

Variation in plant performance in a grassland: Species-specific and neighbouring root mass effects

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Abstract

Question: What characteristics of local biotic neighbourhood is the best proxy of competitive effects experienced by plants in a herbaceous community: (1) total above-ground biomass, (2) root mass or (3) relative above-ground abundance of selected species?

Location: Grassland at ca. 1100 m a.s.l. in the Krkonoše Mts., northern Czech Republic.

Methods: We implanted two phytometer species, *Anthoxanthum alpinum* and *Festuca rubra*, into a mountain grassland, and examined their response to local variation in (1) total above-ground biomass, (2) root mass at three soil depths, and (3) relative abundance of individual species above-ground.

Results: Performance of both phytometer species was determined much more consistently by the mass of neighbouring roots and by species composition of neighbours than by the total above-ground biomass. The two phytometer species showed different responses to these parameters. The most important relationships were (1) negative relationship between performance of *Anthoxanthum* and mass of neighbouring roots at 0-3 cm, (2) positive relationship between performance of *Festuca* and mass of neighbouring roots at 3-6 cm, and (3) negative relationship between performance of *Festuca* and relative abundance of *Festuca* in the neighbourhood.

Conclusions: Neighbouring root mass and above-ground species composition are better determinants of biotic interactions than total above-ground biomass of neighbours in the studied mountain grassland. However, the relationships found are not necessarily due to variation in competitive intensity but can be due to other hidden factors as well, e.g. local availability of resources.

Keywords: Above-ground; *Anthoxanthum alpinum*; Below-ground; Competitive effect; *Festuca rubra*; Species-specific.

Introduction

Intensity of competitive stress has been suggested to be an important determinant of plant performance in the plant community (Goldberg & Barton 1992). This has been supported in numerous studies by the inverse relationship between performance of a plant individual and the size of its neighbours (Goldberg & Landa 1991; Keddy et al. 1994, 2002). However, in reviews of a variety of relevant competition experiments, in only half of the cases this relationship was found for the majority of within-study comparisons (review of Goldberg & Barton 1992, see also more recent studies of Belcher et al. 1995; Peltzer et al. 1998; Herben et al. 2001). Ecological consequences of the results depend on the extent to which size of plant neighbours in the studies substitutes for intensity of encountered competition. Most often, intensity of competition has been substituted by total above-ground neighbouring biomass regardless of neighbourhood composition. This assumes greater importance of above-ground and unspecific competitive interactions, relative to the below-ground or species-specific ones. While this assumption may be reasonable in numerous field systems, it may not be universal. Different parameters capturing the neighbourhood effects should therefore be sought.

First, performance of phytometers may follow variation in root mass, in particular if below-ground competition is stronger than above-ground competition. It has been repeatedly shown that intensity of below-ground competition can be comparable or larger than the intensity of above-ground competition (Belcher et al. 1995; Twolan-Strutt & Keddy 1996; Peltzer et al. 1998; Cahill 1999). This is predicted especially for communities in which variation of plants above-ground is not high enough to produce asymmetric competition for light (Hara & Wakahara 1994; Schwinning & Weiner 1998). Moreover, as spatial pattern of above-ground biomass on a fine scale can differ from that of root mass (Pecháčková et al. 1999; Titlyanova et al. 1999; Casper

et al. 2003, for a review see Schenk & Jackson 2002), above-ground biomass cannot even be used as a proxy for below-ground variation.

Second, species-specific interactions may play an important role in some communities.

In general, species identity typically affects the outcome of competitive interactions between plants to a lesser extent than differences in plant size (Goldberg & Werner 1983; Gaudet & Keddy 1995). However, species-specific effects may become important especially in communities where variation in the size of plant individuals is small (Aarssen 1988; Herben et al. 1997; McLellan et al. 1997). Since spatial distribution of individual plant species often differs from the spatial distribution of the total above-ground biomass, species-specific effects, if present, may modify effects of unspecific above-ground competition.

In the present paper we attempt to compare the amount of variation in phytometer performance explained by several alternative proxies of competition intensity in a grassland where plant performance was weakly linked to neighbouring above-ground biomass (Herben et al. 2001).

