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Long-term Population Development and Spatial Pattern of *Carex curvula* Subspecies

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Abstract

A study of shoot populations of *Carex curvula* subspecies (*Carex curvula* ssp. *rosae* and *C. curvula* ssp. *curvula*) compared predictions from a 3-year observation period with renewed observations after 10 years. The study sites were located in the Dolomites (Mount Latemar), Italy, at 2390–2580 m a.s.l. The first observation period (1990–1992) produced findings on shoot numbers in different plots at five sites. These shoot numbers allowed the finite rates of population increase λ (characterizing the dynamic state of the populations) to be calculated. The values of λ varied modestly within and among populations. The long-term rates of population increase remained close to the equilibrium value of 1.0. The spatial pattern was calculated by means of the patchiness index and patch occupancy. The smaller the plot population, the higher the patchiness and the lower the proportion of occupied patches. To some extent, patchiness can serve as a measure of a population's dynamic state. A correlation between the structural measures (patchiness, patch occupancy) and the rate of population increase λ showed that strongly aggregated populations were small and also decreasing in size. The extinction risks for the next 50 years were found to be very low for populations on the pioneer grassland stand whereas most other populations will decrease and probably reach critical thresholds.

Introduction

Long-term studies of plant populations have been mainly concerned with annuals, biennials (Symonides, 1987; Watkinson, 1990), and perennials of lowland ecosystems (Inghe and Tamm, 1985; Falinska, 1991; Willems and Bik, 1991; Bengtsson, 1993, 2000; Svensson et al., 1993; Woodward, 1997; Menges and Dolan, 1998). Populations of alpine or arctic species have rarely been studied for longer periods (Callaghan, 1976; Carlsson and Callaghan, 1991; Diemer, 1992; Forbis and Doak, 2004). For long-lived species, conclusions based on only 1 or 2 years of study may be misleading, and the importance of long-term demographic studies has frequently been stressed. Long-term observations enable critical stages of population development and environmental factors causing population changes to be detected (Bengtsson, 2000). Population development and/or extinction can then be predicted.

In arctic and alpine environments, recruitment by sexual reproduction is less frequent compared to other ecosystems (review in Carlsson and Callaghan, 1990), and the dominant clonal graminoid species rely mainly on vegetative propagation. However, flowering itself may influence the population dynamics of shoots if they are monocarpic. Additionally, vegetative shoots may die due to environmental stress.

The dynamic state of a population may change in the long run due to changes in environmental factors, e.g., changing competitive pressure from other species or intraspecific density effects. Thus, a population initially growing vigorously may eventually reach a stationary state or even become at increasing risk of local extinction. This risk will be enhanced by the effect of environmental and demographic stochasticities.

In the alpine zone, there is a lack of information on population dynamics, even for dominant species. Therefore, from 1990 to 1992, the shoot numbers of long-lived clonal sedges—*Carex curvula* ssp. *rosae* and *Carex curvula* ssp. *curvula*—were recorded during the

growing seasons in permanent plots in order to observe population development and to understand the species' dynamics in different alpine grassland types (Erschbamer, 1994). In 2002, the sites were revisited and the numbers of shoots were recorded again.

The objective of the present study was to compare the data from 1990–1992 with the return visit to the sites in 2002. Based on the first observation period, a model for shoot population growth was developed and parameterized. The main model parameter was the annual rate of shoot population increase, comprising the annual shoot birth and death rates. This model was used to predict development until 2002. Parameterization of the model on the basis of the complete observation interval 1990–2002 was used to examine extinction risks for further periods. Analysis of temporal dynamics was accompanied by an evaluation of the spatial population structure. The main questions to be answered were: (1) Is there a correlation between the size, dynamic state, and spatial structure of the populations? (2) What predictions on population development for a 10-year period result from the short-term observations of 1990–1992? (3) What conclusions can be drawn about changes in site conditions and population state from comparing predictions with empirical verification? (4) What are the extinction risks of the populations at different sites?

Study Area, Material, and Methods

STUDY AREA

The research areas are located in the Latemar mountain range (western Dolomites, South Tyrol, Italy; 46°22'N, 11°32'E to 46°21'N, 11°35'E) at 2390 m to 2580 m a.s.l. The geological substrate consists of non-dolomitized limestone (= Latemar limestone; Vardabasso, 1930; Leonardi, 1967) intermingled with volcanic rocks (augite porphyry material). The specific grasslands of *Carex curvula* ssp. *rosae* (*Carex rosae*, nomenclature of species: Adler et al., 1994) were described as Elyno-Caricetum rosae (Erschbamer, 1992). Four

TABLE 1

Description of the five observation sites (A–E) at Mount Latemar (Dolomites, Italy).

