomposed by stage, it appeared that the contribution of the different stages to the log-likelihood ratio (G^2) was not equal for all sites. Only in the sites Deelen-2, Dwingeloo-1, Dwingeloo-3 and Terschelling did the fate of the seedling stage differ significantly among years, although this never resulted in a significant variation in elasticities. Significant variation in juvenile fate was detected only in the Terschelling site. The same holds for the fate of the vegetative adults. However, in the sites where this stage made a significant contribution to the total G^2 its contribution often exceeded that of the reproductive adult stage, which contributed significantly (and mostly dominantly) to the overall variation among matrices in all sites. Of course, the (highly variable) seedling and juvenile fecundity components of this matrix column (F_{sg} and F_{lg}) also contribute strongly, but when the analysis was performed without the fecundity entries, the contribution of the reproductive stage was still significant in all sites (statistics not shown). In general, the dormant stage was relatively unimportant for the temporal variation among matrices. The fate of dormants showed significant variation between years only in the Lochem site, while the elasticities of this stage contributed significantly to the overall G^2 in the Deelen-2 and both Texel sites (Table 2a).

When the temporal and spatial components are compared (Table 2b) for the two time steps that are available for all sites ($T = 88/89$ and $T = 89/90$), it appears that both cause significant variation in transition as well as elasticity matrices. Also, there is a significant interaction effect between time and location, implying that the temporal variation depends on the site. Note that the component 'site' also incorporates different management regimes. In the two cases where there are two sites in one population that do not differ in management type, namely Texel-1 and -2 and Dwingeloo-1 and -2, the two sites are significantly different in Dwingeloo ($G^2_{75} = 227.07$, $P < 0.0001$), but not in Texel ($G^2_{100} = 83.15$, $P = 0.889$).

When the matrices were decomposed by stage, it appeared that for the count matrices all stages except the dormants contributed significantly to the overall G^2 for both the site- and time-effect, except that the latter was not significant for the juvenile stage. For the elasticity matrices it was again found that the contribution of the seedling and the juvenile stages did not show any significant temporal or spatial variation (Table 2b).

The average transition matrix, calculated over all available matrices (26 from heathlands and 9 from hay meadows), has a λ of 1.117 (Table 3a). The elasticities of this matrix indicate that, in general, the most important transitions in the life-cycle of *Gentiana pneumonanthe* are juveniles growing into vegetative adults (a_{vj}), vegetative adults remaining veg-

Fig. 2 Life-cycle diagram of *Gentiana pneumonanthe* (a) and the corresponding transition matrix with its different elasticity regions: E_2 , E_4 , E_5 , E_6 and G , L , F (b). The thick arrows in (a) indicate 'fecundity' transitions (value may be > 1), the thin arrows represent the fate of the various stages (values always between 0 and 1).

Table 2 Log-linear analysis of temporal variation in count-(C) and elasticity-(E) matrices within the study sites (a) and of spatial and temporal variation among the study sites (b). The obtained log-likelihood ratios (G^2) for the entire matrices (left) were decomposed into the relative contributions of each State (the sum of G^2 -values of S, J, V, G and D is equal to the total value). The degrees of freedom (d.f.) for both the total and the decomposed analyses (left and right of the slash, respectively) are given on the right. 'Empty' means that there were no matrix entries or elasticities present in the analysis. Model components in (b): S = state, F = fate, T = time, P = site

	Entire matrices	Matrices decomposed by state					d.f.
		S	J	V	G	D	
(a) Temporal variation within sites							
Kooilust (C)	98.76***	7.55	3.30	10.25	76.76***	0.90	50/10
Kooilust (E)	68.05***	3.70	2.57	18.39**	36.88***	6.51	40/8
Deelen-2 (C)	219.93***	45.49***	12.92	92.61***	65.52***	3.38	50/10
Deelen-2 (E)	62.62**	0.51	empty	18.64**	19.35**	24.11***	40/8
Deelen-3 (C)	132.65***	10.36	16.24	8.01	81.55***	16.48	50/10
Deelen-3 (E)	42.73	empty	4.23	3.13	29.39***	5.99	40/8
Lochem (C)	100.61***	1.70	1.64	13.86	62.81***	20.60**	50/10
Lochem (E)	79.29***	0.51	6.48	25.94***	34.98***	11.37	40/8
Dwingeloo-1 (C)	274.59***	42.14***	7.48	16.38	200.95***	7.64	50/10
Dwingeloo-1 (E)	100.64***	2.65	3.37	16.01*	76.46***	2.14	40/8
Dwingeloo-2 (C)	73.09**	4.15	14.76	8.73	40.46***	4.99	50/10
Dwingeloo-2 (E)	69.12***	4.64	27.56***	6.08	30.32***	0.51	40/8
Dwingeloo-3 (C)	162.85***	22.35**	5.55	11.99	118.14***	4.82	50/10
Dwingeloo-3 (E)	53.21	empty	0.57	18.72**	29.61***	4.30	40/8
Texel-1 (C)	164.63***	14.88	6.51	75.25***	56.35***	11.64	75/15
Texel-1 (E)	138.38***	10.78	13.36	30.09***	41.23***	42.91***	60/12
Texel-2 (C)	231.27***	18.67	9.41	31.48***	160.18***	11.18	75/15
Texel-2 (E)	108.54***	2.11	16.87	5.64	53.79***	30.13***	60/12
Terschelling (C)	636.84***	66.70***	92.51***	206.98***	254.33***	16.31	125/25
Terschelling (E)	131.50**	4.22	14.59	69.02***	29.49	14.19	100/20
(b) Temporal and spatial variation, all sites (only $T = 88/89$ and $T = 89/90$)							
Time or Site: STP, SF (C)	2190.79***	215.86***	188.85***	554.08***	1092.88***	139.12***	500/100
Time or Site: STP, SF (E)	945.58***	25.01	63.68	304.96***	424.15***	127.78***	400/80
Site: STP, SFT (C)	1890.98***	167.88***	146.95***	460.42***	1008.39***	107.34	450/90
Site: STP, SFT (E)	857.76***	22.23	61.31	286.54***	378.89***	107.79***	360/72
Time: STP, SFP (C)	997.99***	128.11***	89.58	244.93***	473.70***	61.67	350/70
Time: STP, SFP (E)	463.55***	17.80	38.40	133.73***	220.86***	52.76	280/56
Time $\times$ Site: STP, SFT, SFP (C)	636.84***	—	—	—	—	—	240
Time $\times$ Site: STP, SFT, SFP (E)	131.50**	—	—	—	—	—	192

