

Influence of soil heterogeneity and competition on growth features of three meadow species

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Summary

The effect of competition and artificially created soil heterogeneity was studied in a pot experiment. A tussock grass, *Holcus lanatus*, and the rhizomatous sedge *Carex hartmanii* were grown alone and in combination with another tussock grass, *Molinia caerulea*, in homogeneous and heterogeneous soil treatments. The heterogeneous treatment consisted of four compartments, two nutrient rich and two nutrient poor. In the homogenous treatment total nutrient content was the same as in the heterogeneous treatment. Soil heterogeneity increased *M. caerulea* total production, and increased *C. hartmanii* root:shoot ratio; no effect on *H. lanatus* was observed. Both *M. caerulea* and *C. hartmanii* were able to place their underground organs preferentially into nutrient rich patches. *M. caerulea* and *H. lanatus* total biomass was lower in the presence of the competitor; *C. hartmanii* responded to competition only by increased allocation to rhizoms. *M. caerulea* was more affected by competition in the heterogeneous environment.

Keywords: *Carex hartmanii*, foraging, *Holcus lanatus*, *Molinia caerulea*, root distribution.

Introduction

Soil heterogeneity affects both growth and competition processes in plant communities. The existence of nutrient-rich patches in space and time has been described in several studies (e.g., Jackson & Caldwell 1993; Ryel et al. 1996; Cain et al. 1999), as well as spatio-temporal variability for non-nutrient soil parameters (Jackson & Caldwell 1993). Individual plant species differently take advantage of soil heterogeneity by placing their organs into preferable places (Birch & Hutchings 1994; De Kroon & Hutchings 1995; Humphrey & Pyke 1997; Fransen et al. 1998;

Cahill & Casper 1999; Einsmann et al. 1999; Kleijn & Groenendaal 1999; Fitter et al. 2000; Wijesinghe & Whigham 2001). Differences in plant response to soil patches depend on different plant requirements (i.e., nutrient, water, O₂ and pH requirements) and on the ability of plant species to find and exploit soil resources (Veresoglou & Fitter 1984; Gross et al. 1993) or on the ability for retranslocation of nutrients in stoloniferous plants (Dong et al. 2002). Furthermore, foraging speed is an important factor because patches are dynamic (El-Shatnawi & Makhadmeh 2001; Pickett et al. 2000). Plants may effectively exploit nutrients by both physiological and morpholo-

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gical root plasticity. Derner & Briske (1999) suggested that there is no tradeoff between these two mechanisms and that they may represent complementary, rather than alternative, foraging strategies.

Experiments including cespitose grasses and other “phalanx” species (for phalanx-guerrilla theory see Lovett Doust 1981) demonstrated a foraging ability of this growth form (e.g. Fransen et al. 1999, 2001; Wijesinghe et al. 2001) and showed that root systems of phalanx plants are able to search for favorable soil-patches. After nutrient depletion below a tussock, the phalanx underground strategy, in the sense of overproducing biomass to obtain competitive superiority, does not have any advantage: the roots need to explore new nutrient resources, outside the depleted zone. This is especially important for K and P ions, which diffuse slowly in soil compared with rates at which roots and microbes can absorb them (Robinson 1994). De Kroon & Hutchings (1995) reformulated foraging concepts and recommended incorporation of the foraging behavior of shoots and roots into studies of foraging strategies of clonal plants.

Although many experiments have investigated foraging of numerous plant species in heterogeneous environments, the overwhelming majority of these studies did not include the competition effect. The few studies dealing with the effect of soil heterogeneity on competition suggest that different foraging behaviors in heterogeneous soil environments can separate plant niches and change the relative competitive ability of individual plant species (Schwinning & Weiner 1998; Cahill & Casper 1999; Fransen et al. 2001). Weiner et al. (1997) suggested that soil heterogeneity can increase competition asymmetry between large and small plants due to the ability of large plants to reach and usurp nutrient rich patches. This hypothesis was experimentally supported by de Fransen et al. (2001). Alternatively, Campbell et al. (1991) proposed that dominant species with large root systems tend to be less selective in placing their roots into nutrient rich patches than species with smaller root systems and described the dominant species as “high scale” foragers and the subordinate species as “high precision” foragers. According to this hypothesis there is a tradeoff between scale (size of root system) and precision of root allocation into nutrient rich patches. This hypothesis was recently supported by Wijesinghe et al. (2001). However, all of these authors point to the insufficient number of experimental studies that deal with heterogeneity effects on competitive ability of individual plant species.

