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IS A GRASSLAND COMMUNITY COMPOSED OF COEXISTING SPECIES WITH LOW AND HIGH SPATIAL MOBILITY?

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Abstract: Patterns of grasslands species mobility were compared between communities and within plant species. Data from high spatial resolution permanent plots with fine scale recording system, experiment with removal of the dominant recorded also at a fine scale were used. The permanent plots showed large variation within a community in the patterns of species mobility. The species mobility was partly dependent on the site and was higher in a more nutrient rich and climatically more favourable community. Mobility also varied within species. In some species (*Nardus stricta, Anthoxanthum* spp.) it differed between communities (it was higher in more nutrient rich and climatically more favourable community) and did not respond to removal of the dominant species. In another species, *Festuca rubra*, mobility also differed between plots; in contrast, it did not show consistent variation attributable to community type and showed strongly increased spatial persistence in plots with the dominant species removed. In this species the mobility seems to be dependent on the competitive pressure of the coexisting species.

INTRODUCTION

Vegetation structure is primarily understood as a structure in space. Space does, however, also play an important role in plant species coexistence, since niche and habitat concepts are inseparable in plants (PALMER 1994). Spatial processes of species coexistence are thus the closest interface between studies of species coexistence and vegetation structure.

In temperate grasslands, plant species have been shown to exhibit a considerable spatial mobility over a time scale of years (VAN DER MAAREL & SYKES 1993, HERBEN et al. 1993a). In perennial species, this seems to be related to predominantly clonal growth form of grassland perennials (HERBEN et al. 1993a, LAW et al. 1994); the extent to which the structure of grassland is shaped by this species mobility is, however, generally unknown.

It has become a well established fact in ecology that spatial processes alone have a capacity to enhance species coexistence; see e.g. patch coexistence models (BENGTSSON 1991, CASWELL & COHEN 1991), models based on cellular automata (KARLSON & JACKSON 1981, HOGEVEG et al. 1983, CRAWLEY & MAY 1987, SILVERTOWN et al. 1992, CZÁRÁN & BARTHA 1992), and models based on plant architecture (BELL 1984). However, it is uncertain whether species mobility in grasslands does indeed contribute to species coexistence. To our knowledge, only SCHMID & HARPER (1985) attempted to demonstrate that spatial mobility acts as a factor influencing species coexistence. They demonstrated that coexistence of *Prunella* and *Bellis* in culture is promoted by contrasting growth form of these two species.

Information on spatial mobility within communities is rather scanty. First, it is unclear how much the mobility pattern of individual species changes in relation to their (biotic and abiotic) environment. Several studies demonstrated the potential of clonal plants to change their morphology and spatial behaviour to exploit their environment (for a review, see HUTCHINGS & DE KROON 1994); how much this potential contributes to varying mobility of one species in different communities is unknown. Second, it is unknown whether different communities show any patterns in their overall distribution of species mobility. The aim of this paper is to provide data to answer these two questions.

"High spatial resolution" permanent plots are used to establish the existence of differentiation among species in their mobility and to compare such patterns between contrasting communities. The intraspecific variation of spatial dynamics is demonstrated using a removal experiment testing whether the presence/absence of competitors in the community has an effect on the spatial behaviour of its component species.

METHODS

Study sites

Study sites were located in the mountain grassland in the Krkonoše Mountains, North Bohemia. Data were collected at two localities: One species rich site (referred to as J), with ca. 4-7 species per 10 cm^2 and 25-30 species per 2500 cm^2 (Pec pod Sněžkou, 3.75 km ESE of the centre, Janovy boudy settlement, latitude 50° 41' 28" N, longitude 15° 47' 35" E, altitude 880 m; plots J1 to J4). The second locality (referred to as S) is a species poor grassland with 2-4 species per 10 cm^2 and 6-10 species per 2500 cm^2 (Severka settlement, ca. 3 km NW of Pec pod Sněžkou, latitude 50° 41' 42" N, longitude 15° 42' 25" E, altitude approx. 1100 m; plots S1 to S4). Except for *Euphrasia* sp. at the J locality there were only perennial species at both sites. Both meadows can be classified into *Sileno-Nardetum* (*Nardo-Agrostion, Nardetalia*); the species rich one as subassociation *crepidetosum*, the species poor one as subassociation *pleurozietosum* (KRAHULEC 1990). Traditionally the meadows were mown in summer and grazed late in the autumn. They were manured once every few years.