* $P \leq 0.05$, ** $P \leq 0.025$, *** $P \leq 0.010$.

etative (a_{vv}) or becoming reproductive (a_{gv}), generative adults remaining reproductive (a_{gg}) and juvenile fecundity (F_{gg}), together representing an elasticity of 78%. The average matrix for the hay meadow populations (Table 3b) has a λ of 0.922. It is not fully representative for hay meadows, however, because mowing had ceased in one of the sites (Deelen-2). From the average elasticity matrix, it appears that the younger stages do not contribute much to λ (only 14%). The most important transitions in the hay meadows are a_{vv} , a_{gv} and a_{gg} (together 72%). In the average heathland matrix (Table 3c), λ has a value of 1.156, and the highest elasticities are essentially the same as in the overall matrix.

VARIATION IN THE ELASTICITIES OF G , L AND F

The region elasticities for each site and time step are given in Table 4. The temporal and spatial variation in the relative contribution of the G , L and F regions in the elasticity matrix was analysed as previously

described (Table 5). Overall, both the temporal (for the time steps 88/89 and 89/90) and spatial variation as well as their interaction was highly significant (Table 5b). The sites Kooilust, Deelen-2 and Dwingeloo-3, deviated from the others in that they showed no significant variation in the elasticity of G , L and F between years (Table 5a).

The individual matrices were plotted in the G - L - F ordination triangle (see Silvertown *et al.* 1993; Silvertown & Franco 1993; and Silvertown *et al.* in press), together with their corresponding value of λ (Fig. 3). It can be readily seen that there is a very large variation in the relative contribution of each region of the elasticity matrix between years and sites. The variation is not random, however. The matrices are clearly positioned along a line in the diagram from the upper left to the lower right (Fig. 3a). There is also a very obvious decrease in λ , associated with a change in matrix position to the bottom right of the diagram (Fig. 3b). This association is reflected in the significant regression coefficients that were observed between r ($= \ln \lambda$) and G , L and F , where the coefficient has a

Table 3 Average transition (left) and elasticity (right) matrices for (a) all plots (b) only the plots in hay meadows and (c) only the heathland plots. The transition values are given as means $\pm$ standard errors. Also the dominant eigenvalue, λ , of each average matrix is given. Fecundity transitions are given in bold

Transition					Elasticity				
S	J	V	G	D	S	J	V	G	D
(a) All sites ($\lambda = 1.117$)									
S	0.0004 $\pm$ 0.0003	0	2.4766 $\pm$ 0.6679	0	0.0002	0	0	0.0482	0
J	0.0420 $\pm$ 0.0125	0.0008 $\pm$ 0.0005	1.5757 $\pm$ 0.3844	0	0.0076	0.0001	0	0.1290	0
V	0.1519 $\pm$ 0.0330	0.7417 $\pm$ 0.0373	0.2800 $\pm$ 0.0393	0.3589 $\pm$ 0.0559	0.0340	0.1120	0.1747	0.0283	0.0113
G	0.0051 $\pm$ 0.0024	0.1422 $\pm$ 0.0203	0.5388 $\pm$ 0.0543	0.1777 $\pm$ 0.0351	0.0041	0.0206	0.1645	0.1951	0.0201
D	0.0077 $\pm$ 0.0071	0.0185 $\pm$ 0.0089	0.0274 $\pm$ 0.0072	0.4206 $\pm$ 0.0581	0.0025	0.0040	0.0210	0.0040	0.0190
(b) Hay meadows ($\lambda = 0.922$)									
S	0	0	0.4427 $\pm$ 0.2064	0	0	0	0	0.0272	0
J	0.0267 $\pm$ 0.0177	0	0.1650 $\pm$ 0.0497	0	0.0031	0	0	0.0393	0
V	0.1699 $\pm$ 0.0721	0.6749 $\pm$ 0.0827	0.2508 $\pm$ 0.0456	0.3789 $\pm$ 0.0985	0.0238	0.0380	0.2255	0.0733	0.0157
G	0	0.0126 $\pm$ 0.0110	0.6574 $\pm$ 0.0533	0.1587 $\pm$ 0.0693	0	0.0014	0.1334	0.3654	0.0125
D	0.0021 $\pm$ 0.0021	0.0485 $\pm$ 0.0295	0.0235 $\pm$ 0.0124	0.2957 $\pm$ 0.1169	0.0003	0.0030	0.0174	0.0075	0.0133
(c) Heathlands ($\lambda = 1.156$)									
S	0.0006 $\pm$ 0.0004	0	3.1806 $\pm$ 0.8573	0	0.0003	0	0	0.0520	0
J	0.0473 $\pm$ 0.0157	0.0011 $\pm$ 0.0006	2.0640 $\pm$ 0.4829	0	0.0090	0.0001	0	0.1431	0
V	0.1456 $\pm$ 0.0376	0.7648 $\pm$ 0.0412	0.2901 $\pm$ 0.0508	0.3520 $\pm$ 0.0682	0.0331	0.1199	0.1629	0.0239	0.0103
G	0.0069 $\pm$ 0.0031	0.0470 $\pm$ 0.0160	0.4978 $\pm$ 0.0695	0.1842 $\pm$ 0.0414	0.0064	0.0302	0.1641	0.1686	0.0221
D	0.0096 $\pm$ 0.0096	0.0081 $\pm$ 0.0056	0.0288 $\pm$ 0.0089	0.4638 $\pm$ 0.0662	0.0035	0.0020	0.0231	0.0038	0.0217

