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SPATIOTEMPORAL DYNAMICS IN MOUNTAIN GRASSLANDS: SPECIES AUTOCORRELATIONS IN SPACE AND TIME

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Abstract: Permanent plots with a fine scale recording system were used to trace the spatiotemporal process within two mountain grasslands in the Krkonoše Mts., Czech Republic. The analysis used autocorrelation over increasing lags in space and/or time. Moran's *I* was used to measure the autocorrelation. There was a lot of variation between species both in spatial and temporal correlograms. The spatiotemporal pattern of species correlated well with the growth form of the species and the degree of its clonality. Clonally-growing species tended to have high clumping at distances of a few cells, whereas rosette species often did not show any clumping. The type of clonal growth (compact vs. long spacers) is well correlated with the temporal correlogram (species mobility). There is a relation between low mobility and high clumping at low distances. Attempts to explain the mechanisms of species coexistence in these grasslands should take into account the particular structure of the fine-scale dynamics of these communities of predominantly clonal plants.

INTRODUCTION

In several grassland types, plant species have been shown to exhibit considerable fine scale dynamics over a time scale of years (HERBEN et al. 1990, THÓRHALSDÓTTIR 1990, VAN DER MAAREL & SYKES 1993, SYKES et al. 1994). This is true for both short lived and perennial species (SYKES et al. 1994). In perennial grasslands, these fine scale dynamics have been demonstrated to be related to the predominantly clonal growth form of these species (LAW et al. 1994). Most studies on fine scale dynamics in grasslands up to now have ignored the spatial component of spatiotemporal process (but see MAHDI & LAW 1987, THÓRHALSDÓTTIR 1990). The term "mobility" used sometimes in the literature should, in its strict sense, apply only to explicit treatment of the spatiotemporal process. Significantly, the change of species composition in a particular site over time may show correlation with other events at different spatial scales; disappearance of an individual at one site may be compensated by a new appearance either at a closely neighbouring site, or at a greater distance, depending, inter alia, on the growth form of the particular species.

This study attempts to provide a fuller analysis of the spatiotemporal dynamics of grassland species. It primarily addresses the question of how the fine scale dynamics of species (i.e. rate of change at a particular microsite) are spatially intercorrelated, i.e. whether change in the species frequency at one site is correlated with change at a closely neighbouring site. It

further relates this type of correlation with the growth form of species, namely with different degree and type of the clonal growth. "High spatial resolution" permanent plots are used to record the spatiotemporal process within the community; the analysis is done using standard autocorrelation techniques.

METHODS

Study sites

Study sites were located in the grassland of the Krkonoše Mountains, North Bohemia, the Czech Republic. Data were collected at two localities: A species-rich locality, with ca. 4-7 species per 10 cm^2 and 25-30 species per 2500 cm^2 (Janovy boudy, 3.75 km ESE of Pec pod Sněžkou, latitude 50° 41' 28" N, longitude 15° 47' 35" E, altitude 880 m, slope 5°; plots J1 to J4). The second locality is a species-poor grassland with 2-4 species per 10 cm^2 and 6-10 species per 2500 cm^2 (Severka, 3 km NW of Pec pod Sněžkou, latitude 50° 41' 42" N, longitude 15° 42' 25" E, altitude approx. 1100 m, slope 8°; plots S1 to S4). The meadows are 300-400 years old. The Janovy boudy (species-rich) locality has a milder climate with a longer growing season (ca. 7-8 months), soils richer in magnesium and calcium and a lower C/N ratio than the Severka locality. Traditionally the meadows were mown in summer and grazed late in the autumn; they were manured once every few years. The mowing management was continued during the study. Since the present study was a part of a larger study of mountain grasslands, two plots of each series (S1, S3, J1, J2) were manured in autumn 1985 and 1989 (cow manure in species-poor plots and horse manure in species-rich plots, following the traditional treatment of these sites). This amounted to adding the following amount of nutrients (g/m^2): species-poor sites: Total N = 17, NO_3-N = 0.2, NH_4-N = 3.8, PO_4-P = 2.4; species-rich sites: Total N = 12.7, NO_3-N = 0.54, NH_4- N = 8.4, PO_4-P = 1.8. Both meadows can be classified in the *Sileno-Nardetum* (*Nardo-Agrostion*, *Nardetalia*); the species-rich one as subassociation *crepidetosum*, the species-poor one as subassociation *pleurozietosum* (KRAHULEC 1990). Except for *Euphrasia rostkoviana* at the species-rich locality there were only perennial species at both localities.

