Plant Ecology **174:** 319–336, 2004.

Below-ground spatial pattern of rhizomes in a grassland community and its relevance to above-ground spatial pattern

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Received 14 April 2003; accepted in revised form 8 October 2003

Key words: Clonal growth, Fine-scale, Mountain grassland, Soil block, Spatial autocorrelation

Abstract

Studies of spatial patterns in grassland plant communities have focused on above-ground patterns, ignoring the fact that in clonal plant communities, such as those found in grasslands, above-ground spatial structure must reflect below-ground horizontal growth. The present study examines, at both a fine and a coarse spatial scale, relationships between rhizome and ramet distribution. At the coarse scale, the dominance of species differed between above- and below-ground; some species dominated only above- or below-ground, and others dominated in both layers. At the fine scale, a single species' ramet aggregation above-ground significantly differed from its rhizome aggregation below-ground, for many species. Even for a given species, quantitative relationships between above- and below-ground dominance varied among localities. The variation in spatial pattern among species can be explained by attributes of clonal growth form, including rhizome size, rhizome origin and pattern of above-ground ramet aggregation. Using these parameters of clonal growth, four major space occupation patterns were described for mountain grassland species. For species with a high abundance of evenly distributed rhizomes, ramets either i) reflect rhizome distribution, or ii) do not fully reflect rhizome distribution, but rather are spatially aggregated, and rhizomes are typically developed below-ground. For species with a low abundance of rhizomes, ramets either iii) reflect rhizome distribution and rhizomes are typically of above-ground origin, or iv) do not reflect rhizome distribution and are aggregated only at the growing tips of rhizomes. Spatial correlation above-ground among species was the same as below-ground for some pairs of species but was significantly different for other pairs.

Introduction

Spatial pattern is one of the most conspicuous features of plant communities. Spatial arrangement of plant individuals reflects historical contingencies of the particular community and thus may shed light on processes that have operated in the past (Callaghan 1984; Thórhallsdóttir 1990). At the same time, the spatial pattern of plant individuals constrains their potential to interact and thus has dynamic consequences on future community interactions (Herben et al. 2000). Plant community spatial pattern itself is not static, with recent studies documenting fast dynamics, mainly at small spatial scales (van der Maarel and Sykes 1993; Thórhallsdóttir 1990; Herben et al. 1993a).

To date, almost all studies of plant community spatial patterns have paid attention only to above-ground plant parts. Owing to the scarcity of information on below-ground processes, we know very little about the degree to which above-ground spatial patterns correspond to below-ground patterns (see Casper and Jackson 1997), and how below-ground structures affect dynamics of above-ground spatial patterns. Failure to consider below-ground processes can represent a major oversight, as in many communities such pro-

cesses are likely to be major determinants of the community structure and dynamics. For example, competition for soil resources is often the most important process accounting for species composition and dominance (Wilson 1988).

In temperate climates, below-ground structures (roots, rhizomes, tubers) are often much more persistent than the above-ground plant parts (Palmer 1958; Klimeš et al. 1997; Tamm et al. 2002). Due to short lifespan of shoots, the final above-ground spatial pattern depends on year-to-year variation in the spatial position of shoot-producing buds activated on below-ground structures in a certain year. Thus information on spatial patterns of rhizomes, their growth, and/or bud activation can reveal processes directly responsible for above-ground spatial patterns. However, there is not a one-to-one correspondence between above- and below-ground spatial patterns, as dominance and spatial correlation of species may differ dramatically below the soil surface (Antos 1988).

The other dimension contained in the spatial pattern of a community is a history of species interactions. Plant ecologists have described above-ground spatial correlations among species and have inferred possible mechanisms of species interactions and coexistence from them (Zobel et al. 1994; Herben et al. 1993a; Law et al. 1993; van der Maarel and Sykes 1993). Researchers rarely determine whether these above-ground spatial correlations and the conclusions drawn from them are consistent with what they might find below-ground for a given community. Based on recent studies of roots and above-ground structures (Pecháčková et al. 1999; Titlyanova et al. 1999), Pecháčková et al. (1999) concluded that spatial patterns and processes in root layers and above-ground parts of a grassland community are partly independent of each other. It is very likely that spatial correlations among ramets of different species differ from correlations among their rhizomes, but there are no data to support this expectation or show the level of differences.

Although there is a large body of literature on physiology and ecology of rhizome growth in clonal plants (for reviews see van Groenendael and de Kroon 1990; de Kroon and van Groenendael 1997; Stuefer et al. 2002), most of the available data come from garden or greenhouse experiments on single plants. Very little is known about rhizome spatial patterns or their linkage to above-ground spatial patterns at the community level in the field.

Parameters of clonal growth have often been invoked for the interpretation of spatial pattern and its temporal change in communities of clonal plants (Thórhallsdóttir 1990; van der Maarel and Sykes 1993; Herben et al. 1993a; Klimeš 1999). However, there has never been an attempt to link data for above-ground spatio-temporal patterns and rhizome distribution of component species. The aim of this study, therefore, was to identify to what extent the above-ground spatio-temporal pattern in a community of clonal plants can be ascribed to spatial distribution of rhizomes. A grassland was chosen as the model community as it is largely dominated by clonal plants. In addition, most studies dealing with community spatial pattern have been done in grasslands (see Herben et al. 1993a; Law et al. 1993; Titlyanova et al. 1999; van der Maarel and Sykes 1993) and the major features of spatial and spatio-temporal structure of these communities have therefore already been described.

I attempted to answer the following questions:

1. How closely does community spatial distribution of ramets match distribution of rhizomes?
2. Are fine-scale correlations among ramets of one species matched by similar correlations among its rhizomes?
3. Are there correlations between parameters of spatio-temporal dynamics (ramet longevity, rhizome origin and vegetative mobility) and species spatial distribution, considering both above-ground and below-ground spatial patterns?
4. Do the spatial correlations among species differ between below-ground and above-ground?

In order to collect data on below-ground structure and its correlation with above-ground patterns, I took soil blocks from two grassland communities from which detailed spatio-temporal data were available from earlier studies (Herben et al. 1993a,b, 1995 and 1997a,b). I recorded above-ground (ramet) occurrence at a fine scale, separated all rhizome connections within the soil blocks, identified them to species, and determined below-ground to above-ground pattern correlations using a variety of autocorrelation and cross-correlation techniques. In addition, I compared above-ground spatio-temporal dynamics of these species, known from long-term, fine-scale permanent plots (Herben et al. 1993a), to the spatial structure of their rhizome systems.

Methods

Study sites

The study sites are located in mountain grasslands of the Krkonoše Mountains (Czech Republic). Data were collected at two localities where studies on the above ground spatio-temporal dynamics (Herben et al. 1993a,b, 1995 and 1997a,b) and on root distribution (Pecháčková et al. 1999) have been done. The first site is a species-poor grassland (3 km NW of Pec pod Sněžkou, latitude 50°41'42'' N, longitude 15°42'25''E, altitude approx. 1100 m, slope 8°) with 2-4 species per 10 cm^2 and 6-10 species per 2500 cm^2. The second site is a species-rich grassland (3.75 km ESE of Pec pod Sněžkou, latitude 50°41'28'' N, longitude 15°47'35''E, altitude 880 m a.s.l., slope 5°) with ca. 4-7 species per 10 cm^2 and 25-30 species per 2500 cm^2. These grasslands were established in about the 17th century and may now have reached a more-or-less stable species composition. They have been maintained by annual mowing and by manuring once every few years. The species-poor grassland is classified in the *Nardo-Agrostion* alliance, and the study area is situated in a part of the site influenced by irregular mowing and horse grazing. The species-rich grassland is classified to *Polygono-Trisetion*. The species list for both localities, with species codes and samples in which they occur is in Appendix 1. Species nomenclature follows Tutin et al. (1964-80).