Table 4 Region elasticities (see text), finite rate of increase (λ), and vegetation cover (estimated on a scale from 1 (open) to 5 (closed)) of the 35 matrices for *Gentiana pneumonanthe*. Matrix numbers correspond with Fig. 3(a)

Matrix no.	Population/site	Vegetation cover	Transition (years)	λ	E_2 (= F)	E_4	E_5	E_6 (= G)	$E_4 + E_5$ (= L)
1	Kooilust	3	1988–89	0.93	0.0266	0.2170	0.4931	0.2632	0.7101
2	Kooilust	3	1989–90	1.09	0.1165	0.0000	0.6507	0.2330	0.6507
3	Kooilust	3	1990–91	0.98	0.1039	0.0433	0.5854	0.2674	0.6287
4	De Deelen-2	3	1988–89	1.07	0.0204	0.0578	0.8237	0.0983	0.8815
5	De Deelen-2	4	1989–90	0.68	0.0084	0.0515	0.8830	0.0571	0.9345
6	De Deelen-2	5	1990–91	0.66	0.0000	0.1205	0.7835	0.0960	0.9040
7	De Deelen-3	3	1988–89	1.06	0.0940	0.0795	0.5633	0.2633	0.6428
8	De Deelen-3	3	1989–90	0.94	0.0489	0.0426	0.7870	0.1215	0.8296
9	De Deelen-3	3	1990–91	0.89	0.0024	0.1850	0.6221	0.1907	0.8071
10	Lochem	3	1988–89	0.96	0.0736	0.1537	0.5266	0.2460	0.6803
11	Lochem	3	1989–90	0.97	0.0356	0.1699	0.5810	0.2135	0.7509
12	Lochem	3	1990–91	1.51	0.2282	0.0692	0.2627	0.4399	0.3319
13	Dwingeloo-1	1	1987–88	1.14	0.1863	0.0261	0.4095	0.3781	0.4356
14	Dwingeloo-1	1	1988–89	1.24	0.1309	0.0000	0.6074	0.2617	0.6074
15	Dwingeloo-1	1	1989–90	1.45	0.2528	0.0716	0.1885	0.4871	0.2601
16	Dwingeloo-2	1	1987–88	2.23	0.3098	0.0054	0.2899	0.3947	0.2953
17	Dwingeloo-2	1	1988–89	1.15	0.1340	0.0474	0.5033	0.3153	0.5507
18	Dwingeloo-2	1	1989–90	1.59	0.2615	0.0269	0.2285	0.4831	0.2554
19	Dwingeloo-3	3	1987–88	0.87	0.0106	0.1098	0.7367	0.1429	0.8465
20	Dwingeloo-3	3	1988–89	0.99	0.0318	0.1144	0.7001	0.1536	0.8145
21	Dwingeloo-3	3	1989–90	0.96	0.0171	0.1059	0.7291	0.1480	0.8350
22	Texel-1	2	1987–88	0.78	0.0003	0.0048	0.9902	0.0048	0.9951
23	Texel-1	2	1988–89	0.74	0.1249	0.1249	0.6223	0.1178	0.7472
24	Texel-1	2	1989–90	1.56	0.1895	0.0000	0.4314	0.3790	0.4314
25	Texel-1	3	1990–91	1.29	0.1517	0.0322	0.4889	0.3272	0.5211
26	Texel-2	1	1987–88	0.93	0.0000	0.0000	1.0000	0.0000	1.0000
27	Texel-2	2	1988–89	0.52	0.2121	0.2121	0.3493	0.2265	0.5614
28	Texel-2	2	1989–90	2.04	0.2659	0.0000	0.0596	0.6745	0.0596
29	Texel-2	3	1990–91	1.49	0.1818	0.0087	0.4457	0.3636	0.4544
30	Terschelling	2	1987–88	1.23	0.1837	0.0356	0.4807	0.3000	0.5163
31	Terschelling	2	1988–89	1.59	0.1859	0.0120	0.4321	0.3701	0.4441
32	Terschelling	3	1989–90	0.82	0.0506	0.1126	0.6650	0.1718	0.7776
33	Terschelling	4	1990–91	0.62	0.0171	0.0664	0.8195	0.0970	0.8859
34	Terschelling	5	1991–92	0.74	0.0073	0.0597	0.8584	0.0746	0.9181
35	Terschelling	5	1992–93	0.73	0.0000	0.1158	0.7684	0.1158	0.8842

negative sign for L and a positive for G and F (Table 6). When compared with heathland sites, hay meadow matrices have a different (more restricted) position in the diagram, mostly occupying the lower right corner of the triangle, where $\lambda \leq 1$, and the elasticities of F and G are relatively low (Fig. 3a).