Data collection

Four permanent plots of 50 × 50 cm were established in 1984-1985 at each locality. Plots were selected subjectively, avoiding visible disturbance; within each locality, the distance between the most distant plots was less than 15 m. Plots were recorded either in mid June (species-rich) or mid July (species-poor) until 1993. A grid of 15 × 15 cells (cell size 3.3 × 3.3 cm) was established. The number of morphological units of all plants rooted in each cell was counted. For all grasses and graminoids, morphological units were tillers; for large forbs (*Ranunculus* spp., *Alchemilla* spp., *Polygonum bistorta*) morphological units were basal 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 to a height of 1 cm after recording.

The frequencies of species in the 225 cells are much higher in the species-poor plots (ranging from to ca. 40 in *Festuca rubra* and *Nardus stricta* to almost 200 in *Deschampsia flexuosa*) than in the species-rich plots (between 20 and 60; *Agrostis capillaris, Festuca rubra*

and *Anthoxanthum odoratum* ranged between 60 and 100). Only species occurring with frequency > 20 cells in at least two recordings of one plot were included in the study. Species within the genera *Alchemilla* and *Campanula* were treated as single species in the analyses since they were difficult to identify in the vegetative state.

Data analysis

The spatial pattern of species within individual plots was analyzed using Moran's *I*. In principle, calculation of $I(d)$ involves comparison of the abundance of a species in all pairs of grid cells situated at distance d from each other in a horizontal or vertical direction. If the abundance in both grid cells deviates in the same direction from the mean abundance per grid cell, this represents a positive contribution to $I(d)$; if the abundance is higher than average in one grid cell but lower than average in the other, this means a negative contribution. The formula for Moran's *I* is:

$$I(d) = \frac{n}{S_0} \sum_i \sum_j \frac{W_{i,j} \, (x_i - X) \, (x_j - X)}{(x_i - X)^2}$$

in which $I(d)$ is the autocorrelation for a distance of d grid cells; x_i and x_j denote the number of morphological units of the species in grid cells i and j, respectively; X is the average number of morphological units over all n grid cells; S_0 is the S-statistic according to rook's definition of contiguity of the quadrats and is determined by the dimensions of the grid; and $W_{i,j}$ is an element of the matrix (consisting of zeros and ones) determined by the distance d, indicating which pairs i and j are to be compared (Upton & Fingleton 1985). Clustering at distance d (further referred to as the lag in space d, or d=d) essentially means that relatively many grid cells lying at this distance from each other are similar and thus, results in a high $I(d)$ value for that species in the plot; with a regular distribution, at a distance equal to the average cluster size combinations of dissimilar pairs (one grid cell higher, the other lower than average) would be more common than expected, resulting in a negative $I(d)$ value. Since upper and lower bounds of $I(d)$ are not strictly fixed, values were rescaled to the variable $R(d)$ which lies between -1 and +1 (Upton & Fingleton 1985). This variable (Moran's R) is used in the current paper. These authors also provide formulae for the expected values and standard deviations of $I(d)$, from which a standard normal deviate [O(I) - E(I)] / sd(I) was calculated as a Z-value. For random patterns the Z-value approximately follows the standard normal distribution (Upton & Fingleton 1985). If the absolute value of Z exceeds 1.96, the 5% significance level, we considered the autocorrelation to be significant. The $R(d)$ or Z values may be plotted against distance d in spatial correlograms, showing how the autocorrelation value depends on the lag in space (i.e. the distance over which the autocorrelation is measured).

