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Management and population viability of the pasture plant *Gentianella campestris*: the role of interactions between habitat factors

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Population dynamics of *Gentianella campestris* was studied in a management experiment, involving three levels of grazing intensity and two levels of microsite moisture. The data were evaluated by using matrix population models in order to estimate probability of extinction under various combinations of grazing and moisture. The results showed that population viability of the species was strongly affected by the interaction effects of management and microsite. On dry sites extinction risk decreased with decreasing grazing intensity, while on mesic sites medium grazing intensity showed the lowest probability of extinction. In addition, some other factors are discussed, which may also interact with grazing intensity to affect population viability. These factors are: timing of grazing, population size, environmental stochasticity, geographic location, and flowering phenology. The results are discussed in terms of how they can be used to optimise grassland management based on knowledge of population dynamics of grassland plants.

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Unfertilised fodder-producing grasslands, wooded meadows and similar biotopes are often referred to as seminatural (e.g. Duffey 1974, Rackham 1986). Such biotopes have historically been the basis for agriculture in most temperate regions (Emanuelsson et al. 1985), but introduction of artificial fertilisers and other changes in agriculture have caused a rapid decline during the last 50–100 yr. Today only a fraction remains of the former extension of seminatural grasslands and the area is still decreasing. For example, in Sweden the area of mown seminatural grassland has decreased from ca 1.2 million ha in 1880 to ca 2 400 ha today (Anon. 1990, Bernes 1994). In addition to the decrease in area, the current management is often considerably different from traditional management regimes (e.g. García 1992 ch. 6, Bernes 1993, Beaufoy et al. 1995). One especially important change is the shift from traditional mowing with autumnal grazing, to grazing only (Aronsson and Matzon 1987, Ekstam et al. 1988, Beaufoy et al. 1995). The decline of seminatural grasslands is one of the major threats to European flora and fauna (Wolkinger and Plank 1981, Fuller 1987, Baldock and Long 1987, Fry 1991, Tucker 1991, Bernes 1994, Stanners and Bourdeau 1995, Beaufoy et al. 1995). In Sweden, ca 600 species of plants and animals are threatened by ceased or changed grassland management (Bernes 1994).

When the area of seminatural grasslands decreases, it becomes increasingly important to optimally manage the remaining grassland patches. The current management practice may not always be optimal for biodiversity, as indicated by the fact that many plant species have declined in grassland patches which are still managed (Eriksson 1996, Lennartsson and Svensson 1996). In order to understand and counteract such processes, we need to evaluate how population viability of grassland species is affected by, for example, type, timing and intensity of management. Such fine-scaled variation in management has so far attracted little attention compared to the study of ceased management and loss of habitats.

Management can thus be expected to be an important determinant of population viability of grassland plants and, correspondingly, population modelling to be an important tool for guiding management (e.g. Menges 1997). Management affects population viability in combination with other biotic and abiotic factors. For example, Menges and Dolan (1998) combined fire management with effects of genetic variation, geographic location, population size, and isolation in a viability analysis of *Silene regia*. Oostermeijer (1996) combined effects of management (sod cutting) with that of genetic variation for *Gentiana pneumonanthe*. Lennartsson (1997a) estimated risk of extinction of *Gentianella campestris* by combining different grazing/mowing regimes with environmental stochasticity and population size.

In Scandinavia, most of the remaining grasslands are presently grazed. Therefore, various aspects of grazing are among the most important management factors to include in population viability analyses of grassland plants. Several studies have related grazing to plant demography and fitness (e.g. Widén 1987, Oostermeijer 1992, Bastrenta and Belhassen 1992, Bastrenta et al. 1995), but very few studies have used such data for estimating, for example, extinction risk of populations (cf. Bullock et al. 1994). Especially the intensity of grazing has been much debated among biologists and managers. On one hand, an intense grazing might be needed to counteract detrimental accumulation of detritus (Knapp and Seastedt 1986, Grubb 1988), but on the other hand, such intense grazing may be difficult to combine with economically acceptable growth and productivity of the cattle (cf. Ekstam and Forshed 1996). Intense grazing may also reduce seed production of grassland plants (Oostermeijer 1992, Simán and Lennartsson 1998) and trampling effects may increase mortality (Lennartsson 1997a), thus counteracting the benefits of reduced litter accumulation.