Sites	A 1–5 Pioneer	B 1–5 Pisa 1	C 1–5 Oberholz	D 1–4 Pisa 2	E 1–5 Valsorda
Altitude (m)	2420	2580	2390	2490	2480
Exposure	N–NE	SSE	SW–WSW	SE	ENE
Inclination (°)	20–35	30–40	40–45	25–30	2–12
Cover (%)	70–98	90–93	85–97	95–100	75–90
<i>Carex rosae</i>	Dominant	Frequent	Scarce	Very scarce	—
<i>Carex curvula</i>	—	—	—	—	Dominant

different types of this community were classified (pioneer community, typical subassociation, subassociation with *Festuca norica*, and a subassociation with *Festuca norica-Arnica montana* type). In 1990, permanent plots of 625 cm² were established in these four different communities (5 plots per site, Table 1; Erschbamer, 1994). The plots were selected subjectively according to the presence of a representative tussock system of *Carex rosae* for the specific grassland type. Site A (“Pioneer”) is a relatively small initial grassland patch between rocks and screes, characterized by a pioneer vegetation of *Carex rosae* (Erschbamer, 1990, 1992). At site B (“Pisa 1”), *Carex rosae* is co-dominant with *Kobresia myosuroides*, *Sesleria albicans*, and *Carex rupestris* (typical subassociation). At site C (“Oberholz”), *Carex rosae* is at its lower distribution limit and the species occurs only sporadically within a dense sward of *Carex sempervirens*, *Sesleria albicans*, *Festuca norica*, and *Kobresia myosuroides* (subassociation with *Festuca norica*). On site D (“Pisa 2”), too, together with *Festuca varia* these species form the main grass vegetation (subassociation with *Festuca norica-Arnica montana* type), while *Carex rosae* occurs here on the margins of its distribution area. All plots were extensively grazed by sheep.

In order to compare *Carex rosae* with the closely related *Carex curvula* ssp. *curvula* (= *Carex curvula*), 5 permanent plots were also established on site E (“Valsorda”, Table 1). On this site mainly species of siliceous bedrock occur together with the highly dominant *Carex curvula*. The community was described as Caricetum curvulae seslerietosum varia (Erschbamer, 1992). Grazing pressure by sheep was higher than on the *Carex rosae* plots.

During the 1990–1992 growing seasons, the shoot density within the permanent plots was monitored with a grid frame of 25 × 25 cm divided into 5 × 5 cm subplots (Erschbamer, 1994). Some plots of each site (A1, A2, B3, B5, C4, D2, and D3) were not recorded in 1992. Plot 5 of site D disappeared in 1991 and so is not mentioned here. In 2002, the sites were re-visited. At sites A and C, all the plots were found, and the shoot density per plot was recorded. Sites B and D were located close to tourist paths and marked plots were destroyed by hiking impact within the 10-year period: at site B only two plots were monitored and at site D none of the plots could be detected in 2002. At site E only one permanent plot remained until 2002; the other four had been destroyed by a new hiking trail.

MATERIAL

Carex curvula and *C. rosae* are clonally growing sedges of the alpine zone in the Alps and Pyrenees (Meusel et al., 1965) between 2300 m and about 2800 m a.s.l., following environmental gradients (Choler et al., 2003). *Carex curvula* occurs only on siliceous bedrock, whereas *C. rosae* colonizes calcareous (mica)schists (Gilomen, 1938) and geologically mixed substrates such as limestone interlaced by volcanic intrusions (Erschbamer, 1990, 1992). Both species form long-lived tussocks, reproduction being mainly vegetative by intravaginal

tillering. Reproduction by seedlings is a rare event for the two *Carex* species: in the 1990–1992 period no seedlings were observed in the plots (Erschbamer, 1994).

Shoots of *Carex curvula* live for at least 6–7 years (Grabherr, 1987). During the field work in 1990–1992, new shoots of *Carex rosae* were marked and in 2002 one of these marked shoots was still alive, i.e., the maximum shoot age of *Carex rosae* can be at least 12 years. Flowering shoots are monocarpic.

MODELING OF POPULATION GROWTH

The recording of shoots distinguished between vegetative and generative shoots. As shoot labeling was not possible in the field, the transition rates between these two stages could not be determined. The separate record of generative shoots served the estimation of shoot mortality. Growth modeling pooled all shoots in one plot. The temporal development of the number X of shoots in a plot was described by the growth equation

$$X_{t+1} = \lambda X_t \quad (1a)$$

$$= (1 + b - d)X_t, \quad (1b)$$

where X_t = number of shoots in year t in the plot, λ = annual finite rate of population increase, b = shoot birth rate (vegetative reproduction), and d = shoot death rate. This growth model considered all shoots to be independent of each other, i.e., it neglected the tussock structure of the species and hence any correlated shoot mortality.

