

Small-scale guild proportions and niche complementarity in a Caucasian subalpine hay meadow

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Abstract

Question: Monocot and dicot perennial herbaceous species can be considered two *a priori* guilds, which interact in regularly mown grasslands. Complementary resource use in space is important for diversity and productivity of perennial herbaceous communities, yet small-scale spatial patterns of guilds and niche complementarity have rarely been linked explicitly. We ask: 1. Do guild interactions in our community generate small-scale patterns such as guild proportionality? 2. Do these patterns coincide with overyielding of guilds, that is, can small-scale spatial patterns of guilds be experimentally linked to niche complementarity?

Location: Georgia, central Caucasian mountains.

Methods: We sampled randomly placed small quadrats and used presence-absence data to measure small-scale spatial patterns within plots. We experimentally tested overyielding of monocots and dicots grown separately and in mixtures.

Results: We found measurable small-scale pattern of guilds in our community: monocots and dicots showed significant guild proportionality. However, variance deficit in the number of species per small quadrat was stronger in monocots than in dicots. Experiments found considerable overyielding, which was unaffected by water stress.

Conclusions: Coincidence of measurable small-scale arrangements of guilds with robust overyielding indicates that spatial arrangement is an important manifestation of niche complementarity. Stronger variance deficit of monocot species at small scale suggests that monocots compete with each other more strongly and, as a consequence, are more regularly dispersed at small spatial scale. Conversely, morphologically more diverse and more plastic dicots may more easily fit within the neighbourhood patchwork created by monocots.

Keywords: Monocot; Dicot; Community structure; Small-scale spatial distribution; Complementary resource use; Overyielding.

Introduction

Complementary resource use in space is important for the diversity and productivity of perennial herbaceous communities (van Ruijven & Berendse 2005). However, regularities in distribution of neighbouring plants (a measure of small-scale spatial patterns) and overyielding (a measure of niche complementarity) have never been linked in one study. Rather, there have been reports on non-random patterns of species distribution at a fine scale in managed and natural communities (e.g. Wilson et al. 1992; Stubbs & Wilson 2004) and, independently, many recent papers report overyielding in artificial and reconstructed communities (e.g. van Ruijven & Berendse 2005; Roscher et al. 2005). Linking small-scale spatial patterns and overyielding may reveal important details of plant community organisation.

Guilds are groups of ecologically similar species (Wilson 1999), and interactions within and between guilds may mimic those within and between species. For example, plants belonging to the same species compete for space more strongly among themselves than with plants of other species; such interactions can restrict variation in richness of neighbouring plants (Wilson et al. 1992; Lepš 1995). Likewise, species belonging to the same guild compete for space more strongly among themselves than with species of other guilds (Wilson & Roxburgh 2001), and hence cause restricted variance in guild proportions of neighbouring plants (Wilson & Watkins 1994). Overyielding has been reported for plant functional groups as well (Hooper & Dukes 2004). On the whole, the concept of guilds is important in community ecology, useful for analysing plant communities at a more practicable and general level (Wilson & Roxburgh 2001).

Here, we studied small-scale spatial patterns and the niche complementarity of guilds in a subalpine hay meadow community in the central Caucasus. Traditional management excludes large grazers and their influence on processes and patterns in these species-rich

and productive communities (for an example relevé see Nakhutsrishvili 1999, p. 38). Regular mowing for a historically long time also favours certain growth forms, in particular, non-clonal perennial herbaceous species (Stammel et al. 2003). We distinguished *a priori* two guilds, monocots and dicots, and measured their spatial relations at small (neighbour) scale. We also conducted an overyield experiment to test niche complementarity between these two guilds.

Material and Methods

Study area and sampling design

The study site was located in the subalpine belt of the central Caucasian Mountains, Kazbegi District, Georgia, (42°48' N, 44°39' E, altitude ca. 2100 m a.s.l.). Climate is temperate-humid with cold winters and mild summers. The average annual precipitation is 800-1000 mm. The average temperature of the warmest months (July-August) is 14 °C, with maxima up to 30 °C. Details of climate, soils and vegetation of this area are found in Nakhutsrishvili (1999), Kikvidze (1996) and Kikvidze et al. (2001).