There is a pronounced difference between both localities, namely in the length of the growing season (Tab. 1). At the J site snow disappears in about mid April and appears usually in November; at the S site the growing season begins as late as in mid May when snow disappears and lasts till the beginning of October. The soil in the J plots is significantly richer in calcium and magnesium. Soil pH is also significantly higher. Total soil nitrogen content is similar in both sites (even higher in the S plots). This, together with the higher total soil carbon content in the S plots, strongly indicates slower decomposition rate and nitrogen mineralization and hence lower nitrogen availability for plants (Tab. 1).

Fine scale persistence of species within communities

Eight permanent plots of 50 × 50 cm were established in 1984-1985. Plots were selected subjectively, avoiding visible disturbance; within each site, the distance between the most distant plots was less than 15 m. Plots were recorded in ca. mid June (J) and mid July (S) until 1990. A grid of 15 × 15 subplots (subplot size 3.3 × 3.3 cm) was established. The number of morphological units of all plants rooted in each subplot was counted. For all graminoids,

Table 1. Some ecological parameters of the sites.

	J plots		S plots	
Altitude (m a.s.l.)	880		1100	
Length of the vegetation period (months)	7		5-6	
	manured	not manured	manured	not manured
Peak biomass (g/m^2)	266	176	256	190
Ca (mg/g soil)	1.46	2.40	0.67	0.65
Mg (mg/g soil)	0.37	0.54	0.07	0.06
C/N	11.7	11.9	14.3	13.2

morphological units were tillers; for large forbs (*Ranunculus* spp., *Alchemilla* spp., *Polygonum bistorta*, *Geranium sylvaticum, Solidago virgaurea*) morphological units were leaves, whereas for small forbs morphological units were rosettes or individual stems. Seedlings with cotyledons and juvenile leaves only were not counted. The plots were clipped after recording. Since the present observation was part of the larger experimental study of grasslands, two plots of each series (S1, S3, J1, J2) were manured in autumn 1985 and 1989 (cow manure in S plots and horse manure in J plots, following the traditional treatment done at these plots). This amounted to adding the following amount of nutrients (g/m^2): S plots: Total N = 17, NO_3-N = 0.2, NH_4-N = 3.8, PO_4-P = 2.4, pH = 7.7; J plots: Total N = 12.7, NO_3-N = 0.54, NH_4-N = 8.4, PO_4-P = 1.8, pH = 8.15.

The fine scale dynamics of individual species was expressed using a qualitative measure of autocorrelation in time (temporal carryover, subsequently called persistence). This was based on a 2 × 2 contingency table comparing species presence/absence in grid cells at two sampling times (Tab. 2). The association within this table is a measure of the tendency of a species to remain within the same cells over a given time interval. The point correlation coefficient (PIELOU 1969) was used as a measure of association in this table. Point correlation coefficients were calculated for each species in each plot from all possible pairs of successive years (time lag = 1).

For the purpose of these analyses, species within genera *Alchemilla* and *Campanula* were treated as single species since they were difficult to identify in the vegetative state. Only species occurring with frequency > 20 subplots (out of 225) in at least two recordings of one plot were included in the study. The number of such species varied from 13 to 15 in one plot, with a total of 21 species.