Since the vegetation cover is so clearly correlated with λ , multiple regression was performed to assess its effect on the demographic parameters independently (Table 6). When λ is statistically held constant, it appears that vegetation cover shows a significant positive correlation with the elasticity of fecundity. At the same time, there is a trend ($P < 0.10$) that a denser vegetation also leads to a higher elasticity of survival (L , mainly through increased elasticity for stasis, Table 6). The same trend can be observed within population Terschelling, where the vegetation cover gradually increased after sod-cutting (Table 4, Fig. 3a: matrices 30–35). Figure 4 shows the relationship between the population growth rate (r) and the elasticities of G , L and F . It is clear that survival (retrogression + stasis) is by far the most important life-

history parameter for *Gentiana pneumonanthe*, especially in stable or declining populations, where $r \leq 0$. Only in growing populations ($r > 0.223$) does the sum of fecundity and progression contribute equally or more to the rate of increase than survival.

CORRELATION BETWEEN MATRIX ELEMENTS

There was a significant difference between the observed and expected frequency distribution of correlation coefficients between the matrix elements ($\chi^2_{13} = 31.37$, $P \leq 0.01$). Of the 190 correlation coefficients, 30 are significant at the 5%, and 14 at the 1% level (determined by the randomization test, see Table 7), and most (39) of these are positive.

Some sets of correlations are potentially important. (i) the probability of generative plants remaining generative (a_{gg}) is positively correlated with the recruitment of seedlings and juveniles (F_{sg} and F_{jg}) and with the probability of vegetative adults attaining the flowering stage (a_{gv}), but negatively correlated with the probability of generative adults becoming veg-

Table 5 Log-linear analysis of temporal and spatial variation in the relative contribution of the *G*, *L* and *F* regions to the finite rate of increase within (a) and among (b) the studied populations of *Gentiana pneumonanthe*. Time steps: 1, 1987–88; 2, 1988–89; 3, 1989–90; 4, 1990–91; 5, 1991–92; 6, 1992–93. T, time (temporal component); P, site (spatial component); E, elasticity (*G*, *L* and *F*)

(a) Temporal variation within sites				
site	time steps	d.f.	G^2	P
Kooilust	2, 3, 4	6	8.10	0.231
Deelen-2	2, 3, 4	6	3.65	0.723
Deelen-3	2, 3, 4	6	17.70	0.007
Lochem	2, 3, 4	6	45.28	<0.0001
Dwingeloo-1	1, 2, 3	6	23.99	0.001
Dwingeloo-2	1, 2, 3	6	24.60	<0.0001
Dwingeloo-3	1, 2, 3	6	1.25	0.974
Texel-1	1, 2, 3, 4	9	110.10	<0.0001
Texel-2	1, 2, 3, 4	9	232.52	<0.0001
Terschelling	1, 2, 3, 4, 5, 6	15	122.22	<0.0001

(b) Temporal and spatial variation			
(all sites, only $T = 2$ and $T = 3$)			
model	d.f.	G^2	P
PTE, PE (time effect)	45	185.46	<0.0001
PTE, TE (site effect)	29	485.80	<0.0001
PTE, PE, TE (interaction)	18	167.46	<0.0001

etative (a_{vg}) or dormant (a_{dg}). The latter negative correlations are to be expected, since they probably represent compensation within a matrix column (individuals that go into one state cannot go into another); (ii) the probability that vegetative plants remain vegetative (a_{vv}) is positively correlated with the probability that reproductive adults do not flower the next year (a_{vg}); (iii) the probability that seedlings become established as vegetative (a_{vs}) or even repro-

ductive (a_{gs}) adults is higher in years with favourable germination conditions (F_{sg} , F_{lg}).

Discussion

SPATIAL AND TEMPORAL VARIATION IN TRANSITION MATRICES

During this study, high temporal and spatial variation in demographic parameters was observed within and between populations of *Gentiana pneumonanthe*. Most of the spatial variation is probably caused by the large differences in habitat type and management rather than by differences on a smaller scale. In the two cases where there are two sites in one population that do not differ in management type, namely Texel-1 and -2 and Dwingeloo-1 and -2, the two sites show significantly different transition matrices in Dwingeloo, but not in Texel. This may probably be related to differences in the height of the ground water table between the two sites in Dwingeloo (site 2 is relatively wet as compared to site 1) which are not present at Texel. Similarly, the temporal variation in the heathland populations is probably caused mainly by successional changes in vegetation structure and less strongly by, for instance, climatic differences. This is supported by the significant time-trend observed in population Terschelling. On the other hand, in very closed heathland vegetation or in the hay meadows, in both of which the vegetation structure is relatively stable, temporal variation was also highly significant. Considerable temporal and spatial variation in demographic parameters has been found for several other plant species of open habitats. In these cases, variation could often be attributed to climatic differences or to changes in the environment caused by natural suc-

Fig. 3 (a) Triangular *G*–*L*–*F* ordination of the 35 elasticity matrices of *Gentiana pneumonanthe*, and (b) the same diagram with an additional axis, showing the finite rate of increase, λ , for each matrix. The numbers in (a) refer to individual matrices, and are the same as in Table 4. The circles in diagram (a) represent matrices from heathland sites, the squares represent hay meadows. ‘C’ refers to the matrix derived from Chapman *et al.* (1989) by Silvertown *et al.* (1993). The average matrix for *G. pneumonanthe* is also shown.

