Fine-scale dynamics of rhizomes in a grassland community

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Spatial dynamics in grassland communities are constrained by the belowground spatial distribution of roots and rhizomes. Their dynamics are difficult to measure as underground data collection tends to be destructive and cannot be repeated at the same plot over time. We investigated rhizome dynamics indirectly by examining rhizome spatial structure on long-term grassland study plots where aboveground shoot counts have been recorded using a fine-scale grid over nine years. Number of rhizome apical ends, basal ends and total rhizome length of both live and dead rhizomes were obtained from the data by scanning rhizomes and processing them by GIS vectorization. These rhizome variables were correlated with the above-ground shoot counts in grid cells over varying temporal lags. There was a general decrease in the intensity of correlation between live rhizomes and shoot counts with increasing time lags. Correlation of dead rhizomes increased with increasing time lag, reaching a maximum after several years, and then declined. Species differed strongly in the change of rhizome-shoot counts correlation over varying time lags. These differences were used to infer rhizome growth dynamics, namely rhizome growth rate and lifespan, and rhizome mean decomposition time. The species involved differed in all these traits. Mean rhizome growth rate ranged from 0.2 (*Polygonum bistorta*) to 3.3 cm yr^{-1} (*Deschampsia flexuosa*); mean rhizome lifespan ranged from 5 yr (*Anthoxanthum alpinum*) to over 8 yr (*Nardus stricta*) and mean decomposition time from one growing season (*Anthoxanthum*) to 7 yr (*Polygonum*). Presence of dead rhizomes below living rhizomes or aboveground shoots was taken as an indication of fine-scale replacements between species. These were highly non-random, with some species pairs replacing significantly more frequently. These differences in rhizome growth parameters underlie different strategies of horizontal growth and dieback between species. These can serve as one of the mechanisms of species replacements and contribute to the fine-scale coexistence of species.

Plant community composition is strongly influenced by interactions between individuals. These interactions are constrained by plants' lack of mobility, with plants occupying new space only by seed dispersal or clonal growth. Thus, success of an individual plant largely depends on its spatial position, influenced primarily by the number and identity of its neighbors (Pacala and Levin 1996, Pacala et al. 1996, Keeling 1999, Law and Dieckmann 2000).

In communities of herbaceous perennials, such as grasslands, spatial position is typically constrained by the architecture and growth of belowground plant parts such as rhizomes, and in some cases also roots. These structures directly determine fine-scale spatial dynamics of many clonal species by serving as the spacers between

ramets (Serebrjakov and Serebrjakova 1965, Serebrjakova 1971, Klimes et al. 1997). Nevertheless, most plant community studies of spatial interactions between individuals have looked almost exclusively at above-ground plant parts. Much less attention has been paid to below-ground parts such as rhizomes and roots because of the difficulty of observing them in the soil (Pechackova et al. 1999, Waisel et al. 2002, Sammul et al. 2003).

In contrast to above-ground shoots, which either grow or senesce, rhizomes continually grow at apical ends and slowly die at the basal ends (Czarnecka 1996, Cizkova and Lukavska 1999, Asaeda and Nam 2002). Therefore, rhizomes are linear structures oriented from old to young ends and the nodes along rhizomes

represent growth events in chronological order. Rhizomes produce new ramets at specific distances from senescing ramets, thus influencing fine-scale year-to-year changes in spatial patterns of above-ground stems (Klimes 1992, Stoll et al. 1998, Wildova 2004); they also enable plants to resprout when local environmental conditions become favorable. Differences in rhizome structures are likely to underlie species-specific differences in fine-scale spatial dynamics demonstrated in grassland communities (van der Maarel and Sykes 1993, Herben et al. 1993, Klimes 1999, Tamm et al. 2001).

As most rhizomes live at least several years (Klimes et al. 1997) and often persist in the soil after they die, they could be used as a source of information for reconstructing the history of changes in community spatial patterns over long time periods. Because rhizomes maintain distinguishable marks where shoots had been in the past, the determination of community dynamics should be possible even without having long-term above-ground data (Hossaert-McKey et al. 1996, Tamm et al. 2001, Sammul et al. 2003). The few available studies have shown that rhizomes do carry important information on community spatial patterns (Tamm et al. 2001, Sammul et al. 2003, Wildova 2004). Examining rhizome distributions has revealed that individual species can use different strategies to occupy space, even if their above-ground spatial patterns are similar (Wildova 2004).

Rhizome structures can be also used to determine fine scale interactions between clonal species (Tamm et al. 2001, Sammul et al. 2003) and to interpret them as evidence of past changes in the community. However, lack of information on rhizome dynamics places a major constraint on the interpretation of rhizome structures. Dynamical variables, such as rhizome growth rates, lifespan or senescence, are difficult to record as underground data collection tends to be destructive and therefore cannot be repeated at the same plot over time. This constraint can be overcome in species that leave clear annual growth marks on their rhizomes so that long-term records can be substituted by a single-time record (Tybjerg and Vestergaard 1992, Cain and Damman 1997); in other species, however, the information cannot be easily obtained.

In the present study, we compare the dynamics of rhizome systems in a set of mountain grassland species and examine the species-specific role of rhizomes in spatio-temporal processes in grassland communities. In order to bypass the above constraint we developed a novel indirect approach, in which we examined rhizome spatial structure of five dominant species on plots where spatially explicit time series of aboveground shoot numbers were available. Rhizome data were obtained from harvested belowground cores by scanning rhizomes and processing them by GIS vectorization. The rhizome descriptive parameters that we used (number of basal ends, apical ends and total rhizome length) represented growth events that occurred at different times, and we compared their distributions with species shoot distributions in the same plot recorded annually over a nine-year period. We then correlated individual rhizome parameters with the time series of above-ground shoot distributions for each species and used patterns of these correlations to infer rhizome dynamical variables, such as rhizome growth rate, lifespan, and mean decomposition time. These were compared between species and used to establish the role of rhizome growth for the spatial dynamics of the community.