Removal experiment

In 1990, six plots of the 50 × 50 cm size were established in the S site. In three of them, the dominant grass *Deschampsia flexuosa* has been removed since the spring of 1991. Removal was done by forceps, plants were pulled out of the soil with stem bases and as much as possible also with rhizomes growing at the soil surface. Care was taken not to disturb other plants in the plot and to minimize disturbance to the soil structure. Since *D. flexuosa* regenerated from old rhizomes, removal was repeated at ca. three weeks intervals during the spring and early summer of 1991; further removals were undertaken in autumn 1991, spring and early

Table 2. Frequency table used to measure persistence of individual species. Frequencies (a,b,c,d) are counted in two successive observations of individual 3.3 × 3.3 cm cells. The persistence of the species was expressed using the point correlation coefficient $V=(ad-bc)/\sqrt{[(a+b)(a+c)(b+d)(c+d)]}$.

	Recording time 1	
	Species present in the cell	Species absent in the cell
Recording time 2		
Species present	a	b
Species absent	c	d

summer 1992. In 1990 *D. flexuosa* accounted for 37.4, 40.0 and 57.8% of the living aboveground biomass of the treated plots, and for 25.0, 55.6 and 76.9% of the living aboveground biomass of the control plots. The central areas of these plots (8 × 8 subplots of 3.3 cm side, with coordinates 4 to 11) were recorded using the same fine scale recording system as for the permanent plots. The border zone (0.1 m wide in lower and left parts, 0.133 in upper and right parts) in which *D. flexuosa* was also removed was left unrecorded to avoid edge effects.

The dynamics of individual species was expressed using the point correlation coefficient in the same way as in the large plots. Point correlation coefficients were calculated for each species in each plot from 1990/1991 and 1991/1992 comparisons. The spatial persistence was compared between removed and control plots; the differences were tested with a Student's t-test.

RESULTS

Patterns of species mobility in communities

Since frequencies of studied species did not change significantly over the observation interval (HERBEN et al. 1993a, unpubl.), the point correlation coefficient (persistence) primarily expresses the differences in fine scale mobility of species. Individual species differed strongly in this respect. The persistence over a one year interval measured by the point correlation coefficient ranged from less than 0.1 (*Campanula* spp. in the species rich plots) to more than 0.8 (*Nardus stricta* and *Festuca rubra* in the species poor plots). Within one plot, the values of the species persistence varied much less. The difference between the most persistent and least persistent species within one plot usually ranged between 0.4-0.5 (Fig. 1).

Patterns of species persistence also differed strongly between communities. To show the distribution of persistence values within a community, each recording of each plot can be represented by a histogram of persistence values of the total set of species (Fig. 1). Since such histograms are not easy to compare visually, triangular diagrams (cf. GRIME 1977) were used (Fig. 2). In the more nutrient- and species-rich community the spectrum of persistence was shifted toward lower persistence (Tab. 3). Still there was a large variability among plots of the same grassland type (Tab. 3). Most pronounced was the behaviour of the species poor plot S3, where the mean persistence of the species was much lower than in the rest of the species poor plots. The mobility of most of the species, namely *Festuca rubra, Anthoxanthum alpinum, Deschampsia flexuosa* and *Polygonum bistorta* was higher in this plot (Fig. 3).