Table 6 Multiple regression analysis with population growth rate, r ($= \ln \lambda$), and vegetation cover as independent variables and (summed) matrix region elasticities, E_2 – E_6 , F , L and G as dependent variables. The first row of the table shows the regression between vegetation cover and the population growth rate. $N = 33$ matrices

Dependent variable	Part. regression coefficients	(β)	$t_{(\beta)}$	$P_{(\beta)}$ (2-tailed)	R^2	F -ratio	$P_{(F)}$
r ($= \ln \lambda$)	cover	−0.595	4.148	≤ 0.001	0.357	17.206	≤ 0.001
E_2 ($= F$)	r	0.481	3.467	0.002	0.629	25.484	≤ 0.001
	cover	−0.406	2.933	0.006			
E_4 (retrogr.)	r	−0.640	3.599	0.001	0.389	9.554	0.001
	cover	−0.029	0.160	0.874			
E_5 (stasis)	r	−0.511	3.189	0.003	0.504	15.250	≤ 0.001
	cover	0.274	1.710	0.098			
$E_4 + E_5$ ($= L$)	r	−0.651	5.023	≤ 0.001	0.676	31.292	≤ 0.001
	cover	0.246	1.900	0.067			
E_6 ($= G$)	r	0.729	5.475	≤ 0.001	0.658	28.820	≤ 0.001
	cover	−0.126	0.947	0.351			

cession or due to human disturbance (Bengtsson 1993; Svensson *et al.* 1993; Silvertown & Franco 1993; Bullock *et al.* 1994; Bastrenta *et al.* 1995; Silvertown *et al.*, in press).

SPATIAL AND TEMPORAL VARIATION IN ELASTICITY MATRICES

The simultaneous analysis of count and elasticity matrices allows a comparison between variation in the actual values of life-cycle transitions and their contribution to the finite rate of increase. For instance, it appeared that elasticities for seedling and juvenile survival do not vary significantly in time and space, in contrast to their corresponding transition values. This suggests that although there is variation in seedling survival from year to year and between

sites, this rarely has any strong effect on their relative contribution to the population growth rate. Conversely, the vegetative and reproductive adult stages contribute much more to the overall log-likelihood ratio than the young stages, both for transition and elasticity values. Apparently, variation in the generally most important transitions in the life cycle of this species (survival generally has higher elasticity than the sum of progression and fecundity) has a stronger effect on their corresponding elasticities than it does for the less important transitions.

Not much is known about the variation in elasticities between years for other plant species (Silvertown *et al.* 1993; Silvertown & Franco 1993). In a study of three *Pinguicula* species, elasticities for all three species were reported to vary very little, both over year-to-year transitions and over the various plots (Svensson *et al.* 1993). Also in *Fumana procumbens*, the transitions contributing most to λ (stasis of reproductive adults) were rather similar each year (Bengtsson 1993). In contrast, in the present study the variation in the elasticity matrices is considerable, although generally less than the variation in the transition matrices (Table 2). Only in two of the 10 sites, Deelen-3 and Dwingeloo-3, were the elasticity matrices of different years statistically identical (Table 2a), although when decomposed by stage the elasticities for the adult stages still showed significant variation. Generally speaking, however, in these populations the same stages are most important to population growth (or persistence) in all years.

Fig. 4 Graph showing the relationships between the population growth rate, r ($= \ln \lambda$) and the elasticity values of the matrix regions G , L and F (see text). A regression line was fitted between r and each region elasticity for the 35 available matrices. All three regressions were significant ($P \leq 0.05$). The cross-section shows the (range in) elasticities for G , L and F in a theoretically stable population, at $r = 0$.

VARIATION IN THE RELATIVE CONTRIBUTIONS OF FECUNDITY, PROGRESSION AND SURVIVAL TO λ

As in the total transition and elasticity matrices, there is significant temporal variation in the relative contribution of the G , F and L elasticity regions in all but three sites, namely Kooilust, Deelen-2 and Dwingeloo-3 (Table 5a). The habitat of these populations

Table 7 Matrix of Spearman's rank correlation coefficients between the transition probabilities in the 35 matrices available for *Gentiana pneumonanthe*