Data collection

At each locality, four soil blocks, each 22.5 × 12.5 cm ($\approx$ 280 cm^2) were taken to a depth of 6 cm in 1995, as preliminary studies indicated that rhizomes have a maximum depth of 6 cm in these two localities. Before excavation, the above-ground frequencies of all plant species in the soil blocks area were recorded using a grid with a 2.5 × 2.5 cm cell size (presence/absence of all rooted plants per cell).

A special technique was developed to study the below-ground horizontal separation of plant individuals and species. Soil cores were excavated and then fixed using a special needleboard (size of board corresponded to the size of the soil blocks). The needleboard construction was a modification of the pinboard method of Schuurman and Goedewaagen (1965) used for the vertical study of root systems. The needleboard consisted of a plastic board with 8-cm-long steel needles fixed perpendicular to it following the same grid that was used for the documentation of above-ground frequencies. After the needleboard was pushed into the soil surface the bottom layer with fine roots was removed and the soil was gently washed out from the surface of this layer with a stream of water. The complete spatial structure of species-specific rhizome systems of all species was drawn beginning with the bottom of the soil blocks (at 6 cm depth) and working up to the soil surface (each finished layer was cut after recording and next layer was washed). As a result, each soil blocks was represented by a series of maps with a square grid (2.5 × 2.5 cm), each of them corresponding to one "working" layer. The distance between layers was about 1 cm. The positions of the rhizome penetration from one layer to the adjacent one constituted connections between layers. The diameter of rhizomes was also recorded.

The vector data were created from scanned maps of the drawn rhizome systems, using the geographic information system TOPOL (1996). The rhizome system of each species was given as a set of coordinates for each layer, and layers were exactly connected to each other. These databases of coordinates were connected with "attribute" databases of rhizome diameter and species identification.

Data analysis in GIS

The rhizome features of individual species were evaluated from the coordinate and attribute databases by spatial analysis, using a GIS program, GenaMap (1995). Rhizome volume was calculated from data on diameter and length, assuming rhizomes have a cylindrical shape. The total length and volume of rhizomes were calculated for each species for each cell of the spatial grid in each horizontal layer. This three-dimensional spatial depiction of rhizomes was reduced to a horizontal pattern, by collapsing all the "working" layers to a single layer. The following variables are available for each grid cell: i) presence or absence of species above-ground and ii) rhizome length and volume of each species. Data were recorded in 45 cells per soil blocks. Finally, data for above-ground and rhizome layers at two different spatial scales (soil blocks or cell) were obtained for further analysis. Figure 1 shows a schematic diagram of one soil blocks and one cell.

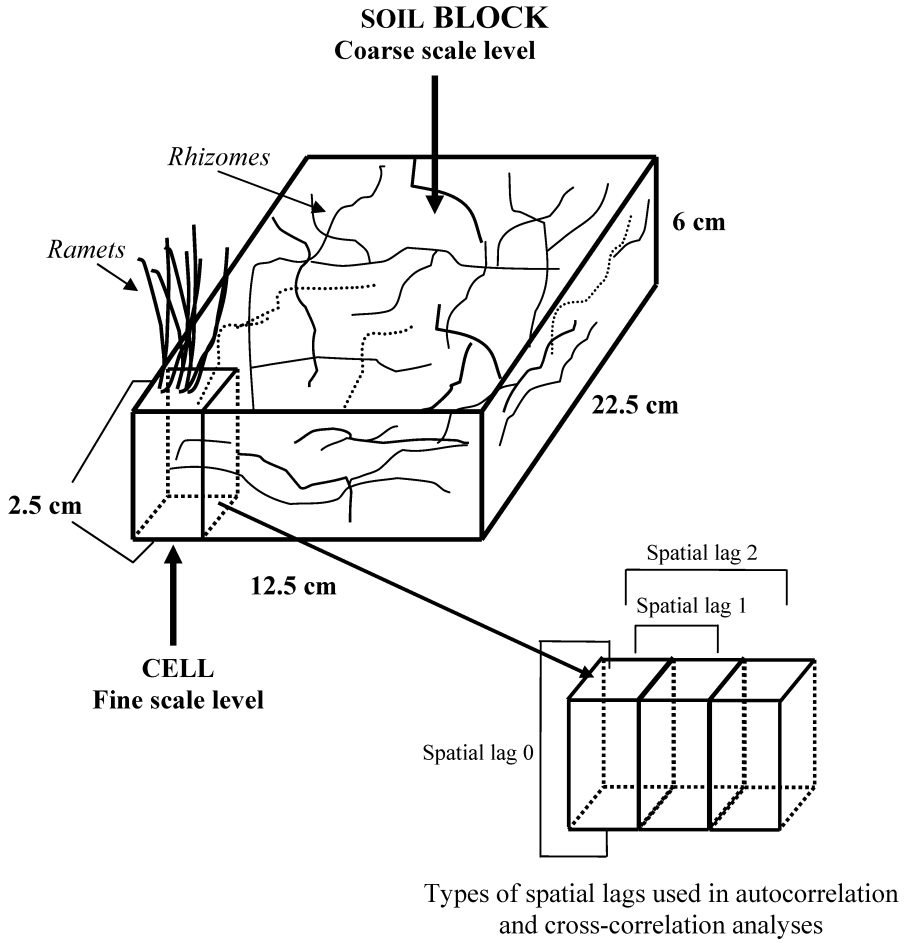

Figure 1. Schematic diagram of rhizome data collection at the soil blocks and cell level, and a close-up of three cells, showing the spatial relations considered in correlation and cross-correlation analysis for ramets, rhizomes, and ramets and rhizomes.

Comparison of diversity in above-ground versus rhizome layer

Species diversity above-ground and in the rhizome layer (defined by the length and volume of rhizomes) was estimated by the Simpson (1949) index of dominance (*SI*). Simpson's index was calculated at the soil blocks (coarse scale) and cell (fine scale) levels. The average values for each locality were calculated as

$$SI = \sum (n_i/N)^2$$

where n_i for above-ground at coarse scale is the number of cells occupied by species i in a soil blocks (frequency) or at the fine scale its presence/absence in a cell; for below-ground n_i is the sum of the rhizome length (volume) of species i in a soil blocks or cell; N is the frequency/presence in above-ground or the sum of the rhizome length (volume) of all species in a soil blocks (cell). The differences in values of the Simpson index between variables and localities were tested with two-tailed t-tests.

Comparison of individual species spatial distribution in above-ground versus rhizome-layer

First, the frequency, represented by the number of cells in which individual species occurred above-ground, was compared with their frequency below-ground for each community. Then, I used a one-way ANOVA to compare the length of rhizome of individual species between cells in which the species was present above-ground and cells in which they were absent.

Table 1. Total rhizome length and rhizome volume in the soil blocks and in the cell. Mean (± S.D.) Simpson index of diversity, given by length of rhizomes, volume of rhizomes and above-ground frequency per soil blocks, and presence per cell for each locality. At the soil blocks level, the differences between Simpson index values and between localities were tested by two-tailed t-tests. Significance of t-test is marked for comparison in columns by letters in superscript ($p < 0.05$). At the cell level, no t-tests were done because of spatial dependence of individual cells.