When repeated recordings of the same (permanent) grid are available, as in this case, the procedure outlined above can be extended in a fairly straightforward way to patterns in space and time. In that case, basically $I(d,t)$ is determined by the deviations of the abundances in grid cells at a specified distance (lag) in space (d) and time (t) from the overall mean abundance per cell. By putting d=0 and varying t, the temporal autocorrelation (related to persistence) can be calculated. Spatio-temporal autocorrelations at specific time and distance lags may be partly due to spatial clumping and carry-over through time. For example, strong spatial

clumping at d=1 in combination with high persistence of the clumps will lead to a positive autocorrelation at d=1, t=1. In addition, however, a high I(d=1, t=1) may result from the effects of processes actually influencing patterns in change. Thus, positive autocorrelation at, say, d=1, t=1 may be due to clonal propagation at a rate of 1 cell per year. In order to detect such effects while partialling out autocorrelations at lower spatial or temporal lags, we calculated partial autocorrelation coefficients according to UPTON & FINGLETON (1985: 202, 204).

Both spatial and temporal correlograms were summarized using principal component analysis. All plots within each site were analyzed together with autocorrelation at different lags as variables and each species within each plot as a separate case. Therefore, the analysis was performed on the $m \times d$ matrix of autocorrelations, where m is the product of number of species and number of plots and d is the maximum number of lags.

Species nomenclature follows TUTIN et al. (1964-1980) except *Anthoxanthum alpinum* Á. LÖVE et D. LÖVE, which is treated as a separate species here. The information on species biology comes from GRIME et al. (1988), HERBEN et al. (1993) and field observations at the localities.

RESULTS

Spatial pattern of species

Species varied greatly in spatial autocorrelation, ranging from very high clustering at lower lags (d=1,2 cells, as, e.g., in *Nardus stricta*; Fig. 1) to almost complete spatial independence (as in *Ranunculus acris*). No species, however, showed any other significant peak except the peak at lag d=1; this indicates there is no regular pattern of spatial distribution of clumps in any species.

The variation in spatial autocorrelation among species was summarized using principal component analysis. The first two axes accounted for 61.1 % of the total variance in the species-poor site and 54.0 % in the species-rich site (7 variables; separate analyses were run for each locality). In both species-rich and species-poor sites the structure of the PCA loadings is very similar (Tab. 1, Fig. 2). Smaller spatial lags (1, 2, 3, 4 cells; up to 6 in the species-poor site) have high positive loadings on the first axis; it expresses an overall strength of the clumping of a species. The second axis has negative loadings for lags of 1 and 2 cells, but positive loadings for higher lags (5,6,7). It then expresses the steepness of decrease of the correlogram curve. The positions in the plot of the first two axes correlate well with the growth form of species (Fig. 2). In the upper left corner there are species which show low overall clumping and no difference between clumping at large and small lags; those are rosette species, e.g., *Ranunculus acris*, *Alchemilla* spp., *Rumex acetosa*, etc. In the lower left, there are tussocky species with small and strong clumps (sharply decreasing correlograms; *Nardus stricta, Luzula multiflora*), whereas in the right there are species with loose tussocks (slowly decreasing correlograms, e.g. *Carex pilulifera, Veronica chamaedrys*).

Fine scale persistence of species

Autocorrelation in time also varied considerably among species both in species-rich and species-poor sites (Fig. 3). The correlogram shape invariably decreased with increasing time

Table 1. PCA axes loadings. Each species and each plot is taken as a separate case; autocorrelations at different lags for the particular species and plot are taken as variables.

	Spatial correlograms			
	Species-poor locality		Species-rich locality	
Lag (cells)	Axis 1	Axis 2	Axis 1	Axis 2
1	0.3060	-0.4808	0.4455	-0.3361
2	0.3665	-0.4627	0.5255	-0.2806
3	0.4596	-0.2226	0.4940	0.0269
4	0.4615	0.0817	0.4434	0.2384
5	0.4225	0.3286	0.2697	0.4478
6	0.3638	0.4241	0.1086	0.5829
7	0.1923	0.4589	-0.0128	0.4587
	Temporal correlograms			
	Species-poor locality		Species-rich locality	
Lag (years)	Axis 1	Axis 2	Axis 1	Axis 2
1	0.3627	-0.5991	0.4699	-0.6655
2	0.4532	-0.4333	0.5201	-0.3057
3	0.5266	0.0298	0.5201	0.3717
4	0.4827	0.3694	0.4881	0.5705
5	0.3908	0.5621		