	a_{ss}	a_{js}	a_{vs}	a_{gs}	a_{ds}	a_{ij}	a_{vj}	a_{gi}	a_{dj}	a_{vv}	a_{gv}	a_{dv}	F_{sg}	F_{jg}	a_{vg}	a_{gg}	a_{dg}	a_{vd}	a_{gd}
a_{js}	0.314*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
a_{vs}	0.179	0.280*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
a_{gs}	-0.100	0.124	0.340*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
a_{ds}	-0.061	0.394*	0.074	-0.100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
a_{ij}	0.327*	0.384*	0.122	-0.124	-0.075	—	—	—	—	—	—	—	—	—	—	—	—	—	—
a_{vj}	-0.127	-0.012	0.030	0.054	0.046	-0.090	—	—	—	—	—	—	—	—	—	—	—	—	—
a_{gi}	0.216	0.451**	0.197	0.289*	0.269*	0.122	-0.228	—	—	—	—	—	—	—	—	—	—	—	—
a_{dj}	0.334*	0.295*	0.382*	-0.236	0.127	0.434**	-0.202	-0.023	—	—	—	—	—	—	—	—	—	—	—
a_{vv}	0.291*	0.340*	0.285*	-0.062	0.027	0.422**	-0.039	-0.141	0.415**	—	—	—	—	—	—	—	—	—	—
a_{gv}	-0.162	-0.065	0.074	0.036	0.042	-0.247	0.245	0.165	-0.085	-0.144	—	—	—	—	—	—	—	—	—
a_{dv}	0.053	0.055	-0.245	-0.095	0.103	-0.081	0.029	0.128	0.060	0.018	0.105	—	—	—	—	—	—	—	—
F_{sg}	0.093	0.047	0.309*	0.492**	-0.319	0.225	0.107	0.079	-0.006	0.174	0.120	-0.304	—	—	—	—	—	—	—
F_{jg}	0.253	0.190	0.356*	0.477**	-0.183	0.293*	0.179	0.239	0.073	0.090	0.029	-0.273	0.676**	—	—	—	—	—	—
a_{vg}	0.043	0.165	-0.005	0.011	-0.164	0.121	-0.147	-0.294	0.201	0.486**	-0.356*	0.333*	-0.197	-0.101	—	—	—	—	—
a_{gg}	0.092	-0.249	0.292*	0.127	-0.118	0.028	-0.065	0.156	0.092	-0.162	0.529**	-0.314	0.380*	0.402*	-0.546**	—	—	—	—
a_{dg}	0.049	-0.004	-0.131	0.052	-0.173	-0.215	0.149	-0.273	-0.120	0.257*	-0.204	0.239	-0.026	-0.053	0.427**	-0.407*	—	—	—
a_{vd}	0.247	-0.023	-0.165	-0.192	-0.236	0.370*	-0.063	-0.122	0.150	0.256*	-0.206	0.322*	-0.247	-0.039	-0.589**	-0.195	-0.130	—	—
a_{gd}	0.105	-0.070	0.047	0.178	-0.275	-0.057	-0.005	0.367*	-0.404*	-0.283	0.332*	-0.069	0.126	0.233	-0.339	0.506**	-0.066	-0.163	—
a_{dd}	-0.195	-0.050	0.111	0.141	0.351*	-0.274	0.145	0.034	-0.156	-0.167	-0.006	-0.071	0.077	-0.118	-0.257	-0.145	-0.177	-0.704**	-0.149

* $P \leq 0.05$, ** $P \leq 0.01$.

may be called relatively stable, either as a result of annual mowing (Kooilust) or the absence of management (Dwingeloo-3, Deelen-2). In such populations, the elasticity of L is highest in all years, which may statistically obscure any differences occurring in the comparatively low elasticities for F and G . These small differences nevertheless may have important consequences for a population. This is demonstrated by Deelen-2, where the elasticity for F declined from an already low 0.02 to zero after mowing ceased, while λ changed from 1.07 to 0.66.

Apart from the three sites discussed above, the relative contribution of G , L and F to the finite rate of increase is generally highly variable between years and sites. The total variation observed within *G. pneumonanthe* is as high as the interspecific variation observed across the whole sample of iteroparous perennials from open habitats analysed by Silvertown *et al.* (1993) and Silvertown & Franco (1993). Some matrices in the ordination diagram for *Gentiana pneumonanthe* (those found in the lower right corner of the G – L – F triangle) are even very similar to those characteristic of woody plants (see Silvertown & Franco 1993).

The present study clearly shows that comparison between species based on elasticity analysis should consider intraspecific variation. This is especially true for species from open, unstable habitats. It has been suggested that comparisons between species should only focus on populations or matrices with a λ of ≈ 1 (Silvertown *et al.*, in press). Figure 4 shows that for *Gentiana* even such 'stable' matrices may show considerable variation in the elasticities for G , L and F . The difficulty of comparing species on the basis of only one (averaged) matrix can immediately be seen from the matrix of *Gentiana pneumonanthe* that is included in the GLF-diagram of iteroparous species of open habitats presented in Silvertown *et al.* (1993). This matrix was derived from a modelling study of the species by Chapman *et al.* (1989) and clearly represents an 'invasive' population (see Oostermeijer *et al.* 1994a) with a λ of 1.53, recolonizing an area after a controlled fire. This matrix is representative for an 'invasive' population but, as the present results show, hardly for the species in general.

DEMOGRAPHY IN RELATION TO VEGETATION SUCCESSION

The distribution of matrices along a long and narrow band in 'GLF-space' probably represents a successional pathway, which is supported by the correlations between λ and the G , L and F elasticities and vegetation cover, and by the trend in the matrices of the Terschelling site. In comparison with similar successional trends observed in six savanna grass species (O'Connor 1993, 1994), in *Cirsium vulgare* (Bullock *et al.* 1994) and in *Pedicularis furbishiae* (Menges 1990), which occupy relatively small parts of

the G – L – F triangle (see Silvertown & Franco 1994; and Silvertown *et al.*, in press), the 'successional pathway' for *Gentiana pneumonanthe* populations seems exceptionally long.

In studies of vegetation succession, the question still arises whether the occurrence of certain plant species in a given successional stage is a consequence of the vegetation structure, which determines if the species can establish, or if the vegetation structure in that stage is created by the species that are able to establish under those conditions (Olf *et al.* 1994). This and other demographic studies may shed some light on this question, since it becomes more and more clear that some species that occur as flowering individuals in a given successional stage may have established several stages earlier. *Gentiana pneumonanthe*, for instance, establishes populations in wet heathlands at the very start of (secondary) succession, in the pioneer community *Lycopodium-Rhynchosporium albo-fuscae* (Westhoff & den Held 1969). In this invasive stage, the density of individual plants is the highest, although not many individuals are flowering. However, in later successional stages (more or less mature wet heathlands that can be classified as *Ericetum tetralicis*, Westhoff & den Held 1969), the species still occurs frequently, but generally in senile populations with a much lower density (Oostermeijer *et al.* 1994a). Hence, in this later stage, the species is no longer able to recruit new individuals to its populations, although it does contribute to the vegetation structure and is even considered a characteristic species for the association (Westhoff & den Held 1969).