In our experiment, two species with different growth strategies (*Carex hartmanii* Cajand. and *Holcus lanatus* L.) were grown alone and with *Molinia caerulea* (L.) Moench as a competitor, both in homogeneous and heterogeneous soil, where the overall nutrient content

was retained. All three species coexist in natural conditions in a wet oligotrophic meadow near České Budějovice (Czech republic). There, *M. caerulea* is dominant, forming a matrix of dense tussocks. Consequently it is the main competitor of the other species. *C. hartmanii* is a typical guerrilla species, forming long underground rhizomes, and *H. lanatus* is a tussock grass. This study complements the field experiments carried at the locality (Lepš 1999 and references therein). Lepš (1999) suggested that species similar to *M. caerulea* take more advantage of *M. caerulea* removal than do dissimilar ones. This would support the idea that niche differentiation (i.e., differences in growth form) leads to reduced competition.

We aimed to answer the following questions:

1. Are plants able to place their roots preferentially into nutrient rich patches and does soil heterogeneity lead to increased plant biomass? Does the ability to do this differ between species?
2. Is species success in competition affected by soil heterogeneity? Is soil heterogeneity advantageous for guerrilla species (*C. hartmanii*), where high precision is expected (Campbell et al. 1991), or for the dominant phalanx species (as follows from Weiner et al. 1997)?
3. Is the investment into rhizomes in *C. hartmanii* positively affected by competition? Is the plant able to selectively place its rhizomes into nutrient-rich patches?

Materials and methods

Study Site and Species

The plants for the experiment were collected at our experimental site Ohrazení, an oligotrophic meadow 10 km south-east of České Budějovice, Czech Republic, 48°57' N, 14°38' E, at 530 m a.s.l., where the mean annual precipitation is 600–650 mm, mean annual temperature is 7.8°C. *M. caerulea* is the dominant species, and *H. lanatus* and *C. hartmanii* are the major species at the locality.

Individual growth units of *M. caerulea*, *C. hartmanii* and *H. lanatus* were randomly selected from different plant individuals on a study field, where the species coexist in nature. *M. caerulea* and *H. lanatus* (*Poaceae*) are perennial non-rhizomatous tufted grasses. *M. caerulea* is dominant in several vegetation types (Taylor et al. 2001), including the vegetation of our study site, where it reaches up to 50% cover, and in samples taken in June 2000 constituted up to 30% of biomass. *Carex hartmanii* is a perennial rhizomatous sedge, penetrating vegetation by long rhizomes (Dostál 1989); in our locality, the plant is able to form rhizomes over 0.5 m long. *H. lanatus* cover increased in our study site after *M. caerulea* had been experimentally removed, but the reaction of *C. hartmanii* was negligible (Lepš 1999 and unpublished data).

Experimental design

Randomly selected growth units of *M. caerulea*, *C. hartmanii* and *H. lanatus* from different individual plants were transplanted into plastic pots (19 cm × 19 cm, 15 cm deep) at the end of April 2001 (*H. lanatus* at early May), and placed in a greenhouse (Fig. 1). The non-competitive pots contained one unit, the competitive two units, each belonging to different species. This corresponds to the simplified target-neighbor design (Gibson et al. 1999; Goldberg & Landa 1991). The transplanted units consisted of two interconnected basal internodes in *M. caerulea*, of two interconnected shoots of *C. hartmanii*, or one shoot of *H. lanatus*. Weight of each individual unit including its roots was estimated before planting using calibration (to avoid cleaning of roots of tillers to be planted). Calibration was based on the regression of weight on easily nondestructively measurable characters (shoot height in *C. hartmanii* and *H. lanatus*, height of basal internodes in *M. caerulea*) in an extra “training sets” of growth units of individual species.

Pots were divided into two soil treatments, heterogeneous and homogeneous. The overall nutrient content in both treatments was retained. In the heterogeneous treatment, each pot was divided into four patches (sectors) of two types: the nutrient-rich patches contained a mix of garden humus and peat in proportion 2:1 (N total = 12,5 g/kg, P total = 120 mg/kg, pH = 5.47), nutrient-poor patches contained only sand (N total < 0.2 g/kg, P total < 6 mg/kg, pH = 6.04). The homogeneous treatment was composed of garden humus, peat and sand in the proportion 2:1:3 (Fig. 1). Five species combinations (each species alone, and *M. caerulea* with each of the other species) were combined with the two soil-treatments. Each of combinations was replicated at least five times (Table 1).

In the middle of August 2001 aboveground biomass was harvested, dried and weighed and number of shoots recorded; root biomass of each species was collected separately in each sector, remnants of soil was washed out carefully, and the roots were dried and weighed. The roots were mostly still attached to the aboveground parts. The unattached roots were identified according to their color and structure, which differs slightly among the species. Rhizomes of *C. hartmanii* were also counted, dried and weighed separately in each sector.