We sampled an old hay meadow of ca. 600 m², with a dense, fully closed canopy reaching a maximum height of 100-150 cm and dominated by *Agrostis planifolia*. The meadow has been under traditional management (mowing once a year) for at least the last 150 years. We established a circular transect, with eight plots, around a small hill. All plots were at the same elevation (ca. 2100 m), non-contiguous, with a distance between plots of ca. 12 m, and the diameter of the transect circle being ca. 30 m. Plot size was 1.28 m × 1.28 m, and each plot was divided into four equal square subplots (64 cm × 64 cm). Subplots were further divided into a grid of 256 small 4 cm × 4 cm quadrats. This size was found to produce results similar to larger quadrats in a preliminary study: the mean richness per quadrat was > 4 and standard deviation was >1.2, reasonable numbers for studying variance of richness at a small scale (Wilson et al. 1995a, b; van der Maarel et al. 1995). We used random numbers generated by a computer to select 25 small quadrats in each subplot, and recorded the presence-absence of all vascular species in these small quadrats (in total 100 small quadrats per plot). Such stratified random sampling reduces spatial autocorrelation and produces reasonably representative samples from large areas (Palmer & van der Maarel 1995; Sutherland 1997). Typically, we recorded about 40-45 species per plot. We constructed community matrices for each plot and analysed frequency distributions using Simpson's index, which discriminates infrequent species (Kikvidze & Ohsawa 2002). On average 15-18 infrequent species

were discriminated from each plot, although they were common elsewhere. Subsequently, we discarded these infrequent species from community matrices for easier handling (Causton 1988; Chiarucci et al. 2004), and analysed spatial patterns within plots.

In regularly mown grasslands such as lawns and hay meadows the majority of plants are non-clonal perennial herbs, with very little contribution from annuals (Stammel et al. 2003). We *a priori* distinguished two guilds: monocots and dicots, which is a usual guild structure for this type of meadow (Wilson & Watkins 1994; Martinkova et al. 2002).

Spatial patterns

We followed randomization tests described earlier for both guilds and species (Wilson et al. 1992; Wilson & Watkins 1994). These tests are based on the variance ratio $RV = V_{\text{obs}} / V_{\text{exp}}$, where V_{obs} is the observed variance of guild proportions or species richness in quadrats and V_{exp} is the variance expected under the null model, which assumes that plants occur near to each other at random (see below for details). A value of $RV = 1$ points to a random distribution of plants, but values of RV less than 1 indicate that plants belonging to the same guild or to the same species occur near to each other less frequently than would be expected if plants are randomly distributed. We performed 1000 randomizations and determined significance level from the number of randomization variance ratios equal or more extreme than that observed.

With respect to guilds, a constancy of guild proportion in small quadrats can result from limitations to coexistence of similar species belonging to same guilds (Wilson & Roxburgh 2001). The null-model takes as fixed the observed frequency of each species per plot, but assigns species to quadrats at random within this constraint, i.e., with no limitation on the ability of members of the same guild to co-occur. We calculated proportions of monocots relative to the total number of species in each quadrat. Then we calculated the observed between-quadrat variance in proportion of monocots. The expected variance we calculated as mean of similar calculations from randomizations under the null model.

With respect to species, a reduced variance of their richness in quadrats can result from limitations to coexistence of conspecific plants (Stubbs & Wilson 2004). The null model takes as fixed the observed frequency of each species, but allocates these species occurrences at random to quadrats independently for each species. In this case we used the observed and expected variances of quadrat richness to calculate their ratio RV . In this way, it is also possible to calculate RV for different subcomponents within the community, e.g., separately for monocots and dicots. However, RV values will de-

pend on the size of the subcomponent (i.e. on the number of species within it) since the potential deviation of RV from 1 accumulates as the number of species within any subcomponent of the community increases. To correct for this effect, we calculated the difference $RV - 1$ for each subcomponent and divided this value by species number in the subcomponent. Such a correction gives a decrement of RV per species, which then may be compared for the two guilds. For purely intuitive reasons (as RV decreased with species number), we rendered the decrement a negative value. Decrements were compared by paired t -test using software Statistix8 (Analytical Software, Tallahassee, Florida).

Overyield experiment

We collected seeds from all possible species during the growing season, and thoroughly mixed them to prepare three stocks: monocots, dicots and their mixture (1:1 by volume). After germination, we were able to identify seven monocot and 23 dicot species usually abundant in our experimental community. During the winter, the seeds were stored in ceramic pots buried outside in the soil near the experimental community at ambient soil temperature. In general, we followed the outline of Špačková & Lepš (2001). We started our experiment the next year, after snow melt in late April, by sowing seeds into pots. Pots were 16 cm in diameter and 16 cm deep, filled with a 1:1 mixture of sand and common commercial soil substrate. We sowed 5 ml of seed material from each of three stocks per pot. The use of volume in stead of weight to prepare seed stocks was beneficial for easy handling, despite the risk of underrepresentation of large-seeded plants. During the first two months, the plants were grown under natural daylight regime in a greenhouse, and watered when needed. By the end of June pots were put outdoors and divided into two treatments. One treatment was well watered when needed, but the other received exactly two times less water. There were 12 replicates for each seed composition (monocots, dicots, and mixture) and treatment (high vs. low watering regime), giving a total of 72 pots. At mid-August we harvested plants from pots, dried them to constant mass (three days at 70°C) and weighed them. We calculated overyield simply as:

$$\text{Overyield} = 2B_{\text{mixture}} / (B_{\text{monocots}} + B_{\text{dicots}}), \quad (1)$$

where B is mean biomass of the corresponding guild and their mixture measured as grams of dry mass per pot. We also compared dry mass per pot between different watering regimes to test stress resistance of plants. We compared the obtained dry mass data using two-way ANOVA and Tukey's multiple comparison test using the Statistix8 software.