	Species-poor community	Species-rich community	t-test
Per soil blocks	n = 4	n = 4	Comparison in rows
Total rhizome length [cm]	759.02 ± 455.16	930.21 ± 513.95	p = 0.047
Total rhizome volume [cm^3]	7.99 ± 3.04	15.27 ± 5.00	n.s.
Simpson index			
Rhizome length	0.49 ± 0.12[a]	0.25 ± 0.10[a]	p = 0.039
Rhizome volume	0.31 ± 0.04[a]	0.33 ± 0.12[b]	n.s.
Above-ground frequency	0.27 ± 0.05[a]	0.20 ± 0.07[ab]	n.s
Per cell	n = 180	n = 180	
Total rhizome length [cm]	16.45 ± 15.47	20.67 ± 15.76	
Total rhizome volume [cm^3]	0.17 ± 0.33	0.34 ± 0.27	
Simpson index			
Rhizome length	0.67 ± 0.21	0.47 ± 0.21	
Rhizome volume	0.68 ± 0.23	0.56 ± 0.22	
Above-ground presence	0.69 ± 0.28	0.58 ± 0.29	
Number of species below-ground	2.18 ± 0.95	3.81 ± 2.09	
Number of species above-ground	1.58 ± 1.03	2.12 ± 1.06	

Table 2. Analysis of variance (ANOVA) of species relative abundance at the core level as an effect of species, locality, and placement. The variable placement means that abundance of species was defined either by ramets or by rhizomes.

Tested variable	df	MS	F	P
Placement	1	0.138	2.807	0.099
Locality	1	0.629	12.834	0.001
Species	15	0.380	7.751	0.000
Placement* Locality	1	0.079	1.622	0.208
Placement* Species	15	0.035	0.716	0.759
Locality * Species	8	0.093	1.897	0.076
Placement * Locality * Species	8	0.040	0.811	0.595

Species contribution to community structure

The dominance of individual species in above-ground and in rhizome layer for both localities together was characterized by the average relative abundance (RA) of individual species in the soil blocks.

$$RA_i = n_{ij} / \sum N_j$$

where n_{ij} is the frequency in above-ground or the sum of the rhizome length of species i in soil blocks j; N_j is the frequency in above-ground or the sum of the rhizome length of all species in a soil blocks (cell) j. ANOVA was used to identify the effects of locality, species and reference to above-ground or rhizomes (SPSS version 10; ANONYMOUS, 2000).

Multivariate analysis of above-ground versus below-ground community structure at fine scale

The above- and below-ground community spatial structure for each locality was characterized by principal component analyses (PCA) based on individual grid cells. The relative abundance of species below-ground calculated from rhizome lengths and above-ground calculated from ramet presences in each cell were used for the analysis. Reference of single case to individual cores was used as a covariate. Separate analyses were performed for each locality.

Autocorrelations and cross-correlations of individual species spatial pattern

Spatial distribution of the rhizomes and the occurrence of individual species above-ground were analysed by an index Moran's *I*. Moran's *I* is a measure of spatial autocorrelation of a variable value at a given spatial position with that same variable moved by a defined horizontal distance (termed the spatial lag). If

the value of the Moran's *I* is positive at a given spatial lag, it indicates the existence of periodic structures of the same range as the lag value, whereas a negative value indicates a negative co-variation at that scale. Moran's *I* can also be used for cross-correlation where the value of one variable at a given position is correlated with the value of a different variable at another position (for definition of Moran's *I* see Upton and Fingleton 1985).

Moran's *I* was used to analyse above-ground and rhizome spatial pattern for each species separately (above-ground autocorrelation A-A and rhizome autocorrelation R-R) and across above-ground and rhizome structures (cross-correlation A-R). Autocorrelation analyses were assessed at spatial lags of 1 and 2 neighborhood cells (1 lag = one cell = 2.5 cm) and cross-correlation at 0, 1 and 2 spatial lags. The spatial lag 0 means correlation of the same cell but between two different layers, above-ground and below-ground. Analyses were conducted for each of the eight soil blocks separately, but only the mean values across soil blocks is presented. The significance was determined using Monte Carlo permutations: i) by full randomisation for autocorrelations and ii) by toroidal shifts, rotation and reflection for cross-correlation; each soil blocks was permuted independently (Palmer and van der Maarel 1995). The spatial performance of individual species was summarised by the centred PCA of the correlation matrix of the seven correlation parameters given by Moran's values (A-A lag 1; A-A lag 2; R-R lag 1; R-R lag 2; AR-lag 0; AR-lag 1 and AR-lag 2).

Relationship of spatial structure and other plant attributes

The correlation between species spatial pattern (= autocorrelation and cross-correlation parameters) and explanatory variables such as ramet longevity (data from Herben et al. 1993a; in that study authors defined above-ground ramet longevity as "plant mobility"), rhizome origin (above-ground or below-ground) and vegetative mobility (=size of rhizome) (Klimeš et al. 1997; data from CLO-PLA1 database http:/www.butbn.cas.cz/klimes/) was assessed by redundancy analysis (RDA). RDA is a canonical form of PCA that identifies major gradients within the set of dependent variables (Jongman et al. 1995). The significance of the maximum amount of explained variance was tested using Monte Carlo permutation tests; each soil blocks was permuted independently by toroidal shifts, rotation and reflection (Palmer and van der Maarel 1995). The species growth forms (rhizome origin and rhizome size) and mobility characteristics are summarized in the Table 3. All multivariate analyses (PCA and RDA) were done using the program CANOCO version 4 (ter Braak and Šmilauer 1998).

Results

Overall rhizome structure description and comparison with above-ground

Total rhizome length and volume per cell and total rhizome volume per soil blocks differed significantly between the two localities, though overall rhizome distribution was highly variable between soil blocks within each site (Table 1). Dominance, defined by Simpson index, on the coarse spatial scale depended on which measure of abundance was used (Table 1). In the species-poor site, the dominance was greatest (showed more uniform pattern) when assessed by rhizome length and the least (showed more diverse pattern) when assessed by above-ground frequency, although the differences between variables were not significant. In the species-rich site, dominance was higher when assessed by rhizome volume than by rhizome length or above-ground frequency, but these differences were also not significant. In the comparison of localities, the dominance index based on length was significantly higher for the species-poor grassland, whereas the dominance index based on volume was the same for both grasslands.

At the cell level in the species-poor site, dominance was similar regardless of measure of abundance used. In the species-rich site, results were similar to those for the coarse scale; dominance was significantly greater when assessed by rhizome volume than by rhizome length. For more detailed below-ground distribution of individual species see Appendix 1.

Comparison of individual species' spatial distribution in above-ground versus rhizome-layer

Frequency of species' occurrence in cells differed among species and localities for above-ground and rhizome portions (Figure 2). Species like *Agrostis capillaris, Hypericum maculatum, Deschampsia flexuosa, Luzula multiflora, Galium pumilum* occurred much more frequently in below-ground than above-ground. Interestingly, in the species poor community,

Table 3. Clonal growth attributes and spatial pattern characteristics of individual species, above-ground ramet longevity (low or high), rhizome origin (above-ground, AG, or below-ground, BG), and size of rhizome (long versus short rhizomes). For better illustration of autocorrelation and cross-correlation projection of species in PCA (in Figure 5), the rough estimation of species correlation to individual spatial variables is presented (+ positive correlation, – negative correlation, 0 – no correlation). The table is divided into the four groups of species of similar spatial pattern (marked as I-IV).