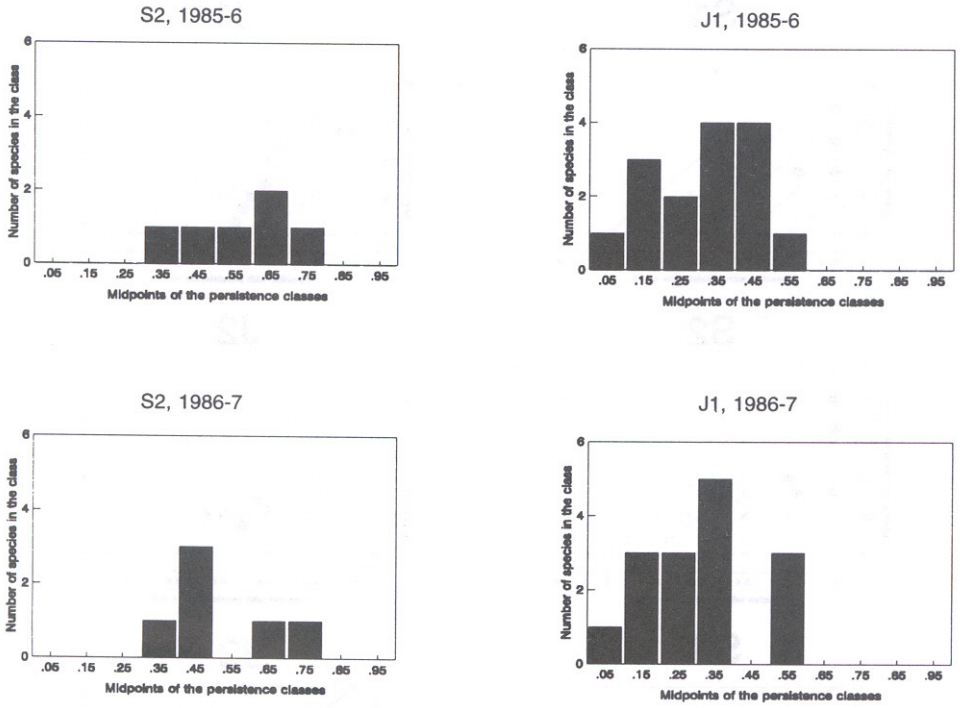

Fig. 1. Example of distribution of persistence values in two plots and two recording times. Persistence is expressed using a measure of association (point correlation coefficient) within a 2 × 2 contingency table comparing species presence/absence in grid cells at two sampling times. The association within this table is a measure of the tendency of a species to remain within the same cell over a given time interval.

Variation of persistence of individual species

Spatial behaviour of individual species was also variable between plots and communities. Of the species common to both community types, only *Polygonum bistorta* showed the same mobility in both sets (Fig. 3). In contrast, *Nardus stricta*, a species with a compact growth form showed much lower persistence at the species rich site (Fig. 3). The same pattern was shown also by *Deschampsia flexuosa* and *Anthoxanthum* spp. Some species, for example *Festuca rubra* and *Anthoxanthum* spp., showed large variability in the spatial persistence between sites both in more nutrient rich and less nutrient rich (species rich and species poor) plots. This variability was not related to the difference in community types, since the plots with high *F. rubra* persistence occur both at species rich and species poor site (Fig. 3).

In four taxa which were present in all the plots (*Nardus stricta, Deschampsia flexuosa, Anthoxanthum* spp. and *Festuca rubra*) there was a large covariation in their spatial persistence. This could be expressed by the magnitude of the first eigenvalue in the PCA based on persistence values (persistence of each species was taken as variables; all plots and recording times were taken as separate cases; correlation matrix was used). The first eigenvalue accounted for 65.5% of the total variation of persistence of four species.