Data analysis

In all the analyses, we used the weight of tillers before planting as a covariate (to account for the possible variability caused by unequal size of tillers at the beginning of the experiment). Although the effect of the covariate was not significant in all the analyses, in some cases, dropping of the covariate lead to decrease of the significance in the main effects (clearly because the covariate was able to account for part of the variability in the response, and in this way to decrease the unexplained variation). Because of this, and because the effect of covariates could be expected a priori, we decided to keep the covariates in all the models, regardless whether they were significant or not.

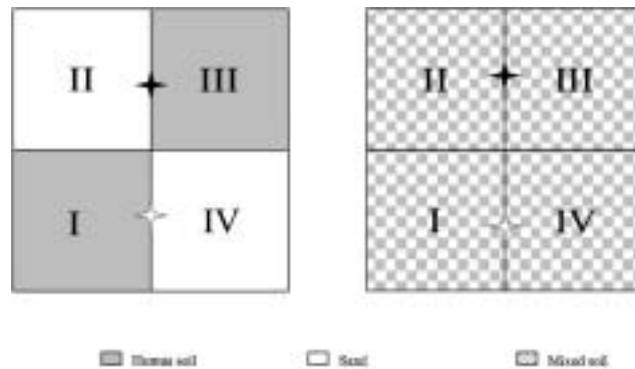


Fig 1. The experimental design. Both heterogeneous (left) and homogeneous (right) treatments were performed in square 19 × 19 cm pots. I, II, III, IV-sector numbers. ◇ The place, where one growth unit of *M. caerulea* in plant combinations 1,4 and 5 was planted. ♦ The place, where one growth unit of *H. lanatus* (combination 3 and 5) or one growth unit of *C. hartmanii* (combination 2 and 4) was planted (for plant combination see Table 1). Note, that for the monospecific combinations 1, 2 and 3, one of the positions remained empty.

Table 1. Number of pots analyzed in individual treatments and plant combinations. M-*M. caerulea*, C-*C. hartmanii*, H-*H. lanatus*.

Combination	Plant species	Heterogeneous soil	Homogeneous soil
1	M	8	8
2	C	7	8
3	H	5	5
4	M*C	7	8
5	M*H	8	8

We first analyzed the characteristics of each species. We used the Analysis of Covariance (using STATISTICA 5.5, Anon 1996) to test the effect of heterogeneity and presence of competitor on total biomass, R:S ratio, and number of shoots.

Biomass allocation into individual organs (roots, shoots and rhizomes) of *C. hartmanii* was analyzed by MANCOVA (STATISTICA, Anon 1996). Heterogeneity, presence of competitor and interaction were used as predictors and percentage allocation into individual organs as dependent variables. ANCOVA was used to test differences in allocation to different plant organs.

We then analyzed the selective placement of underground organs into differing sectors of the heterogeneous treatment. This was analyzed by ANCOVA with split-plot design, where humus-rich soil versus sand placement was used as a within plot factor.

Data on biomass placement and number of shoots or rhizomes were log-transformed and square-root transformed respectively to improve normality and homoscedasticity.

Results

Response of individual plant species to the heterogeneity and competition

At the end of our experiment plant canopies in the competition environment exhibited little overlap. Hence, we can reasonably assume that competition was predominantly underground.

Total biomass production and number of shoots of *M. caerulea* was higher in the heterogeneous soil environment (Table 2). Both total biomass and number of shoots of *M. caerulea* were negatively affected by competition with *C. hartmanii*. Competition effect of *C. hartmanii* on total biomass of *M. caerulea* was higher in heterogeneous environment, and R:S ratio of *M. caerulea* was positively affected by the presence of *C. hartmanii* as a competitor (Table 2, Fig. 2). There was no significant effect of *H. lanatus* on *M. caerulea* (Table 2, the non-significant results are not portrayed in Figures).

There was no effect of either soil heterogeneity or competition (of *M. caerulea*) on the total biomass production and number of shoots of *C. hartmanii* (Table 2). However, both heterogeneity (MANCOVA, Wilk's $F = 0.74$, $p = 0.029$) and competition (MANCOVA, Wilk's $F = 0.68$, $p = 0.009$) affected *C. hartmanii* biomass allocation into shoots, rhizomes and roots; their

interaction was not significant (MANCOVA, Wilk's $F = 0.95$, $p = 0.563$). Biomass allocation to the rhizomes was positively affected by the presence of the competitor (ANCOVA, $F = 5.94$, $p = 0.022$). Allocation of biomass to the roots was higher in heterogeneous treatment (ANCOVA, $F = 5.49$, $p = 0.027$), whereas allocation to the shoots was higher in homogeneous treatment (ANCOVA, $F = 9.46$, $p = 0.005$) and in the non-competitive environment (ANCOVA, $F = 5.23$, $p = 0.031$). This results correspond to significant effect of heterogeneity on R:S ratio of *C. hartmanii* (Table 2, Fig. 3).