Species	Ramet longevity[1]	Clonal growth characteristics		Species projection onto vectors of autocorrelation and cross-correlation variables in PCA							
		Rhizome origin[2]	Rhizome size[2]	A-R lag 0	A-R lag 1	A-R lag 2	A-A lag 1	A-A lag 2	R-R lag 1	R-R lag 2	
Poa pratensis	low	AG, BG	long, short	+	+	+	+	+	+	+	I.
Deschampsia flexuosa	low	AG	long,short	0	+	+	+	+	+	+	
Hypericum maculatum	low	BG	long	–	+	+	+	+	+	+	II.
Agrostis capillaris	low	BG	long	–	–	0	+	+	+	+	
Veronica chamaedrys	low	BG	long	–	0	0	+	+	+	+	
Festuca rubra ssp. *rubra*	high	AG, BG	long, short	–	–	–	0	+	+	+	
Cardaminopsis halleri	low	AG	long	0	0	0	0	0	0	0	III.
Trifolium repens		AG	long	–	–	–	0	0	0	0	
Galium pumilum	low	BG	long	–	–	–	–	0	0	0	
Achillea millefolium	low	AG, BG	long, short	–	–	–	–	–	–	–	
Luzula multiflora	high	AG	long	0	–	–	–	–	–	–	
Alchemilla sp.	high	AG	short	0	–	–	–	–	–	–	
Potentilla aurea		AG	short (long)	+	0	0	–	–	–	–	IV.
Rumex acetosa	low	AG	short (long)	+	+	0	–	–	–	–	
Ranunculus acris	high	AG	short	+	+	0	–	–	–	–	
Deschampsia cespitosa	high	AG	short	+	+	+	–	–	–	–	
Polygonum bistorta	high	AG, BG	short (long)	+	+	+	0	–	–	–	
Nardus stricta	high	AG	short (long)	+	+	+	+	0	–	0	

[1]Ramet longevity after Herben et al. (1993 a); [2]Clonal growth mode characteristics after CLO-PLA1 database Klimeš et al. (1997)

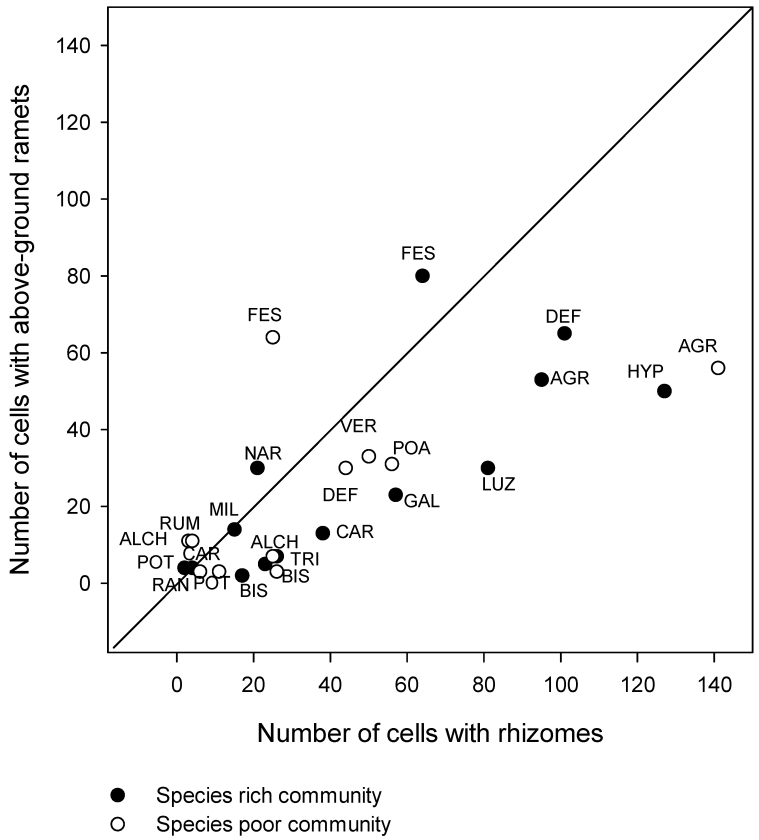

Figure 2. Number of cells that contained rhizomes of individual species versus number of cells with ramets of the same species above-ground. For species abbreviations see Appendix A.

Agrostis capillaris also occurred more frequently below-ground than above-ground. On the other hand, there were several species that had higher above-ground frequencies, such as *Festuca rubra* and *Nardus stricta*.

At the cell level, all species had the greatest amounts of rhizomes in cells in which they also produced ramets above-ground ($P = 0.033$ for *Poa pratensis* and $P <= 0.001$ for other species). Nevertheless closer inspection showed species-specific spatial relationship between rhizomes and ramets (Figure 3). The species *Cardaminopsis halleri*, *Festuca rubra*, *Nardus stricta,* and *Veronica chamaedrys* often developed ramets where they had rhizomes below-ground; there were few cells with rhizomes without ramets above-ground. The species *Agrostis capillaris, Deschampsia flexuosa, Galium pumilum*, *Hypericum maculatum, Luzula multiflora,* and *Poa pratensis* had a lot of cells with rhizomes and ramets above-ground but also had cells only with rhizomes. In comparison to other species, *Agrostis capillaris, Hypericum maculatum,* and *Poa pratensis* had many cells with rhizomes but no ramets above-ground.

Species contribution to community structure

The relative abundance of individual species at the soil blocks level differed between above-ground and rhizome layers (Figure 4). The significant effects of species and locality are shown in Table 2. Three basic relationships between above-ground and rhizome relative abundance can be defined. For the first group of species, above-ground and rhizome abundance did not differ (*Alchemilla* sp., *Achillea millefolium*, *Cardaminopsis halleri*, *Galium pumilum*, *Polygonum bistorta,* and *Potentilla aurea*). The species in the second group dominated more above-ground (*Festuca rubra*, *Nardus stricta,* and *Rumex acetosella*). The last group of species showed higher relative abundance below-ground (*Agrostis capillaris*, *Deschampsia flexuosa*, *Hypericum maculatum, Luzula*

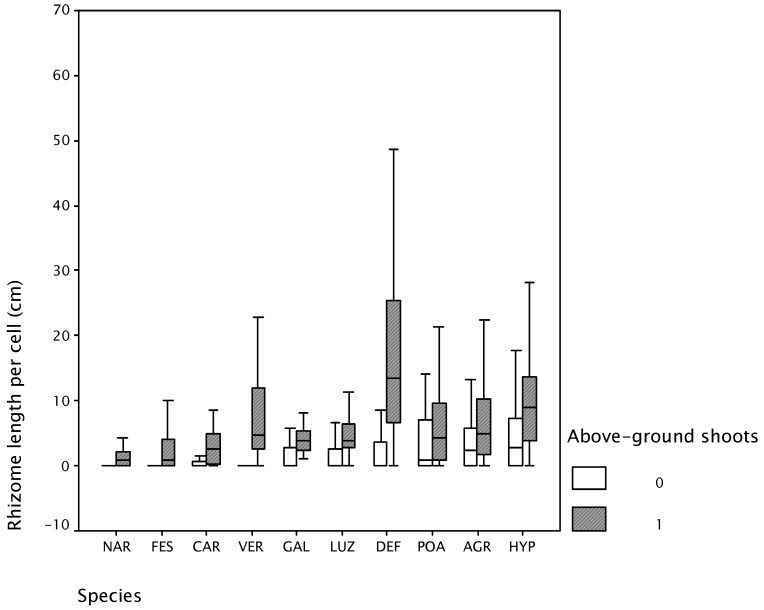

Figure 3. Sums of rhizome lengths of individual species in cells in which the species was present above-ground compared with those in which it was absent. The box plots are shown only for frequently occurring species. The bottom and top of each box plot marks the 25- and 75-percentile, respectively. The midline is the median and the whiskers extend to the minimum and maximum values.