DETERMINATION OF RATES

If shoot numbers X were recorded in subsequent years, the rate of population increase was calculated from the records by

$$\lambda = X_{t+1}/X_t. \quad (2)$$

In the general case where the interval between records was n years, the average rate of population increase $\lambda(n)$ was given by

$$\lambda(n) = \sqrt[n]{X_{t+n}/X_t}. \quad (3)$$

Weighted values and standard deviations from m different rates of population increase λ_i ($i = 1, \dots, m$) were calculated in a simplified manner by arithmetic averaging:

$$\bar{\lambda} = \frac{\sum_i n_i \lambda_i}{\sum_i n_i} \quad (4)$$

$$s = \sqrt{\frac{\sum_i n_i (\lambda_i - \bar{\lambda})^2}{\left(\sum_i n_i - 1\right)}}. \quad (5)$$

The weights n_i were given by the number of annual steps n that featured in the calculation of λ_i values via Equation 3.

Death rates (and indirectly birth rates, via Equation 1b) were estimated from the proportion of the monocarpic generative shoots, neglecting other causes for mortality. The following values were used for the percentage of generative shoots in order to estimate death rates d (Erschbamer, 1994):

- (A) Pioneer 5% $d = 0.05$
- (B) Pisa 1 8% $d = 0.08$
- (C) Oberholz 10% $d = 0.10$
- (D) Pisa 2 8% $d = 0.08$
- (E) Valsorda 5% $d = 0.05$

SIMULATION OF POPULATION DEVELOPMENT

Population development was projected on the basis of Equation 1a using RAMAS Ecolab software (Akçakaya et al., 1999). Rates of

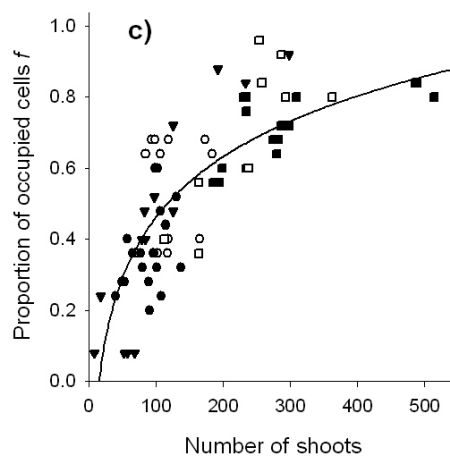
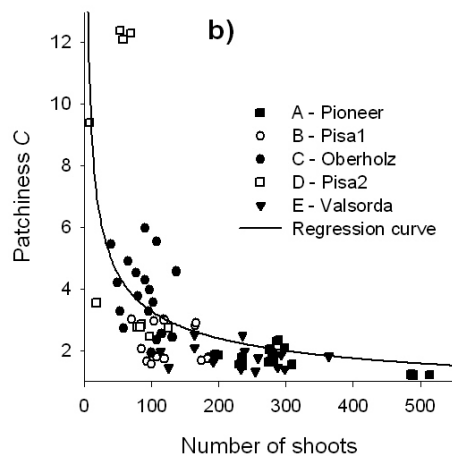
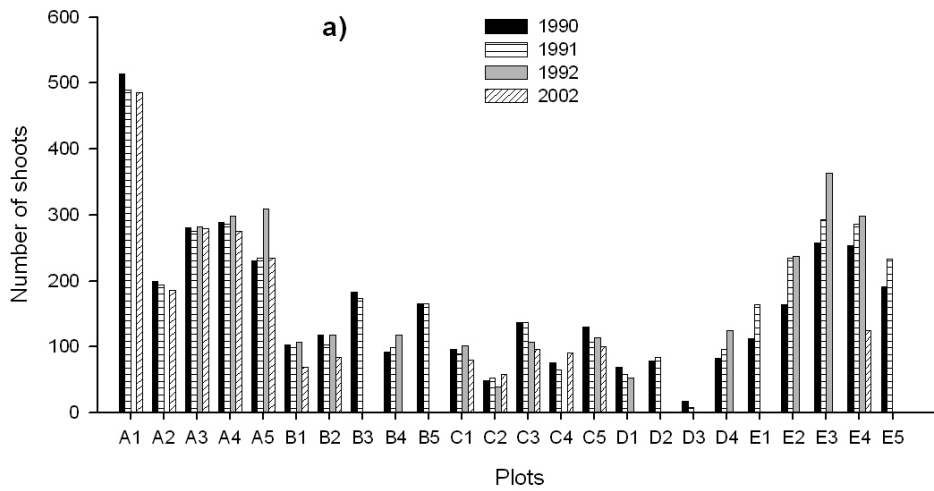