M. caerulea competition negatively affected the number of shoots and total biomass of *H. lanatus* (Fig. 4), and the increase in the R:S ratio of *H. lanatus* in the presence of *M. caerulea* was only marginally significant (Table 2). There was no significant effect of heterogeneity on either total biomass or biomass allocation of *H. lanatus* (Table 2).

Root placement

In heterogeneous treatments, *M. caerulea* and *C. hartmanii* significantly translocated root biomass into nutrient rich patches, whereas the root biomass of *H. lanatus* was similar in nutrient rich and nutrient poor patches (Table 3, Fig. 5). There was no significant effect of pre-

Table 2. Effect of heterogeneity, presence of a competitor and their interaction on biomass, root: shoot ratio (R:S) and number of shoots of the species *M. caerulea*, *C. hartmanii* and *H. lanatus* tested by ANCOVA. Symbol * indicates significance level $0.05 < p < 0.1$. The data on number of shoots was square-root transformed prior to analysis. Initial growth unit weight was used as a covariate. Superscript + at the significance value means positive effect of heterogeneity or competitor on the variable under consideration, superscript - means negative effect. For replication number see Tab. 1.

Species (competitor)	Dependent variables	Predictors					
		Heterogeneity		Competitor		Interaction	
		p	F	p	F	p	F
<i>M. caerulea</i> (<i>C. hartmanii</i>)	Total biomass	0.0001 ⁺	19.8759	0.0001 ⁻	20.8338	0.0237	5.7777
	R:S ratio	n.s.	0.6545	0.0109 ⁺	7.5116	n.s.	1.0347
	Number of shoots	0.0332 ⁺	5.0607	0.0000 ⁻	29.3354	n.s.	2.2371
<i>H. lanatus</i>	Total biomass	0.0016 ⁺	12.3352	n.s.	0.1261	n.s.	0.7405
	R:S ratio	n.s.	0.0662	n.s.	0.6442	n.s.	0.0007
	Number of shoots	0.0007 ⁺	14.6838	n.s.	0.3662	n.s.	0.0343
<i>C. hartmanii</i> (<i>M. caerulea</i>)	Total biomass	n.s.	1.6835	n.s.	0.3515	n.s.	0.5412
	R:S ratio	0.0093 ⁺	7.2852	n.s.	1.8519	n.s.	0.5159
	Number of shoots	n.s.	0.0931	n.s.	1.7419	n.s.	1.5871
<i>H. lanatus</i> (<i>M. caerulea</i>)	Total biomass	n.s.	0.7985	0.0413 ⁻	4.7252	n.s.	2.3468
	R:S ratio	n.s.	0.9134	n.s.*	3.3540	n.s.	0.0381
	Number of shoots	n.s.	0.0025	0.0029 ⁻	11.3357	n.s.	1.2777

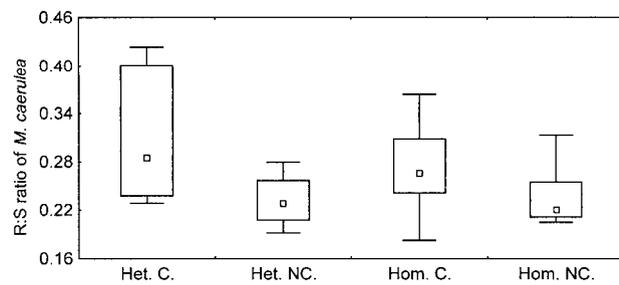
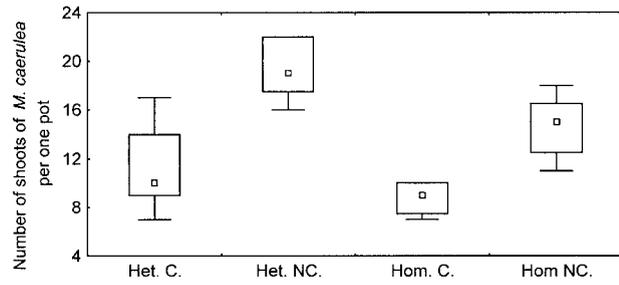
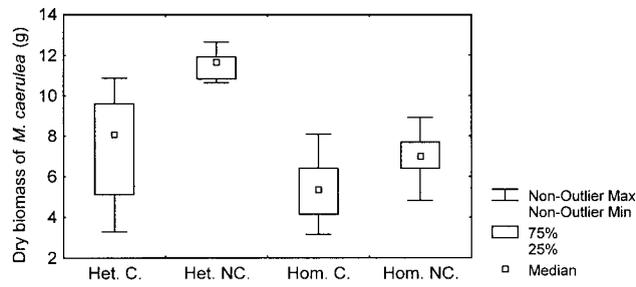