Methods

Study site

The study site is located in a grassland in the Krkonoše Mts., in the northern part of the Czech Republic (Severka settlement, ca 3 km NW of Pec pod Sněžkou, 50°41′42″N, 15°42′25″E, altitude ca 1100 m). Mean temperature in the warmest month (July) was 16.5°C (1995), 12.3°C (1996) and 13.2°C (1997) at the nearby weather station (Pec pod Sněžkou, ca 900 m a.s.l.). The study site has a long winter with thick snow cover, which usually lasts from November until the end of April with annual average precipitation of 1300 mm. The grassland has been maintained by a mowing regime since its establishment in the 17th century, and has reached a stable species composition owing to its consistent management practices (Krahulec et al. 1997). This management consists of mowing once a year and manuring once every few years.

Four dominant grasses: *Anthoxanthum alpinum*, *Deschampsia flexuosa*, *Festuca rubra* and *Nardus stricta*, and a single common dicot, *Polygonum bistorta* (henceforth referred to as *Anthoxanthum*, *Deschampsia*, *Festuca*, *Nardus* and *Polygonum*) occurred in the plots. Although the system is species-poor at the large scale, the species coexist at the fine scale with no obvious coarse tussocks. There are ca 2−4 species 10 cm^{-2}, 7−53 shoots 10 cm^{-2} (average over 9 yr) and 6−10 species 2500 cm^{-2}.

Data collection

We used two permanent plots of 26.6 × 26.6 cm that had been established at the site in 1990 as part of a larger removal experiment (Herben et al. 1997a). In one of the two plots (R3), *Festuca rubra* had been removed in 1990, while in the other (R12) it had not. However, because the density of *Festuca* in R3 had been low, there was no observable effect of its removal on the plot's

community composition, and both plots were treated as replicates for the present study (with the exception of the absence of *Festuca* in R3). In each plot, the numbers of above-ground modules (shoots for grasses, leaves for *Polygonum*) of each species occurring within each 3.3×3.3 cm cell of a 6×8 cell grid were recorded in mid July every year between 1990 and 1998. Small *Polygonum* seedlings with only juvenile leaves were not counted. Plots were clipped after recording data to simulate mowing, ensuring that there was no successional trend associated with the observations.

In 1998, each plot was carefully excavated as a soil block with a 5 cm wide horizontal buffer zone. The top 6 cm layer of each of these blocks was then inverted and maneuvered into a needleboard having needles oriented vertically and horizontally (Fig. 1). Rhizomes in the study community were concentrated mostly in the first 3 cm from the soil surface and did not go deeper than 6 cm Beginning with what was originally the bottom of each soil block (i.e. at 6 cm depth) the soil was carefully washed out 0.5 cm at a time, with all the rhizomes and roots exposed within each 0.5 cm layer scanned. The resulting images had square (3.3×3.3 cm) grids formed by the points of the vertical needles. Each image was then printed out and a transparency overlaid on it. Colored markers – with one color for each species – were then used to trace each rhizome, living or dead, onto the transparencies. Dead rhizomes were denoted with special symbols so that they could be treated separately in subsequent analyses. Dead rhizomes were identified as rhizomes with no connected, living above-ground shoots and no attached roots (occasionally a few old, thick roots). For each soil block, the resulting series of transparencies were then scanned in sequence corresponding to their depth, and the spatial data builder Cartalinx 1.2 (Clark Labs) was used to convert the rhizome images to vector data. We processed the vector images using ArcView ver. 3.2 (Anon. 1996) to yield spatial distribution data. This provided species-specific information on the spatial (horizontal and vertical) distributions of processed rhizomes to yield summary rhizome parameters (Appendix 1). ArcView was also used to overlay below-ground data with horizontal grids.

In some cases, especially for *Deschampsia* which has many long rhizomes, parts of rhizomes had been cut at the borders of soil blocks, and rhizomes were fragmented to smaller pieces. Therefore we used data from a separate study on rhizome sizes from the same grassland (Juklickova 2003) to estimate the average rhizome size for *Deschampsia* instead of data from the excavated soil blocks (Table 1).

Definition of rhizome parameters used in analyses

For each species, the numbers of apical ends, basal ends, and the total rhizome length in each cell were calculated separately for living and dead rhizomes. For all rhizomes, basal ends represented the oldest ends of rhizomes where fragmentation due to dieback occurred or where original seedling growth initiated. Apical ends represented the youngest portions of live rhizomes, and often bore the youngest ramets. In live rhizomes, they typically correspond to growing tips; in dead rhizomes they indicate the youngest parts of rhizomes before they died. For all species basal to apical orientation indicates the direction of rhizome growth. Rhizome length represented the sum of the lengths of all rhizomes of a given species in a single grid cell.

Estimation of dynamic parameters of rhizome systems

The correlations between the rhizome variables and shoot counts were used to infer values of dynamical
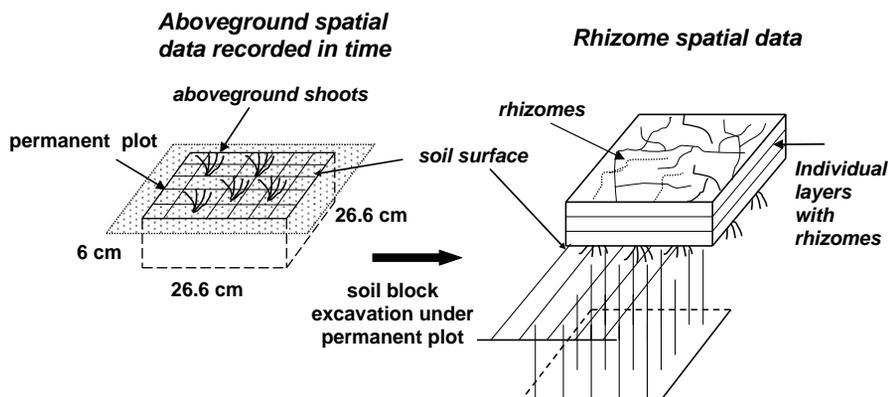
Fig. 1. Schematic diagram of rhizome data collection from the soil blocks after they were excavated from permanent plots, where the spatial data of aboveground shoot densities were collected for 9 yr before soil excavation.

Table 1. Average rhizome fragment length (mean±SE, and maximum value), of the five species studied at both study plots. [1] Independent measurements of *Deschampsia* from the same grassland done at larger plots where the edge effect was smaller (Juklickova 2003). N – number of examined rhizome fragments.