lag; absolute higher values indicate species with higher persistence at the site. The pattern in these correlograms was also summarized using principal component analysis. The first two axes account for 95.4 % of the total variation in the species-rich site and 96.2 % in the species-poor site (Fig. 4; 4 variables in the species-rich site and 5 variables in the species-poor site). The first axis separates species with high overall autocorrelation in time (high persistence, i.e. low mobility) from species of low autocorrelation. The position along this axis (persistence) is well correlated with the species growth form. In the species--rich site, the annual *Euphrasia rostkoviana* has a very low persistence; also stolon-forming species, e.g., *Campanula* spp., *Achillea millefolium, Veronica chamaedrys, V. officinalis* show a low persistence. Conversely, rosette-forming *Ranunculus acris* and *Carex pilulifera* have a high persistence. The same patterns occur in the species-poor site, where the stolon-forming species *Vaccinium myrtillus* and *Deschampsia flexuosa* show low persistence, whereas tussocky species (*Nardus stricta, Festuca rubra*) show high persistence.

The second PCA axis (accounting for 13.2 % in species-rich site, and 28.2 % in species-poor site) separates species with decreasing autocorrelation with increasing time lag (sloping correlogram) from species with non-sloping correlograms. Both in the species-poor and species-rich sites, grasses (*Anthoxanthum* spp., *Nardus stricta, Festuca rubra, Poa pratensis, Deschampsia flexuosa*) have negative scores on the second axis (i.e. show decreasing autocorrelation), no matter whether they show low or high overall persistence. In contrast, dicots (mainly rosette ones) are in the upper (non-sloping) part of the graph. In the species-poor site, clearly non-sloping correlograms are shown by the only dicot *Polygonum bistorta*, and by *Festuca rubra* (in some plots only).

Spatiotemporal autocorrelations

Partial autocorrelation based on Moran's R for lag = 1 in space and time (i.e. the correlation with the neighbouring cell over a time interval of one year) shows variation between species, and clearly separates species with and without clonal growth (Fig. 5). In the species-rich site, of the species with the lowest persistence, the stoloniferous *Veronica officinalis* has high

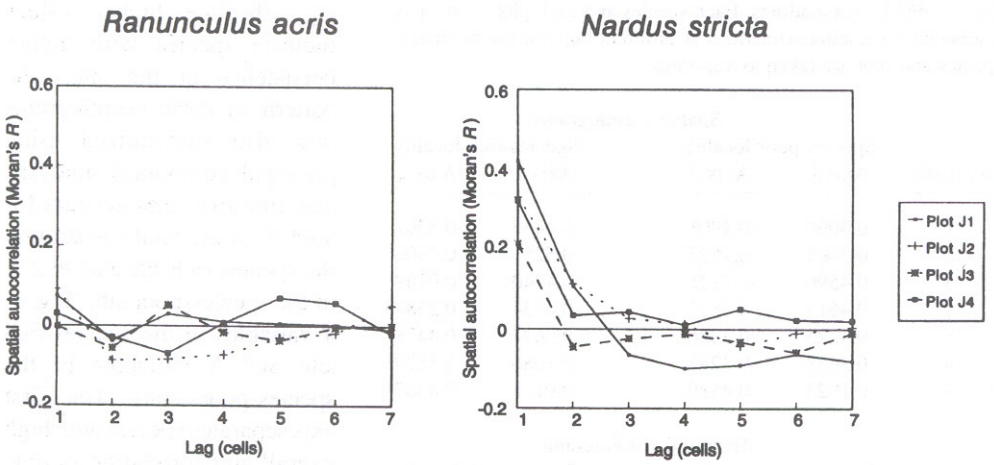

Fig. 1. Examples of spatial correlograms. Each line represent average correlograms of all recordings of the plot.

partial autocorrelation, whereas the annual *Euphrasia rostkoviana* has almost zero partial autocorrelation. Species with high persistence and low partial autocorrelation are rosette species with seed reproduction (most typically *Ranunculus acris*, then *Polygonum bistorta*, *Alchemilla* spp., *Rumex acetosa*); species with low persistence and high partial autocorrelation are non-rosette non-tussocky stoloniferous plants (*Galium pumilum*, *Campanula* spp., *Agrostis capillaris*, *Hypericum maculatum*, *Deschampsia flexuosa*, *Veronica chamaedrys*). In the species-poor locality, there is considerably less variation in autocorrelation between individual species. Still, on a qualitative level, it separates species of high persistence and clonal growth (*Nardus stricta*), species of low persistence and high clonal growth (*Deschampsia flexuosa*), from species of clonal growth at different rates or other means of propagation through the community. These three species also differ in their persistence.