Methods

Study site

The study site was located in a mountain 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). The whole area has a harsh climate; mean temperature in the warmest month (July) was 12–17 °C (1986–2001) at the nearby climatic station (Pec pod Sněžkou, ca. 900 m a.s.l.). The study area has a long winter with a thick (> 1 m) snow cover; the total number of days with snow per year in the study period ranged from 137 to 182. The soil at the site is podzolic, with dark brown humus (0–3 cm) and a grey leached layer (3–6 cm) above a reddish brown iron-enriched horizon, and is covered by a litter layer approximately 1 cm thick. Total soil nitrogen decreases with depth (1.6 %, 0.5 % and 0.3 % for individual layers), as does mean soil moisture (Pecháčková unpubl. data). The studied grassland is not natural, but has been maintained by human management, namely mowing and manuring. Since their establishment in about the 17th century the grasslands in this area have reached a relatively stable species composition owing to the stable management practices (see also Krahulec 1990).

There are only five principal species in the plots: *Anthoxanthum alpinum*, *Deschampsia flexuosa*, *Festuca rubra*, *Nardus stricta* and *Polygonum bistorta*. Although

the system is species-poor at a large scale, the species intermingle at a fine scale; the species density is 2–4 species/10 cm². The average height of vegetation in the peak vegetation season (July) is 15–20 cm.

Study species

Festuca rubra ssp. *rubra* is a common perennial grass species of temperate grasslands in Europe. It forms long-lived (> 1 yr) monocarpic shoots. Architecture of its tussocks is variable, ranging from compact to rather loose, and is under both genetic and environmental control (Skálová et al. 1997). *Anthoxanthum alpinum* (hereafter *Anthoxanthum*) grows in grasslands, shrub communities, and open woodlands through Arcto-Alpine parts of Europe. It forms compact tussocks consisting of short-lived (most frequently < 1 yr) monocarpic shoots. It is a phenologically early species, showing its peak of growth about a month earlier than *Festuca*.

Experimental design

In 1990 11 plants of *Festuca* were collected from the studied grassland. These plants were shown to be different clones by a molecular marker study (Skálová et al. 1997). Six clones of *Anthoxanthum* were collected at the study site at least 5 m apart. Their genetic identity was not tested because *Anthoxanthum* tussocks are known to be unique genotypes (Suzuki et al. unpubl.).

The clones were multiplied vegetatively in an experimental garden. In June 1997, 18 well developed individual shoots of each *Festuca* clone, and six shoots of each *Anthoxanthum* clone were taken from the mother tussocks. They were rooted in water and subsequently planted into filter paper tubes 1 cm in diameter and 5 cm long filled with a mixture of compost and peat. When they reached 5–8 cm height, the tubes were implanted into the grassland at the study site in 12 rows 100 cm apart. Attention was paid to cover the full range of the variation in shoot density at the site; the minimum planting distance within individual rows was 20 cm.

A few implants did not survive (probably due to mechanical damage during the implanting); therefore only 178 plants of *Festuca* and 33 of *Anthoxanthum* were used for later observations. The initial mortality was not included in the analyses, and no other implants died later in the experiment. Because of daughter shoot formation, small tussocks (hereafter phytometers) were formed from the implanted shoots. After establishment in 1997, phytometer growth was monitored twice a year until July 2001. The recordings were made in late May (ca. 10–14 days after snow melting) and in mid-July, and number of surviving shoots and the length of the longest leaf of the phytometer were measured.

To collect information on neighbouring vegetation, a circle of 12 cm in diameter was laid over each phytometer with the phytometers positioned in the centre of the circle. The size was derived from the distance of autocorrelation in environmental properties and species composition in the grasslands (Herben et al. 1995; Skálová et al. 1999). As the phytometers moved a little by means of horizontal growth, it was necessary to change the absolute position of the circles between individual years of the experiment in order for the phytometers to remain in the centre of the sampled area. After the July recordings, neighbour plants within each circle were clipped at a height of 2.5 cm, sorted by species, and dried at 60 °C. This dried biomass represented the species composition of the neighbourhoods of the phytometers. The phytometer plants were also clipped at this time to obtain their above-ground biomass. After sampling, the whole study area was clipped at a height of 2.5 cm to simulate the traditional management of the grassland.