Species	N	Rhizome fragment length		
		Mean	SE	Max
Anthoxanthum	91	4.36	0.31	18.81
Deschampsia	397 (53)	6.15 (19.50)[1]	0.31 (2.33)[1]	56.77 (78.10)[1]
Festuca	23	5.41	0.98	20.27
Nardus	9	13.18	4.50	42.20
Polygonum	94	1.48	0.13	5.71

variables of rhizomes, i.e. growth rate and lifespan, and spatial positioning of shoots on rhizomes. These calculations were based on the following assumptions: 1) if rhizomes grow horizontally and annual above-ground shoots reappear every growing season mostly at the apical ends of the rhizomes, the spatial correlation of rhizome apical ends with number of aboveground shoots will decline with the age of the record. The correlation of rhizome length with aboveground shoots will also decline with the age of the record, but less steeply. The spatial correlation disappears whenever the above-ground record reaches back to the point when the observed rhizome structure did not yet exist. The time interval from the point when rhizome structure was recorded to the point when spatial correlation between this structure and historical above-ground records disappears is rhizome lifespan. Rhizome growth rate was estimated as the average size of a rhizome system divided by the rhizome lifespan. 2) If rhizomes are preserved in the soil for long periods after they die then the length of dead rhizomes would not be correlated with aboveground shoots that were alive at the time of excavation. However, the correlation should increase with past above-ground records that would correspond with the time period when those rhizomes were alive and bore above-ground shoots. The time span from the time of excavation to the point when correlation increases from zero and then continues to increase is determined as a minimum rhizome decomposition time. These variables were compared across species to identify whether different species show different rhizome dynamics. Predicted shapes of relationships between these variables are shown in Fig. 2.

Finally, we used the spatial information of co-occurrence of live rhizomes and above-ground shoots and dead rhizomes to identify possible species replacement patterns in the community. If past records of above-ground shoots of species A were positively correlated with dead rhizomes of species B during the time period equal to "rhizome decomposition time" of species B, we assumed species A replaced species B. Similarly, if live rhizomes of species A were positively correlated with dead rhizomes of species B we assumed species A replaced species B. However, if this positive correlation was not accompanied by a corresponding positive correlation for above-ground shoots, then, on the contrary, we assumed that species B invaded places occupied by rhizomes of species A and then died, while species A remained alive, so that this was a "failed" replacement.

Intraspecific replacements were considered only if dead rhizomes co-occurred with live rhizomes of the same species but not with above-ground shoots, because we cannot distinguish if recorded aboveground shoots were from the same plant or from a new plant of the same species.

Statistical analyses

To estimate dynamic rhizome parameters we correlated spatial position of rhizome systems excavated in 1998 with spatially explicit shoot densities of individual species recorded in each year from 1990 to 1998. Differences between the excavation year and the year of above-ground data record are referred to as the time lag. Pairwise relationships (one rhizome variable vs density aboveground over a given time lag) were examined by Moran's I (Upton and Fingleton 1985); this was done separately in each plot. These pairwise autocorrelations were then used to make gross estimates of rhizome dynamic parameters. The time lag where correlation of live rhizome length or apical ends with above-ground shoots reached zero was taken as rhizome lifespan, the time lag when the correlation between dead rhizomes and above-ground records continuously increased and became significant as mean rhizome decomposition time. The annual rhizome growth rate was estimated by dividing the average length of live rhizome fragment by rhizome lifespan.

To explore the overall correlation between rhizomes and above-ground spatial pattern the multivariate relationships (involving all rhizome parameters of one species) were examined by standardized redundancy analysis. Redundancy analysis is a generalized version

Species A with live rhizomes at the time of harvest

Species B with dead rhizomes at the time of harvest

year of record

1995 No shoots

1996

1997

Aboveground data

1998

Rhizome data

basal end

apical ends
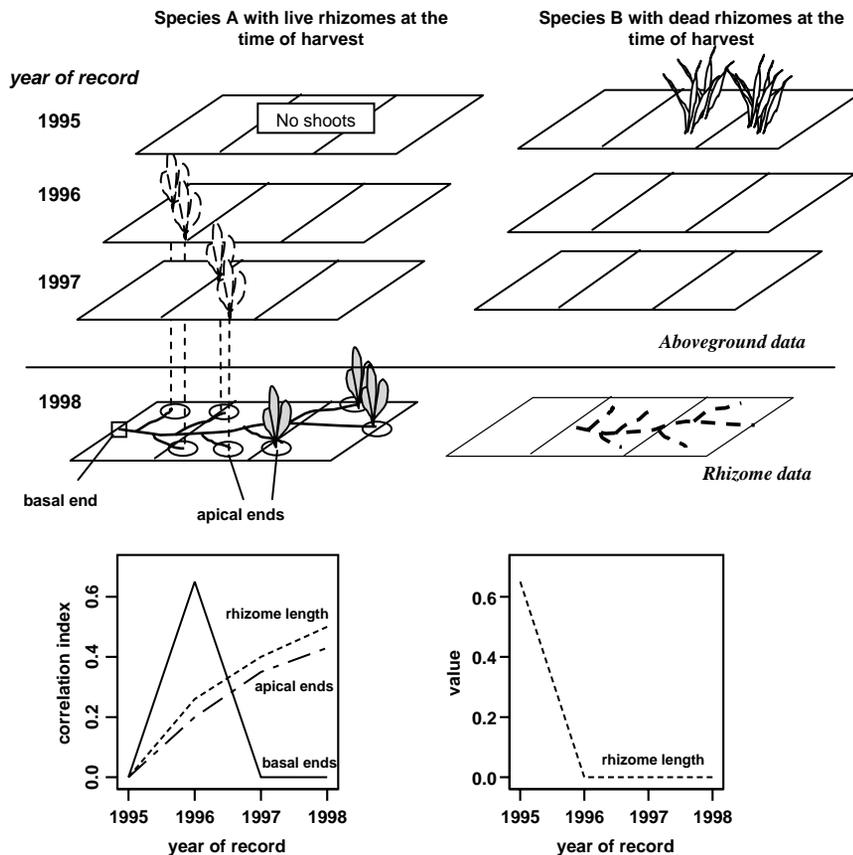
Fig. 2. Schematic picture of aboveground and belowground spatial data for two different hypothetical clonal plants observed over time. Species A first appears in 1996 and for the next two years spreads vegetatively, bearing shoots only at the youngest ends of new rhizomes. Species B dies after year 1996, therefore the only record for aboveground shoots is for 1996, but the dead rhizomes are still present belowground at the year of harvest two years later. The adjacent schematic diagrams show the expected spatial correlations over time between parameters of rhizomes (apical ends, basal ends, and rhizome length) and frequency of aboveground shoots recorded in a spatial grid. The shape of curves is projected from the overlap of layers of spatial data (top part of the figure). Note: the shape of correlation curves depends on the size of the grid used, growth rate of rhizomes and type of rhizome (see discussion part of the paper for details).

