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Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands

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Summary

1. After analysis of population age-state spectra of *Gentiana pneumonanthe* in a variety of vegetation types, three different population types could be distinguished: (a) 'invasive' or 'dynamic' populations, characterized by high densities of seedlings and juveniles relative to the adult age states, (b) 'normal' or 'stable' populations with adult age states prevailing, but with low densities of seedlings and juveniles, and (c) 'regressive' or 'senile' populations, consisting only of adult flowering and adult vegetative individuals.

2. The structure of the surrounding vegetation appears to be very important in determining the population structure of the marsh gentian. In particular the percentage of bare soil surface and the cover of the litter layer explain most of the variation in the density and proportion of different age states in the populations. The area of bare soil surface in the vegetation increases the percentage of seedlings and juveniles in the population and, consequently, decreases the proportion of generative adults, while the reverse is true for the cover of the litter layer.

3. In heathlands, a clear trend can be observed in the age state structure from 'invasive' populations in young successional stages, via 'normal' populations in relatively stable situations, to 'regressive' populations in late successional stages or unmanaged areas dominated by grasses or shrubs. In hay meadows, 'normal' populations are usually observed, except where mowing has been stopped or where a combination of early mowing and acidification exists. This leads to closure of the community by grasses or bryophytes, respectively, and therefore to a 'regressive' population structure.

4. Individuals in heathland and grassland populations seem to have a different life-strategy because of the differences in vegetation dynamics between these two habitat types. Ecotypic differentiation in life-history characteristics may therefore be expected.

5. It is argued that, as a basis for conservation and management, monitoring the age state structure of populations of rare perennial plant species is far more effective than counting only the flowering individuals, as is mostly done.

Key-words: age states, conservation biology, herbs, life history, monitoring.

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Introduction

A better understanding of the relationship between the populations of plants and the vegetation of which they are part of is a useful tool in the conservation and management of rare and threatened plant species (Synge 1985; Harvey 1985; Bakker 1989; Hutchings

1991). Demographic studies can reveal the critical stages in the life cycle of rare plants and, if the results are related to different management practices and the structure and composition of the surrounding vegetation, they may allow prediction of the effects of changes in management on threatened populations (Hutchings 1991). Detailed demographic studies are,

however, laborious, and often take many years to complete, which prevents their wide use in conservation biology (Harvey 1985).

Another less time-consuming way to relate demographic performance of populations of (herbaceous) perennials to vegetation is to analyse their structure in different plant communities (phytocoenoses). The structure of a population may be described by classifying the individual plants either by age, size or their life stage (Rabotnov 1969, 1985). However, it is often impossible in practice to establish the age of individuals, except by following them from germination onwards. Moreover, especially in herbaceous perennial plant species, both size and reproductive capacity are poorly correlated with actual age (Harper 1977). Therefore, the best way of describing populations of such species in a single census is by determination of the relative proportions of individuals in the different ontogenetic stages in the life cycle, generally called 'age states'. This method has proved to be successful in a number of studies on perennial plant species (see Gatsuk *et al.* 1980; Rabotnov 1985; Barkham 1980a,b; Zhang 1983; Mehrhoff 1989).

Preliminary data from a long-term demographic study of the marsh gentian (*Gentiana pneumonanthe**) have suggested that two types of population may be distinguished: 'dynamic' populations, with relatively high turnover of individual plants, high numbers of seedlings and juveniles present each year, and low percentages of adult generative individuals; and 'senile' or 'static' populations, in which the same generative plants are found every year, and practically no germination and seedling recruitment takes place (Oostermeijer *et al.* 1992). From the viewpoint of conservation and management, it is interesting to test whether these 'dynamic' and 'senile' populations occur in vegetation types which differ in structure and composition. If they do, the age-state spectrum for a population of a plant such as the marsh gentian (and possibly also of other species with a similar life cycle) in a nature reserve could be used as an indicator of its present vitality, and also as a basis for evaluating and predicting the effects of different management strategies (Oostermeijer, van't Veer & Broerse 1990; Oostermeijer *et al.* 1992).

Materials and methods

STUDY SPECIES

Gentiana pneumonanthe is a long-lived, polycarpic herbaceous perennial characteristic of wet heathlands, unmanured grasslands and hay meadows (alliances *Ericion tetralicis* (Schwick 1933), *Violion caninae*

(Schwick (1941) em. Preising 1949) and *Junco (subuliflori)-Molinion* (Westhoff 1969); Westhoff & Den Held 1969). The species is a good example of a plant formerly common in the Netherlands that has become quite rare during recent decades due to land reclamation, excessive use of fertilizers, atmospheric deposition, ground water abstraction, and also the lack of suitable management in nature reserves (Mennema, Quené-Boterbrood & Plate 1985). However, numerous populations still exist, although many are now very small and isolated due to intense fragmentation of the habitat, which may lead to reduced gene flow, inbreeding and reduced fitness (Oostermeijer *et al.* 1992).

Gentiana pneumonanthe overwinters as a rosette of short shoots with small, scale-like leaves formed at the end of each flowering season. Reproduction takes place only by seeds, which are normally produced in large quantities and clearly adapted to (short-range) wind dispersal. There is no persistent seed bank (Oostermeijer *et al.* 1992).

DETERMINATION OF DIFFERENT AGE STATES

Since the actual age of individual plants of *Gentiana pneumonanthe* cannot be determined, the population structure analysis was based on the numbers of individuals in the different ontogenetic stages of the life cycle that are in some way related to age (age states: Rabotnov 1969; Gatsuk *et al.* 1980). Based on our demographic studies, we have distinguished six different age states in populations of *Gentiana pneumonanthe*. These categories are as follows (Fig. 1).