In this paper, I estimate how population viability of the grassland plant *Gentianella campestris* (L.) Börner is affected by grazing, alone and in interaction with other factors. I present data from a 6-yr field experiment in which three levels of grazing intensity were combined with two levels of microsite moisture in simulations with a stochastic matrix model with variable frequency of summer drought. The model also includes population size as a parameter. With this study as a base, I discuss how grazing intensity may interact with other habitat factors, such as timing of grazing, geographic location, and flowering phenology, to influence population viability of *G. campestris*.

Methods

Study species

Gentianella campestris ssp. *campestris* is a European biennial herb (Pritchard and Tutin 1972, Hultén and Fries 1986). It is spring germinating, forms a rosette the first summer, and overwinters as a taproot and a bud (Lennartsson 1997b). The plant flowers the second summer, either in early July (aestival type, Wettstein 1895) or in August (autumnal type). The size at flowering is normally 5–20 cm high with 5–15 lilac flowers (Fig. 1). The life cycle is strictly biennial as all plants flower their second summer and die after flowering, and the species lack mechanisms of vegetative reproduction (Fig. 2). The adult plant has a main stem with a top meristem and 6–12 nodes, each of which with two opposite, decussate leaves and up to six flowers. Some nodes produce branches with secondary

Fig. 1. *Gentianella campestris* ssp. *campestris* (L.) Börner, field gentian. Autumnal type from the Björnvad population.

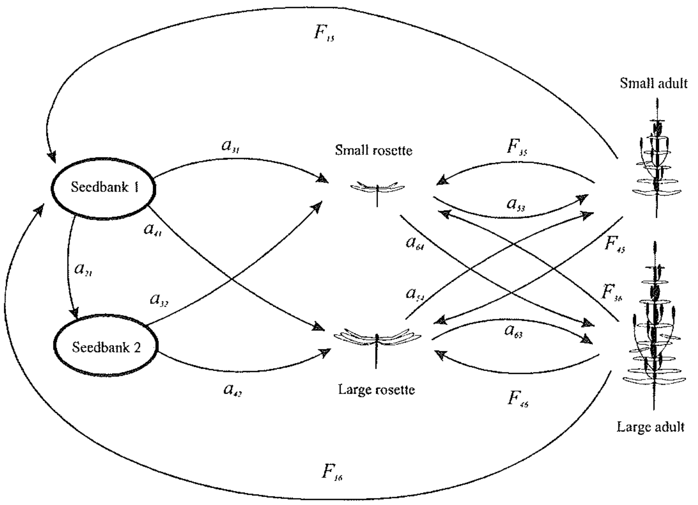

Fig. 2. Life cycle graph and basic projection matrix of *Gentianella campestris* ssp. *campestris* (L.) Börner (Gentianaceae). F_{ij} indicate fecundity transitions, a_{ij} indicate probability of transitions from stage *j* to stage *i*. Size of rosettes is defined by the number of leaves × rosette diameter index, where rosettes with an index > 15 are considered "large rosettes". Size of adult plants is defined by the number of nodes on the main stem and on the branches. Plants with > 10 nodes are assigned "large adults".

	1 Seedbank 1	2 Seedbank 2	3 Small rosette	4 Large rosette	5 Small adult	6 Large adult
1 Seedbank 1	-	-	-	-	F_{15}	F_{16}
2 Seedbank 2	a_{21}	-	-	-	-	-
3 Small rosette	a_{31}	a_{32}	-	-	F_{35}	F_{36}
4 Large rosette	a_{41}	a_{42}	-	-	F_{45}	F_{46}
5 Small adult	-	-	a_{53}	a_{54}	-	-
6 Large adult	-	-	a_{63}	a_{64}	-	-

nodes. The plants are frequently visited by bumblebees (Müller 1881, Lennartsson unpubl.), which serve as the only known pollinators, but the species is highly self-compatible and obtains a high seed set without insect pollination (Lennartsson 1997a). The seed bank is short-lived (Milberg 1994).

Gentianella campestris contains bitter glycoside substances (e.g., Inouye et al. 1967, Hostettmann-Kaldas and Jacot-Guillarmod 1978) which give some protection against herbivory, but on pasture localities 15–80% of the plants are grazed, depending on grazing agent, grazing intensity and vegetation structure. Grazing or other damage can release vigorous regrowth of new branches and flowers (Zopfi 1991, Lennartsson et al. 1998).