When comparing heathland and hay meadow matrices, it appears that the former occupy a much broader region of the triangle than the latter, which are positioned only at the lower right corner. This is also a result of the stronger changes in vegetation structure that occur in heathlands as compared with meadows. In heathlands, the percentage bare soil surface can be nearly 100% directly after sod-cutting, falling to almost 0% in the course of the secondary succession. In hay meadows there is hardly ever any bare soil. Even when regularly mown, the total vegetation cover is still high, and when mowing ceases, the grass cover closes rapidly to 100% (see site Deelen-2). The occurrence of recruitment in this habitat is probably more related to climatic differences.

The detailed demographic results presented here agree very well with the 'invasive', 'stable' and 'regressive' types of population structure, that were distilled from single censuses of 60 Dutch populations (Oostermeijer *et al.* 1994a). Invasive populations, with high densities and a higher proportion of seedlings and juveniles than adult plants, are positioned on the top left of the successional pathway in the G – L – F diagram ($\lambda > 1$). Stable populations, with intermediate densities and more adult individuals than seedlings and juveniles, are found in the middle

($\lambda \approx 1$). Regressive (or senile) populations, which have low density, show no recruitment and hence consist only of adult plants, occupy the lower right corner of the triangle ($\lambda < 1$).

In general, it can be concluded that disturbance is necessary to prevent populations of *Gentiana pneumonanthe* from (local) extinction. A major disturbance, such as sod-cutting, sets a population back to the upper left side of the triangle, after which the successional pathway is followed until a new disturbance occurs. Disturbances of lower intensity that occur on a regular basis, such as trampling, grazing and mowing, will most likely result in populations remaining in the middle (stable) section of the pathway.

MATRIX MODELS AS A TOOL IN CONSERVATION AND MANAGEMENT

The information described above provides a very strong basis for assessing the viability of a population (by determining the population structure, but preferably by constructing a transition matrix) or for evaluating the success of conservation and (new) management strategies.

The elasticity of survival (retrogression + stasis) is very high in declining populations. This implies that λ is most sensitive to a change in these transitions, so management should focus on keeping them relatively constant. However, although focusing on the survival of the remaining plants is important to prevent immediate extinction, it will not reverse the decline of the population. Figure 4 shows that growing (regenerating) populations of *Gentiana pneumonanthe* are characterized by relatively high elasticities for fecundity and growth. The optimal management strategy would thus be to keep the survival of the remaining plants as high as possible (by preventing any unnatural damage) while at the same time increasing the possibilities for germination and recruitment (e.g. by creating gaps in the vegetation). Only then can fecundity and growth become more important to the population, allowing λ to increase. The same conclusion was drawn by Silvertown *et al.* (in press), based on comparative data from other plant species. The results teach us that in conservation and management decisions, elasticity values should not be interpreted without considering the corresponding value of λ .

CORRELATIONS BETWEEN THE TRANSITION PROBABILITIES OF DIFFERENT LIFE STAGES

Several of the matrix entries were significantly positively correlated. This suggests that they will not vary independently of each other when the environment changes. It may be expected that positive correlations between matrix elements increase the risk of extinction, as under adverse conditions several stages are

affected negatively at the same time, causing the effects of environmental stochasticity to be more extreme (Menges 1992). Negative correlations may be advantageous, since there is an increased probability that some stages will survive even when others do not (Caswell 1983). In *Gentiana*, some of the observed positive correlations between matrix entries are possibly important in this respect., but most of the negative correlations probably represent compensations within the matrix columns. Interesting positive correlations are those between recruitment (F_{sg} and F_{gg}) and seedling progression (a_{es} and a_{gs}), between recruitment and the probability of reproductive plants remaining reproductive (a_{gg}) and between stasis of vegetative adults (a_{vv}) and the probability that reproductive adults become vegetative (a_{vg}). Apparently, when conditions are favourable for recruitment (germination), they also favour establishment and growth of the newly recruited individuals, while at the same time the reproductive adults have a higher probability of flowering again the next year. Of course this relationship also works in the opposite way, leading to correlated negative responses of various life stages to unfavourable conditions. This reduces the opportunities for spreading risks between life stages and can therefore increase the probability of extinction. Simulation studies will shed more light on this in the near future.

Acknowledgements

The authors would like to thank all students and field assistants for their help with the demographic analyses of the permanent plots. The first author especially wants to thank Dr Eric Menges for the many fruitful discussions on this subject and for critically reading a previous version of the manuscript. Dr J. Silvertown, Dr M. Franco and an anonymous referee also improved the paper with several useful suggestions. Dr L. Haddon kindly corrected the English. Our thanks also go out to Prof. Dr J. van Groenendael, for good suggestions and for explaining some basics of matrix analysis, and to Prof. Dr K. Bachmann for his critical comments. We are very grateful to several nature management and conservation organizations for providing the necessary research permits and to many local reserve managers who discussed important aspects and problems of nature management with us.