Fig 2. Effect of soil treatment and presence of *C. hartmanii* as a competitor on total biomass, number of shoot and R:S ratio of *M. caerulea*. Het. – heterogeneous soil treatment, Hom. – homogeneous soil treatment, C – competition environment, NC – non-competition environment. Statistical analyses are given in Table 2.

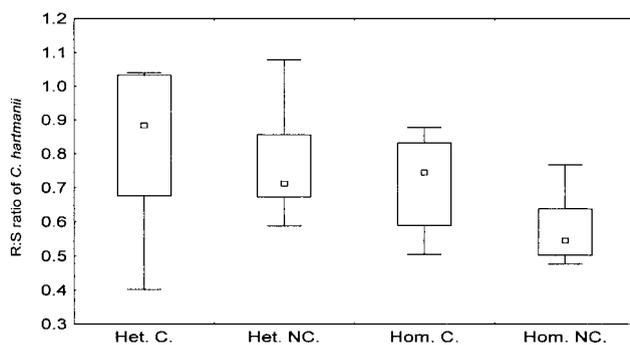


Fig 3. Effect of soil treatment and presence of *M. caerulea* as a competitor on R:S ratio of *C. hartmanii*. Het. – heterogeneous soil treatment, Hom. – homogeneous soil treatment, C – competition environment, NC – non-competition environment. Statistical analyses are given in Table 2.

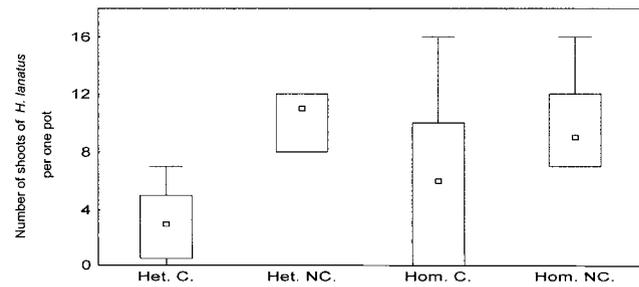
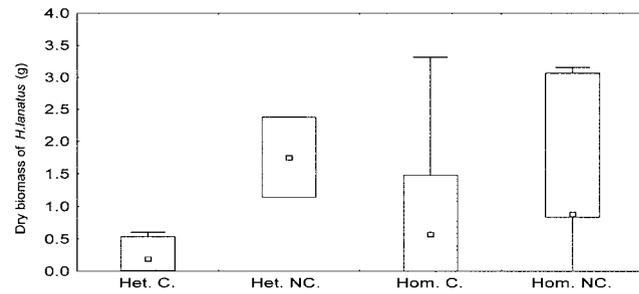


Fig 4. Effect of soil treatment and presence of *M. caerulea* as a competitor on total biomass and number of shoots of *H. lanatus*. Het. – heterogeneous soil treatment, Hom. – homogeneous soil treatment, C – competition environment, NC – non-competition environment. Statistical analyses are given in Table 2.

sence of a competitor on root placement of either species (Table 3). *C. hartmanii* translocated a significantly higher proportion of root biomass into nutrient-rich patches (66.9%) than did *M. caerulea* (62.8%) in the absence of competitor (t-test, $t = 2.44$, $p = 0.03$), but there was no significant difference in translocation between *M. caerulea* and *C. hartmanii* in the presence of a competitor (t-test, $t = 1.02$, $p = 0.32$).

Rhizome placement of *C. hartmanii*

Both rhizome number and biomass were greater in the nutrient-rich patches (Table 4, Fig. 6). Moreover, the presence of a competitor affected the mode of rhizome biomass translocation with preference for nutrient rich patches stronger in the absence of a competitor (Interaction effect, Table 4, Fig. 6).