Gentianella campestris occurs almost exclusively in managed seminatural grasslands. Very few natural habitats are known, for example river banks and mountain scree slopes (Nilsson et al. 1999). The species has undergone a rapid decline during the last 50 yr, mainly due to ceased management of seminatural grasslands. In a studied region in central Sweden, the species has disappeared from ca 90% of its localities during the last 50 yr (Lennartsson and Svensson 1996). It is red-listed as "care demanding" in Sweden (Aronsson et al. 1995) as well as in several other European countries (e.g., Ingelög et al. 1993). *Gentianella campestris* is associated with grasslands with high biodiversity and conservation value (Anon. 1987, Lennartsson 1997a), and it may therefore serve as an appropriate indicator species for evaluating management regimes in species rich grasslands.

Experimental design and data analysis

The grazing experiment was performed in a horse pasture, Björnvad in the Province of Södermanland in central Sweden (59°20′21″N, 16°51′31″E, see Fig. 3). The site is an open, species-rich grassland pasture of ca 15 ha, dominated by *Avenula pratensis* – *Festuca rubra* meadow and herb-rich *Agrostis capillaris* meadow (Rydberg and Vik 1992, Påhlsson 1994). The topography of the grassland creates a mosaic of dry, sandy sites and mesic sites with a higher content of clay in the soil. Average population size of *Gentianella campestris* (autumnal type) is ca 5 000 adult plants, largely fluctuating between years.

The grazing intensity by horses varied within the site. In order to create three grazing intensities that were not varying between years, grazing was controlled by fencing.

Fig. 3. Part of the pasture at Björnevad in wich the study took place, just before onset of grazing in June.

Three adjacent, ca 50 × 15 m areas were selected, located in a row with the following sequence: intense grazing – weak – medium grazing. The sequence was thus nonlinear with respect to grazing intensity, which contributes to separate effects of grazing from effects of location. Grazing intensity was estimated every 10 d by measuring average vegetation height in each 2 × 2 m plot in all three treatment areas (Ekstam and Forshed 1996). Grazing was considered "intense" if average vegetation height was reduced by at least 75% during June–early September. The corresponding figures for "medium" and "weak" grazing are 40–50% reduction and 20–30% reduction, respectively. Plots which showed a varying grazing intensity during the study were omitted from the analyses. The number of omitted plots per treatment area was < 10 (< 5%). All plots with a certain grazing intensity were situated within the same treatment area.

Gentianella campestris occurred scattered over all three treatment areas. The mortality and growth of all individual adults and rosettes was followed from 1990 (start of experiment) through 1995, together with seed production of adults, herbivory and trampling. The plants were assigned to two size classes. For adult plants, these classes were defined by the number of stem and branch nodes (≥10 nodes: large adults; <10 nodes: small). For rosettes, the size classes were defined by a size index given by the number of leaves times the rosette diameter in cm (index >15: large rosettes; <15: small, see Lennartsson 1997a for a detailed description of data sampling). Germination of last year's and older seeds was estimated from batches of seeds sown in pots in a common garden. Approximately 200 seeds from ten plants per treatment were sown each year and the germination from each batch was monitored annually throughout the study. Seedling emergence in the field was counted each year in random plots. From these data, combined with data by Milberg (1994) on seed mortality, it was possible to estimate the longevity of the seed bank (Lennartsson 1997a). Correspondingly, the recruitment of large and small rosettes from large and small adults and from the seed bank could be estimated, assuming that the origin of seeds did not affect the fate of the seedlings (cf. Lennartsson et al. 1997).

The life cycle graph for *Gentianella campestris* was translated into a projection matrix with i rows and j columns in which the matrix elements a_{ij} and F_{ij} define transitions from stage j to stage i in one-year time intervals (Fig. 2). a indicates yearly transition probabilities (ranging between 0–1), F indicates fecundity (may be >1). Transition matrices are treated in greater detail by Caswell (1989) and Akçakaya (2000). Analysis of a projection matrix at asymp-

Table 1. Finite rate of increase, λ, for *Gentianella campestris* in three grazing intensities over two types of microsites, mesic and dry, respectively.