FIGURE 1. Shoot numbers and spatial population characteristics. (a) Shoot numbers X in the plots for the years 1990, 1991, 1992, and 2002. (b) Correlation between Lloyd's patchiness index C and shoot numbers X . Regression function: $C = a * X^b$ with $a = 26.5 \pm 7.3$, and $b = -0.454 \pm 0.063$. Correlation coefficient: $r = 0.58$. Correlation was significant at a 0.1% level. (c) Correlation between proportion of patch occupancy f and shoot number X . Regression function: $f = y_0 + a * \ln(X)$ with $y_0 = -0.676 \pm 0.112$ and $a = 0.248 \pm 0.0224$. Correlation coefficient: $r = 0.79$. Correlation was significant on a 0.1% level. Both regressions summed over all sites.

population increase were calculated from the field records as described above. Demographic stochasticity was included in all projections. Therefore, it was needed to specify death rates (and indirectly birth rates) that figured in the rates of population increase (Equations 1a and 1b). Simulation showed that their impact hardly depended on a precise estimation if $d < 0.20$. If possible, the effect of environmental stochasticity was included via mean values and standard deviations of the rates of population increase (Equations 4 and 5). Projection intervals and the probabilities of reaching a given threshold were computed from 1000 simulation runs.

PATCHINESS INDEX

The spatial structure of the shoot population within one plot was characterized by Lloyd's Patchiness Index (Lloyd, 1967; Pielou, 1977). This patchiness index C of a 25×25 cm plot with 5×5 cm subplots as counting units was calculated by:

$$C = m^*/m. \quad (6)$$

The mean shoot density m in a plot sums over all subplots:

$$m = \sum y_i / N, \quad (7)$$

where y_i is the shoot numbers in the subplots ($N = 25$).

"Mean crowding" m^* is determined by:

$$m^* = \sum y_i(y_i - 1) / \sum y_i. \quad (8)$$

If $C = 1$, all individuals are distributed randomly over the area, whereas

$C > 1$ denotes an aggregation of shoots within some subplots. The maximum patchiness value is given by $C = N = 25$, when all shoots are concentrated within one subplot.

PATCH OCCUPANCY

The proportion of occupied subplots in a plot was calculated by:

$$f = z/N, \quad (9)$$

where z = number of subplots with at least one shoot, and N = total number of subplots ($N = 25$). In our context, patch occupancy f varied between 0.04 and 1.0.

REGRESSION ANALYSES

Nonlinear regression analyses were performed by the unweighted nonlinear least-squares method using the SigmaPlot 7.0 statistical suite. The regression functions that best described the shape of the data are specified in the legends of Figures 1 and 2. Two-tailed significance tests for correlations were based on F statistics.

Results

SHOOT POPULATIONS, PATCHINESS, AND PATCH OCCUPANCY

The numbers of shoots X for all plots were determined, if possible, for the years 1990, 1991, 1992, and 2002. The results are given