of multiple regressions that can account for a relationship of a set of dependent variables to another set of independent variables (ter Braak and Smilauer 1998). In these multivariate tests, time series of shoot counts of a given species were used as independent variables and all live rhizome variables (number of apical and basal ends and rhizome length) of that species as dependent variables. For each species we used a stepwise approach to find the date of above-ground record

that fit best with extant rhizome spatial pattern. A categorical variable coding for the plot was used as a covariable.

To determine relationships between rhizome growth and shoot turnover at a community level, a separate redundancy analysis was used to examine multivariate relationships between rhizome data and time series across species. Time series of shoot counts of species in a given year were used as independent variables, and

Fig. 3. Correlations (Moran's I) between rhizome variables: number of apical (youngest) ends, number of basal (oldest) ends, and total rhizome length per cell and number of aboveground shoots recorded at these cells over different time lags back to the past. 1998 corresponds to the year of rhizome excavation, 1997 is temporal lag = 1, 1996 lag = 2 etc. Correlations significant at $\alpha = 0.05$ are indicated by two asterisks left to the point; one asterisk indicates a marginally significant correlation ($\alpha = 0.1$). Captions in the figure: plot R12 marked with squares, plot R3 with circles, filled symbols are for live rhizomes and empty for dead rhizomes.
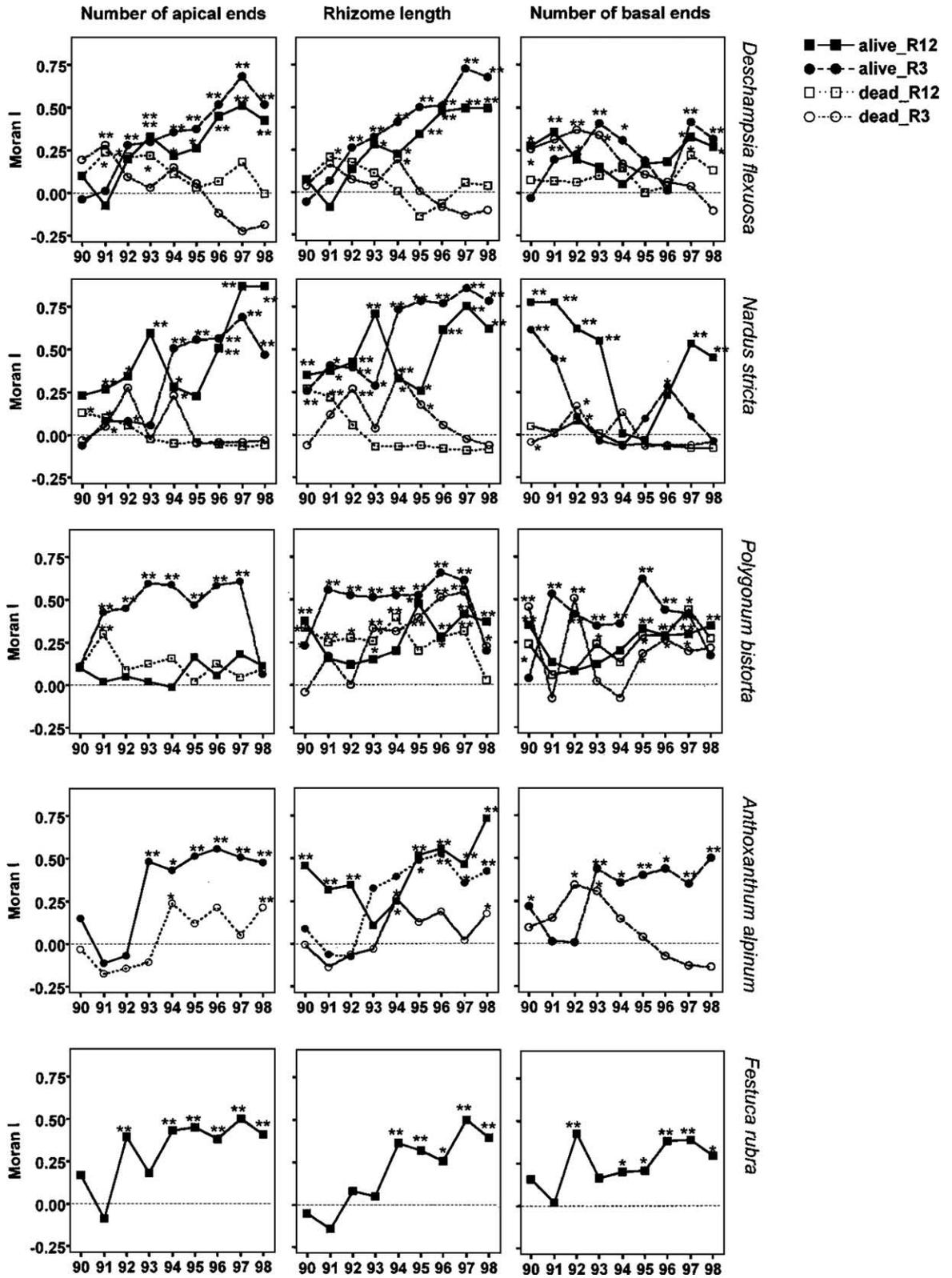
Fig. 3 (*Continued*)

species-specific rhizome lengths per cell as dependent variables. Separate analyses were performed for each time lag.