	Intense grazing		Medium grazing		Weak grazing	
Matrix	Mesic	Dry	Mesic	Dry	Mesic	Dry
91–92	0.89	0.57	1.3	0.81	0.91	0.95
92–93	0.85	0.58	0.97	0.81	0.85	0.93
93–94	0.41	0.17	0.44	0.21	0.25	0.28
94–95	0.8	0.41	0.77	0.54	0.61	0.51
Average	0.74	0.44	0.87	0.59	0.66	0.67

totic population growth gives the population's finite growth rate, $\lambda = N_{t+1}/N_t$, where N is the population size. Analysis of a population matrix also shows how population growth rate changes due to a change in a certain matrix element a_{ij}. To compensate for differences in absolute values of a_{ij}, elasticity was used, defined as the proportional change in λ caused by a proportional change in a_{ij} (de Kroon et al. 1986). Elasticities sum to one and reflect the relative importance of matrix elements for population growth rate (Silvertown et al. 1996).

The probability of extinction was estimated by combining four autumn – autumn transition matrices per treatment in a stochastic model, where the probability of summer drought (probability of the 1993–1994 matrix, Ultuna Climate and Bioclimate Station unpubl.) was varied (cf. Grime and Curtis 1976, Hopkins 1978, Bengtsson 1993). I ran 1 000 replicates per simulation over 200 yr, using the computer programs KARISMAT, developed by Kari Lehtilä, and POPPROJ2, by Menges (1992). The proportion of simulations resulting in a population size equal to zero after a certain time period gave the extinction probability for that time period (Wilcox and Murphy 1985, Quinn and Hastings 1987, Menges 1997).

When discussing how grazing intensity may interact with other factors than microsite moisture, I refer to data from two earlier clipping experiments with *G. campestris*. One of the experiments investigated how compensatory growth following clipping damage varied with the timing of damage (Lennartsson et al. 1998). The second experiment investigated how compensatory growth varied between early flowering, intermediate and late flowering seasonal types of the species (Lennartsson et al. 1997). In both experiments plants were damaged by removing about half of the biomass. Seed production was compared with that of unclipped control plants of the same initial size as the clipped ones.

Results

Grazing intensity affected λ for the studied population of *Gentianella campestris* (Table 1), that in turn influenced the probability of extinction (Fig. 4). The most unfavourable grazing pressure yielded an extinction risk that was up to six times higher than the optimal one, other factors being constant. However, the relationship between probability of extinction and grazing intensity differed considerably between dry and mesic sites, thus indicating an interaction effect of grazing intensity and microsite moisture (Fig. 4). At mesic sites, an intermediate grazing pressure yielded the lowest extinction risk, whereas at dry sites extinction risk decreased with decreasing grazing intensity. Extinction risk was always lower at the mesic sites than at the dry sites, the difference being largest for the medium grazing intensity.

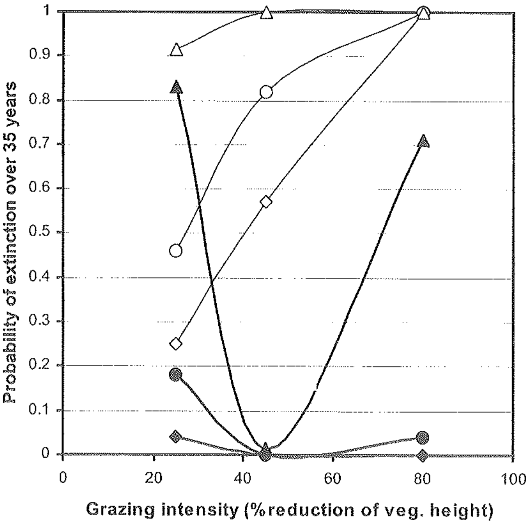

Fig. 4. Probability of extinction of *Gentianella campestris* as a function of grazing intensity. Thick lines and filled symbols indicate mesic site, thin lines and unfilled symbols indicate dry site. Lines with triangles indicate a probability of summer drought of 0.25; circles a probability of 0.1; diamonds a probability of 0.05. Initial population size, n_0 = 1 000, where the respective numbers of large and small rosettes and adults = $n_0/4$; the number of seeds in seedbank 1 = $n_0 \times 500$; and in seedbank 2 = $n_0 \times 225$.