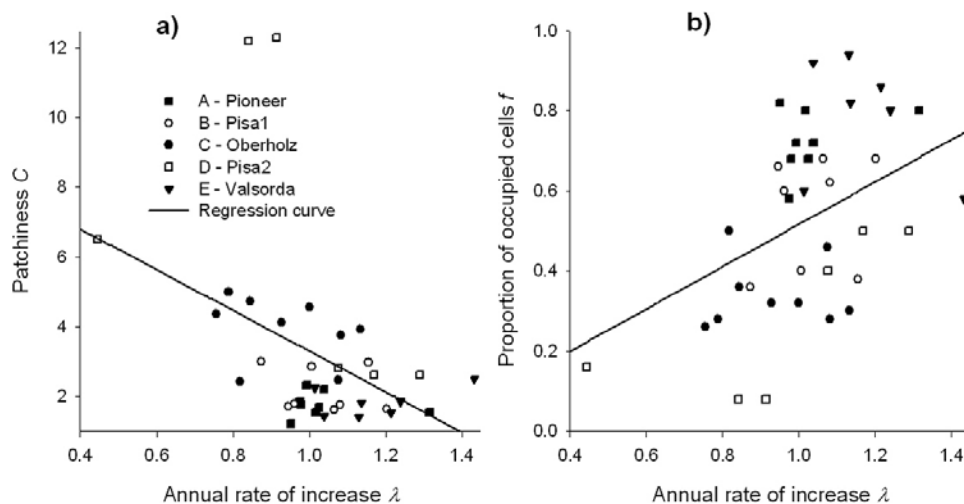


FIGURE 2. Relations between structural and dynamic population characteristics. (a) Correlation between Lloyd's patchiness index C and annual rates of population increase λ_1 and λ_2 (Table 2). Patchiness values C were averaged in the same way as the occupancy values f . Regression function: $C = y_0 + a\lambda$, with $y_0 = 9.1 \pm 2.0$ and $a = -5.8 \pm 1.9$. Correlation coefficient: $r = 0.44$. Correlation was significant at a 5% level. (b) Correlation between proportion of patch occupancy f and annual rates of population increase λ_1 and λ_2 (Table 2). Occupancy values f were averaged over the values from 1990 and 1991 or from 1991 and 1992 for plotting against λ_1 or λ_2 , respectively. Regression function: see Figure 2a, with $y_0 = -0.0116 \pm 0.192$ and $a = 0.528 \pm 0.184$. Correlation coefficient: $r = 0.43$. Correlation was significant on a 5% level.

in Figure 1a. For the same plots and years, patchiness indices C (Equation 6) and patch occupancy values f (Equation 9) were calculated. The patchiness index C was linearly correlated with patch occupancy f ($r = 0.90$; results not shown).

Both structural measures were nonlinearly correlated with shoot number X (Figs. 1b and 1c): the smaller the plot population, the higher the patchiness C ($r = 0.58$; Fig. 1b) and the lower the proportion of

occupied patches f ($r = 0.79$; Fig. 1c). Both correlations were significant with $P < 0.0001$. In no case did patch occupancy reach the maximum value of $f = 1.0$, whereas 46% of all values were below $f = 0.5$. Together with the C values, this result indicates a strong overall aggregation of shoots.

RATES OF POPULATION INCREASE

The rates of population increase λ_1 and λ_2 (Equation 2) as well as mean values λ_3 (Equation 4, with $n = 1$ for each λ_i) are listed in Table 2 for the annual steps 1990–1991 and 1991–1992. At least the first rate could be determined for all plots. Of these 1-year rates λ_1 and λ_2 , 31% were within the interval 0.95–1.05, 26% were below 0.95, and 44% were higher than 1.05. For the averaged rate λ_3 , the distribution of values was similar (33%, 27%, and 40%). When shoot numbers X were available for both 1992 and 2002, average rates λ_4 for the 1992–2002 population increase were computed (Equation 3), along with weighted averages λ_5 (Equation 4 with $n = 1$ for λ_1 and λ_2 and $n = 10$ for λ_4) for the whole period 1990–2002 (Table 3). These rates λ_5 included all the dynamic information available for a plot. No significant differences were apparent, either between the populations or between years. The long-term values were much more concentrated around the stationary value of $\lambda = 1.12$ of 13 values (92%) were within the 0.95–1.05 interval, and only one value fell below it.

CORRELATIONS BETWEEN DYNAMIC AND STRUCTURAL MEASURES

Increase rates for 1-year steps λ_1 and λ_2 were correlated with the two structural measures patchiness index C and patch occupancy f (Figs. 2a and b). For each annual step $t \dots t+1$, the measures C_t and C_{t+1} as well as f_t and f_{t+1} , respectively, were averaged over the 2 years t and $t+1$. Correlations between the dynamic measure λ and the spatial measures C and f , respectively, were significant with $P = 0.0066$ and 0.0046 , respectively. The patchiness C decreased linearly with increasing λ , while vice versa, the proportion of occupied cells f increased with λ .

TABLE 2

Rates of population increase λ for 1990–91 (λ_1), 1991–1992 (λ_2), and mean values λ_3 of both rates including standard deviations (SD). Sites: A—Pioneer, B—Pisa 1, C—Oberholz, D—Pisa 2, E—Valsorda.

Plots	λ_1	λ_2	λ_3	SD
A1	0.951			
A2	0.975			
A3	0.979	1.025	1.002	0.033
A4	0.993	1.038	1.016	0.032
A5	1.017	1.315	1.166	0.021
B1	0.961	1.081	1.021	0.085
B2	0.873	1.155	1.014	0.199
B3	0.9456			
B4	1.0645	1.202	1.133	0.097
B5	1.005			
C1	0.928	1.133	1.030	0.145
C2	1.082	0.755	0.918	0.231
C3	1.00	0.788	0.894	0.15
C4	0.844			
C5	0.817	1.075	0.946	0.182
D1	0.841	0.914	0.878	0.052
D2	1.076			
D3	0.444			
D4	1.169	1.289	1.229	0.085
E1	1.451			
E2	1.433	1.013	1.223	0.297
E3	1.136	1.239	1.188	0.073
E4	1.13	1.038	1.084	0.065
E5	1.214			