In July 2001, soil cores 12 cm in diameter and 15 cm in depth were taken around each phytometer using a specially constructed steel corer. The cores were split into layers 0-3, 3-6, 6-9, 9-12 and 12-15 cm. Roots in each layer were separated from soil and from rhizomes in a laboratory, dried at 60 °C, and weighed.

Data processing

The performance of the two phytometer species was assessed by biomass of above-ground parts in mid-July, total number of shoots in late May, and length of the longest vegetative shoot in the tussock. Maximum shoot length occurred in late May for *Anthoxanthum* and in mid-July for *Festuca* (hereafter max. spring and summer length) because of differences in phenology. The growth parameters were not expressed separately for individual years of the experiment because of strong between-year covariation of phytometer growth (data not shown). Instead, they were expressed as the above-ground biomass at the end of the experiment (hereafter above-ground biomass) and the number of phytometer shoots and maximal length of the phytometers averaged across the four experimental years (hereafter number of shoots and maximal length of the phytometers, respectively). Number of phytometer shoots was square-root transformed to satisfy the assumption of normality for statistical analysis.

The neighbouring vegetation was characterized by total above-ground biomass and by proportions of three species (*Nardus*, *Festuca* and *Anthoxanthum*) in the above-ground biomass averaged over the four experimental years, and by root mass in individual soil layers at the end of the experiment. The proportions of *Nardus*, *Festuca* and *Anthoxanthum* were used as the

three independent variables representing the main components of uncorrelated variability in species composition at the study site. Principal Components Analysis of species composition showed that the proportion of the fourth major species at the site, *Deschampsia flexuosa*, explained little additional variation in species composition (data not shown). The below-ground neighbourhood was defined by root mass in 0-3 cm, 3-6 cm and 6-15 cm soil layers. Root mass in soil layers below 6 cm were strongly correlated (data not shown) and were therefore combined.

Statistical analysis

The relationships between individual parameters of the neighbouring vegetation were assessed by means of correlations. The effect of individual predictor variables on growth parameters of phytometers were analysed using GLM. We compared amount of variation in growth parameters of phytometers explained by a model involving all predictors with the amount of variation explained by the model where the predictor variables were deleted in an alternate fashion. The direction and significance of relationships between growth parameters of phytometers and predictor variables were assessed by linear regression. All statistical calculations were done using S-plus 2000 (Anon. 2000).

Results

Structure of the neighbourhoods

Mean above-ground biomass of the neighbourhoods was 326 g.m⁻² (SD = 157) and mean mass of roots within this area down to 15 cm depth was 537 g.m⁻² (SD = 153). The three species used to assess the species-specific effects in this experiment (*Nardus stricta*, *Festuca rubra* and *Anthoxanthum alpinum*) were the first, second and fourth-ranked species in terms of mean above-ground biomass, and the third, fourth and first species according to frequency (Table 1, the remaining species was *Deschampsia flexuosa*).

The species composition, as well as the proportion of the three selected species in individual neighbourhoods were rather stable over time. There was a highly significant positive relationship between the amount of total above-ground biomass and proportion of *Nardus*. Proportions of both *Festuca* and *Anthoxanthum* were negatively correlated to the proportion of *Nardus* and total amount of above-ground biomass (for all relationships between individual properties of neighbourhood, see Table 2). The mass of roots in 3-6 cm and 6-15 cm layers were positively correlated. The mass of roots in

Table 1. Neighbourhood structure in the experiment (expressed as g/100 cm² for above-ground biomass and g/100 cm³ for root mass).