References

- Bastrenta, B., Lebreton, J. & Thompson, J.D. (1995) Predicting demographic change in response to herbivory: a model of the effects of grazing and annual variation on the population dynamics of *Anthyllis vulneraria*. *Journal of Ecology*, **83**, 603–611.
- Bengtsson, K. (1993) *Fumana procumbens* on Öland: population dynamics of a disjunct species at the northern limit of its range. *Journal of Ecology*, **81**, 745–758.

- Boeken, B. & Canham, C.D. (1995) Biotic and abiotic control of the dynamics of gray dogwood (*Cornus racemosa* Lam.) shrub thickets. *Journal of Ecology*, **83**, 569–580.
- Bullock, J.M., Clear-Hill, B. & Silvertown, J. (1994) Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology*, **82**, 101–111.
- Caswell, H. (1983) Phenotypic plasticity in life history traits: demographic effects and evolutionary consequences. *American Zoologist*, **23**, 35–46.
- Caswell, H. (1989) *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer Associates Inc., Sunderland, MA.
- Chapman, S.B., Rose, R.J. & Clarke, R.T. (1989) The behaviour of populations of the marsh gentian (*Gentiana pneumonanthe*): a modelling approach. *Journal of Applied Ecology*, **26**, 1059–1072.
- Franco, M. & Silvertown, J. (1990) Plant demography: what do we know? *Evolutionary Trends in Plants*, **4**, 74–76.
- Franco, M. & Silvertown, J. (1994) On trade-offs, elasticities and the comparative method: a reply to Shea, Rees & Wood. *Journal of Ecology*, **82**, 958.
- Gleason, S.K. & Tilman, D. (1990) Allocation and the transient dynamics of succession on poor soils. *Ecology*, **71**, 1144–1155.
- Gray, A.J., Crawley, M.J. & Edwards, P.J., eds. (1987) *Colonisation, Succession and Stability*. Blackwell Scientific Publications, Oxford.
- Keddy, P.A. (1981) Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology*, **69**, 615–630.
- de Kroon, H., Plaisier, A., van Groenendael, J.M. & Caswell, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*, **67**, 1427–1431.
- Manly, B.F.J. (1991) *Randomization and Monte Carlo methods in biology*. Chapman & Hall, London.
- Margadant, W.D. & During, H.J. (1982) *Beknopte Flora van Nederlandse Blad- en Levermossen*. Bibl. K.N.N.V., Thieme, Zutphen.
- Meijden, R. van der (1990) *Heukels' Flora van Nederland*, 21st edn. Wolters-Noordhoff, Groningen.
- Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.
- Menges, E.S. (1992) Stochastic modeling of extinction in plant populations. *Conservation Biology: the Theory and Practice of Nature Conservation, Preservation and Management* (eds P. L. Fiedler & S. K. Jain), pp. 253–275. Chapman & Hall, New York.
- Meusel, H., Jäger, E., Rauschert, S. & Weinert, E. (1978) *Vergleichende Chorologie der Zentral-europäischen Flora*. Band II. Fischer Verlag, Jena.
- O'Connor, T.G. (1993) The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. *Journal of Applied Ecology*, **30**, 119–132.
- O'Connor, T.G. (1994) Composition and population responses of an Africa savanna grassland to rainfall and grazing. *Journal of Applied Ecology*, **31**, 155–171.
- Økland, R.H. (1995) Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. *Journal of Ecology*, **83**, 697–712.
- Olf, H., Pegtel, D.M., van Groenendael, J.M. & Bakker, J.P. (1994) Germination strategies during grassland succession. *Journal of Ecology*, **82**, 69–77.
- Oostermeijer, J.G.B., den Nijs, J.C.M., Raijmann, L.E.L. & Menken, S.B.J. (1992) Population biology and management of the marsh gentian (*Gentiana pneumonanthe* L.), a rare species in The Netherlands. *Botanical Journal of the Linnean Society*, **108**, 117–130.
- Oostermeijer, J.G.B., van 't Veer, R. & den Nijs, J.C.M. (1994a) Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in The Netherlands. *Journal of Applied Ecology*, **31**, 428–438.
- Oostermeijer, J.G.B., Eijck, M.W. van & den Nijs, J.C.M. (1994b) Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). *Oecologia*, **97**, 289–296.
- Pickett, S.T.A., Collons, S.L. & Armesto, J.J. (1987) A hierarchical consideration of causes and mechanisms of succession. *Vegetatio*, **69**, 109–114.
- Raijmann, L.E.L., Leeuwen, N.C. van, Kersten, R., Oostermeijer, J.G.B., Nijs, J.C.M. den & Menken, S.B.J. (1994) Genetic variation and outcrossing rate in relation to population size in *Gentiana pneumonanthe* L. *Conservation Biology*, **8**, 1014–1026.
- Shea, K., Rees, M. & Wood, S.N. (1994) Trade-offs, elasticities and the comparative method. *Journal of Ecology*, **82**, 951–957.
- Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. (1993) Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology*, **81**, 465–476.
- Silvertown, J., Franco, M. & Menges, E.S. (in press) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology*, in press.
- Silvertown, J.W. & Franco, M. (1993) Plant demography and habitat: a comparative approach. *Plant Species Biology*, **8**, 67–73.
- Svensson, B.M., Carlsson, B.Å., Karlsson, P.S. & Nordell, K.O. (1993) Comparative long-term demography of three species of *Pinguicula*. *Journal of Ecology*, **81**, 635–645.
- Westhoff, V. & den Held, A.J. (1969) *Plantengemeenschappen in Nederland*. Wolters-Noordhoff, Groningen.

Received 9 January 1995

revised version accepted 11 September 1995