Results

In total we recorded 76 species, all of which had been recorded previously in this area (Nakhutsrishvili 1999, p. 38). After excluding infrequent species from the matrices, 48 species (12 monocots and 36 dicots) were left and were included in the analyses (Table 1). Mean proportions of guilds varied between plots from 0.178 to 0.3575 for monocots, and from 0.822 to 0.6425 for dicots. However, the variance of guild proportions was restricted within small quadrats – the mean value of RV was significantly less than 1 (0.64 ± 0.04 SD, $p < 0.0001$ by a t -test) – thus demonstrating guild proportionality. The variance of species richness in small quadrats was also strongly restricted as values of RV were significantly less than 1 (0.44 ± 0.06 SD, $p < 0.0001$ by a t -test). However, the decrement of RV per species was significantly steeper in monocots than that in dicots (-0.078 ± 0.004 SD vs. -0.0275 ± 0.00001 SD, $p < 0.0001$, by a paired t -test), which points to considerably stronger deficit of variance in monocot species than in dicots.

In the pot experiment, mixed monocots and dicots showed strong overyield compared to average yield in 'monocultures' (monocots or dicots alone) in both watering regimes (Fig. 1). Overyield values were 1.203 and 1.229, respectively, for high and low watering regimes. This overyield was statistically highly significant ($p = 0.00196$ and $p = 0.0004$ for high and low watering regimes, respectively). At the same time, the difference in overyield between watering regimes was small and insignificant. Another way of expressing this is that the proportional increase in biomass due to diversity is the same irrespective of watering regime. Watering regime, however, had a pronounced effect on overall biomass production: mean dry mass obtained under the low watering regime was 1.49 times less than under the high watering regime (Fig. 1, $p < 0.0001$ by ANOVA). In monocultures, monocots were significantly less sensitive to water deficit: the low watering regime reduced the dry mass of monocots 1.27 times, whilst dicot biomass was reduced by 1.70 times (Fig. 1).

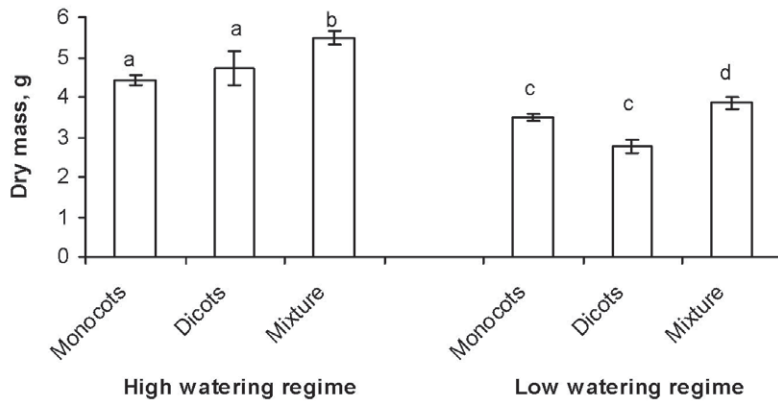


Fig. 1. Dependence of dry mass production on seed composition and water availability; bars show mean per pot values, different letters above bars show statistically significant differences between cases ($p < 0.05$).

Discussion

The results of our investigation show that well-expressed small-scale patterns for guild proportions coincide with robust overyielding in our community. This coincidence indicates that spatial arrangements at a small scale are an important manifestation of niche complementarity (see also van Ruijven & Berendse 2005). In general, morphological differences between monocots and dicots can be linked to their spatial interactions. In our community, monocots are characterised by erect, tall shoots, while dicots occupy the lower strata of the canopy but with a more diverse morphology of above-ground parts (Kikvidze 1996). Below-ground, monocot roots are generally shallow and later-

ally spread (Kutschera & Lichtenegger 1982), whilst dicot roots penetrate deeper but less laterally (Kutschera & Lichtenegger 1992). For a more detailed interpretation of our results, let us consider three situations.

First, all plants in a community are morphologically similar and thus try to capture resources from the same strata of canopy and soil. As a consequence, neighbouring plants interfere with each other, reducing productivity. This situation corresponds to the monocultures in our overyield experiments.