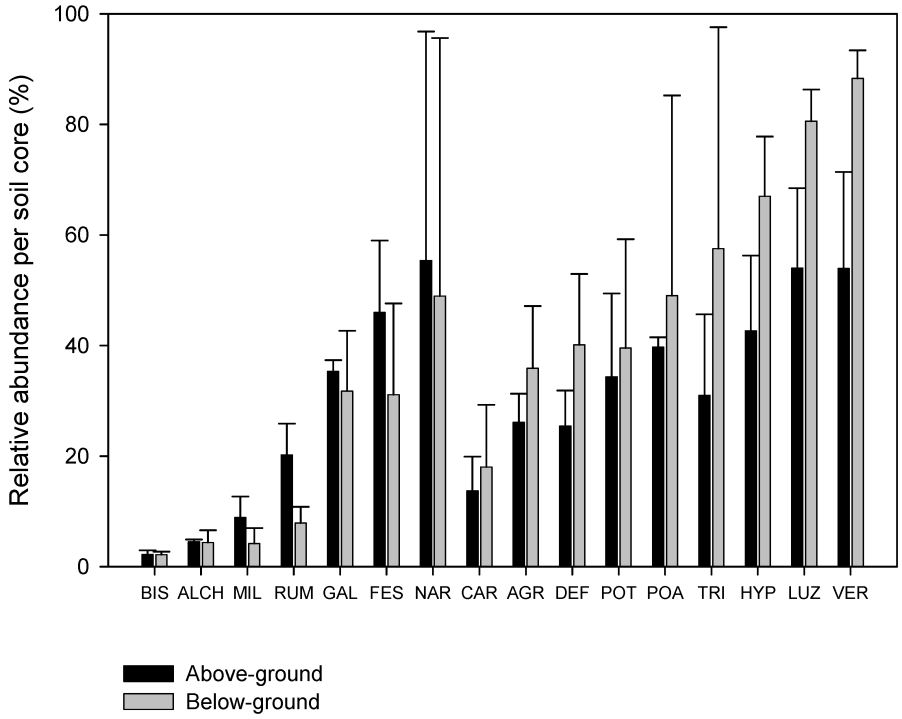

Figure 4. Dominance of individual species in above-ground and in rhizome layers for both localities, presented by means (± S.E.) of relative abundance of individual species in the soil blocks.

multiflora, Poa pratensis, Trifolium repens, and *Veronica chamaedrys*).

Spatial pattern of individual species

The autocorrelation analyses revealed a high positive and significant spatial autocorrelation of rhizomes at spatial lag 1 for *Achileea millefolium*, *Alchemilla* sp., *Deschampsia flexuosa*, *Festuca rubra*, *Galium pumilum*, *Hypericum maculatum*, *Luzula multiflora*, *Poa pratensis*, *Polygonum bistorta,* and *Veronica chamaedrys* (for exact values for spatial lags 0 and 1, see the Appendix 1). The positive significant autocorrelation of rhizomes at the larger spatial lag 2 was found only for *Hypericum maculatum* (Moran's I, MI = 0.27) and was slightly negative for *Potentilla aurea* (MI = 0.05). Significant autocorrelations were less apparent above-ground; a significant positive autocorrelation at spatial lag 1 was found for species *Deschampsia flexuosa*, *Festuca rubra,* and *Galium pumilum* and at spatial lag 2 there was a slightly negative autocorrelation for *Polygonum bistorta* (MI = 0.06). The cross-correlation between rhizomes and above-ground showed a high spatial correlation at spatial lag 0 for species *Achileea millefolium*, *Alchemilla* sp., *Deschampsia flexuosa*, *Hypericum maculatum*, *Luzula multiflora*, *Polygonum bistorta, Potentilla aurea,* and *Rumex acetosa*; at spatial lag 1 for species *Achileea millefolium, Deschampsia flexuosa, Hypericum maculatum,* and *Polygonum bistorta*; and at spatial lag 2 for species *Hypericum maculatum* (MI = 0.12). A slightly negative cross-correlation was revealed at spatial lag 2 for species *Potentilla aurea* (MI = 0.05) and *Trifolium repens* (MI = 0.04).

The principal component analysis of spatial autocorrelations within above-ground (A) or rhizome (R) abundances (A-A lag 1, 2 and R-R lag 1, 2) and cross-correlations between above-ground and rhizome abundance (A-R lag 0, 1, 2) over all species and soil blocks showed high correlation among these coefficients (Figure 5). The first axis (39.6% of the total variation) had positive loading for all variables; the second axis (24.3%) had positive loading for the cross-correlation variables and negative loading for the autocorrelation variables. The species with similar projection in PCA were sorted to the same functional group (Table 3) reflecting their common spatial characteristics. In the first group (upper right quadrant) are species (*Poa pratensis, Deschampsia flexuosa*) that showed high autocorrelation of above-ground and of rhizome spatial pattern over all spatial lags and high cross-correlation between above-ground and rhizome abundance over all spatial lags. In the second group (lower right quadrant) are species (*Hypericum maculatum, Agrostis capillaris*, *Veronica chamaedrys*) with low cross-correlation between above-ground and rhizome spatial pattern mainly at zero spatial lag, and they have high autocorrelation in above-ground and also high autocorrelation of rhizome spatial pattern. In the third group are species (*Cardaminopsis halleri*, *Galium pumilum*, *Achillea millefolium*, *Trifolium repens*) with negative correlation for all spatial variables over all spatial lags. In the forth group are species (*Ranunculus acris*, *Rumex acetosa* group, *Polygonum bistorta*, *Potentilla aurea* and *Nardus stricta*) that showed a high cross-correlation of rhizome layer and above-ground at zero spatial lag and a low spatial autocorrelation in above-ground and also low autocorrelation in rhizome pattern over all lags. Some species differed from this general scheme. For example, *Nardus stricta* from group IV had a high autocorrelation of above-ground spatial pattern at spatial lag one and *Festuca rubra* ssp. *rubra* from group II had low au-

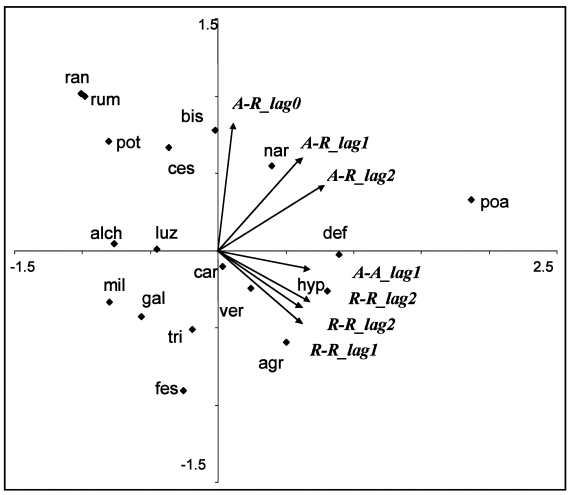

Figure 5. PCA of the individual species' spatial autocorrelations and cross-correlations, analysed with seven Moran's I parameters as variables. Variables used were autocorrelations of above-ground: A-A lag 1, A-A lag 2; autocorrelations of rhizomes: R-R lag 1; R-R lag 2; and cross-correlations between above-ground and rhizomes AR-lag 0; AR-lag 1 and AR-lag 2. Each point represented a centroid of several correlation values for individual species. Correlation values were obtained from soil blocks in which this species was present. Scores of Moran's parameters and means of individual species scores in the first two PCA axes are shown. For species abbreviations see Appendix 1.

tocorrelation of above-ground spatial pattern at spatial lag one.

RDA revealed that origin of rhizomes explained 19.7% ($p = 0.01$), rhizome size 17.6% ($p = 0.035$) and ramet longevity 14.2% ($p = 0.04$) of variance of species spatial pattern by separate analyses for each explaining variable. The origin of rhizome and rhizome size explained 30.4 % of variability ($p = 0.01$). The ramet longevity was correlated with rhizome origin and rhizome size and did not contribute to explained variability of species spatial pattern.