	Mean ± SD	Minimum	Maximum	Mean proportion ± SD (%)	Maximal proportion (%)	% occupied neighbourhoods
Total above-ground	3.26 ± 1.57	0.63	11.11			
<i>Anthoxanthum</i>	0.36 ± 0.32	0	2.13	12.5 ± 10.5	73.7	98
<i>Festuca</i>	0.47 ± 0.54	0	3.43	15.9 ± 16.4	74.3	84
<i>Nardus</i>	1.13 ± 1.18	0	7.42	29.8 ± 23.7	81	88
Roots 0 - 3 cm	1.21 ± 0.45	0.42	2.97			
Roots 3 - 6 cm	0.31 ± 0.16	0.05	1.3			
Roots 6 - 15 cm	0.09 ± 0.04	0.03	0.44			

Table 2. Correlation coefficients between individual above-ground properties of the neighbourhoods averaged over the four experimental years and mass of roots in individual soil layers at the end of the experiment. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	df	Above-ground biomass	<i>Festuca</i> proportion	<i>Anthoxanthum</i> proportion	<i>Nardus</i> proportion	Mass of roots, 0 - 3 cm	Mass of roots, 3 - 6 cm
<i>Festuca</i> proportion	1	-0.22***					
<i>Anthoxanthum</i> proportion	1	-0.32***	-0.18**				
<i>Nardus</i> proportion	1	0.69***	-0.51***	-0.39***			
Mass of roots, 0 - 3 cm	1	0.15*	0.03	-0.15*	0.09		
Mass of roots, 3 - 6 cm	1	0.13	-0.05	-0.31***	0.29***	0.08	
Mass of roots, 6 - 15 cm	1	0.06	-0.08	-0.16*	0.23**	-0.02	0.64***

the 0-3 cm layer was positively related to the amount of above-ground biomass in the neighbourhoods. There was a negative relationship between proportion of *Anthoxanthum* averaged over the time of experiment and mass of roots in 3-6 cm and 6-15 cm layers; the same relationship was positive for *Nardus*.

Sources of variation in phytometer performance

Total above-ground biomass of neighbours explained small amount of variation in all growth parameters of both phytometer species in GLMs, relative to the amount of variation explained by most successful predictors (for all relationships see Table 3). The only significant relationship in which it was involved was the positive regression with maximum summer length of *Festuca* leaves.

According to the GLMs, most successful neighbour predictor of *Festuca* performance was proportion of neighbouring *Festuca*. It explained ca. four times larger amount of variation in above-ground biomass of *Festuca*

Table 3. Comparison of the amount of variation in growth parameters of phytometers explained by particular predictor variables in GLM. The values show the decrease of explained variability (in %) after deletion of particular sets of predictor variables (shown in the first column of each row) from maximum model. df indicates total number of degrees of freedom of a particular set of the predictor variables and their interactions. ‘-’ and ‘+’ signs indicate direction of significant ($p < 0.05$) relationships between growth parameters and predictor variables in linear regression.

	df	<i>Festuca</i>			df	<i>Anthoxanthum</i>		
		Above-ground biomass	Number of shoots	Maximal summer length		Above-ground biomass	Number of shoots	Maximal spring length
Clone	10	20.78	20.22	28.81	6	58.11	50.67	20.88
Total above-ground biomass	1	1.82	3.93	(+) 3.35	1	1.08	2.67	5.52
Proportion of <i>Anthoxanthum</i>	1	0.69	(-) 5.1	0.53	1	25.45	9.01	15.13
Proportion of <i>Festuca</i>	1	(-) 7.56	(-) 14.68	0.42	1	28.28	4.57	7.80
Proportion of <i>Nardus</i>	1	0.02	1.06	0.16	1	(-) 20.69	11.73	5.80
Mass of roots in 0-3 cm	1	0.05	0.07	0.01	1	(-) 19.18	10.18	11.84
Mass of roots in 3-6 cm	1	(+) 5.14	(+) 5.6	0.58	1	0.3	3.91	0.26
Mass of roots in 6-15 cm	1	2.68	0.35	(-) 4.08	1	(-) 6.94	0.52	(-) 7.09