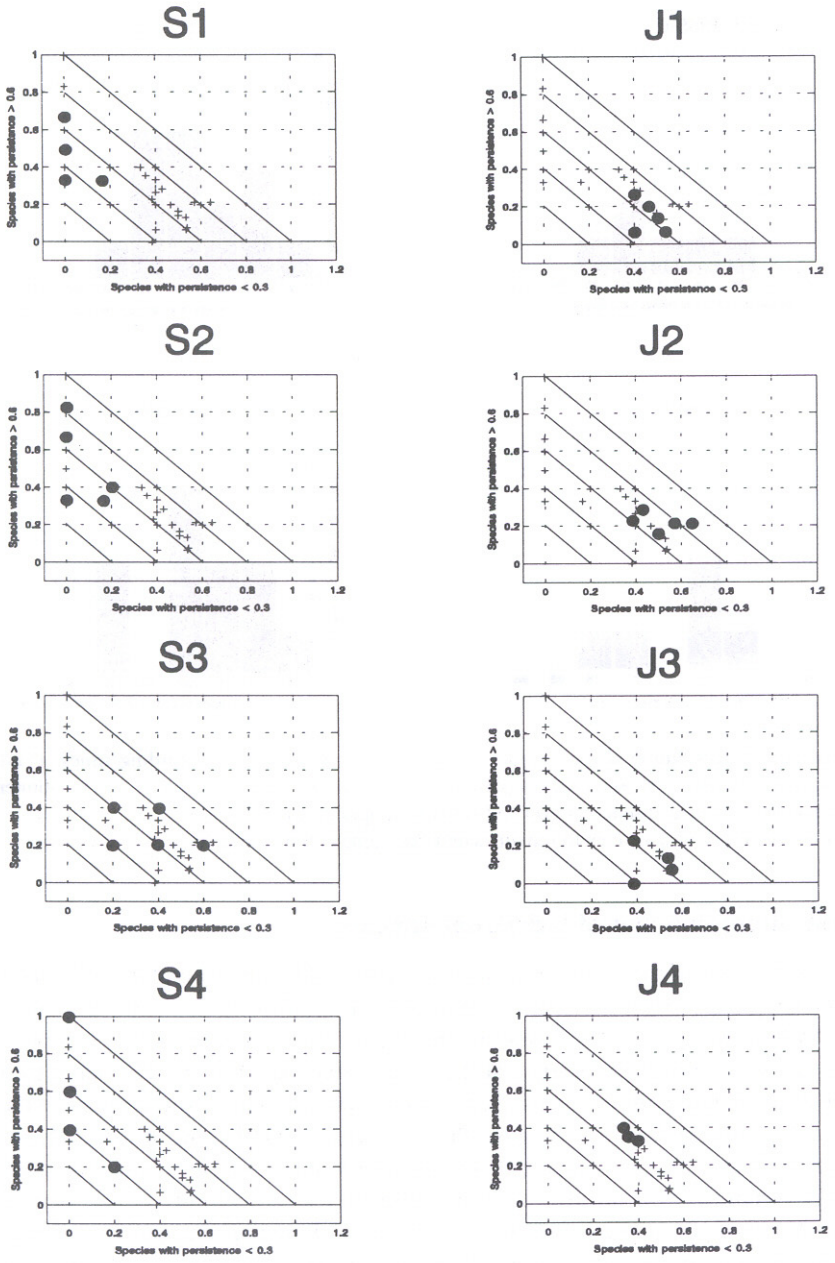

Fig. 2. Triangular diagrams of species persistence spectrum in individual plots. Persistence values of all species within a plot were divided into three classes (less than 0.3, 0.3-0.6, more than 0.6). These limits are chosen arbitrarily. If the proportion of species in the lowest and highest presistence class are plotted on X and Y axis, respectively, diagonal lines connect points having the same proportion of species with persistence within interval 0.3-0.6. To enable comparison, positions of all recordings of all plots are indicated in all eight plots (by crosses); closed circles represent recordings of the plot indicated at the top of the plot. Plots J1, J2, S1, S3 were manured.