The transition values for rosettes and adult plants growing large (transition elements a_{63-64} and F_{45-46}, respectively) were considerably higher for mesic than for dry sites (Fig. 5). The transition values $a_{31-32, 41-42}$ consequently show that a seed from the seed bank was more likely to develop a large rosette at mesic sites, and a small rosette at dry sites. These differences in size between "dry" and "mesic" plants are also reflected by the fact that production of seeds to the seed bank (F_{15-16}) was higher at mesic than at dry sites (Fig. 5).

The probability that a seed developed a large rosette (e.g. a_{41}) increased with increasing grazing intensity at mesic sites. At dry sites, growth of rosettes was on the contrary favoured by weak grazing (Fig. 5). In general, large adult plants were more often formed by large rosettes (a_{64}) than by small rosettes (a_{63}). The probability that a large rosette developed a large adult increased with decreasing grazing intensity at both mesic and dry sites. The probability that a small rosette developed a large adult plant (a_{63}) showed a peak in medium grazing intensity at mesic sites, whereas at dry sites, the probability increased with decreasing grazing pressure.

The probability of summer drought in general increased the probability of extinction in all treatments (Fig. 4). At mesic sites, an interaction effect of environmental stochasticity and grazing intensity was also shown, because summer drought increased extinction risk more in intense grazing than in weak grazing. For example, with a probability of summer drought of 0.1, weak grazing yielded a 4.5 times higher extinction risk than intense grazing. With a drought probability of 0.25, the corresponding value was 1.2 times (Fig. 4).

The risk of extinction varied with initial population size in interaction with grazing intensity and microsite moisture (Fig. 6). This interaction is reflected both by the position and the shape of the curve extinction risk as a function of population size.

Intense mesic	1	2	3	4	5	6
1					210.0 (37.40)	366.3 (56 70)
2	0.681 (0.032)					
3	0.67×10^{-4} (0.12×10^{-4})	0.10×10^{-4} (0.02×10^{-4})			0.092 (0.021)	0.160 (0.036)
4	2.70×10^{-4} (0.96×10^{-4})	0.42×10^{-4} (0.14×10^{-4})			0.290 (0.098)	0.550 (0.195)
5			0.592 (0.155)	0.286 (0.106)		
6			0.086 (0.051)	0.452 (0.200)		

Intense dry	1	2	3	4	5	6
1					116.7 (27 59)	181.1 (60.48)
2	0.690 (0.037)					
3	2.28×10^{-4} (0.84×10^{-4})	0.38×10^{-4} (0.15×10^{-4})			0.138 (0.026)	0.181 (0.070)
4	0.65×10^{-4} (0.38×10^{-4})	0.09×10^{-4} (0.05×10^{-4})			0.053 (0.031)	0.085 (0.050)
5			0.711 (0.181)	0.246 (0.088)		
6			0.000 (0 000)	0.175 (0.118)		

Medium mesic	1	2	3	4	5	6
1					382.9 (73.04)	626.0 (123.9)
2	0.701 (0.024)					
3	1.11×10^{-4} (0.37×10^{-4})	0.16×10^{-4} (0.06×10^{-4})			0.205 (0 048)	0.323 (0 062)
4	1.96×10^{-4} (0.79×10^{-4})	0.26×10^{-4} ($0 10\times10^{-4}$)			0.379 (0.182)	0.645 (0.293)
5			0.521 (0.165)	0.139 (0.053)		
6			0.405 (0.173)	0.545 (0.199)		

Medium dry	1	2	3	4	5	6
1					258.4 (66.07)	292.2 (98.19)
2	0.680 (0.031)					
3	2.43×10^{-4} (0.89×10^{-4})	0.38×10^{-4} (0.16×10^{-4})			0.293 (0.080)	0.284 (0.133)
4	0.59×10^{-4} (0.35×10^{-4})	0.08×10^{-4} (0.05×10^{-4})			0.108 (0.064)	0.129 (0 077)
5			0.702 (0.185)	0.314 (0.183)		
6			0.020 (0 020)	0.274 (0.158)		

Weak mesic	1	2	3	4	5	6
1					392.8 (68.94)	500.2 (72.92)
2	0.671 (0.039)					
3	1.10×10^{-4} (0.29×10^{-4})	0.16×10^{-4} (0.05×10^{-4})			0.234 (0 068)	0.300 (0.081)
4	0.84×10^{-4} (0.30×10^{-4})	0.13×10^{-4} (0.04×10^{-4})			0.205 (0.084)	0.258 (0.100)
5			0.603 (0.073)	0.125 (0.079)		
6			0.064 (0.064)	0.698 (0.189)		