1. Seeds: individuals in an enforced dormant state on, or directly below, the soil surface.
2. Seedlings: individuals developed directly after germination of seeds, with cotyledons, often also with one or two leaf-pairs, and without a stem or an overwintering shoot.
3. Juveniles (immatures): plants with one or (rarely) more stems and/or overwintering shoots, still carrying cotyledons, although these have frequently started to wither. The leaves differ from those of adult age states in that they are thinner, not revolute and mostly more ovate. Juveniles and vegetative adults cannot be distinguished by means of their size, since juveniles especially may be either very small (0.5–2 cm) in short, open vegetation, or rather elongated (>10 cm) in tall vegetation.

The transition between juveniles and immatures is very difficult to distinguish morphologically. Therefore, immatures are considered as juveniles here.

4. Vegetative adults: individuals without cotyledons, with one or more flowerless stems and with overwintering shoots in late summer. The leaves are thick and mostly revolute.
5. Generative adults: plants with one or more flowering stalks (frequently also bearing vegetative

* Plant nomenclature follows Margadant & During (1982) for bryophytes and van der Meijden (1990) for vascular plants.

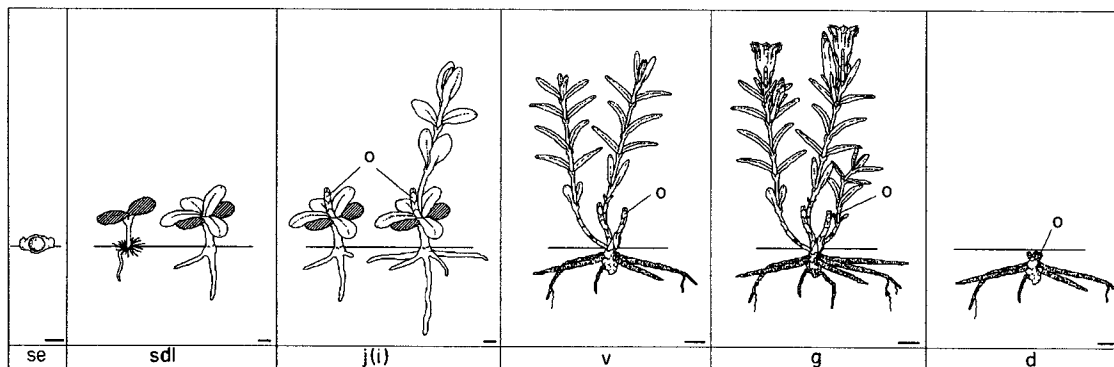


Fig. 1. Schematic drawing of different age states of *Gentiana pneumonanthe*: se, seed; sdl, seedling; j(i), juvenile (and immature); v, adult vegetative; g, adult generative; d, dormant. Note the overwintering shoots (o) and cotyledons (shaded). Scale bars indicate 1 mm for the se, sdl and j(i) classes, and 1 cm for the v, g and d age states.

stems) and in late summer with overwintering shoots. The leaves are identical to those of vegetative adults.

6. Dormants: plants in a dormant state, without any organs visible above ground.

The normal developmental sequence of an individual is from seed to generative adult. Although the seedling and juvenile age states usually each last 1 year, there is considerable variation in the time it takes different adult individuals to proceed from the vegetative to the generative age state, and many of the adult vegetatives never reach the flowering state at all. This means that large differences in age occur among individuals within the adult age states.

ANALYSIS OF THE VEGETATION AND DETERMINATION OF AGE-STATE SPECTRA

Vegetation relevés and population analyses were made for populations of the marsh gentian occurring in a total of 60 nature reserves in different parts of the Netherlands (Fig. 2). When subpopulations of the marsh gentian occurred in clearly different phytocoenoses in one reserve, more than one quadrat per site was analysed, leading to a total of 133 samples.

In each phytocoenosis, quadrats representing a homogeneous stand were selected for population analysis. The quadrat area varied from 4 to 16 m², depending on the density of the population and the nature of the vegetation. In these quadrats, the vegetation was described by estimating the actual cover percentages and average height of all vegetation layers, and the cover of all species of vascular plants and bryophytes. In each quadrat, the number of individuals in each of the different age states of *Gentiana pneumonanthe* was also counted, so that an adequate estimate of the density of each age state (in plants m⁻²) could be made. The 'seed' and 'dormant' age states had to be omitted from the population analysis, because it is not possible to assess the number of individuals in these categories without a detailed long-term demographic study.

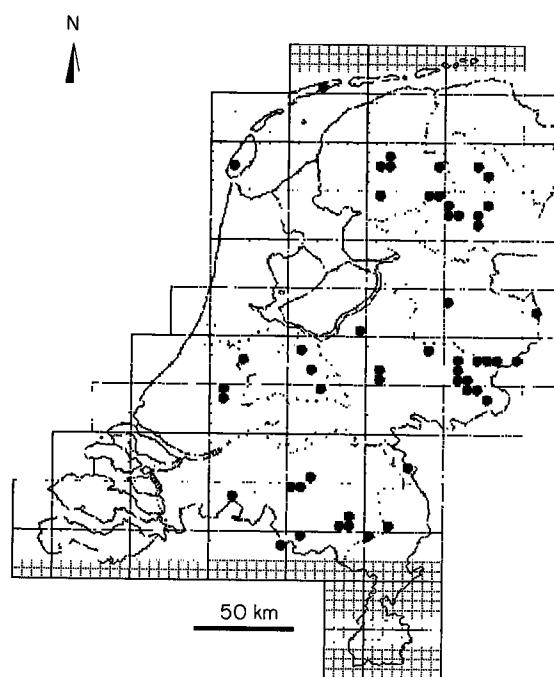


Fig. 2. Location of the sampling areas in the Netherlands.