Discussion

Both *C. hartmanii* and *M. caerulea* roots exhibited foraging behavior, i.e., they were able to translocate their biomass into nutrient-rich patches, whereas *H. lanatus* did not so. Under competition-free conditions, precision foraging by *C. hartmanii* was higher than by *M. caerulea*. However, in the presence of a competitor, this

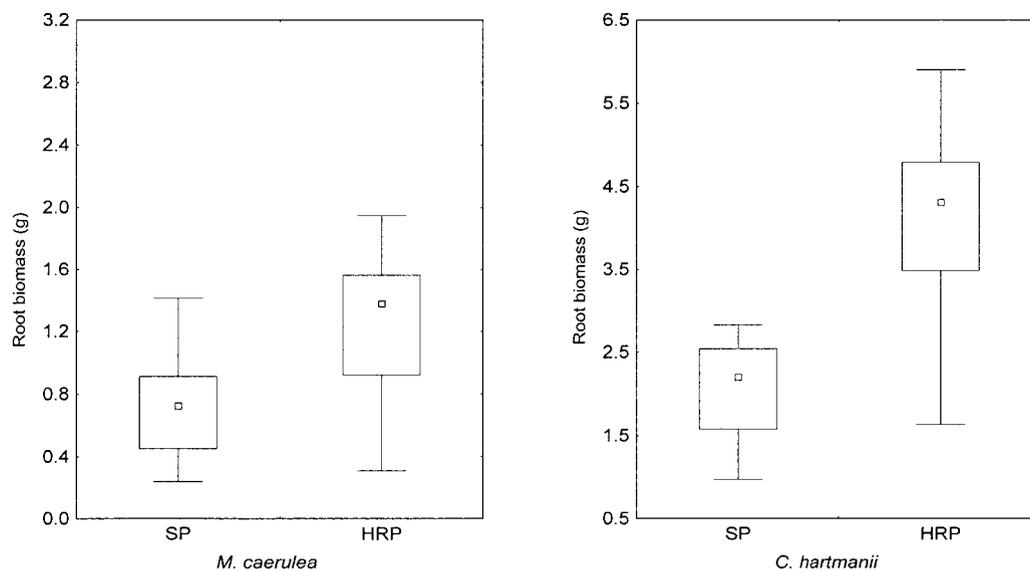


Fig 5. Translocation of root biomass of *M. caerulea* and *C. hartmanii* into sand (SP) and humus-rich (HRP) patches. Statistical analysis is given in Table 3. As the competition had no effect on the root placement, the results are pooled for the competition/without competition treatments.

Table 3. Effect of presence of a competitor on root production and placement (interaction) of studied species and placement-effect in the heterogeneous treatment (see text). Analyzed by split-plot analysis of covariance. Initial growth unit weight was used as a covariate. Humus-rich soil versus sand placement was used as a within plot factor. Symbol * indicates significance level $0.05 < p < 0.1$. The data were log-transformed.

Species	Competitor		Placement		Interaction	
	p	F	p	F	p	F
<i>M. caerulea</i>	n.s.	1.1936	0.0000	68.3569	n.s.	0.5001
<i>C. hartmanii</i>	n.s.	0.0283	0.0000	217.9538	n.s.	0.4710
<i>H. lanatus</i>	n.s.*	5.0266	n.s.	1.3491	n.s.	1.7889

difference disappeared. *H. lanatus* behavior contradicted the results of Fransen et al. (1999), who found its ability to utilize both spatial and temporal nutrient patches. We assume that the differences were caused by different experimental design and/or by the very small root biomass of *H. lanatus* in our experiment. Moreover the study of Fransen & de Kroon (2001) has shown that *H. lanatus* is able to distinguish nutrient-rich patches at a high overall level of nutrient availability only.

Total biomass production was positively affected by environmental heterogeneity in *M. caerulea* only. Heterogeneity also affected biomass allocation in *C. hartmanii*, which, in the heterogeneous environment, invested more into roots and less into shoots, and showed very high precision foraging by placing its roots into nutrient-rich patches. It seems that *C. hartmanii* was able to take advantage of the soil heterogeneous environment by increasing its R:S ratio.

In concordance with other studies (e.g. Einsmann et al. 1999) we can answer the first question: Plant species differ in their ability to find and exploit nutrient rich patches. Two of the three studied species exhibited the ability to forage, but only one of them (the dominant plant, with lower foraging precision) increased its total biomass. However, we should be aware that plant success over the studied time interval need not be manifested by an increase in total biomass production.

Our study showed that *M. caerulea* is more negatively affected by *C. hartmanii* in a heterogeneous than in a homogenous environment. This might be caused not only by increased competition pressure when the resources are concentrated into a smaller soil volume, but also by increased investment of *C. hartmanii* into root production in a heterogeneous environment. Moreover, the presence of *M. caerulea* increased the relative invest-

Table 4. Effect of presence of a competitor, placement-effect and interaction on rhizome biomass production and rhizome orientation of *Carex hartmanii* in the heterogeneous treatment. Analyzed by split-plot analysis of covariance. Humus-rich soil versus sand placement was used as a within plot factor. Initial growth unit weight was used as a covariate. Rhizome biomass data were log-transformed, and number of rhizomes was square-root transformed prior to analysis. Symbol * indicates significance level $0.05 < p < 0.1$. Superscript +/- at the significance value means positive/negative effect of competitor or increased amount in the nutrient rich sectors. For replication number see Tab. 1.