The positive values of partial autocorrelations for lags d=2 and t=1 separate highly stoloniferous species (*Carex pilulifera, Galium pumilum, Veronica chamaedrys, Achillea millefolium* at the species-rich site, and *Polygonum bistorta* and *Vaccinium myrtillus* at the species-poor site; data not shown), from other species. The latter group comprises species not able to form longer stolons (with high partial autocorrelations at d=1, t=1) and non-clonal species (with low partial autocorrelations at d=1, t=1). The partial autocorrelations at lag d=3 and t=1 seem to yield very little information; they show high non-systematic spread both within and between species (data not shown).

Relation between spatial and temporal correlograms

There is only a weak relation between the degree of spatial clustering and species persistence. Correlation of Moran's *I* for spatial lag = 1 with Moran's *I* for temporal lag = 1 is very low for the species-rich site (R^2=0.043); it is higher in the species-poor site (R^2=0.20). There is also a marginally significant relation between overall persistence (expressed as the score on

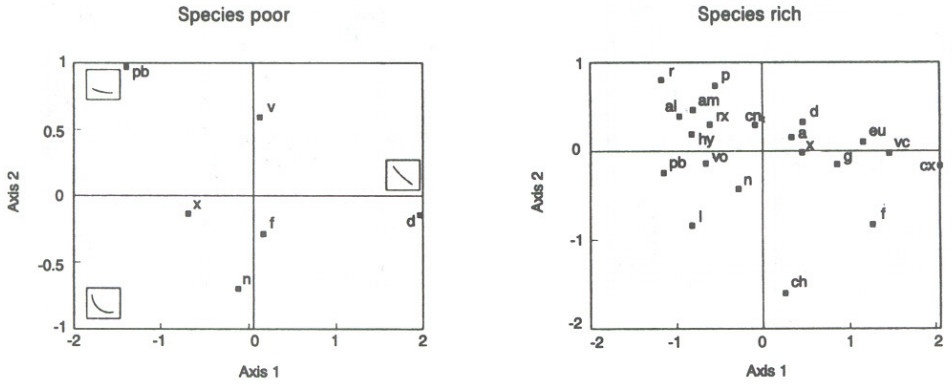

Fig. 2. Ordination of spatial correlograms in the plane of the first two PCA axes. Each point is the mean position of a species, averaged over plots and recording times. Typical correlograms for extreme values of the PCA scores are shown in the plot corners. Species abbreviations: a: *Agrostis capillaris*, al: *Alchemilla* spp., am: *Achillea millefolium*, ch: *Cardaminopsis halleri*, cn: *Campanula* spp., cx: *Carex pilulifera*, d: *Deschampsia flexuosa*, eu: *Euphrasia rostkoviana*, f: *Festuca rubra*, g: *Galium pumilum*, hy: *Hypericum maculatum*, l: *Luzula multiflora*, n: *Nardus stricta*, p: *Poa pratensis*, pb: *Polygonum bistorta*, r: *Ranunculus acris*, rx: *Rumex acetosa*, v: *Vaccinium myrtillus*, vc: *Veronica chamaedrys*, vo: *Veronica officinalis*, x: *Anthoxanthum* (*A. odoratum* in the species-rich site, *A. alpinum* in the species-poor site).