DATA ANALYSIS

The vegetation data were classified by means of the computer package TWINSpan (Hill 1979). The TWINSpan program constructs a classification of vegetation types by means of an ordered two-way (species by sites) table (Jongman, ter Braak & van Tongeren 1987). A *K*-means clustering (Hartigan 1975) was performed on the population structure data (proportion of each age state in a population sample). This multivariate clustering method splits a set of samples into a selected number of groups by maximizing between-group relative to within-group variation. Differences in mean parameter values between the population types found by this method were then tested statistically with Student's *t*-test. To meet the assumptions of statistical analyses, percentages were subjected to angular transformation

(Sokal & Rohlf 1981). The observed densities (in plants m^{-2}) and transformed percentages of plants of *G. pneumonanthe* in different age states were investigated in relation to the structural parameters of the surrounding vegetation by means of multiple regression analysis (Sokal & Rohlf 1981). All statistical analyses were performed using the computer application SYSTAT (Wilkinson 1989).

This paper will focus more on the relationship between vegetation and population structure than on the classification of vegetation types, because the latter plays only a secondary part in the present study. A more detailed syntaxonomical and synecological interpretation of the vegetation data in relation to soil parameters will be presented elsewhere.

Results

COMPOSITION AND STRUCTURE OF THE VEGETATION TYPES

Based on the TWINSpan analysis, 12 different main vegetation types and a number of subtypes were distinguished within the complete dataset. A short description of the characteristic species combination, synecology and management of the communities is given in Table 1.

At the first level, the vegetation relevées were divided into two main groups that may be characterized as 'heathlands' (community types H1–H8) and 'grasslands' (types G1–G4). The community types G1 and G2, which occurred mostly on loamy soil,

Table 1. Description of the plant communities as classified by TWINSpan, together with their characteristic (name-giving) species, synecology and management

TWINSpan plant community	Synecology/management
(a) Heathland communities	
Type H1 <i>Drosera intermedia</i> community	Sod-cut areas, paths and tracks, grazed areas inundated in winter, relatively wet in summer.
H1.1 subtype with <i>Rhynchospora fusca</i> and <i>Lycopodium inundatum</i>	
H1.2 subtype with <i>Agrostis canina</i> , <i>Juncus bulbosus</i> and <i>Hydrocotyle vulgaris</i>	
Type H2 <i>Sphagnum cuspidatum</i> – <i>Sphagnum auriculatum</i> community	Former sod-cut areas, borders of moorland pools, heathland depressions, inundated in winter, wet in summer, rarely grazed or mown.
Type H3 <i>Scirpus cespitosus</i> – <i>Erica tetralix</i> community	Grazed or unmanaged heathlands, borders of moorland pools, often inundated in winter, wet in summer. Subtype 2 occurs where horizontally running water is present.
H3.1 subtype with <i>Sphagnum compactum</i> and <i>Sphagnum tenellum</i>	
H3.2 subtype with <i>Narthecium ossifragum</i> and <i>Hypnum cupressiforme</i> var. <i>ericetorum</i>	
Type H4 <i>Molinia caerulea</i> – <i>Erica tetralix</i> community	Wet to moist, unmanaged and/or nutrient-enriched heathlands.
Type H5 <i>Calluna vulgaris</i> – <i>Dicranella heteromalla</i> community	Wet to rather dry heathlands, disturbed by lowering of the water table and/or introduction of cattle or sheep (grazing, trampling, etc.).
H5a wet variant, with dominance of <i>Erica tetralix</i>	
H5b dry variant, with dominance of <i>Calluna vulgaris</i>	
Type H6 <i>Calluna vulgaris</i> – <i>Agrostis capillaris</i> community	Relatively dry, grazed areas, enriched in nutrients.
Type H7 <i>Carex trinervis</i> – <i>Empetrum nigrum</i> community	On sod-cut sites and along tracks in wet, leached secondary dune valleys, rarely mown periodically.
Type H8 <i>Myrica gale</i> – <i>Cephalozia bicuspidata</i> community	Unmanaged heathland depressions with large summer–winter fluctuations in the water table.
(b) Grassland communities	
Type G1 <i>Carex nigra</i> – <i>Agrostis canina</i> community	Former sod-cut sites and mown (every 1–4 years) areas in wet to moist heathlands on loamy soil.
Type G2 <i>Succisa pratensis</i> – <i>Pseudoscleropodium purum</i> community	Annually mown (September–October) areas in wet to moist heathlands on loam.
G2.1 subtype with <i>Parnassia palustris</i> , <i>Carex pulicaris</i> and <i>Polygala serpyllifolia</i>	
G2.2 subtype with <i>Rhynchospora squarrosus</i> and <i>Cirsium dissectum</i>	
Type G3 <i>Molinia caerulea</i> – <i>Leucobryum glaucum</i> community	Annually mown (July–October), wet to moist, unmanured hay meadows on peat.
G3.1 subtype with <i>Sphagnum palustre</i> , <i>Cirsium dissectum</i> and <i>Eriophorum angustifolium</i>	
G3.2 subtype with <i>Festuca ovina</i> , <i>Nardus stricta</i> and <i>Galium saxatile</i>	
Type G4 <i>Sphagnum flexuosum</i> – <i>Odontoschisma sphagni</i> community	Annually mown (August–September), unmanured hay meadows on floating vegetation mats ('kraggen').

exhibit certain floristic and structural characteristics of both heathlands and grasslands, but have been placed in the grassland group because of the mowing regime. In the following they are referred to as 'grass heaths'.

The mean number of species in the grassland communities was significantly higher than in the heathlands (23.2 vs. 12.2 species per sample, respectively, $P \leq 0.01$, Student's *t*-test).