Whenever an empirical value X for 2002 was available for a plot, this observation was compared with projections of population development for 2002 starting from the records in 1990. If average rates of population increase could be used (λ_3 in Table 2), projections factored in both environmental and demographic stochasticities, whereas in exceptional cases (A1, A2, and C4) only demographic stochasticity could be included in the simulations (projection with only λ_1), making projections too precise. Both projections and empirical verifications are compared in Figure 3. The error interval for the projections in Figure 3 is calculated by $\pm 2s$ (where s denotes the standard deviation) of the results of the stochastic simulation runs, giving the 95% confidence interval of projection results. In all cases where environmental stochasticity could not be estimated (3 plots), the empirical value was outside the projection interval. When stochasticity was fully taken into account, in only 3 of 10 cases did the projection interval not include empirical verification (plots C2, C3, E4).

PROJECTION INTO FUTURE: ESTIMATION OF EXTINCTION RISKS

Projections of future population development were based on all the information available for population dynamics combined into λ_5 (Table 3). The projection results gave the probabilities of small population values (25 or 10 shoots per plot) or population extinction (0 shoots per plot; Fig. 4) being reached over the next 50 years. In 6 out of 13 cases (B1, B2, C1, C3, C5, E4), the probability of a population becoming small, i.e., its size falling below the threshold of 25 shoots per 625 cm², exceeded 25%. However, the danger of full extinction within the next 50 years was still low for almost all populations: only in 1 case (E4) was the probability of total extinction higher than 1%.

Discussion

The study addressed the problem of evaluating long-term population development on the basis of observations over periods that are significantly shorter than the mean lifetime of individuals. Usually, population dynamics are recorded over 2 or at most 3 years. Observations allow population development to be projected into the future via simulation modeling, so that the risks of population extinction can be calculated. Such projections can be done by simple rate models if all the individual shoots are pooled together, or age- or stage-based matrix models (Caswell, 2001) if the transition rates can be determined. Simulations should include all the knowledge available on stochastic aspects (demographic and environmental stochasticities). The range of stochastic projection outcomes may be rather large: many new observations will fit into this interval and thus may validate the projection. On the other hand, significant deviations between projections and verifications will not disqualify the model forecast, but will elucidate gradual changes in external conditions for the population, e.g., caused by disturbance or succession. When there are several observations under similar conditions, even modest differences between projections and observations may enable some general trends to be elucidated.

One-year values for the rate of population increase λ were scattered over a broad interval of $\lambda = 0.4$ – 1.50 , denoting high temporal and site-dependent stochasticity in growth conditions. By contrast, almost all the averaged values were within a small interval of $\lambda = 0.95$ – 1.05 . These long-term rates of population increase of the *Carex curvula* subspecies were similar to those reported for long-lived perennials which reproduce by vegetative means, also remaining close to the equilibrium value of 1.0 (Callaghan, 1976; Fetcher and Shaver, 1983;

TABLE 3

Average rate of population increase λ_4 for 1992–2002 (Equation 3), weighted average λ_5 for the interval 1990–2002 (Equations 4 and 5) including standard deviation (SD).

Plot	λ_4	λ_5	SD
A1	0.999	0.995	0.014
A2	0.996	0.994	0.061
A3	0.999	1.00	0.010
A4	0.992	0.996	0.013
A5	0.973	1.00	0.100
B1	0.958	0.968	0.035
B2	0.967	0.975	0.063
C1	0.976	0.985	0.049
C2	1.038	1.018	0.084
C3	0.988	0.972	0.058
C4	1.031	1.015	0.054
C5	0.986	0.979	0.057
E4	0.916	0.944	0.068

McGraw and Antonovics, 1983; Callaghan, 1984; Svensson and Callaghan, 1988; Carlsson and Callaghan, 1991; Jonsdottir, 1991; Nault and Gagnon, 1993; Silvertown et al., 1993; Wikberg et al., 1994). If λ remains more than 1.0, it may be assumed that the population size can be steadily maintained by clonal reproduction (Shimizu et al., 1998). Clonality has already been recognized as one of the essential features of plants growing under harsh arctic and alpine conditions (Callaghan, 1988; Stöcklin, 1999).

Parallel to the determination of size and the actual dynamic state of populations, the spatial structure of the plot populations was also evaluated. Shoot populations varied spatially depending on the grassland type they occupied. This suggests that population dynamics may change as a result of natural changes in the grassland within the course of succession to denser swards. Similar results were found by Valverde and Silvertown (1998) for *Primula vulgaris* in different forest canopies.