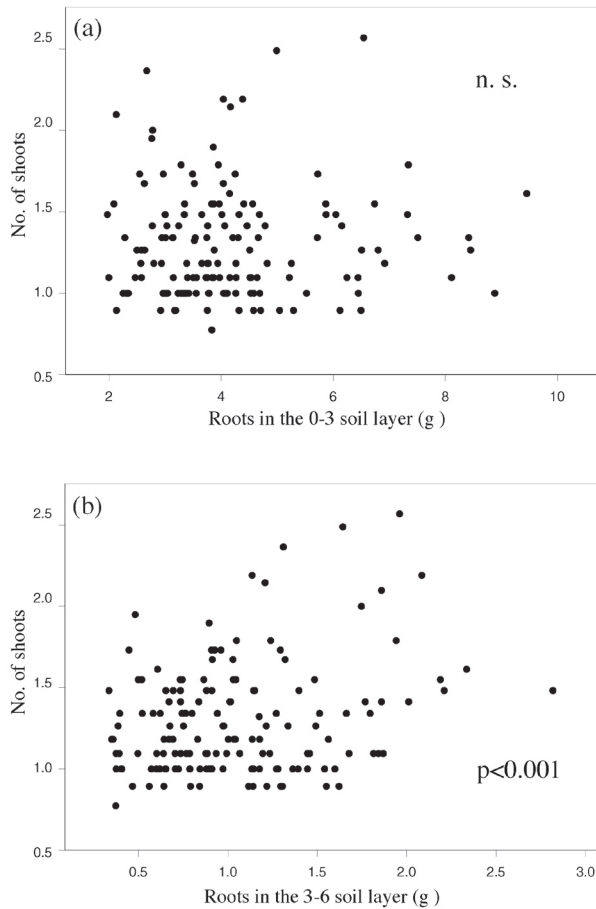


Fig. 1. Relationship between number of *Festuca* shoots averaged over the four experimental years and mass of roots in different soil layers at the end of experiment. The values of the root mass are calculated for 100 cm³. Significance indications refer to the significance of the relationships in linear regression; n.s. = non-significant.

phytometers than total above-ground biomass of neighbours and more than ten times larger amount of variation than proportion of *Anthoxanthum* and *Nardus*. The relationship was significantly negative when assessed in linear regression (Fig. 1). Out of the root variables, the most successful predictor of *Festuca* performance was the mass of neighbouring roots in the 3-6 cm soil layer. It explained the ca. three times larger proportion of variation in its above-ground biomass than total above-ground biomass of neighbours and ca. two times larger than mass of neighbouring roots in the 6-15 cm soil layer. This relationship was positive (Fig. 2). The most successful predictor of *Festuca* performance was their clone identity, however.

Almost all predictors explained more variance in growth parameters of *Anthoxanthum* phytometers than in those of *Festuca* phytometers in GLM. There was not