Species interactions above-ground versus below-ground

Species spatial interactions at the cell level differed between above-ground and below-ground (Figure 6). However, several pairs of species showed similar positive or negative spatial relationship in above-ground and below-ground. Such positive occurrence was revealed for *Deschampsia flexuosa* with *Veronica chamaedrys* at the species poor site or *Hypericum maculatum* with *Veronica chamaedrys* at the species rich site. Some species avoided each other above-ground and below-ground, such as *Agrostis capillaris* with *Veronica chamaedrys* at the species poor site or *Hypericum maculatum* and *Galium pumilum* at the species rich site. Some species placed rhizomes together but avoided placing ramets at the same spatial position, such as *Deschampsia flexuosa* with *Festuca rubra* at the species poor site or *Agrostis capillaris* with *Festuca rubra* at the species rich site. On the other hand, some pairs of species had the opposite strategy, such as *Poa pratensis* with *Festuca rubra* at the species poor site or *Agrostis capillaris* with *Hypericum maculatum* at the species rich site; they placed ramets at the same position but their rhizomes did not overlap in space.

Discussion

Individual species spatial pattern below-ground and above-ground

Species dominance or rarity above-ground significantly differed from that below-ground, and showed many interesting patterns. Some species dominated more above-ground, such as *Festuca rubra* and *Nardus stricta*. For *Festuca,* this pattern probably results from the presence of dense, long-branched above-ground trailing shoots with rhizomes developed only at the bases of these shoots (Serebrjakov and Serebrjakova 1965). In contrast, there are species that were dominant below-ground with rare above-ground shoots, such as *Galium pumilum, Agrostis capillaris, Polygonum bistorta,* and *Hypericum maculatum*. These species had high proportions of rhizomes without ramets and may even be temporally "invisible" from above-ground. Such "invisibility" was confirmed for *Polygonum bistorta,* which has a large number of "sleeping" rhizomes waiting below-ground for favorable conditions above-ground (Pecháčková and Krahulec 1995). In the grasslands studied, there were also species with very short, slowly growing rhizomes that were found at the same spatial position above-ground and below-ground (*Rumex acetosa, Ranunculus acris, Alchemilla* sp., and *Achillea millefolium*).

Space occupation strategies of species

Trends in autocorrelation and cross-correlation parameters suggest that there are specific space occupation strategies based on combinations of (i) rhizome spatial distribution (length of spreading, rhizome density below-ground) and (ii) ramet distribution along rhizome length (ramets either aggregated or evenly distributed). These two spatial traits are likely to reflect differences in rhizome size (long or short rhizomes; Klimeš & Klimešová 1999), rhizome origin (rhizome either developed above-ground or below-ground, and this feature determines where and when ramets can form; Klimeš & Klimešová 1999; see also Serebrjakov and Serebrjakova 1965; van Groenendael et al. 1996) and processes of interactions among species and individuals.

In this study I classified species into four distinct types (Figure 7) of spatial distributions that are correlated with rhizome size, rhizome origin and ramet longevity (Table 3). Group I (*Poa pratensis*, *Deschampsia flexuosa*) includes species with high density of long rhizomes and ramets that occur along the entire length of rhizomes. In this group, above-ground abundance is a good predictor of rhizome abundance, although the dominance of species in this group tends to be higher in the rhizome layer. Such species have great potential to be dominant in the community because they successfully occupy space above-ground and also below-ground. It is important to note that the tendency to produce dense rhizome systems is a

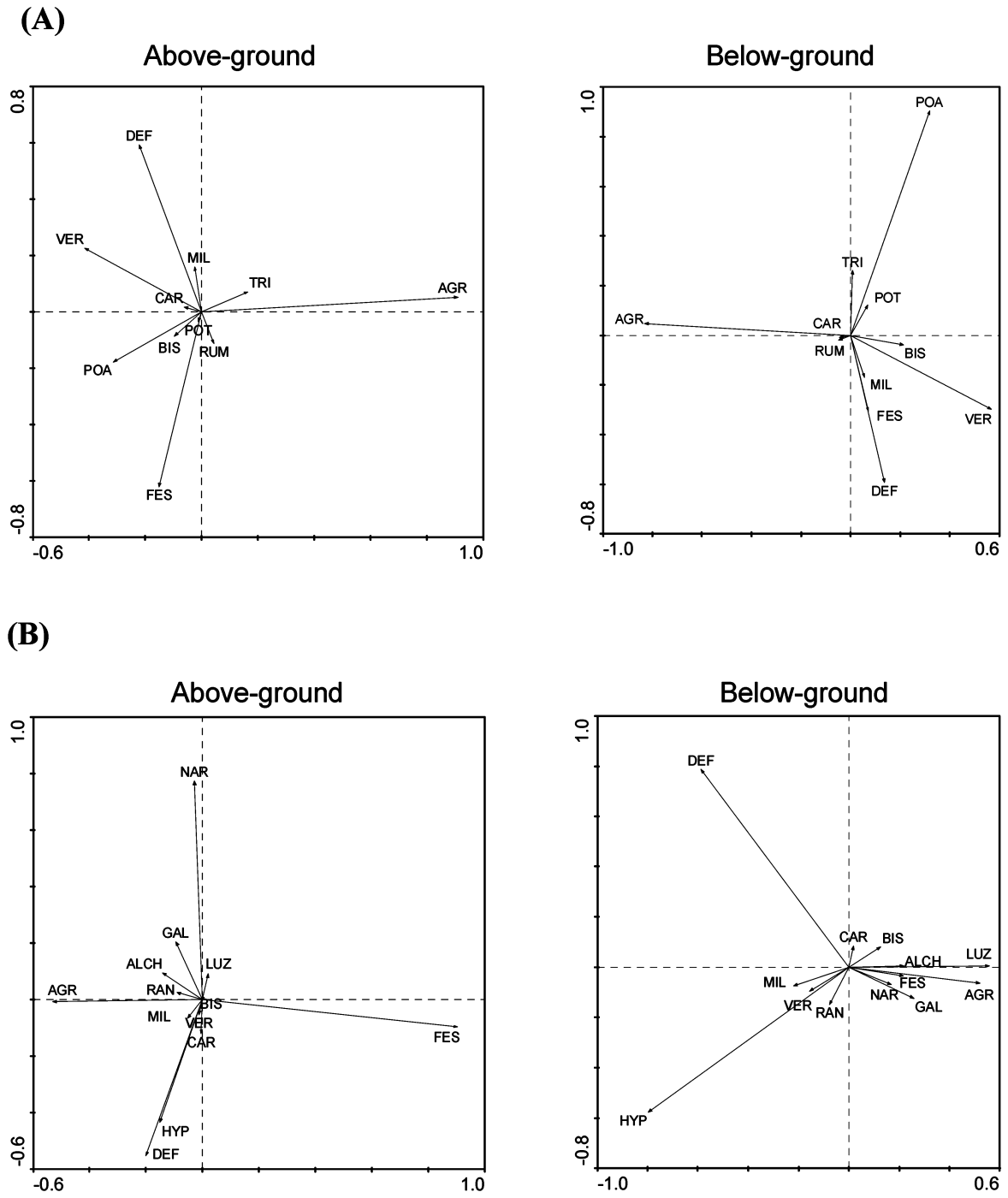

Figure 6. PCA of the above- and below-ground community spatial structure for species poor (A) and species rich (B) localities. Relative abundance of rhizomes and ramets of each species in each cell were used for the analysis. Reference of single case to individual cores was used as a covariate. Arrows pointing in the same direction indicate a positive spatial correlation of species and arrows of opposite directions indicate a negative correlation. Arrows that are perpendicular to each other indicate that there is no correlation between species. For species abbreviations see Appendix 1.