The mean values of the most important structural variables for the vegetation types are given in Table 2. Important differences in structure between the heathland and the grassland group were the presence in the former group of a shrub layer and a high percentage cover of litter. Both the shrub and litter layer had a variable cover in the different heathland communities, but were practically absent in the grassland vegetation types. Within the heathland group, there was considerable variation in all structure parameters. In the vegetation types of sod-cut areas and tracks (types H1.1, H1.2 and also H7, Tables 1 & 2), the vegetation structure was very open, with low cover percentages of the shrub, herb, bryophyte and litter layers. The other heathland communities were much more closed, with low percentages of bare soil. In vegetation type H2, there was a high cover percentage of *Sphagnum* spp., mostly *Sphagnum cuspidatum*, while in communities H3 and H4 the relatively closed structure was caused by dominance of *Sphagnum compactum*, *Erica tetralix* or *Molinia caerulea*. The *Myrica*-*Erica* community (type H8) stood out because of a very closed shrub layer and a relatively high cover of litter.

Within the grassland vegetation types, the bryophyte cover was sometimes especially high, often almost reaching 100%. Within this bryophyte layer, there were sometimes considerable differences in microstructure, depending on the dominant bryophyte species. In vegetation type G2, for instance, these were mostly relatively low pleurocarpous species, for example *Rhytidiadelphus squarrosus* and *Hypnum cupressiforme*, while in the vegetation types G3 and G4 there was often a relatively thick, closed carpet of acrocarpous species, such as *Leucobryum glaucum*, *Polytrichum commune* var. *perigoniale* and *Sphagnum palustre*.

POPULATION AGE-STATE SPECTRA

Using the *K*-means clustering, three main groups (containing more or less equal numbers of samples) with different population age-state structures (Fig. 3a, b) could be distinguished in the dataset (Table 3). When other numbers of groups were selected for the analysis, the clusters were either too heterogeneous (in the case of two pre-selected groups) or entire clusters consisted of only few (deviating) samples (four and five groups). Within the three groups, the first main type (the 'invasive' type) was characterized by high proportions of seedlings and juveniles, relative to the adult age states. This was the opposite of the second ('normal') type, where there were still seedlings and juveniles present in the population, but the adult flowering individuals had the highest proportion. The proportion of seedlings and juveniles in the 'invasive' type was significantly higher than in the 'normal' type (*t*-test, $[74 \text{ df}] = 6.450$,

Table 2. Mean values (\pm SE) of variables describing vegetation structure in the different plant communities (see Table 1)

Plant community	Variable						
	Bare soil surface (%)	Cover of litter (%)	Cover of bryophytes (%)	Cover of herbs (%)	Cover of shrubs (%)	Height of herbs (cm)	Height of shrubs (cm)
(a) Heathlands							
H1.1 ($n = 14$)	54.1 \pm 8.4	19.7 \pm 6.7	3.1 \pm 1.9	40.6 \pm 6.1	12.1 \pm 3.9	23.5 \pm 2.6	16.9 \pm 3.5
H1.2 ($n = 8$)	31.6 \pm 12.4	6.5 \pm 2.2	21.0 \pm 12.5	63.1 \pm 7.7	7.0 \pm 1.8	21.9 \pm 3.9	13.8 \pm 2.3
H2 ($n = 10$)	3.5 \pm 3.0	19.0 \pm 3.3	71.5 \pm 8.7	47.8 \pm 6.8	28.3 \pm 10.5	37.7 \pm 4.3	29.7 \pm 4.0
H3.1 ($n = 12$)	1.3 \pm 0.5	23.0 \pm 5.7	30.1 \pm 9.6	49.0 \pm 8.1	43.7 \pm 10.2	30.4 \pm 2.5	28.3 \pm 2.7
H3.2 ($n = 5$)	8.0 \pm 8.0	44.0 \pm 15.0	8.2 \pm 5.7	44.4 \pm 14.1	61.4 \pm 14.7	42.0 \pm 3.0	33.0 \pm 4.3
H4 ($n = 9$)	11.6 \pm 8.1	36.7 \pm 8.0	0.1 \pm 0.1	71.7 \pm 9.1	10.7 \pm 3.9	38.0 \pm 6.8	22.0 \pm 4.0
H5a ($n = 7$)	7.1 \pm 4.8	27.1 \pm 10.8	3.6 \pm 2.1	60.0 \pm 13.2	39.4 \pm 14.5	37.9 \pm 7.6	42.9 \pm 14.2
H5b ($n = 7$)	8.6 \pm 6.9	18.3 \pm 4.6	17.0 \pm 9.8	54.3 \pm 6.3	27.4 \pm 6.8	34.0 \pm 2.9	26.0 \pm 5.5
H6 ($n = 10$)	1.6 \pm 0.6	30.5 \pm 7.6	16.2 \pm 8.4	76.8 \pm 4.2	20.0 \pm 4.5	40.6 \pm 6.3	52.5 \pm 17.1
H7 ($n = 4$)	23.3 \pm 10.1	3.7 \pm 3.2	14.3 \pm 12.8	45.0 \pm 16.1	18.3 \pm 13.5	20.0 \pm 10.0	10.0 \pm 0.0
H8 ($n = 4$)	0.0 \pm 0.0	65.0 \pm 15.6	7.3 \pm 5.2	57.5 \pm 12.5	50.0 \pm 11.7	44.5 \pm 3.2	55.5 \pm 6.1
(b) Grasslands							
G1 ($n = 14$)	4.5 \pm 1.6	5.9 \pm 2.0	48.4 \pm 10.9	81.0 \pm 4.3	13.8 \pm 4.1	30.3 \pm 3.1	23.5 \pm 3.5
G2.1 ($n = 5$)	18.6 \pm 14.1	6.0 \pm 2.1	12.8 \pm 8.2	65.0 \pm 12.2	18.0 \pm 9.7	20.6 \pm 1.2	18.0 \pm 3.4
G2.2 ($n = 9$)	1.1 \pm 0.8	6.6 \pm 2.3	80.0 \pm 9.0	89.9 \pm 5.4	5.0 \pm 3.2	23.9 \pm 2.2	14.3 \pm 1.4
G3.1 ($n = 7$)	0.1 \pm 0.1	4.6 \pm 2.0	94.3 \pm 3.5	81.0 \pm 5.5	0.1 \pm 0.1	27.3 \pm 3.4	10.0 \pm 10.0
G3.2 ($n = 5$)	0.2 \pm 0.2	19.4 \pm 6.6	23.8 \pm 15.5	97.0 \pm 0.6	0.0 \pm 0.0	19.6 \pm 5.4	0.0 \pm 0.0
G4 ($n = 4$)	0.3 \pm 0.3	9.0 \pm 3.6	96.3 \pm 2.4	89.5 \pm 6.9	4.3 \pm 1.8	48.8 \pm 10.1	23.5 \pm 9.1