To identify community dynamics, Moran's I was used to examine spatial relationships across species. First, pairwise correlations were calculated between lengths of dead rhizomes of the target species and aboveground shoot counts of all other species. Second, pairwise correlations were calculated between dead rhizomes of the target species and all three variables of live rhizomes of all other species.

Pairwise and multivariate relationships were tested for statistical significance using Monte Carlo randomisations under a null hypothesis that accounted for spatial dependence in the data (rotation, reflexion and positional shift of the grid). 1000 permutations, unless noted otherwise, were used to generate the expected distribution of the test statistic under the null hypothesis. All multivariate calculations were performed by CANOCO ver. 4.5. (ter Braak and Smilauer 1998).

Results

Rhizome sizes and densities

Excavation revealed considerable numbers of rhizomes in the soil, allowing differences to be identified in rhizome densities between species. *Deschampsia* was by far the dominant species. There were ca 380 m of live rhizomes 1 m^{-2}, consisting of 230 m of *Deschampsia*, 50 m of *Festuca*, 50 m of *Anthoxanthum*, 13 m of *Nardus* and 13 m of *Polygonum* (for details, see Appendix 1). The proportion of dead rhizomes to live rhizomes differed between study plots and species; dead rhizomes were 11–68% of live rhizomes for *Deschampsia*, 1% for *Anthoxanthum*, 13–23% for *Nardus* and 22–82% for *Polygonum*. No dead rhizomes were found for *Festuca*. Most of the live rhizomes of all species were concentrated in the surface layer of the soil, up to 1.5 cm, except for *Polygonum* that had most rhizomes at 2.0–2.5 cm depth. *Polygonum* and *Nardus* were also occasionally present even deeper down to 3 cm, where otherwise, mostly dead rhizomes occurred. In contrast, live rhizomes of *Festuca* and *Anthoxanthum* occurred strictly on the soil surface (Appendix 1). The average length of a single rhizome fragment ranged from 20 cm for *Deschampsia*, to 13 cm for *Nardus*, 5 cm for *Festuca*, 4 cm for *Anthoxanthum,* and 1.5 cm for *Polygonum* (Table 1). Appendix 2 shows the quantitative relationship between rhizome length and number of aboveground shoots, ratio of shoots to rhizome length and above-ground shoot density over time.

Single species correlations of rhizome variables with shoot densities

For live rhizomes, there were strong and significant correlations in the year of excavation between aboveground shoot counts and number of apical ends and total length for all species except *Polygonum* (Fig. 3). However, the intensity (variance explained by all canonical axes) of correlations of both variables differed among species. It decreased in the order from *Nardus*, *Deschampsia*, *Anthoxanthum* to *Festuca*, and *Polygonum*.

The intensity of correlations between length of live rhizomes and shoot densities decreased with increasing time lag, although species differed in the steepness of this decrease (Fig. 3) with *Deschampsia*, *Festuca* and *Anthoxanthum* being faster and *Polygonum* and *Nardus* much slower. In contrast, correlation between the number of basal ends of live rhizomes and shoot densities increased with time lag. This was particularly pronounced in *Nardus*, where the correlation increased up to a time lag of eight years (i.e. the shoots that had been observed eight years before the rhizomes were harvested), and it is conceivable that it could have increased even further, had there been a longer observation period (Fig. 3).

The multivariate approach showed that shoot distribution in the past explained significant amounts of variation in rhizome distribution (Table 2). The correlation remained significant even when the variation explained by above-ground records from either 1997 or 1998 (the years closest to excavation) were excluded (Table 2). This indicates that past ramet distributions brings independent information for interpretation of rhizome patterns. Comparison of different time lags showed that aboveground shoot distribution in the year of excavation never explained the highest proportion of variation in rhizome distribution in multivariate analyses (Table 2). In *Deschampsia*, *Festuca*, and *Nardus*, one year (1997), in *Anthoxanthum*, 2–3 yr (1996 and 1995) and in *Polygonum* 3 yr (1995) preceding excavation explained most of the variation.

The correlation of shoot densities with apical ends of dead rhizomes increased with increasing time lag but eventually reached a maximum. Specifically, dead rhizomes of *Deschampsia* showed maximum correlation at a time lag of 6 yr and *Polygonum* at a lag of 7 yr. The time of the maximum correlation is taken as an estimate of mean decomposition time. Dead rhizomes of *Nardus* showed very low correlations in one plot (likely remnants of very old rhizomes), whereas in the other plot the correlations were bigger and peaked twice at lags of 4 and 6 yr. For *Festuca*, we did not find any dead rhizomes. This is likely because in the one plot where this species was present, it only invaded the study plot

Table 2. Percentage of variation in rhizome variables (number of apical ends, number of branchings, number of basal ends and rhizome length per cell) explained by cell-wise aboveground shoot counts over different time lags. Simple – analysis involving the given year only. Partial – additional variation explained by aboveground shoot counts in individual years (if significant) after variation explained by aboveground shoot counts in 1998 (year of excavation, i.e. lag =0) or 1997 (lag = 1) is removed, values for 1998 and 1997 were not applicable and marked as N/A in the whole table. The significance is given as: ns =not significant, * =p <0.05; ** =p <0.01; *** =p < 0.001. Year when aboveground shoot counts explained most of the variation in rhizomes is indicated in bold.