Weak dry	1	2	3	4	5	6
1					299.6 (71 56)	342.9 (114.4)
2	0.675 (0.033)					
3	2.03×10^{-4} (0.59×10^{-4})	0.31×10^{-4} (0.10×10^{-4})			0.328 (0.091)	0.329 (0.146)
4	0.75×10^{-4} (0.44×10^{-4})	0.10×10^{-4} (0.06×10^{-4})			0.169 (0 099)	0.200 (0.118)
5			0.695 (0.123)	0.252 (0.146)		
6			0.070 (0.042	0.304 (0.176)		

Fig. 5. Average transition matrices for each treatment. Intense, medium and weak refers to three levels of grazing intensity, mesic and dry to two levels of microsite moisture. Mean transition values and standard errors (in brackets) of four matrices.

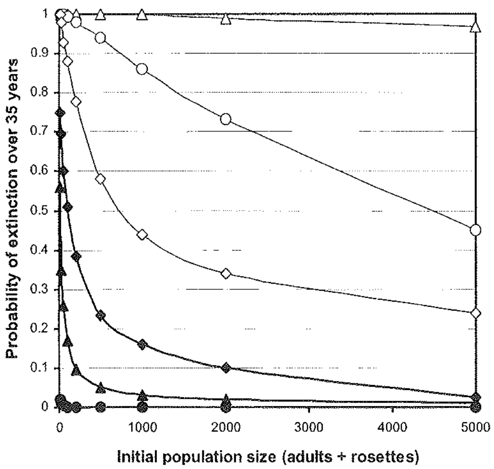

Fig. 6. Probability of extinction of *Gentianella campestris* as a function of intial population size. Thick lines and filled symbols indicate mesic site, thin lines and unfilled symbols indicate dry site. Triangles indicate intense grazing, circles medium grazing, and diamonds indicate weak grazing. Number of adults, rosettes and seeds in seedbank 1 and seedbank 2 are related to initial population size as in Fig. 4.

Discussion

This study shows that grazing is an important determinant of population viability of the grassland plant *Gentianella campestris*. It also emphasises that the effects of grazing intensity need to be evaluated together with other interacting factors. Thus, to optimise population viability by manipulating the grazing, we need some estimates on how grazing influences the population in interaction with other relevant factors. Below, I discuss some properties of environment and population, which can be assumed to interact with grazing to yield differences in population viability of *G. campestris*.

Grazing intensity in interaction with microsite and population size

Implications for management

The optimal grazing intensity for *G. campestris* differed considerably between sites with different soil moisture. This result highlights two important implications for conservation of the species: 1) if possible, dry parts of a site should be managed with a lower grazing pressure than mesic parts; 2) a viability analysis of a certain population of *G. campestris* needs to estimate the extinction risk for "dry" and "mesic" subpopulations separately, preferably by combining grazing intensity with population size (Fig. 6).

The λ values obtained by analysis of the population matrices (Table 1) were congruent with the observed number of plants at the study site. During the first three years of the study, all subpopulations except for the intense/dry treatment were stable or increased (medium/mesic), whereas the low λ values during the last years were shown by a drastic decrease in population size in all treatments.

Even with an optimal grazing intensity, the probability of extinction was much higher for subpopulations on drier soils, and even very large populations would face a high risk of extinction, if no mesic sites are available (Fig. 6). A medium grazed, "dry" population with an initial size of 100 000 plants would still have a probability of extinction of 0.75 over 50 yr, which implies that a minimum viable population size (MVP, cf. Menges 1997) is hardly possible to find in dry habitats. In most populations of *G. campestris*, a certain proportion of the plants grow at dry microsites, in spite of reduced subpopulation viability in such habitats. Judging from the λ values, one would expect a source-sink relationship between mesic and dry patches within a population. This relationship may however be reversed during occasional periods with very weak or no grazing (cf. Fig. 4 with curves extrapolated to, for example, 10% grazing intensity). Also in very rainy years, population viability can be expected to be high at dry microsites.