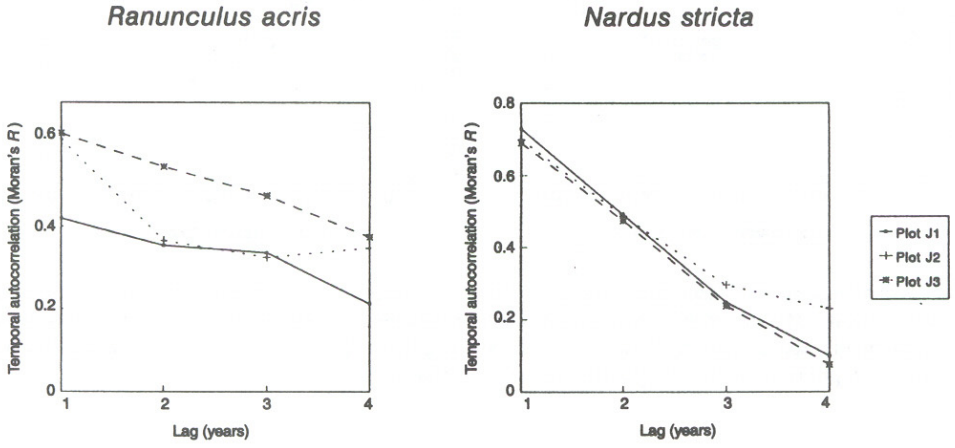

Fig. 3. Examples of temporal correlograms.

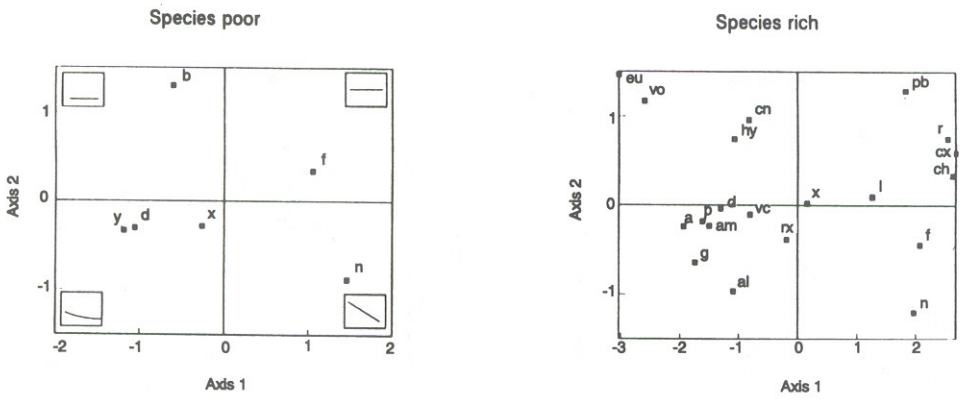

Fig 4. Ordination of temporal correlograms in the first two PCA axes. Each point is the mean position of a species, averaged over plots and recording times. Typical correlograms for extreme values of the PCA scores are shown in the plot corners. Species abbreviations see Fig. 2.

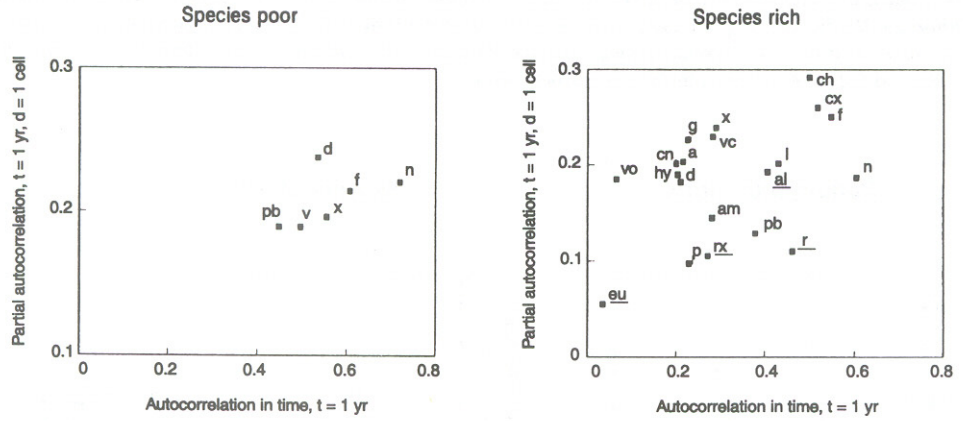

Fig. 5. Spatiotemporal autocorrelations of species. Abscissa: Moran's *R* of temporal autocorrelation over lag t=1, d=0; ordinate: Moran's *R* of partial spatiotemporal autocorrelation over lag t=1, d=1. Each point is the mean position of a species, averaged over plots and recording times. Species abbreviations see Fig. 2. Names of species with primarily non-clonal growth form are underlined.