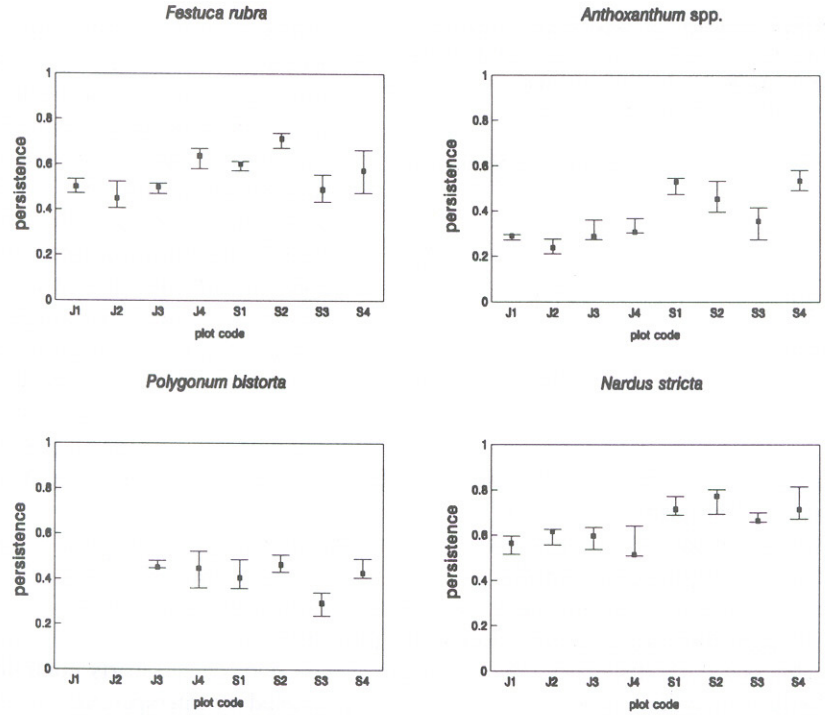

Fig. 3. Persistence of four principal taxa in the permanent plots. J1 to J4 are species rich plots, S1 to S4 are species poor plots. The points are median values, the bars indicate 25% and 75% percentiles of the data. Plots J1, J2, S1, S3 were manured.

Removal experiment

Removal of a dominant species, *Deschampsia flexuosa*, did not have a significant effect on the total number of tillers in the two years following the treatment except in *Nardus stricta* (unpubl.). Some changes in the spatial dynamics of species were detected (Tab. 4). The most pronounced response was shown by *Festuca rubra*, whose persistence increased in treated (i.e. with dominant removed) plots.

DISCUSSION

In both community types much interspecific variation in the species persistence was found. This finding, however obvious it may seem, has not often been reported from plant communities (but see VAN DER MAAREL & SYKES 1993, LAW et al. 1994, SYKES et al. 1994). Though persistence is the composite variable dependent on several factors (module life span, module size, mean runner/rhizome length), the previous study showed it is primarily related to the type of clonal growth (HERBEN et al. 1993a). We thus interpret differences in persistence as differences in mobility (primarily mean runner/rhizome length).

The mean values of persistence differed between species rich and species poor communities. Simple statistical effects of fixed number of modules or species per cell could be dismissed, since both module and species numbers per cell varied considerably, both within plots and

Table 3. ANOVA of the species persistence in permanent plots. Individual effects are tested by comparison of log likelihood of models with these effects set to zero with unconstrained models using the program BMDP3V (DIXON 1993).

Variance component	Chi-square	Significance
Fixed effects		
Site	5.962	0.015
Species	300.093	< 0.001
Site*species	32.126	< 0.001
Random effect		
Plot	51.610	< 0.001

between plots. The most likely explanation for the difference in persistence is a variation in growth dynamics between the two sites. This variation is due to nutrient richness and climate differences (Tab. 1). As a result, at the species rich plots plants may be able to grow faster, which in turn could increase their spatial mobility (decrease persistence). The results of plot S3, which shows higher overall mobility and is also the richest in nutrients among the S plots, may indicate this. The strong plot effect for the persistence of all species is also supported by the large covariation in the persistence patterns among four principal species.

However, it remains to be answered how (if at all) the greater species richness in the J plots is related to their higher mean spatial mobility. It would be attractive to conclude that the higher mobility of species contributes to the ability of more species to coexist. However, the plot S3, whose spatial dynamics was close to the plots in the species rich community, but its species richness did not differ from the rest of the species poor plots, clearly contradicts this pattern. Modelling studies show that coexistence is promoted by interspecific differences in spatial mobility (BELL 1984, CASWELL & COHEN 1991), not by the mean of all species. Though mean values for species rich and species poor communities differed in the studied cases, the difference between the most mobile and least mobile species were approximately same in both community types.