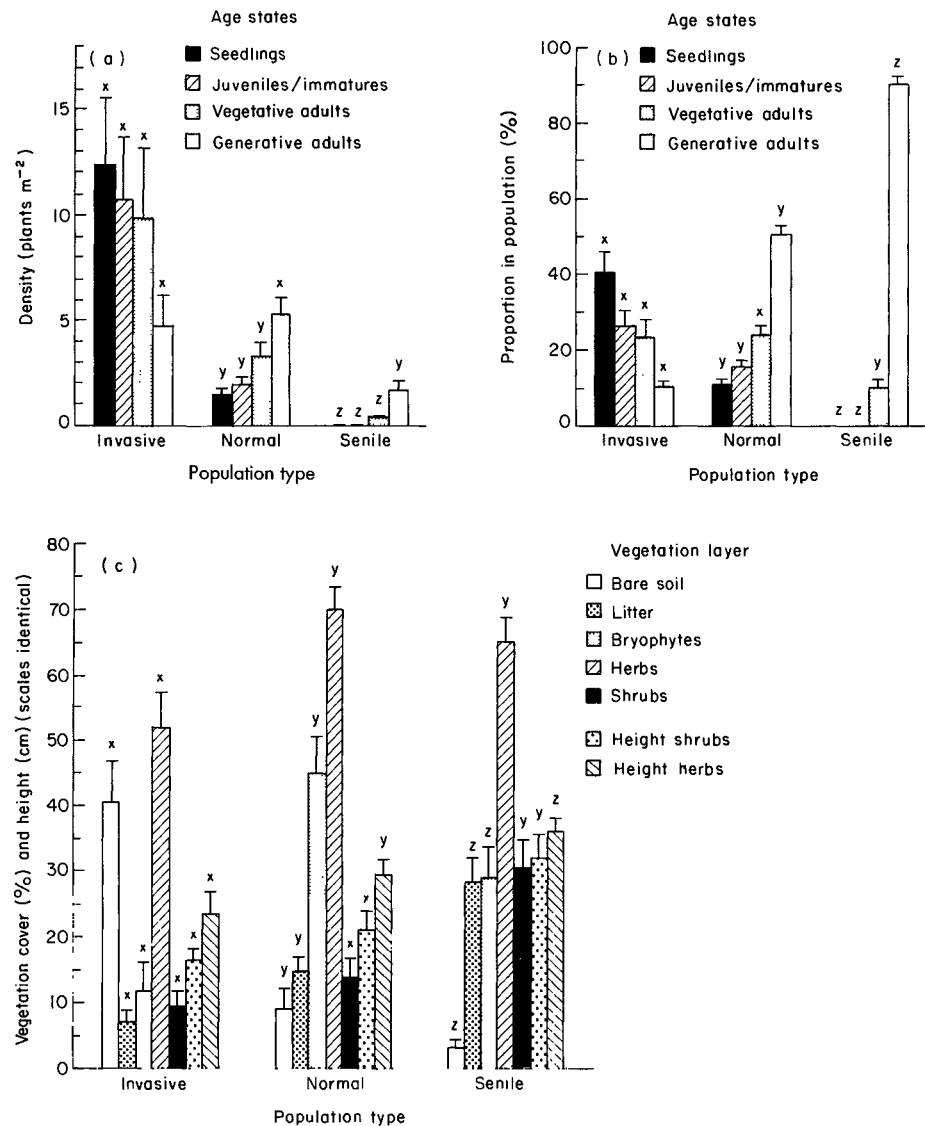


Fig. 3. (a) and (b) age-state structure and (c) mean values of vegetation structure variables in the three different population types of *Gentiana pneumonanthe*. The age-state structure is given as (a) mean plant density and (b) mean percentage in the population. Vertical bars indicate standard error of the mean. Age-state performances or structure variables marked with different letters differ significantly at $P \leq 0.05$.

Table 3. Analysis of variance statistics of the *K*-means clustering of the population age-state structures (percentage of different age states in the populations), with three pre-selected groups (see text). The mean values per variable per group are given in Fig. 3b

Variable	SS		SS		<i>F</i> -ratio	<i>P</i>
	between groups	df	within groups	df		
Seedlings (%)	27970.31	2	12287.33	130	147.96	≤0.0001
Juveniles (%)	13094.57	2	15493.01	130	54.94	≤0.0001
Vegetatives (%)	23256.82	2	14074.87	130	107.40	≤0.0001
Generatives (%)	77543.76	2	14995.10	130	336.13	≤0.0001

SS, sum of squares; df, degrees of freedom; *F*, variance ratio.

$P \leq 0.0005$ and $t[74 \text{ df}] = 3.215$, $P \leq 0.0005$, respectively), while the proportion of adult generative plants was significantly lower ($t[74 \text{ df}] = 9.286$, $P \leq 0.0005$). In the third population type (the 'regressive' or 'senile' type), seedlings and juveniles were totally absent from the population, and only adult plants were present. The proportion of adult generative

plants in this type was significantly higher than in the 'invasive' and 'normal' type ($t[77 \text{ df}] = 14.873$, $P \leq 0.0005$ and $t[109 \text{ df}] = 13.109$, $P \leq 0.0005$, respectively), while that of the vegetative adults was lower ($t[77 \text{ df}] = 3.155$, $P \leq 0.0005$ and $t[109 \text{ df}] = 4.485$, $P \leq 0.0005$).