In the second situation, the two different morphological types are mixed, but their spatial distribution is random. As a result, some neighbour plants are similar and some dissimilar. Morphologically dissimilar neighbours absorb resources from different strata of the

Table 1. The analysed species and their relative abundances (calculated from the total frequency of occurrence in the eight plots); M = monocot; D = dicot.

Species	Group	Proportion	Species	Group	Proportion
<i>Agrostis planifolia</i>	M	0.099	<i>Alchemilla caucasica</i>	D	0.009
<i>Trifolium trichocephalum</i>	D	0.062	<i>Betonica macrantha</i>	D	0.009
<i>Leontodon hispidus</i>	D	0.06	<i>Luzula multiflora</i>	M	0.009
<i>Campanula collina</i>	D	0.057	<i>Taraxacum stevenii</i>	D	0.007
<i>Carum meifolium</i>	D	0.057	<i>Carex huetiana</i>	M	0.006
<i>Potentilla recta</i>	D	0.056	<i>Cephalaria gigantea</i>	D	0.006
<i>Calamagrostis arundinacea</i>	M	0.052	<i>Alchemilla retinervis</i>	D	0.005
<i>Prunella vulgaris</i>	D	0.052	<i>Crepis caucasica</i>	D	0.005
<i>Ranunculus oreophilus</i>	D	0.048	<i>Cruciata laevipes</i>	D	0.005
<i>Trifolium spadicum</i>	D	0.046	<i>Geranium ibericum</i>	D	0.005
<i>Astrantia maxima</i>	D	0.041	<i>Helictotrichon asiaticum</i>	M	0.005
<i>Festuca varia</i>	M	0.04	<i>Polygala alpicola</i>	D	0.005
<i>Veronica gentianoides</i>	D	0.032	<i>Veronica chamaedrys</i>	D	0.005
<i>Arenaria rotundifolia</i>	D	0.027	<i>Alchemilla sericata</i>	D	0.004
<i>Sedum oppositifolium</i>	D	0.026	<i>Anthoxanthum odoratum</i>	M	0.004
<i>Carex tristis</i>	M	0.02	<i>Bromus variegatus</i>	M	0.004
<i>Trifolium montanum</i>	D	0.02	<i>Trifolium ambiguum</i>	D	0.004
<i>Nardus stricta</i>	M	0.015	<i>Hieracium umbellatum</i>	D	0.003
<i>Silene ruprechtii</i>	D	0.015	<i>Pyrethrum coccineum</i>	D	0.003
<i>Thymus nummularioides</i>	D	0.015	<i>Bupleurum polyphyllum</i>	D	0.002
<i>Koeleria albovii</i>	M	0.013	<i>Euphrasia hirtella</i>	D	0.002
<i>Viola oreades</i>	D	0.012	<i>Hypericum nummularioides</i>	D	0.002
<i>Lotus caucasicus</i>	D	0.011	<i>Phleum alpinum</i>	M	0.002
<i>Plantago lanceolata</i>	D	0.011	<i>Viola caucasica</i>	D	0.002

community space, thus avoiding interference. Such cases will increase the performance of plants in mixtures and contribute to overyielding. This situation corresponds to the mixed community in the overyield experiment.

The third situation is similar to the second, but plants are arranged spatially so that neighbouring plants are the most dissimilar. In this way, even more interference is avoided, which thus results in amplified overyielding. The spatial patterns observed in our community clearly point to the third situation: dissimilar species were more frequently found near each other and, *vice versa*, more similar species were more dispersed over space than expected on a random basis.

We may infer two predictions from the above interpretation. First: long-term experiments found that overyielding increases gradually over a number of years (van Ruijven & Berendse 2005). These years were probably necessary for the development of small-scale patterns, which gradually amplify overyielding. Second, the patterns of limited similarity of species at small scale have also been reported for other grassland communities (e.g. Wilson et al. 1992; Wilson & Watkins 1994; Stubbs & Wilson 2004). We may expect that experiments will find significant overyielding in these communities.

Our measurements also revealed more strongly restricted variance of richness in monocots than in dicots in our community. In other words, monocots were more regularly dispersed over space than dicots. In all probability, the variance of species richness is limited by the competition for space (Lepš 1995), and the competition among similar plants is stronger than among dissimilar ones (Stubbs & Wilson 2004). We suspect that monocots are morphologically less varied than dicots (in line with our finding that monocots are less sensitive to water deficit than dicots). As a result, monocots on average compete with each other more strongly, and this stronger competition drives a more regular distribution of monocots over space. Conversely, morphologically more diverse and more plastic dicots fit more easily into the neighbourhood – around the patchwork built by monocots ('subordinate guild behaviour', Bartha 2001).

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