On the other hand, the difference in mobility between species within each of these communities could be one of the mechanisms for coexistence of component species. This is generally difficult to demonstrate; at any rate, such demonstration will have to rely on a deductive approach. A spatially explicit model could be used to determine how big a difference in mobility should be to help species coexist. Data on mobility are not, however, sufficient input for such a model. Primarily, it would be needed to relate mobility of species and their phalanx/guerrilla behaviour (LOVETT DOUST 1981, LOVETT DOUST & LOVETT DOUST 1985). The high mobility species could well be those showing more guerrilla strategy, i.e. forming longer internodes, looser tussocks and easily exploring open spaces within the community. Though preliminary data seem to support such a relationship (HERBEN et al. 1993a, LAW et al. 1994), much more data are needed here.

The species spatial dynamics was also variable within individual species among plots. In general, this variability can be explained either as (a) differential response to different competitive environment in both sites, (b) differential response to the abiotic (e.g. nutrient) regime, or (c) genetic differences within species. The data available are only partly helpful for separation between these effects. Different species show different patterns in this variation; *Nardus stricta* and *Anthoxanthum* spp. have lower persistence in species rich plots with higher nutrient status. However, their behaviour did not change appreciably when the dominant species of the species poor community was removed. This indicates that they were probably

Table 4. Mean persistence of four principal species in the removal experiment. The difference for each species between treatment and control is tested using two tailed t-test.

	Deschampsia flexuosa			
Species	Removed	Present	t statistic	Significance
Anthoxanthum alpinum	0.437	0.449	0.87	n.s.
Festuca rubra	0.592	0.414	3.22	$P < 0.05$
Nardus stricta	0.686	0.704	0.13	n.s.
Polygonum bistorta	0.493	0.441	0.41	n.s.

more influenced by the different nutrient status of the communities, not their species composition. *Polygonum bistorta* showed the same mobility in the species poor and species rich plots. It also did not respond to the removal of the dominant species. This species had constant spatial dynamics within a larger range of environmental conditions. In contrast to *N. stricta* or *Anthoxanthum* spp. the variation of mobility of *Festuca rubra* ran across the richness/climate favourability division. This species also responded strongly to the removal of the dominant species, indicating a plastic response in mobility to competition pressure (TURKINGTON et al. 1991). The apparent low persistence of *F. rubra* in some (namely species poor) plots seems to be due to the competition effect of its neighbours. When these species are absent, it behaves as a phalanx species. The gap colonization (the guerrilla component of its spatial behaviour) in this species is attained by the formation of extravaginal tillers; the known variability in the extravaginal/intravaginal tiller proportion (HERBEN et al. 1993b) may be one of the reasons for mobility difference.

Models such as those by BELL (1984) or CRAWLEY & MAY (1987) assume the species spatial dynamics is a species stable feature; this clearly does not hold for *F. rubra* (changes with competition) and for *N. stricta* (changes between sites). Whether the plasticity in the species mobility could contribute to the species coexistence remains to be demonstrated. However, KARLSON (1985) has demonstrated the role of genotypic differentiation in spatial growth pattern of a species for its coexistence with other species and the resulting community richness.

Though the present data demonstrate the grasslands are composed of coexisting species with high and low mobility, it does not enable one to determine whether this variation underlies the species richness of these grasslands. Demonstration of direct action and relative prevalence of such mechanism in the field is not a simple task. There are indirect ways to approach this problem. First, it is possible to assemble experimental communities with different sets of species differing in their spatial behaviour, as done by SCHMID & HARPER (1985). Ideally, different experimental communities should be assembled, with species differring in their spatial mobility parameters. The same approach could also be taken using a formal model with parameter values taken from the culture or field (BELL 1984, SILVERTOWN et al. 1992).

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