Source Dependent variable	Competition		Placement		Interaction	
	p	F	p	F	p	F
Rhizome biomass ^a	n.s.* ⁺	4.6655	0.0001 ⁺	31.2504	0.0394	5.339
Number of rhizomes ^b	0.0404 ⁺	5.3914	0.0365 ⁺	5.5403	n.s.	2.5199

^a translocation of rhizomes biomass to the sand or humus-rich soil patches.

^b number of rhizomes penetrating to the sector II (sand) or sector III (humus-rich soil), see Fig. 1.

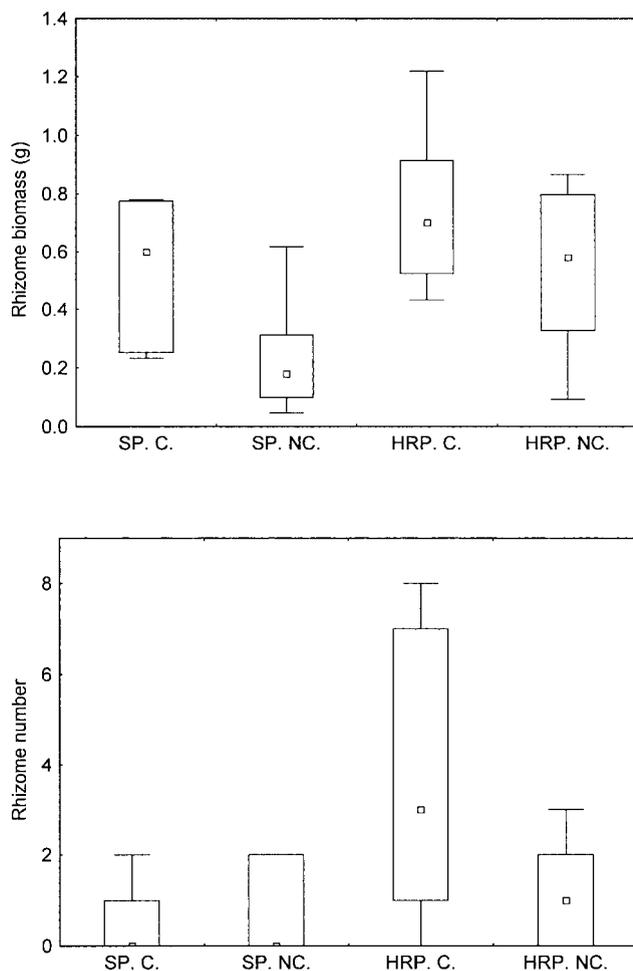


Fig 6. Translocation of rhizome biomass of *C. hartmanii* into sand (SP) or humus-rich (HRP) soil patches in competition (C) versus non-competition (NC) treatments and number of rhizomes penetrating to the sand patch (SP) and humus-rich patch (HRP), see Fig. 1. Statistical analyses are given in Table 4.

ment of *C. hartmanii* into rhizomes, but did not affect its total biomass. These results correspond to the hypothesis of Campbell et al. (1991) about the relative advantage of high precision foraging of subordinate species in heterogeneous environments. On the other hand, the increased biomass of the dominant species *M. caerulea* in a heterogeneous environment shows that this advantage of *C. hartmanii* may only be temporary. As demonstrated by Humphrey & Pyke (1998), the competition outcome could change during time. Their study demonstrated a decrease in biomass of guerrilla *Elymus lanceolatus ssp. lanceolatus* compared with phalanx *E.l. ssp. wawawaiensis* in the second year of the experiment. Recently Fransen et al. (2001) demonstrated a competition shift between *Festuca rubra* and *Anthoxanthum odoratum* in a heterogeneous environment in the second year of their experiment. One should, however, be aware of the limitations of pot experiments. Under natural conditions, *C. hartmanii* is able to escape the competition of *Molinia caerulea*, because in two years its daughter ramets can reach more than 0.5 m apart from the mother ramet (and consequently, also from the competitive *Molinia* tussock). Owing to its long spacers, *C. hartmanii* is able to forage on a much larger spatial scale. *C. hartmanii* is able to acquire a competitive advantage by rapid investment of roots into nutrient-rich patches, whereas the dominant *M. caerulea*, although able to put roots preferentially into nutrient rich patches, does not change its R:S ratio. The behaviour of *C. hartmanii* is probably more favorable in dynamically changing heterogeneous environments, whereas that of *M. caerulea* in more stable heterogeneous environments. Whereas the first part of the second question could be unequivocally answered: Competition is clearly affected by soil heterogeneity, the answer to its second part is less clear. We suppose

that both subordinate guerrilla plants (as suggested by Campbell et al. 1991) and dominants (as suggested by Weiner et al. 1997) can under certain circumstances benefit from soil heterogeneity – probably the spatial scale and temporal dynamics of the spatial mosaic determines which of them will be more successful.