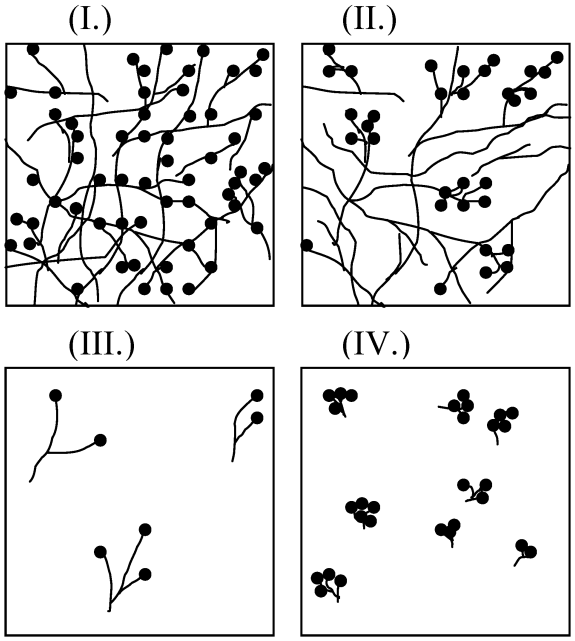

Figure 7. Four different species' spatial patterns based on the results from the PCA of the autocorrelation and cross-correlation parameters of individual species. One hypothetical representative species was drawn for each group of spatial distributions. Linear objects represent rhizome structures and points represent ramets. The numbers I-IV correspond to the numbers used for these groups in the text.

growth strategy and cannot be confused with rarity or dominance.

Group II (*Hypericum maculatum, Agrostis capillaris*, *Veronica chamaedrys*) includes species with long rhizome systems that densely fill below-ground space, but with ramets that are aggregated above-ground and therefore do not predict rhizome distribution very well. One possible explanation for this ramet aggregation is that ramets mainly form at the densely branched youngest parts of rhizomes (Wildova upubl.data). Although rhizomes of different clonal fragments cross each other below-ground, they are not able, under competition of other species, to fill the space evenly by placing the youngest parts of rhizomes close to each other. They can fill space evenly under some circumstances; for example, *Hypericum maculatum* is able to form essentially monospecific patches a few meters large in abandoned mountain grasslands (Krahulec et al. 2001). This group typically has a below-ground origin of rhizomes and short ramet lifespan. The regular mowing or grazing maintains these species that invest more in below-ground than in above-ground parts, and they may become dominant after a catastrophic event like fire when the above-ground parts of vegetation are killed.

Group III (*Cardaminopsis halleri*, *Galium pumilum*, *Achillea millefolium*, *Trifolium repens*) includes species with medium-sized rhizomes and ramets placed mainly at the growing tip of rhizomes. Older parts of rhizomes do not have ramets attached to them and rhizomes are not densely distributed below-ground. Therefore their above-ground abundance does not predict their rhizome distribution well. This group includes species with rhizomes formed both above-ground or below-ground and with both low or high ramet lifespan. Those species could stay for a long time at one place because of their slow horizontal growth. Those species probably have a very good start at the beginning of the growing season when they produce ramets only at the tips of rhizomes, because their large below-ground rhizome system supports ramet growth with stored resources.

Group IV (*Ranunculus acris*, *Rumex acetosa* group, *Polygonum bistorta*, *Potentilla aurea* and *Nardus stricta*) includes species with distant and non-overlapping short rhizomes, in which ramets showed exactly the same spatial distribution as rhizomes. This group typically has an above-ground rhizome origin and a long ramet lifespan, and ramets stay at the same place for many years (see Herben et al. 1993a). In this group, above-ground abundance predicts rhizome distribution well. Under competitive conditions these species are probably very successful because they are very good at maintaining space above-ground and also below-ground. However, because their growth is slow (very short rhizome fragments), they have a lower potential to become dominant in communities if species of the first group with long faster growing rhizomes are also present. On the other hand, they can be dominant species in habitats with intensive below-ground disturbance like freeze-and-thaw cycles in cryogenic soils. Examples of such situation are alpine meadows in Krkonoše Mts. that occur above the timberline and are dominated by one of those species, *Nardus stricta*.

This description of spatial occupation strategies is relevant for the spatial scale used in this study. Placing a species with long non-overlapping rhizomes, such as *Achillea millefolium* from this study, into one of the above mentioned categories could be confusing. The occupation strategy of this species, with low correlation between above-ground and below-ground, is between groups II and III. This species produces

very long rhizomes, but their growth can be limited by environmental conditions or can even differ between genotypes (Warwick and Briggs 1980; Bourdot et al.1985). The specific scale used in this study revealed the spatial distribution of *Achillea millefolium* only as several shorter fragments that could represent either entire plants or fragments of longer rhizomes.

While definitions of these groups are perhaps quite general, however, assignment of individual species to them is likely to be valid for the particular study system. Individual species may fall into different spatial occupation patterns under different conditions. There are examples of this even in the studied grasslands after a parts of them were abandoned; nitrogen-dependent species that have very different growth forms, such as *Polygonum bistorta* (short rhizomes, annual ramets), *Hypericum maculatum* (long rhizomes, annual ramets), or *Deschampsia cespitosa* (tussock, persistent ramets) began to dominate both above-ground and below-ground and completely change the spatial structure of the grassland (Pecháčková & Krahulec 1995; Krahulec et al. 2001).

Species spatial interactions above-ground versus below-ground

In the rhizome layer, higher numbers of species occurred together at the small spatial scale than above-ground. Rhizomes densely filled the rhizome layer and the amount of rhizomes increased with species richness of the community. The most fascinating differences in spatial arrangement of species were found at the fine spatial scale. Inter-species spatial aggregation differed between above-ground and below-ground (Figure 8).

There were two types of spatial interactions with similar inter-species aggregation above-ground and below-ground. The first type represents species that avoided each other even at fine scale, whereas the second type of species spatially overlapped at a very fine scale. Two other spatial arrangements emerged, one in which two species overlapped in the rhizome layer but spatially avoided each other above-ground, and one in which two species placed ramets together but their rhizomes did not spatially overlap. What processes and interactions can produce such spatial patterns? The first two types of spatial aggregation could be a result of dominance and rarity of individual species.

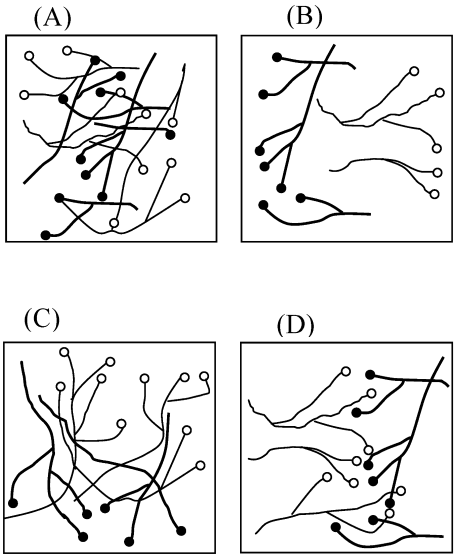

Figure 8. Four fine-scale inter species spatial interaction patterns drawn from bird's-eye perspective for two species. Linear objects represent rhizome structures and points represent ramets. (A) Ramets of two species occur together and their rhizomes overlap; (B) Ramets and rhizomes of two species do not occur together; (C) Rhizomes of two species overlap but ramets are spatially segregated; (D) Rhizomes of two species do not overlap but ramets are spatially aggregated.