There was also a significant decrease in the total

density of *Gentiana* individuals, from 37.6 plants m^{-2} in the 'invasive', 11.9 plants m^{-2} in the 'normal', to 2.0 plants m^{-2} in the 'regressive' type. All three types differed significantly from each other in total plant density ($3.898 \leq t \leq 6.097$, $P \leq 0.0005$).

Another descriptor of the different age-state structures is the ratio of the numbers of seedlings plus juveniles to the number of generative individuals ($K+J:G$ ratio). This ratio had a mean value of 23.9 (range 2–100) in the 'invasive' type, 0.672 (0.03–2) in the 'normal' type and 0 in the 'regressive' type. All means were significantly different ($4.661 \leq t \leq 8.914$, $P \leq 0.0005$).

CORRELATION BETWEEN AGE-STATE SPECTRA AND VEGETATION STRUCTURE

The mean values of the measured vegetation structure variables in the different population types are given in Fig. 3c. Except for the percentage cover and the height of the shrub layer, all variables were significantly different (t -test, $P \leq 0.05$) in each of the three population types of *Gentiana pneumonanthe*. It appears that the vegetation structure was rather open in the 'invasive' populations, as can be seen from the high percentage of bare soil surface and the low cover percentages of the litter, bryophyte, herb and shrub layers. The vegetation in the 'normal' populations had, in comparison with the 'invasive' populations, lower percentages of bare soil and a higher cover of the litter, bryophyte and herb layers, but the height and cover of the shrub layer was not significantly different (height: $t[74 \text{ df}] = 0.989$, $P > 0.10$; cover: $t[74 \text{ df}] = 0.987$, $P > 0.10$).

In all vegetation structure variables the 'invasive' population type differed significantly from the 'regressive', the latter having a much more closed structure (Fig. 3c). The same is true for the differences between the 'normal' and the 'regressive' type. The 'regressive' populations had a very low percentage of bare soil, and both the litter and the shrub layer had a high cover.

Multiple regression analysis shows that among all measured vegetation structure variables there were three that were most important for the variation in population structure and density of *Gentiana pneumonanthe*, namely, the percentage of bare soil and the cover of the bryophyte and litter layer (Table 4). The variation in total density of *G. pneumonanthe* individuals in the vegetation is significantly explained by the first two factors. Apparently, high densities may be found both in very open vegetation types and in types with a high cover of the bryophyte layer. The regression analysis on separate age states shows that these high total densities were mostly due to seedlings and juveniles in vegetation with a high percentage of bare soil, while it was mostly the adult generative plants that occurred at high density in vegetation with a high cover of bryophytes (Table 4).

Regression on the percentage of age states in a *Gentiana* population revealed that, in open vegetation types, populations occurred that have high percentages of seedlings and juveniles and a low percentage of adult generative plants (i.e. 'invasive' populations), while the reverse was true for the closed vegetation types with a low percentage of bare soil surface (i.e. 'regressive' populations). In contrast, the litter layer affects the percentage of seedlings and juveniles negatively, but is correlated positively with the proportion of adult generative plants (Table 4).

OCCURRENCE OF THE POPULATION TYPES IN THE OBSERVED PLANT COMMUNITIES

The occurrence of the three types of age-state spectra of *Gentiana* in the observed plant communities is given in Table 5. In general, there appeared to be no strict association between plant community and population type, in the sense that in certain communities only one type of age-state spectrum was found. While this certainly occurred in some instances, as in types H3.2 and H8 (only 'regressive' populations) and in type H7 (only 'invasive'), in the other communities more than one population type could be found, although often one seemed to prevail. In the types H4, H5b and H6, populations mostly belonged to the 'regressive', and rarely to the 'normal' type. The latter type was most frequent in the grassland communities G2.2, G3.1 and G3.2. The 'invasive' type was frequent only in community H1, where also 'normal' and rarely 'regressive' populations could be found. 'Invasive' populations also occurred occasionally in communities H2, H4, H5a, G1 and G2.1.

Discussion

In the different vegetation types that were distinguished in this study, populations of *Gentiana pneumonanthe* were observed in three clearly different age-state structures: (i) populations in which the seedling and juvenile age states were predominant; (ii) populations in which seedlings and juveniles still occurred in fairly high numbers, but where adult individuals predominated; and (iii) populations that consisted of vegetative and generative adults only. This extends our earlier view, in which we put forward only two different types of demographic behaviour of the marsh gentian, the one 'dynamic' and the other 'regressive' or 'senile' (Oostermeijer *et al.* 1992).

The different population types correspond well with the 'invasive', 'normal' and 'regressive' populations, respectively, as distinguished by Rabotnov (1969, 1985). From the results of the vegetation analysis, it could be demonstrated that the differences

Table 4. Multiple regression of all measured vegetation structure variables against (a) the density of age states in the vegetation and (b) the percentage of age states in the population. No statistics are given for the mature vegetative age state, since there was no significant regression model with any of the variables. Only the significant models, with the constituent factors and their statistics, are given here. Left column: R_y^2 = the squared multiple regression coefficient (proportion of variance explained by the model); coefficient \pm SE = regression coefficient with its standard error; std coeff = standardized regression coefficient; t = t -statistic, testing whether the standardized regression coefficient differs from zero; this is followed by its two-tailed probability P . All percentage data subjected to angular transformation prior to analysis