Time lag (yr) Covariate		Simple %	Partial 1998 %	Partial 1997 %
Deschampsia flexuosa				
0	1998	17.8 **	N/A	4.4 **
1	1997	**21.7 ****	8.3 **	N/A
2	1996	12.7 **	ns	ns
3	1995	7.5 **	ns	ns
4	1994	5.4 *	ns	ns
5	1993	6.1 *	1.4 *	1.4 *
6	1992	ns	ns	ns
7	1991	ns	ns	ns
8	1990	ns	ns	ns
All years		30.4	12.6	8.7
Festuca rubra				
0	1998	9.1 *	N/A	ns
1	1997	**13.3 ***	2.9 *	N/A
2	1996	7.2 *	ns	ns
3	1995	7.5 *	ns	ns
4	1994	10.2 *	4.5 *	4.4 *
5	1993	ns	ns	ns
6	1992	7.5 *	6.9 *	ns
7	1991	ns	ns	ns
8	1990	ns	ns	ns
All years		29	19.9	15.6
Nardus stricta				
0	1998	25.4 ***	N/A	ns
1	1997	**33.3 *****	11.3 ***	N/A
2	1996	22.9 ***	1.3 *	1.8 **
3	1995	11 **	1.5 *	1.4 *
4	1994	17.9 **	7 **	6.3 **
5	1993	14.2 **	ns	ns
6	1992	11.6 **	2.4 *	3.5 **
7	1991	13.9 **	9.8 **	11.8 ***
8	1990	12.3 **	ns	ns
All years		61.0	35.6	27.7
Anthoxanthum alpinum				
0	1998	16.6 **	N/A	8.6 **
1	1997	12.7 *	ns	N/A
2	1996	**20.2 ***	ns	ns
3	1995	18.6 *	9.8 *	ns
4	1994	ns	ns	ns
5	1993	12.9 *	ns	ns
6	1992	ns	ns	ns
7	1991	ns	ns	ns
8	1990	ns	ns	ns
All years		34.4	17.8	21.7
Polygonum bistorta				
0	1998	ns	N/A	ns
1	1997	10.6 **	2.4 *	N/A
2	1996	9.3 **	ns	ns
3	1995	**11.4 ***	9.2 **	3.1 *
4	1994	5.4 **	ns	ns
5	1993	6.9 **	ns	ns
6	1992	4.3 *	ns	ns
7	1991	5.6 **	ns	ns
8	1990	2.6 *	ns	ns
All years		17.7	15.3	7.1

during last four years of above-ground data collection. Therefore we do not have enough data to estimate probable decomposition time for *Festuca*. For *Anthoxanthum*, the correlation patterns for rhizome parameters of live and dead rhizomes with above-ground shoots were very similar because dead and live rhizomes are highly spatially correlated (data not shown). For dead rhizomes, correlations of shoot distribution with the distributions of length of the same species were significant for *Anthoxanthum* and *Polygonum*.

A similar pattern was revealed by multivariate analysis of community composition. Rhizome length explained 30–45% of the variation in aboveground species distribution in the year of excavation. With increasing time lag, the proportion of explained variation declined. In one plot, it first increased up to almost 60% for lags 1 and 2 after the excavation, and then steeply declined again (Table 3). For both plots, the relationship ceased to be significant 5 yr (1994) before excavation and earlier.

Using the information on temporal correlations, it was possible to make gross estimates of rhizome dynamic parameters (Table 4). Rhizome lifespans differ among species from 5 for *Anthoxanthum* and 8 for *Nardus* and *Polygonum*. Horizontal growth of most of our study species was about one centimeter per year with the exception of *Deschampsia* with a growth rate more than three times faster, and *Polygonum* about three times slower than the remaining species. The mean decomposition time is species-specific with some species persisting for just one year (*Anthoxanthum* and *Festuca*) and other for many years (*Polygonum*, 7 yr) after they die.

Species replacements aboveground and belowground

Both pairwise correlations of lengths of dead rhizomes with shoot densities of other species and with rhizome parameters of other species showed significant patterns between species (Table 5). Both data sets (shoot densities in the past and live rhizomes) yielded a rather similar picture. The majority of species pairs demonstrated significant replacement between species, although species differ strongly in the direction of replacement. Dead rhizomes of *Anthoxanthum* were not found correlated with *Deschampsia* and *Festuca* shoots from any year, and rarely with other species with the exception of *Nardus*. *Festuca* was not found to grow

Table 3. Intensity (variance explained by all canonical axes) of multivariate relationships between aboveground density of all species in individual years and species-specific rhizome lengths in spatial grid data (standardized redundancy analysis with species-specific rhizome lengths as predictor variables). Each year was analyzed separately. Significance tests are based on 200 permutations by toroidal shifting within rectangular spatial grid. Significance is given as: ns =not significant and ** = values were significant at α =0.05.

Year	Time lag (yr)	Variance explained by all canonical axes	
		Plot R3	Plot R12
1998	0	32.4**	46.3**
1997	1	55.2**	40.5**
1996	2	56.9**	43.1**
1995	3	38.1**	39.1**
1994	4	33.2**	36.6**
1993	5	25.5 ns	27.2 ns
1992	6	26.7 ns	24.3 ns
1991	7	28.4 ns	20.9 ns
1990	8	21.6 ns	27.6 ns

over *Nardus* and *Polygonum*, whereas it grew freely over other species. *Nardus, Deschampsia*, and to a lesser extent *Anthoxanthum* were found over dead rhizomes of most other species (with the exception of *Deschampsia* not being found over *Anthoxanthum*). For all species, their live rhizomes were positively spatially correlated with their dead rhizomes, which means that species are generally replacing themselves at the same positions allowing species to occupy certain space for long time.

Discussion

Reconstructing dynamics of the rhizome layer

As far as we are aware, this paper presents the first explicit attempt to link rhizomes and their position preserved in the soil to a temporal data series of aboveground shoot densities and to compare species in these parameters. A number of studies focus on rhizome growth parameters of individual species

Table 4. Rhizome parameters of the five species studied, based on correlations between number of growing and basal ends and rhizome length of live and dead rhizomes with time series of above-ground shoot distributions (Appendix 2). [1] Data from Juklickova (2003); [2] no dead rhizomes of *Festuca* were found, probably due to its low density and recent invasion of the plot.

Species	Rhizome growth rate (cm yr^{-1})	Lifespan (yr)	Mean decomposition time (yr)
Anthoxanthum	0.73	5−6	0−4
Deschampsia	3.33[1]	6	6
Festuca	0.83	6	?[2]
Nardus	<1.63	≥8	4−6
Polygonum	0.20	7−8	7

(Bernard et al. 1985, Klimes 1992, Stoll et al. 1998, Charpentier and Stuefer 1999, Meyer and Schmid 1999), but do not link them spatially and temporally to the dynamics of other species in the community. Our approach, on the other hand, allows comparison of rhizome dynamic parameters of co-occurring species, so that we can explore mechanisms of species coexistence in communities of clonal plants.