PCA axis 1 in Fig. 4) and clumping at lesser distances (expressed as the score on PCA axis 2 in Fig. 2). Species showing a tendency to clump are also less dynamic over time (Fig. 6). One species (*Ranunculus acris*) does not fit into this overall pattern, showing high persistence and almost no clumping.

DISCUSSION

Spatial pattern

The differences in spatial pattern between the species are clearly related to their growth form (cf. GREIG-SMITH 1979), with plants growing in tussocks or with short runners showing most pronounced clumping. In the species-poor site, a higher proportion of the species shows clumped patterns than in the species-rich site. Similarly, the pattern of *Agrostis tenuis* (= *A. capillaris*) in species-poor Snowdonian uplands was strongly clumped (KERSHAW 1958), while clumping was much less pronounced and restricted to smaller distances/scales in species-rich chalk grasslands (MAHDI & LAW 1987, VAN DER HOEVEN et al. 1990). Whether this is a more general phenomenon remains to be seen, however.

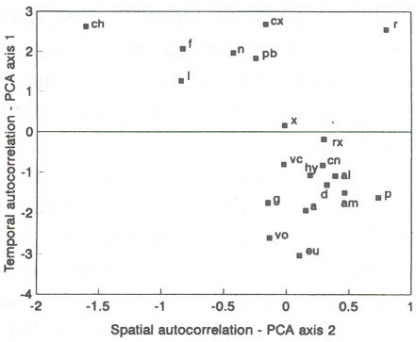

Fig. 6. Relation between spatial and temporal correlograms in the species-rich site. Abscissa: average species score on axis 2 of PCA of spatial correlograms (in Fig. 2; low scores indicate strong clumping at small distances); Ordinate: average species score on axis 1 of PCA of temporal correlograms (in Fig. 4; low scores indicate low overall persistence). Spearman's correlation coefficient R=-0.421, P=0.067. Each point is the mean position of a species, averaged over plots and recording times. Species abbreviations see Fig. 2.

Some species occurring in both localities show interesting shifts in the PCA plots. In *Polygonum bistorta*, clumping is less in the species-poor than in the species-rich site; perhaps this simply reflects differences in average size of the individuals. In contrast, the grasses (*Anthoxanthum* spp., *Deschampsia flexuosa*, *Festuca rubra* and *Nardus stricta*) show stronger clumping in the species-poor site. *Deschampsia* and *Festuca* show opposite trends along the first axis: while *Festuca* tends to have larger, more diffuse clumps in the species-rich locality, *Deschampsia* does so in the species-poor locality. We are not able to offer an explanation for these differences.

Clonal growth and spatiotemporal dynamics

Rather high values of temporal autocorrelation indicate that many species are present over long term intervals in at least part of the cells. Obviously, the only annual differs from the perennials in this respect, but there is a lot of variation even among the rest of the species. This variation corresponds well with the growth form of the species (see also LAW et al. 1994). The shape of the temporal autocorrelograms (sloping vs. non-sloping) may be explained by differential mortality of plant individuals. If the mortality chances for all individuals are similar, the species will show a regular sloping autocorrelogram (as, e.g., in *Nardus stricta*). These are mainly grasses, i.e. the species with almost identical modules and a strong clonal component of spreading. They also show high partial autocorrelation at d=1, t=1. In contrast, the non-sloping curves shown, e.g., by *Ranunculus acris*, are of those species which show different mortality rates for different individuals. These are often non-clonal species with

modules varying in size, with several "core" long-lived individuals; outside them, there is a continuous establishment and disappearance of small seedlings.

The partial autocorrelation over nonzero spatial lags and time lag = 1 yr may be interpreted as a net component of expansion into neighbouring cells at the horizontal speed of d cells per year. This type of dynamics is most likely due to clonal growth. The species with highest partial autocorrelation at d=1, t=1 are indeed species with a strong clonal component of spreading (*Cardaminopsis halleri, Carex pilulifera, Festuca rubra, Anthoxanthum* spp., *Veronica chamaedrys*, *Polygonum bistorta*; unpubl. data). The species with high values at both d=1 and d=2 are most probably those able to expand clonally at a higher speed (higher than one cell per year), but not with spacers with a length beyond the size of one cell (*Veronica chamaedrys, Carex pilulifera*). In contrast, negative partial autocorrelations at d=2 combined with relatively high positive ones at d=1 mean that in such species increase is strictly limited to the immediate neighbourhood of the clumps (*Festuca rubra, Nardus stricta, Cardaminopsis halleri*).