Small, decreasing populations were on average more aggregated than large populations in an expanding state. These correlations are rather plausible: a growing population increasingly fills a plot and thus lowers shoot patchiness. The increase in aggregation parallel to a decrease in size corresponds to theoretical conclusions: patchiness arises when population densities become low, and dispersal occurs only over short distances and where interactions between individuals are localized (Freckleton and Watkinson, 2002). Short vegetative “dispersal” distances are due to the phalanx growth form of the *Carex* species. At best, a dispersal of shoots was only observed between neighboring subplots of 5×5 cm.

The results showed that patchiness can serve as a measure of the dynamic state of a population: from Figure 2b it can be deduced that a population increases ($\lambda > 1$) whenever more than 50% of all patches have at least one shoot ($f > 0.5$). Values for patch occupancy f can be determined in the field much easier than for patchiness C or even the increase rate λ (which needs at least a 2-year observation period) and may be used for a screening of the population state. However, it should be borne in mind that such structural values can only serve as a snapshot: a strict relationship between λ and C or f will not hold over longer periods of population development (Winkler and Matthies, unpub.).

The correlation found in Figure 2 cannot hold any longer when new subpopulations arise from established seedlings. Here, initial aggregation may be high even though such a population will be in a growth state ($\lambda > 1$). However, during the research period, seedlings were never recorded for either *Carex rosae* or *Carex curvula* (Erschbamer, 1994). On the other hand, the potential to recruit by

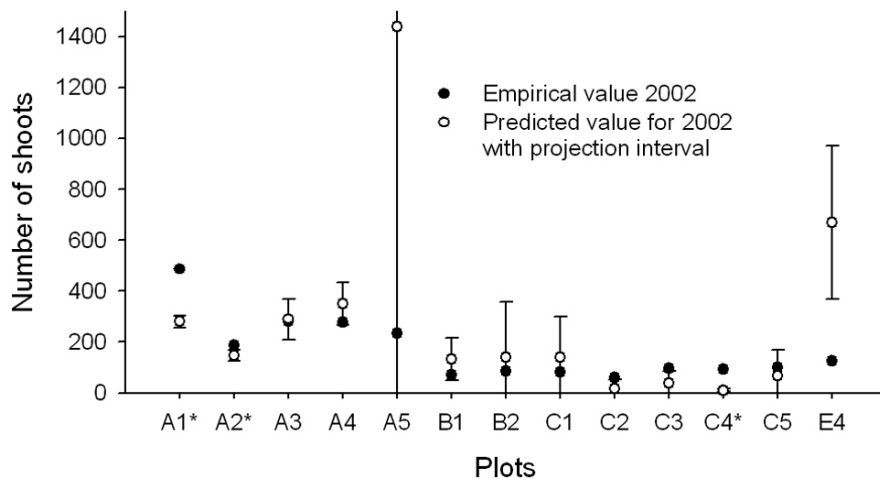


FIGURE 3. Simulation projection from 1990 to 2002 (white symbols with error bar) using averaged rates of population increase λ_3 (Table 2). An asterisk marks the cases where values for only one time-step 1990–1991 (λ_1 in Table 2) were available. Simulations (1000 runs) included demographic and, where possible, environmental stochasticity. Projection intervals were given as the twofold standard deviation of the projection results for 2002. Simulation results are compared with empirical values for shoot number X in 2002 (black symbols).

seedlings has to be assumed at least occasionally, as seeds of both subspecies were found for instance in the soil of a central alpine grassland site (Niederfringer Schlag, unpubl.). The degree to which populations can be rejuvenated by occasional successful germination remains uncertain.

Predictions for 2002, over 10 years, were made from observations of size changes and of aggregation over two annual steps 10 years before. These predictions were compared with the empirical findings and judged in the light of general knowledge about the conditions at the observation sites.

Site A—Pioneer. Initially there was a large potential for expansion: the overall cover of the vegetation was lower than in closed grassland, with low interspecific competition and open gaps. This is reflected by the average values for the plots of the site: $\lambda = 1.037 \pm 0.166$ and $f = 0.72 \pm 0.08$. They seemed to be strong indicators of an increase in population size, the population growing in its optimum environment. However, the high average λ may be due to the “outlier” λ_2 of A5 (average λ without this value is 0.997). Indeed, in the period until 2002, the plot populations did not change in size. On average, λ was a better predictor of development than f : all the relevant values in Figure 2a lie above the regression line. The population evidently left the growth stage in the last decade and approached a stationary state. Similar to *Carex curvula* which does not exceed a certain density of shoots per plot (Grabherr, 1987), intraspecific regulation may be suggested for *Carex rosae*, too.

Site B—Pisa 1. In this grass sward, high competition between *Carex rosae* and *Kobresia myosuroides* has to be assumed. Hence, the *Carex* tussocks were smaller, with lower shoot density. The average plot values were $\lambda = 1.036$ and $f = 0.55$ (for all plots and both annual steps). They still indicated a tendency for population growth. However, stronger competition compared to site A was reflected by the much lower value for f . Indeed, the population size decreased (Fig. 1a), and the shoot values observed were lower than those predicted using the growth model (Fig. 3). Here, patch occupation f was a better indicator of population development and a valuable addition for determining λ .