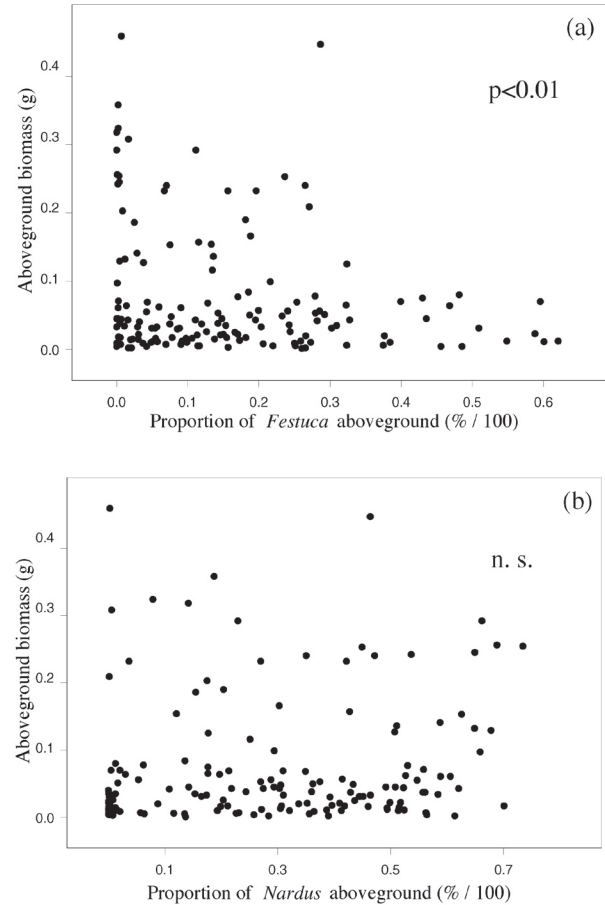


Fig. 2. Relationship between above-ground biomass of *Festuca* phytometers at the end of the experiment and proportion of selected species in their neighbourhood averaged over the four experimental years. Significance indications refer to the significance of the relationships in linear regression; n.s. = non-significant.

any outstanding predictor of *Anthoxanthum* performance. The proportion of all neighbour species explained similar amount of variation in its above-ground biomass; this was more than twenty times larger than the amount of variation explained by total above-ground biomass of neighbours. The most successful root predictor of *Anthoxanthum* performance was the mass of neighbouring roots in the 0-3 cm soil layer. It explained a similar amount of variation in its above-ground biomass to proportion of neighbour species. This amount was ca. three times larger than the amount of variation explained by mass of neighbouring roots in the 6-15 cm soil layer. Similarly to the *Festuca* phytometers, the most successful predictor of *Anthoxanthum* performance was the factor clone.

Discussion

Variation in root mass and variation in proportions of neighbour species each explained an at least three times larger proportion of variation in growth parameters of phytometers than did variation in above-ground biomass (for quantification of variance in phytometer performance explained by individual predictor variables, see Table 3). The only exception was large explanatory power of above-ground biomass on height of *Festuca* phytometers. This is probably due to simple etiolation of shoots when shaded. This implies an important role of below-ground as well as species-specific above-ground processes, which have been reported from other herbaceous communities (for below-ground processes, see Belcher et al. 1995; Twolan-Strutt & Keddy 1996; Peltzer et al. 1998; Cahill 1999; for species-specific processes, see Aarssen 1988; Herben et al. 1997; McLellan et al. 1997). Lack of knowledge on species-specific distribution of roots does not allow us to specify extent of interdependence of the two processes. It might be large, however, as species-specific effects are more probable to proceed below-ground than above-ground due to larger potential of below-ground resources to be partitioned between species in time and space (Veresoglou & Fitter 1984; Fitter 1986; Mc Kane et al. 1990).

While the effects of neighbouring root mass were strong in both phytometer species, the two species responded differently. Above-ground biomass of *Anthoxanthum* phytometers was affected negatively by the mass of neighbouring roots in 0-3 cm soil layer whereas above-ground biomass of *Festuca* phytometers was related positively to mass of neighbouring roots in the 3-6 cm soil layer. In the case of *Anthoxanthum* the relationship most likely reflects variation in below-ground competitive intensity, and corresponds well with results of the only other field study in which the relationship between mass of neighbouring roots and performance of plants has been observed (Cahill & Casper 2000). In the case of *Festuca*, the relationship is hard to interpret without additional data as it can be due to (1) facilitation of *Festuca* performance by its neighbours below-ground, (2) high performance of *Festuca* at sites with thick, heavy but sparse *Nardus* roots, as well as due to (3) high *Festuca* performance at nutrient enriched sites concentrating large root mass due to nonspecific proliferation of roots of all neighbouring plants. We can neither fully exclude the possibility that the relationship is due to the *Festuca* phytometers themselves, although according to our experience, the root system of grass shoots similarly sized to *Festuca* phytometers does probably not affect the root mass within the whole neighbourhood. Interestingly, vertical differentiation of below-ground neighbourhoods having most pronounced relationships with *Festuca* and

Anthoxanthum performance agrees well with vertical differentiation of root mass of the species at the study site (Pecháčková et al. 1999). This strongly suggests that the statistical responses of both phytometers to neighbouring root mass are really due to below-ground interactions, independent of their exact nature, rather than due to any hidden interaction between plants above-ground.