It can be assumed that if grazing intensity varies between years (which is often the case), population viability of *G. campestris* may be highest in patchy grasslands, because a temporal variation in grazing seems to be buffered by a spatial variation in microsite moisture. This is supported by a field survey of 65 populations of *G. campestris* and the closely related *G. amarella* (L.) Börner in the Province of Uppland (Lennartsson and Svensson 1996). This survey showed that under managed conditions, populations were significantly larger at mesic than at dry sites, whereas unmanaged populations were less reduced at dry than at mesic sites. This may thus be explained by slightly higher λ at dry sites than at mesic, when grazing intensity is low (Table 1).

The reduced population viability in some combinations of grazing intensity and microsite is also reflected by the shape of the curves in Fig. 6, especially regarding threshold values for population size. The curve for intense grazing at mesic sites shows that a small change in population size will cause a large change in extinction risk, if population size is smaller than ca 250–500 plants (Fig. 6). The corresponding threshold size for the weak/mesic curve is 500–1 000 plants, and for the weak/dry curve 1 000–2 000 plants. For the medium/dry treatment there is a more or less linear relationship between population size and extinction probability up to 5 000 plants.

Grazing intensity in interaction with timing of grazing and environmental stochasticity

One important aspect of the life cycle of pasture plants is mechanisms for increasing the tolerance to grazing (Belsky et al. 1993, Rosentahl and Kotanen 1994, Järemo et al. 1999). In *G. campestris*, such tolerance is accomplished by high capacity for compensatory growth of branches, flowers and fruits after grazing (Lennartsson et al. 1997). Under certain conditions the plants may even overcompensate for damage, that is, damaged plants produce more seeds than undamaged ones of the same initial size. In the transition and elasticity matrices, overcompensation and compensatory growth in general is indicated by high values of the matrix element a_{63} (and to some extent a_{64}), i.e., development of large adults by small rosettes (Fig. 2). a_{63} has a high elasticity value in the treatment "medium grazing/mesic site" (Fig. 5), but lower values in all other matrices. This indicates that compensation is influenced by an interaction effect of grazing intensity and microsite moisture. Furthermore, Lennartsson et al. (1998) showed that vigorous compensatory growth could be induced by damage during a limited time period only, thus an effect of the timing of grazing. Full compensation or overcompensation was induced only if damage occurred during ca 1–25 July. Under circumstances which allow high compensation (essentially the medium/mesic treatment), this tolerance mechanism can be assumed to be an important component of the population dynamics of *G. campestris*. This implies that the same grazing intensity can be expected to yield different probabilities of extinction, depending on the timing of grazing, thus indicating an interaction effect of intensity and timing of grazing.

Implications for management

Such an interaction effect has important implications for management. In *Gentianella* populations with a significant proportion of "mesic" plants, an intermediate grazing intensity should be the objective. In sufficiently large grasslands, medium grazing intensity can be attained by using relatively few grazers during a longer time period. In small grasslands, however, even a low number of grazers would give a high grazing intensity, if grazing is extended over the whole season. In small grasslands, therefore, a shorter grazing period is needed to create an optimal grazing intensity, and the timing of that grazing period should as often as possible fall within ca 1–25 July.

Compensatory growth also varied between years, as indicated by between-year differences in the elasticity matrices (Fig. 7). During the dry summer 1994 elasticity for the matrix element a_{63} was zero in the treatment medium grazing/mesic site, which indicates that tolerance to grazing was decreased by summer drought. The matrix elements related to compensatory growth and growth of large adult plants (a_{63} and a_{64}), are in general among the most variable elements between years (Fig. 7). Between-year variation in compensation is therefore an important explanation for the interaction effect of grazing intensity and environmental stochasticity on population viability of *G. campestris*.

Grazing intensity, geographic location and flowering phenology

One prerequisite for compensatory growth is that the grazed plants have enough time for regrowth before the autumn frost. Lennartsson et al. (1998) hypothesised,

Med.mes. 91-92	1	2	3	4	5	6
1					0.013	0.056
2	0.005					
3	0.020	0.001			0.023	0.097
4	0.045	0.003			0.052	0.222
5			0.029	0.059		
6			0.111	0.263		

Med.mes. 92-93	1	2	3	4	5	6
1					0.010	0.071
2	0.007					
3	0.022	0.002			0.013	0.097
4	0.052	0.005			0.032	0.233
5			0.025	0.030		
6			0.110	0.292		