Variable	Coefficient	SE	std coeff	t	P	ANOVA [†]				
						Source	SS	df	MS	F
(a) Density of age states in the vegetation										
Total plant density (sdl + juv + veg + gen)										
$R_y^2 = 0.136$										
CONSTANT	-0.149	3.576	0.000	-0.042	0.967	REGRESSION	9655.2	2	4827.6	10.237***
BRYOPHYTES	10.134	3.874	0.235	2.616	0.010	RESIDUAL	61303.3	130	471.6	
BARE SOIL	27.976	6.283	0.401	4.452	0.000					
Density of seedlings										
$R_y^2 = 0.148$										
CONSTANT	0.623	0.731	0.000	0.853	0.395	REGRESSION	1087.1	1	1087.1	22.834***
BARE SOIL	8.644	1.809	0.385	4.778	0.000	RESIDUAL	6231.9	131	47.6	
Density of juveniles										
$R_y^2 = 0.125$										
CONSTANT	0.853	0.680	0.000	1.253	0.212	REGRESSION	770.2	1	770.2	18.672***
BARE SOIL	7.276	1.684	0.353	4.321	0.000	RESIDUAL	5404.0	131	41.3	
Density of generative adults										
$R_y^2 = 0.208$										
CONSTANT	0.147	0.754	0.000	0.195	0.846	REGRESSION	716.6	2	358.3	17.102***
BRYOPHYTES	4.765	0.816	0.503	5.836	0.000	RESIDUAL	2723.5	130	21.0	
BARE SOIL	3.737	1.324	0.243	2.821	0.006					
(b) Percentage of age states in the population										
Percentage of seedlings										
$R_y^2 = 0.230$										
CONSTANT	0.211	0.047	0.000	4.448	0.000	REGRESSION	2.820	2	1.410	19.459***
BARE SOIL	0.361	0.074	0.394	4.913	0.000	RESIDUAL	9.418	130	0.072	
LITTER	-0.187	0.081	-0.184	-2.299	0.023					
Percentage of juveniles										
$R_y^2 = 0.261$										
CONSTANT	0.237	0.039	0.000	6.052	0.000	REGRESSION	2.270	2	1.135	22.956***
BARE SOIL	0.311	0.061	0.403	5.122	0.000	RESIDUAL	6.428	130	0.049	
LITTER	-0.189	0.067	-0.221	-2.807	0.006					
Percentage of generative adults										
$R_y^2 = 0.230$										
CONSTANT	0.959	0.071	0.000	13.527	0.000	REGRESSION	7.079	2	3.539	21.814***
BARE SOIL	-0.561	0.110	-0.403	-5.099	0.000	RESIDUAL	21.094	130	0.162	
LITTER	0.315	0.122	0.205	2.586	0.011					

[†] SS, sum of squares; df, degrees of freedom; MS, mean square; F , variance ratio; ***denotes significance at $P = 0.0001$.

in the age-state spectra were strongly related to the vegetation structure. In particular, the percentage of bare soil in the vegetation had a very significant effect on the density and proportion of the different age states in the gentian population. This explains why populations of the first ('invasive') type were found mainly in plant communities of younger (secondary) successional stages in heathlands and (less frequently) in grass heaths where the vegetation structure was very open. The second, 'normal' type of population was found in heathlands only where there was some kind of regular disturbance, such as grazing or winter inundation (communities H3.1 and

H5a), or in older sod-cut sites where the 'invasive' populations had more or less stabilized (communities H1 and H2). On the borders of heathland pools some germination could take place on wet litter of *Molinia caerulea*, while the periodic inundations retarded the successional closure of the vegetation. In extensively grazed wet heathlands, bare patches in the vegetation created by trampling provided suitable germination sites.

In the grassland communities, the 'normal' population type was more frequent. In these cases, the annual mowing regime usually caused a medium-open vegetation structure in which germination and

Table 5. Frequency of occurrence (in %) of the three population structure types of *Gentiana pneumonanthe* in the different TWINSPLAN plant communities. *n* is the number of relevées per community

Plant community	Population type		
	'Invasive'	'Normal'	'Senile'
(a) Heathlands			
H1.1 (<i>n</i> = 14)	57.1	42.9	0.0
H1.2 (<i>n</i> = 8)	50.0	25.0	25.0
H2 (<i>n</i> = 10)	20.0	50.0	30.0
H3.1 (<i>n</i> = 12)	0.0	50.0	50.0
H3.2 (<i>n</i> = 5)	0.0	0.0	100.0
H4 (<i>n</i> = 9)	66.7	22.2	11.1
H5a (<i>n</i> = 7)	14.3	57.1	28.6
H5b (<i>n</i> = 7)	0.0	14.3	85.7
H6 (<i>n</i> = 10)	0.0	20.0	80.0
H7 (<i>n</i> = 4)	100.0	0.0	0.0
H8 (<i>n</i> = 4)	0.0	0.0	100.0
(b) Grasslands			
G1 (<i>n</i> = 14)	7.1	42.9	50.0
G2.1 (<i>n</i> = 5)	40.0	40.0	20.0
G2.2 (<i>n</i> = 9)	0.0	66.7	33.3
G3.1 (<i>n</i> = 7)	0.0	85.7	14.3
G3.2 (<i>n</i> = 5)	0.0	80.0	20.0
G4 (<i>n</i> = 4)	0.0	50.0	50.0

establishment remain possible for many years, but only in relatively few suitable microsites.

'Regressive' populations were frequently observed in both heathlands and grasslands, especially in vegetation types with a very closed structure. In heathlands, these were the communities dominated by dwarf shrubs, such as *Erica tetralix* or *Calluna vulgaris* (H3.2 and H5b), by bryophytes, such as *Sphagnum* spp. (H3.1) or by grasses, such as *Molinia caerulea*, *Agrostis capillaris* or *Deschampsia flexuosa* (communities H4 and H6), and also the *Myrica gale*-*Cephalozia bicuspidata* community (type H8).

Besides the presence of bare soil, the cover of the litter layer was also an important structure variable in the vegetation of heathlands, since it diminished the proportion of the younger individuals. It apparently did not influence the density of adult plants, so that the proportion of this age state increased in the population. The suppressive influence of the litter layer on the germination and survival of many plant species has been stressed before (Grime 1979; Bakker 1989).