The overall variation in partial autocorrelations (lags d=0 to d=2, at t=1) is highly multidimensional. This is most probably due to the fact that different growth patterns may lead to very different combinations of values at d=1 and at d=2, and these seem to be nonlinear responses, which are not well summarized by the PCA.

Differences between species-poor and species-rich localities

It is remarkable that a species-rich site shows much more variation in both spatial and temporal autocorrelation values of species. This may be the simple effect of a limited species pool in the species-poor site and the restricted variation may be simply due to a rarefaction process. However, some growth forms which are richly represented by species in the species-rich locality are missing from the species-poor locality, where mainly grasses are prevalent. There are several possible explanations of this fact. (a) It is possible that the limited nutrient supply in the species-poor site, possibly in combination with a short growing season, allows only plants of a few specific growth forms (rosettes or tufts, meristems at ground surface, strong root system) to grow there, while the environment in the species-rich site is more conducive to several growth or life forms. (b) The adversity of conditions at the species-poor locality may also underlie a more functional explanation: higher species-richness (due to ameliorated growing conditions) is only possible if additional species are in some way complementary in their behaviour (for a discussion, see WERGER et al. 1987). This would involve a limit on number of species able to coexist having the same growth form, and expect some form of "niche differentiation" to be necessary for coexistence (WILSON & ROXBURGH 1994). More data from different grassland types would be necessary to exclude or support any of these hypotheses.

Coexistence of clonally growing species

With a few exceptions, the majority of the plants in the studied grasslands grow clonally; this type of growth seems to account for a large part of the observed dynamics. Current research on clonal plants, based on concepts of foraging and clonal integration (for a review, see HUTCHINGS & DE KROON 1994), studies clonal growth and resulting spatial dynamics of a target plant, but its neighbouring plants are often treated as immobile "blocks" in the spatial

mosaic of the environment (LOVETT DOUST & LOVETT DOUST 1985). The environment is thus understood as spatially heterogeneous, but the dynamics of this heterogeneity is not taken into account (but see OBORNY 1994b). If this heterogeneity is due to other clonal plants present, it may show a considerable dynamics of its own, as shown also by the present study. These dynamics depend on the entire composition of the community, since the strengths and maximum lags of spatiotemporal correlations differ between species, though virtually no species in the current study was truly "immobile". The biotic environment of a module of any given species then depends not only on the spatial pattern of the habitat, but also on the dynamics of this spatial pattern (OBORNY 1994a, b) with important implications for the selective forces acting in such a community (TURKINGTON 1989, SCHMID 1990). The prevalence of short range clonal growth (which manifests itself as a partial spatiotemporal correlation at nonzero time and space lags) determines also the type of the models suitable to analyze such systems. Whereas systems with interactions over longer distance are best modelled using lottery models (CHESSON & WARNER 1981), cellular automata are much more suitable for systems with correlation at small spatial lags (CZÁRÁN & BARTHA 1992), since they are capable to account for spatially structured processes.

Grasslands are not an exception in their high proportion of clonally growing species (PRACH & PYŠEK 1994). In communities with prevailing non-clonal plants (as most forests, for example) the species persistence depends on successful seedling establishment which may be independent of the spatiotemporal pattern of the community. In contrast, in communities of clonal plants, the structure of the spatiotemporal mosaic may be critical for a species with given growth form and type of clonal growth to persist. Since clonal plants do not spread over long distances, the regeneration gap should appear at the particular point in time **and** space. Modelling studies show that species coexistence in such communities is dependent on the reciprocal ability of neighbouring plants of different species to match each other in their spatial dynamics (BELL 1984) and there is even experimental evidence for this (SCHMID & HARPER 1985, TURKINGTON 1989, TURKINGTON et al. 1991). Attempts to explain the mechanisms of species coexistence in these grasslands should take into account this high fine scale dynamics.

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