Site C—Oberholz. Strong competition by other species (*Carex sempervirens*, *Sesleria albicans*, *Kobresia myosuroides*, *Festuca norica*) allows only small tussocks of *Carex rosae*. Due to its thin leaves, a low aboveground biomass was found for *C. rosae* (Erschbamer et al., 1998), and the species may be assumed to be a weak competitor. Both λ and f (0.936 and 0.34) indicated population decline. Indeed, the population did decline, albeit significantly less rapidly than expected (Fig. 3).

Site D—Pisa 2. Both λ and f (0.955 and 0.29 on average) predicted population decrease. These values may reflect strong competition. However, no observations were available for 2002. Sites D and C represent the lower distribution limits of *C. rosae* and fitness may be reduced, as was found for several other species growing at the margins of their distribution area (Bengtsson, 2000; Gaudeul et al., 2000).

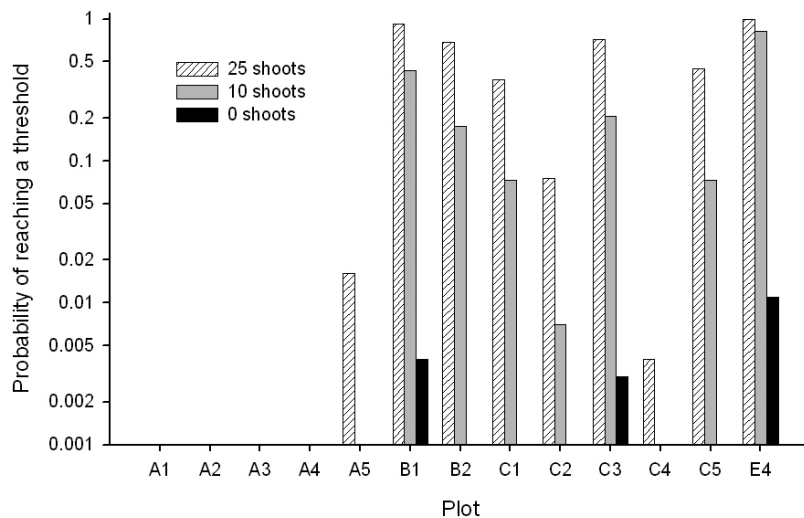


FIGURE 4. Probabilities of reaching threshold values for shoot number X within a 50-year period from 2002. Simulations (1000 runs) used rates of population increase λ_5 from Table 3 that averaged over all available dynamic information for the plots.

Site E—Valsorda. Following all λ and f values (average values 1.21 and 0.74) population sizes of *Carex curvula* should strongly increase. This may be the typical situation of a dominant species close to carrying capacity. However, the short-term observation 1990–1992 could not include all relevant external effects. In the last decade the whole area was strongly affected by tourists and by grazing. Although the predictions could be compared only in one case with the actual state, a remarkable decline in population size compared to the initial observations was detected. It must remain open if this deviation between prognosis and verification is due to an increasing competitive stress in the course of community development not reflected in the first observation period or simply due to disturbance by tourists.

On a short term, within the next decades, the risk of the various populations going extinct is still very low (Fig. 4). However, the populations of the species-rich climax grasslands will decrease, probably even below some critical threshold. Only the populations at site A (“Pioneer”) seem to be far-removed from any danger of population decline. Inevitably, such prognoses depend on different preconditions. Because of the phalanx growth form of the *Carex curvula* subspecies, the simulation Equation 1, which assumes independent shoots, is unlikely to hold when populations become small. Moreover, we had to assume that environmental conditions will remain in the same state as averaged over the period 1990–2002. It is unlikely that this will really be the case. Therefore, a continuous monitoring of population development of long-living species combined with an updating of prognoses must be a task for future research.

Conclusions

- The *Carex curvula* subspecies are able to maintain more or less stable population sizes over decades.
- The most endangered populations occur in species-rich climax grasslands where the patch occupation of *Carex rosae* is already low.
- Besides the analysis of rates of population increase, structural measures such as patchiness index and patch occupancy can serve as indicators of the dynamic state of a population. The proportion f of occupied patches and the spatial distribution of occupied patches are especially good indicators, the recording of which may markedly reduce the observational effort.
- Strongly aggregated populations were small and also decreased in size.
- The systematic continuation of plot observations over the next few years or even decades to answer questions about the impact on population development of environmental fluctuations and of long-term environmental changes is highly desirable.

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