Remarkably, the above-ground biomass and number of shoots of *Festuca* phytometers responded negatively to the relative abundance of neighbouring *Festuca*, whereas the proportion of other species affected performance of *Festuca* phytometers to a much lesser extent. The negative relationship between *Festuca* performance and proportion of neighbouring *Festuca* is triangular, with high variation in *Festuca* phytometer performance in neighbourhoods without *Festuca*, but with consistently low performance in neighbourhoods with *Festuca*. This indicates that *Festuca* presence, although important, is only one of the many factors that determine phytometer performance. The relationship may suggest that *Festuca* performance was controlled more intensively by intra-specific than inter-specific competition. This is surprising as in most cases, including *Anthoxanthum* in a present experiment, the intensity of intra- and inter-specific competition per unit biomass is similar (for a review, see Goldberg & Barton 1992). However, it is unlikely that this relationship is caused by the low quality of sites occupied by *Festuca*. If this were the case, we would expect a positive relationship between performance of *Festuca* phytometers and the total amount of above-ground biomass and/or a negative relationship between the proportion of *Festuca* in the neighbourhood and mass of neighbouring roots. No such relationship was found. Large sensitivity of *Festuca* phytometers to species composition of neighbours, relative to *Anthoxanthum* phytometers, might be due to differences in their growth: small and slowly growing *Festuca* tussocks probably experienced differences in effects of neighbouring plant species to a larger extent than large and dynamic *Anthoxanthum* tussocks.

The findings may have important implications for coexistence of plants within the studied grassland: the probability of plants to coexist increases when intra-specific frequency-dependent regulation of plant abundance is stronger than inter-specific regulation (McArthur & Levins 1967; Goldberg & Barton 1992). The mechanism underlying this pattern cannot be inferred from our results. This might be due to inter-specific differentiation in the way plants use soil resource heterogeneity, or to vertical distribution of their below-ground zones of influence as suggested by different patterns of relationships between neighbouring root mass and performance of *Festuca* and *Anthoxanthum* along a gradient of soil depth (see Table 1). Alternatively, the pattern can be

explained by a larger spatial range of intra-specific negative interactions, relative to the inter-specific ones (Murrell & Law 2003); this can be, for example, caused by species-specific root herbivores or allelopathy (Murrell & Law 2003 and references therein). Remarkably, the performance of phytometers of both species pronounced considerable intra-specific variation (see the effect of clone in Table 3). Potentially, competitive outcomes of intra-genotypic and inter-genotypic interactions may differentiate by analogous mechanisms to those differentiating intra-specific and inter-specific interactions. Such a differentiation would explain high genotypic diversity of *Festuca* tillers found in the studied grassland (Suzuki et al. 1999) as well as high genotypic diversity of clonal plants in other studies (Ellstrand 1987).

Implications and conclusions

Our results suggest that a large part of the variation in plant performance that did not match the spatial variation in above-ground biomass in grassland communities reflects variation in below-ground processes and/or in species-specific competitive effects. The important role of below-ground and species-specific processes in grassland communities is thought to be due to low vertical variation of plant sizes due to regular disturbance or seasonal growth and a low consequent role of asymmetric competition for light (Hara & Wyszomirski 1994; Rajaniemi 2003 and references therein). However, our results also suggest that the small role of above-ground unspecific competition at the study site cannot be easily inferred from the range of variation of above-ground biomass *per se*. First, while the range of variation of above-ground biomass in this community was larger than the range of variation of the root mass, the root mass explained a larger part of variation in the phytometer performance. Further, the range of variation of above-ground biomass at our study site was larger than at several other communities where the phytometer performance did respond to variation in the above-ground biomass (for a review, see Belcher et al. 1995).

This is in line with Law et al. (1993) who showed that variation in above-ground plant sizes has to encompass the non-linear (sloping) part of the density-performance relationship in order to show the systematic effect of crowding on performance. This supports the notion that the thresholds beyond which the variation in vertical plant sizes can induce variation in performance of plants may differ between communities. They may reflect positioning of the non-linear part of the density-performance relationship which itself may be determined by the role of above-ground unspecific competition, relative to all other sources of variation in plant performance.

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