The spatial aggregation of species pairs that differ between above-ground and below-ground brings an entirely new view on species interactions. *Deschampsia flexuosa* with *Festuca rubra* or *Agrostis capillaris* with *Festuca rubra* showed overlapping below-ground but avoidance above-ground. *Festuca* is a species with dense tussocks of above-ground shoots and thin rhizomes that grow essentially on the soil surface. Both species, *Deschampsia* and *Agrostis,* that avoided *Festuca* in above-ground have more loose shoots and very long rhizomes. Rhizomes of *Deschampsia* grow on the surface and rhizome of *Agrostis* can grow deep under the surface. One possible scenario could be that long rhizomatous species avoid placing ramets close to the dense tussocks of *Festuca* and they use different strategies to do that. *Deschampsia* produces long creeping shoots that eventually become rhizomes, and with which they could actively avoid of *Festuca* tussocks. *Agrostis* produces below-ground growing rhizomes and could place its shoots selectively (Macdonald and Lieffers 1993) outside of *Festuca* tussocks. *Agrostis capillaris* showed opposite phenomenon with *Hypericum maculatum*; their ramets appeared at the same place but rhizomes did not overlap. Those species have large

rhizome systems under the soil surface that could compete for below-ground space (Wildova unpubl. data). They may stop horizontal growth of rhizomes under unfavourable conditions (e.g., when they run into other dense rhizome structures) and replace it with vertical growth of above-ground shoots. These scenarios illustrate possible mechanisms of species interactions that were not yet considered in the community ecology of clonal plants.

There is no information on how plants compete in the rhizome layer. Clonal plants are known to exploit resource-rich "windows of opportunity" by rhizome growth only to a limited degree (Stuefer 1996). It is likely that to some extent rhizomes respond to changes of light conditions (Palmer 1958; Hutchings and de Kroon 1994) and they also could compete for physical space (Wildova unpubl. data). Dense rhizome structures of some species in below-ground can mirror dense tussocks of clumper species in above-ground. Species with large and persistent rhizome systems could have a better chance to develop ramets in places with good light conditions and could also suppress vegetative spreading of other species with slowly growing or short-lived rhizomes.

These findings indicate possible mechanisms of species interactions that could be tested in the future. For example, do space occupation strategies of individual species change under different environmental conditions or across different communities? If we understood the relationship between environmental conditions and presence of certain occupation strategies, we could use this information to reconstruct the history of clonal plant communities and even predict their future development under changed conditions.

Acknowledgements

Deborah Goldberg and Tomáš Herben helped me very much by reading, criticizing and editing earlier drafts of this paper. I am grateful to Jonathan Rosenthal for linguistic corrections of the paper and for helpful comments. Nia Pauliukonis helped me a lot by correcting English of the final version. I thank Zuzana Münzbergová and the discussion group Sněhurka for critical comments on the manuscript. I thank Tomáš Herben for help with autocorrelation analyses, Luboš Ursta with GIS analyses, and Jan Wild for designing technical equipment. I am indebted to František Krahulec and Sylvie Pecháčková for valuable discussions. The research was funded by the GAČR grant no 206/02/0578.

Appendix

Table A1. Summary information for study species. Species codes are used in Figure 2, Figure 3, Figure 4, Figure 5. Soil cores 1-4 were from species-poor community and 5-8 from species-rich community. Means and standard deviations of rhizome density given by length and volume in the whole soil blocks across localities are presented. Means of Moran's *I* and their confidence intervals (lower and upper limits) for i) spatial autocorrelations of rhizomes (R) and ramets (A), respectively, at the spatial lag 1 and ii) cross-correlations between rhizomes and ramets (AR) at the spatial lag 0 and 1 are shown. Bold means are significantly different from zero (i.e., confidence interval does not contain zero).

pecies	Species Code	Soil cores where species was present	Rhizome density per soil blocks		Autocorrelations						Cross-correlations					
			Mean ± S.D.		Mean and confidence interval						Mean and confidence interval					
			Length [cm]	Volume [cm^3]	R_lag 1			A_lag 1			AR_lag 0			AR_lag 1		
					Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
Achillea millefolium	MIL	3, 4, 6	52.40 ± 70.50	0.024 ± 0.044	**0.16**	0.22	0.62	**0.01**	0.04	0.43	**0.14**	0.10	0.50	**0.09**	0.02	0.26
Agrostis capillaris	AGR	1, 2, 3, 6, 7, 8	223.24 ± 119.09	0.042 ± 0.048	0.42	−0.29	0.62	0.23	−0.11	0.14	0.30	−0.31	0.59	0.14	−0.19	0.38
Alchemilla sp.	ALCH	7, 8	26.26 ± 2.77	0.107 ± 0.240	**0.30**	0.21	0.39	0.05	−1.88	1.98	**0.62**	0.07	1.18	−0.01	−0.24	0.22
Cardaminopsis halleri	CAR	2, 5, 8	41.75 ± 23.29	0.007 ± 0.013	0.36	−0.03	0.76	0.25	−0.06	0.55	0.42	−0.05	0.90	0.11	−0.07	0.30
Deschampsia cespitosa	CES	1, 4	1.70 ± 0.65	0.012 ± 0.074	−0.04	−0.17	0.08	0.32	−4.35	4.98	0.65	−3.54	4.85	0.17	−2.59	2.93
Deschampsia flexuosa	DEF	4, 5, 6, 7, 8	404.90 ± 397.02	0.015 ± 0.023	**0.50**	0.36	0.63	**0.35**	0.19	0.51	**0.51**	0.31	0.70	**0.24**	0.09	0.38
Festuca rubra ssp. *rubra*	FES	4, 5, 6, 7, 8	81.83 ± 59.16	0.005 ± 0.012	**0.29**	0.04	0.54	**0.26**	0.02	0.49	0.19	−0.18	0.56	0.05	−0.14	0.24
Galium pumilum	GAL	7, 8	122.94 ± 32.67	0.056 ± 0.082	**0.37**	0.27	0.48	**0.18**	0.03	0.34	0.35	−0.13	0.82	0.01	−0.94	0.97
Hypericum maculatum	HYP	5, 6, 7, 8	264.90 ± 207.16	0.104 ± 0.117	**0.51**	0.35	0.66	0.15	−0.11	0.41	**0.33**	0.13	0.53	**0.20**	0.09	0.32
Luzula multiflora	LUZ	5, 7, 8	94.78 ± 51.57	0.066 ± 0.088	**0.28**	0.10	0.45	0.17	−0.15	0.48	**0.42**	0.28	0.56	0.09	−0.16	0.33
Nardus stricta	NAR	5, 8	19.55 ± 26.97	0.071 ± 0.188	0.18	−2.20	2.56	0.29	−3.41	3.98	0.74	−2.59	4.06	0.14	−1.72	2.01
Poa pratensis	POA	1, 3	206.68 ± 216.84	0.035 ± 0.047	**0.36**	0.08	0.63	0.48	−2.49	3.45	0.50	−0.27	1.26	0.34	−1.63	2.31
Polygonum bistorta	BIS	1, 3, 4, 5, 7, 8	11.67 ± 5.44	0.050 ± 0.264	**0.34**	0.09	0.58	0.15	−0.05	0.35	**0.54**	0.32	0.77	**0.29**	0.14	0.44
Potentilla aurea	POT	3, 4, 8	7.78 ± 2.46	0.006 ± 0.035	0.15	−0.03	0.34	0.05	−0.32	0.42	**0.60**	0.07	1.12	0.18	−0.01	0.37
Ranunculus acris	RAN	6, 7	0.48 ± 0.09	0.002 ± 0.013	−0.02	−0.11	0.06	0.05	−0.79	0.88	0.78	−1.99	3.55	0.07	−1.06	1.20
Rumex acetosa	RUM	2, 4, 6	1.29 ± 1.38	0.009 ± 0.054	0.09	−0.34	0.51	−0.02	−0.05	0.02	**0.92**	0.59	1.25	0.03	−0.15	0.21
Trifolium repens	TRI	2, 3	28.52 ± 33.51	0.015 ± 0.086	0.09	−0.87	1.06	−0.03	−0.07	0.00	0.02	−0.58	0.62	0.28	−0.86	1.42
Veronica chamaedrys	VER	1, 2, 6, 7, 8	85.71 ± 154.80	0.013 ± 0.029	**0.41**	0.15	0.66	0.19	−0.26	0.64	0.29	−0.20	0.78	0.16	−0.17	0.50

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