In the grassland group, 'regressive' populations were found especially in early (July) mown hay meadows, in which acrocarpous mosses such as *Sphagnum* spp., *Leucobryum glaucum* or *Polytrichum longisetum* had very high cover percentages (belonging to community types G1, G3 and G4). In grasslands with an equally high bryophyte cover, but of pleurocarpous species, 'normal' age state spectra were mostly observed (community G2.2). In the Netherlands, dominance of *Sphagnum*, *Leucobryum* and *Polytrichum* in wet, acidic grasslands was most probably a result of atmospheric

acidification in combination with an early mowing regime (July) and absence (or a low level) of fertilization. In field and greenhouse experiments, *Sphagnum palustre*, *Polytrichum longisetum* and *Leucobryum glaucum* appeared to reduce emergence and survival of *Gentiana* seedlings dramatically (Oostermeijer, de Boer & van't Veer, unpublished data). A similar reduction of seedling emergence in patches with a high cover of (pleurocarpous) bryophytes has been shown for short-lived forbs in chalk grasslands (van Tooren 1988). The adult generative plants were apparently not adversely affected by the presence of a dense bryophyte layer. It may even have served as protection for the overwintering shoots and thus reduced winter mortality. This could partly explain the positive correlation of the density of adult plants with the cover of bryophytes (Table 4).

Because the mortality rate of adult individuals of *Gentiana pneumonanthe* is very low, and individual plants have been observed to reach a high age (more than 30 years), 'regressive' populations may persist in a closed vegetation for a long period (Oostermeijer *et al.* 1992). By means of computer modelling of the population dynamics in burned heathlands, it was estimated that without regular disturbance, populations of the marsh gentian would become extinct after 30–50 years (Chapman, Rose & Clarke 1989).

Gentiana pneumonanthe may be described as a 'demutational explorer' *sensu* Ramenskii (in Rabotnov 1985): a species that fills gaps after the vegetation has been set back to its initial successional state by some form of disturbance. Following the

classification of Grime (1979), the species may be characterized as a 'ruderal'. In heathlands, the species typically invades bare patches in the closed vegetation, created by sod-cutting, trampling, burning or grazing. In such patches, development towards a population with flowering individuals usually takes place very rapidly, before the vegetation starts to close again. There is no persistent seed bank, but normally large quantities of seeds are produced. On the other hand, the long persistence of vegetative and generative adults in closed vegetation, and the ability to remain underground in a dormant state (Oostermeijer *et al.* 1992) are more characteristic of 'patients' (Rabotnov 1985).

In its other main habitat type, unmanured hay meadows, *Gentiana pneumonanthe* appeared to have a somewhat different life strategy, corresponding more with that of a 'C-S-R-strategist' *sensu* Grime (1979). In this type of vegetation, invasion of a population was probably slow, with low numbers of seedlings emerging on the few, scattered microsites suitable for germination. Once established, an individual may have faced a relatively low mortality risk, taken a longer period before first time of flowering and reached a high age, as long as regular mowing prevented closure of the vegetation, and thus reduced competition for light. In this way, 'normal' populations were formed in which adult individuals predominated, but seedlings and juveniles were also present at low densities. Whether or not heathland and hay meadow populations of the marsh gentian show ecotypic differentiation in morphological and life-history traits is presently under study.

The close relationship of the population structure of the marsh gentian with the structure of the vegetation has important implications for conservation and management of the species. It has to be stressed that, at present, many of the populations belong to the 'regressive' or 'senile' type, because the vegetation structure has become too closed. In the few studies that are currently available, other rare perennial plant species have also been reported to occur in 'regressive' populations, such as *Arnica montana* (Schwabe 1990a; Fennema 1990), *Antennaria dioica* (Schwabe 1990b), *Peucedanum palustre* (Harvey & Meredith 1981), *Isotria medeoloides* (Mehrhoff 1989) and *Narthecium ossifragum* (Summerfield 1972). In most of these studies, an increase in the cover of the surrounding vegetation is mentioned as a possible cause for the decline.

In general, all management practices leading to a more open vegetation structure, but ensuring the presence of at least some seed-producing individuals, will be favourable for regeneration of the marsh gentian (cf. Oostermeijer *et al.* 1992). In heathlands, these management types may be either small-scale sod-cutting in the vicinity of the remaining flowering individuals, grazing by sheep or cattle (making sure that the flowers are not grazed), or mowing with

removal of the product every second year. In hay meadows, annual mowing and haymaking after seed dispersal is the most suitable management practice. In the case of acidic, unmanured hay meadows, special attention should be paid to the bryophyte layer, which may prevent germination and establishment of seedlings. In general, the development of a dense carpet of *Leucobryum glaucum* and *Sphagnum* spp. seems to be favoured by an early mowing regime (July), so this should be avoided if possible.

After a change in management strategy has been decided upon, the performance of the population can best be followed by monitoring the age state structure or, even better, by following the fate and performance of individual plants in the population (Hutchings 1991; Oostermeijer *et al.* 1992). Of course, in a single census of the age-state structure there is a risk of missing seedlings due to normal variation in germination from year to year. Juveniles (seedlings from the year before that have survived) may serve as a control for this type of variation. However, in most populations with suitable safe-sites for germination, seedlings are found nearly every year, albeit in strongly varying numbers.

After a change in management, a positive development may be considered to have taken place when shifts occur towards a population structure in which all age-states are present, as in the 'invasive' and 'normal' populations described here. At the same time, it is highly probable that such a shift indicates that the structure of the vegetation has become more suitable for the establishment of several other species as well. When the whole population is taken into account, rather than just the flowering individuals, as is mostly the case in monitoring of the species at present, *Gentiana pneumonanthe* may serve as an excellent indicator species for management and conservation of its habitats, namely wet heathlands and unmanured hay meadows.

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