Med.mes 93-94	1	2	3	4	5	6
1					0.123	0.001
2	0.021					
3	0.100	0.020			0.292	0.002
4	0.003	0.001			0.010	0.000
5			0.414	0.011		
6			0.000	0.003		

Med.mes. 94-95	1	2	3	4	5	6
1					0.019	0.063
2	0.009					
3	0.029	0.004			0.035	0.115
4	0.043	0.006			0.052	0.171
5			0.106	0.000		
6			0.077	0.271		

Fig. 7. Four elasticity matrices for the treatment medium grazing/mesic site, showing between-year variation. Note especially the variation in the matrix element a_{63} (cf. Fig. 2).

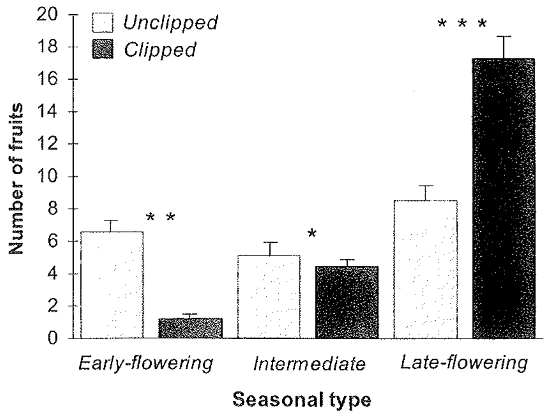

Fig. 8. Average number of mature fruits produced by clipped and unclipped *Gentianella campestris* plants in three seasonal (early-flowering, intermediate and late-flowering) subgroups from the locality Hyttan (Lennartsson et al. 1997). Clipping experiments were performed in cultivation on plants of equal initial sizes. One standard error is indicated, and t-test statistics for paired comparisons of experimental plants from the same mother plants (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). The number of pairs in each subgroup is 21, 18 and 21, respectively.

based on a field experiment, that compensation may be weaker or more occasional at high altitudes and latitudes. This would imply that the plants' tolerance to grazing varies over the species' range of distribution, and thus an interaction effect of grazing intensity and geographic location on population viability of *G. campestris*.

As mentioned earlier, *G. campestris* exhibits a wide intraspecific variation, especially regarding flowering phenology (Lennartsson 1997b). One important difference between early and late flowering plants is that early plants show much lower tolerance to damage (Fig. 8; Lennartsson et al. 1997). This indicates an interaction effect of grazing intensity and flowering phenology, which can be assumed to decrease viability of early flowering populations under intense grazing.

Implications for management

A lower grazing pressure can be recommended for early-flowering populations of *G. campestris*. An even better alternative would be a late onset of grazing, after completed seed maturation of the plants in mid-July.

Linking population data and PVA with management and conservation

Estimation of the relative importance of single factors, and of the interactions between them, is a key task in population viability analysis and in recovery planning for threatened species (cf. Schemske et al. 1994). The viability of a plant population is affected by a number of biotic and abiotic factors (see references in Silvertown and Franco [1993], Silvertown et al. [1996] and Menges [1997]), and *G. campestris* is no exception. In this paper I have discussed seven factors, all being important determinants of the population viability of *G. campestris*: grazing intensity, microsite, environmental stochasticity, population size, timing of grazing, geographic location, and flowering phenology. Of these factors, only intensity and timing of grazing are possible to directly influence by conservation efforts. Hence, even if other factors may be equally or more important for population viability of a grassland species, management can be regarded as the tool with which we may manipulate the effect of other factors.

If we have or intend to make a PVA for a grassland species and want to translate this knowledge to management recommendations, I suggest the following method: first, evaluate known relevant factors in terms of how they affect population viability of the target species in interaction with management. Second, design theoretical management regimes which optimise population viability for each interacting factor separately. Third, design or choose one or a set of management regime(s) which make the best compromise. In many cases, as for *G. campestris*, different types of management, varying between years, would probably be the best alternative.

Even without a PVA and population data, we usually have some knowledge about how grassland species react to management. When designing management recommendations on such a basis, I recommend that knowledge from as many different conditions as possible are used (different years, microsite, geographic locations etc.). This study of *G. campestris* clearly shows that management recommendations or recovery plans may be of little use if they are based on data from only a narrow range of biotic and abiotic conditions.

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