Dynamic parameters of rhizome growth can be inferred from patterns of correlations between rhizome parameters and shoot densities both in the year of excavation and in the past. Individual species show correlation of shoot densities with different rhizome variables; moreover they differ in the temporal lag with which these correlations decrease. These differences reflect differences in rhizome growth and lifespan and decomposition times that are, in turn, responsible for the size and age distribution of rhizomes. While some correlation is necessary for the data from the year of excavation (shoots are necessarily attached to rhizomes and therefore must be correlated with them), there is no inevitable correlation over nonzero temporal lags, meaning that existing correlations are directly indicative of processes of growth and death. We explored three types of correlations between above and belowground structures and their implications for dynamics of the plant community.

First, correlations of live rhizomes with shoot distributions going back in time are indicative of rhizome growth rates. In the mountain grassland we studied, the correlations indicate rather slow overall spatial dynamics belowground, with horizontal growth of most of our study species between 0.2 and 1.6 cm yr^{-1}. This seems reasonable for a community with a short growing season and rather poor soil conditions. However, the most abundant species of this community (Appendix 1), *Deschampsia*, grew more than three times faster than the other species (3.3 cm yr^{-1}). This species is thus able to reach most sites within the community by clonal growth faster than any other species.

Second, information on positions of shoots on rhizomes and potential architectural constraints can be obtained by examination of which rhizome parameters (number of apices vs rhizome length) are best correlated with the extant shoot distribution. The actual correlation depends on the exact positioning of the shoots and on the presence of long rhizomes without any shoots. Species differ considerably in this respect. *Nardus* and *Festuca* have low density of intermediate-sized rhizomes (in our study their lengths exceeded the size of individual cells), without overlap of individual rhizomes (Wildova 2004). Therefore, for these species, the high correlation of rhizome length with shoot abundance within a cell indicates presence of shoots not only at the apical ends but also laterally along rhizomes. For *Deschampsia,* with abundant

Table 5. Species replacement patterns revealed by correlating length of dead rhizomes per cell with time series of 1) above ground shoot counts (1990–1998; each year analyzed separately) of each species – "Aboveground shoots"; and 2) rhizome parameters (number of apical and basal ends and rhizome length) of live rhizomes of all species – "Live rhizomes". Years of significant positive correlation are marked by symbol "X". Significance was tested by Monte Carlo test ($\alpha = 0.05$). Highlighted years show estimated length of mean decomposition time, during which we can assume true species replacement as in contrast just a presence at the same spatial location. Correlations with dead rhizomes of *Festuca* are not included as there were no dead rhizomes of that species.

	Significan positive spatial correlation of									
	Aboveground shoots									Live rhizomes
with dead rhizomes of *Anthroxanthum*										
Year of record	90	91	92	93	94	95	96	97	98	98
Anthoxanthum	X								X	X
Deschampsia										X
Festuca										
Nardus	X	X	X				X	X	X	X
Polygonum			X							X
with dead rhizomes of *Deschampsia*										
	90	91	92	93	94	95	96	97	98	98
Anthoxanthum	X		X	X	X	X	X	X	X	X
Deschampsia	X	X	X	X	X	X	X			X
Festuca	X	X				X	X	X	X	X
Nardus	X	X	X	X	X	X	X			X
Polygonum	X	X	X	X	X	X	X	X	X	X
with dead rhizomes of *Nardus*										
	90	91	92	93	94	95	96	97	98	98
Anthoxanthum	X						X		X	X
Deschampsia			X		X	X	X	X	X	X
Festuca	X									
Nardus	X	X	X	X	X	X	X	X		X
Polygonum			X	X	X	X				
with dead rhizomes of *Polygonum*										
	90	91	92	93	94	95	96	97	98	98
Anthoxanthum	X	X	X	X	X	X	X	X		X
Deschampsia				X	X	X	X		X	X
Festuca	X									
Nardus	X	X	X					X		X
Polygonum	X	X	X	X	X	X	X	X	X	X

overlapping long rhizomes, the correlation between rhizome length and shoot abundance is blurred by co-occurrence of apical ends of one individual alongside of rhizomes of other individuals within the cell. For *Anthoxanthum* with very short rhizomes, the high correlation is due to the fact that entire rhizome systems and their shoots co-occur within the same cell. *Polygonum bistorta* (the only dicot species) showed almost no correlation between rhizomes and above-ground shoots over time in one of the study plots. This species had high proportions of rhizomes without ramets and may even be temporarily "invisible" from above-ground as it has a large number of dormant rhizomes waiting below-ground for favorable conditions (Pechackova and Krahulec 1995).

Although one would expect that rhizome variables would best correspond with the shoot distribution in the year of excavation, our data demonstrate that this is often not the case. This is likely due to the nature of shoot arrangement on rhizomes. Whether or not shoots are present at apical ends of rhizomes is determined by the type of rhizome growth: 1) it may develop directly as a below-ground organ and grow first horizontally before switching to vertical growth to produce a shoot or 2) it may start as a shoot, and later the basal part of shoot lies on the soil surface and transforms to a rhizome by rooting in at its nodes (Serebrjakov and Serebrjakova 1965, Klimes et al. 1997, Klimes and Klimesova 1999). In the first type, it is likely that some apical ends have not yet produced shoots, whereas in the latter type rhizomes regularly bear shoots at their ends. All of our study species except for *Nardus* produce both rhizome types (Freiova 1996). Therefore, in the year of excavation, the basal parts of shoots are creeping, but the rhizome apical ends, which are transitional between rooted rhizome and shoots, are spatially offset from the perpendicular projection of vertical stem.

Finally, species differ in rhizome die-off and consequently in their rate of accumulation of dead rhizomes in the soil. The data generally show that rhizome lifespan and persistence of dead rhizomes in the soil differs between species, although typically rhizomes stay in the soil for a long time for all species. The estimated long-term persistence of dead rhizomes explains the large amount of dead relative to live rhizomes in the soil for species like *Deschampsia*, *Polygonum* and *Nardus* (Appendix 1). This dead biomass may have considerable influence on community dynamics, although little is known on its effects (Pucheta et al. 2004). On the other hand, *Anthoxanthum* shows a sharp decrease of the correlation between shoot density and rhizomes with increasing time lag indicating fast rhizome turnover, which agrees with the observation that it has very few dead rhizomes in comparison to the amount of its live rhizomes.

The reconstruction of rhizome dynamics thus allows accurate interpretation of clonal species growth strategy and role in a community. For example, *Deschampsia* is the only species with overlapping rhizome systems and fast horizontal growth rate. Thus, while aboveground morphology of this species (thin and short shoots, Fig. 4) is similar to other co-occurring grass species, it strongly differs in its rhizome system. Its pattern of fast growing rhizomes with many attached shoots combined with its ability to form rather dense rhizome mats that slowly decompose after rhizome death makes *Deschampsia* a dominant species in the community.

Rhizome dynamics in the community context

Species differences in dynamics of rhizome growth can be responsible for replacement patterns observed aboveground and competitive hierarchies in clonal plant communities (Fig. 3). All species show fine-scale replacement processes, but with marked differences in patterns of spatial replacements over time. Three species, *Deschampsia*, *Nardus* and *Festuca* form a basic matrix of species replacing each other by growing new rhizomes over dead rhizomes, with *Festuca* lower on the competitive hierarchy than the other two and able to replace only *Deschampsia*. This replacement hierarchy is the same as that inferred from long-term spatio-temporal data based on frequency changes of aboveground shoots from the same grassland (Herben et al. 1995, 1997a, b). However, for the other two species, *Anthoxanthum* (very high spatial turnover) and *Polygonum* (very slow spatial turnover), the data provided here on belowground processes are not consistent with data on shoot turnover (Herben et al. 1993). Rhizome observations showed spatial overlap of new rhizomes of these two species with dead rhizomes of other matrix species, even though the occurrence of new shoots aboveground was independent of spatio-temporal changes of shoots of other species (Herben et al. 1993). The processes independent to vegetative spreading are responsible for this inconsistency. The independent dynamic to rhizome growth for *Anhtoxanthum* is likely driven by very high seed production and generative recruitment (Flegrova and Krahulec 1999,
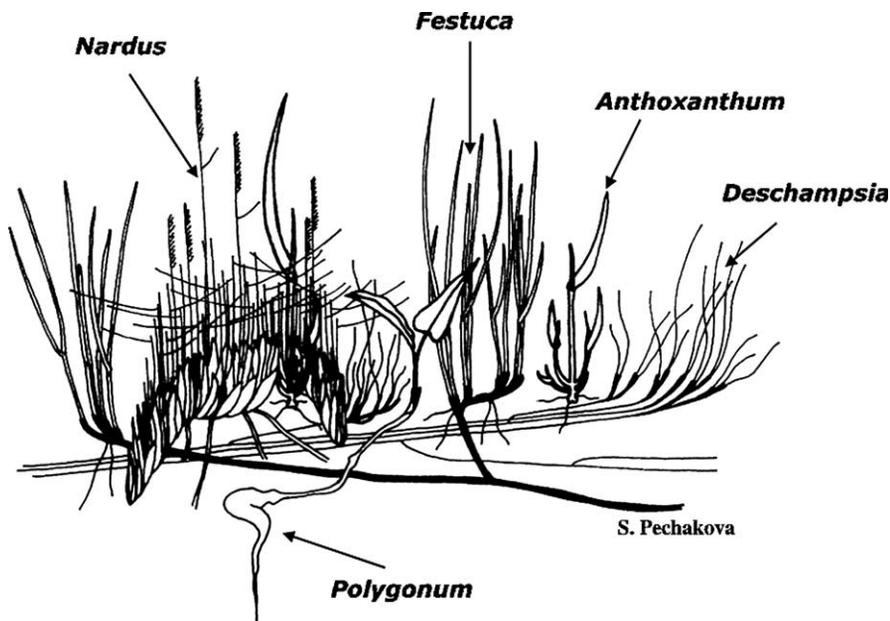
Fig. 4. Idealized structure of studied grassland community showing spatial distribution of layers of rhizomes, original adapted from Herben et al. (1997b) with permission.

J. Suzuki pers. comm.), whereas *Polygonum* seems to be strongly influenced by environmental conditions increasing rapidly shoot densities from dormant rhizomes, when all grass species are suppressed (for example by short growing season and high snowfall, Wildova et al. unpubl.).

Replacements in the community seem to be driven by small-scale gaps due to directional rhizome growth. Rhizomes of all species, even *Nardus*, with tussock-like growth, grow at one end and die at the other, bearing shoots mainly at the apical ends. Thus, they leave behind older parts of rhizomes without shoots (Fig. 4). These become aboveground gaps; although their accessibility to other species may be limited for some time by the dense rhizome network, they eventually become colonized by other species or other individuals of the same species.

The whole system thus functions on the basis of a kind of colonization-competition tradeoff: species differ in their ability to colonize and replace/compete. Good colonizers like *Deschampsia* and *Anthoxanthum* are able to reach the gaps first, albeit using very different mechanisms for colonization (rhizome long distance growth versus fast generative recruitment, respectively), Longer-term, these fast colonizers also make gaps relatively quickly and eventually some of these gaps are colonized by slower matrix species, which will then occupy that space for a long time period. The differences in rhizome growth and architectural constraints combined with differences in mortality patterns allows co-existence of both types of species and succession stages are continuously cycling at a small spatial scale (Herben et al. 1994, Sammul et al. 2004). The system does not depend on gaps generated externally, but generates open microhabitats by rhizome growth coupled with architectural constraints. This mechanism of community assembly is a likely mechanism to maintain long-term species coexistence in nutrient poor communities of clonal plants (Otsus and Zobel 2002, Sammul et al. 2004).

Conclusions

The data show rather convincingly that similar species such as perennial grasses differ in parameters such as rhizome growth rate, lifespan and mean decomposition time. These differences in clonal growth parameters are responsible for species-specific differences in horizontal growth and dieback over time that had been repeatedly shown by aboveground recordings. Further, types of rhizome growth have strong bearing on interactions between species as replacement of species in space is also constrained by the same rhizome growth pattern. It is therefore likely that rhizome growth patterns determine rates and directions of within-community fine-scale

dynamics and underlie the fine-scale coexistence of these grassland species.

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