The third question yielded also unequivocal answer: Rhizome formation in *C. hartmanii* is positively affected by the presence of a strong competitor, and more rhizomes were placed into favorable locations in the heterogeneous treatment. Rhizome foraging behavior (without the competition effect) has been demonstrated in several other rhizomatous and stoloniferous species (e.g., Birch & Hutchings 1994; Kleijn & van Groenendael 1999; De Kroon & Knops 1990; Salemaa & Sievänen 2002). Our study demonstrated not only a strong effect of heterogeneity, but also an interaction between heterogeneity and competition (see Fig. 6). Preference for nutrient rich patches was weaker when the nutrient-rich patches had high root density of the competitor. Generally, the rhizome biomass was higher in the presence of competitor in both treatments. Without competitor, rhizome biomass in the sand patches was much lower than in humus patches, whereas in the presence of the competitor, the difference was considerably smaller. *C. hartmanii* rhizomes are not only able to differentiate between rich and poor spots in the soil, but this differentiation is also affected by the presence of a competitor.

Lepš (1999) suggested that *H. lanatus*, because of its similarity to *M. caerulea*, increased in cover after *M. caerulea* removal. This suggestion is consistent with our results that in contrast to *C. hartmanii*, *H. lanatus* is more affected by *M. caerulea* (Table 2). Thus, the result is consistent with the idea of increased competition with increasing species similarity.

For a generalization of this hypothesis more competition studies with plants of various growth forms are required. Pot experiments are necessarily limited in their ability to mimic natural conditions. This is particularly true for experiments studying effects of spatial heterogeneity. Further studies should include effects of both temporal and spatial heterogeneity, effects of different patch size and nutrient content and longer time span. Not only biomass allocation, but also physiological and morphological responses of species to the environments should be investigated. In addition, the creation of experimental environments should reflect the field situation as far as possible. Nevertheless, even with the limitations typical for the pot experiments, the present study was able to demonstrate the foraging behavior of underground structures of *Molinia caerulea* and *Carex hartmanii* (in contrast to *Holcus lanatus*), and how it is affected by competition and soil heterogeneity.

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References

- Anon. (1996): STATISTICA for Windows [Computer program manual]. Stat Soft, Tulsa, OK.
- Birch, C. P. D. & Hutchings, M. J. (1994): Exploitation of patchily distributed resources by the clonal herb *Glechoma hederacea*. – *J. Ecol.* **82**: 653–664.
- Cahill, J. F. & Casper, B. B. (1999): Growth consequences of soil nutrient heterogeneity for two old-field herbs, *Ambrosia artemisiifolia* and *Phytolacca americana*, growth individually and in combination. – *Ann. Bot.* **83**: 471–478.
- Cain, M. L.; Subler, S.; Evans, J. P. & Fortin, M. J. (1999): Sampling spatial and temporal variation in soil nitrogen availability. – *Oecologia* **118**: 397–404.
- Campbell, B. D.; Grime, J. P. & Mackey, J. M. L. (1991): A trade-off between scale and precision in resource foraging. – *Oecologia* **87**: 532–538.
- De Kroon, H. & Hutchings, M. J. (1995): Morphological plasticity in clonal plants: the foraging concept reconsidered. – *J. Ecol.* **83**: 143–152.
- De Kroon, H. & Knops, J. (1990): Habitat through morphological plasticity in two chalk grassland perennials. – *Oikos* **59**: 39–49.
- Derner, J. D. & Briske, D. D. (1999): Does a tradeoff exist between morphological and physiological root plasticity? A comparison of grass growth forms. – *Acta Oecol.* **20**: 519–526.
- Dong, M.; During, H. J. & Werger, M. J. A. (2002): Root and shoot plasticity of the stoloniferous herb *Ajuga reptans* L. planted in a heterogeneous environment. – *Flora* **197**: 37–46.
- Dostál, J. (1989): Nová květena CSSR. [New Flora of Czechoslovakia. In Czech.] – Academia, Praha.
- Einsmann, J. C.; Jones, R. H.; Pu, M. & Mitchell, R. J. (1999): Nutrient foraging traits in 10 co-occurring plant species of contrasting life forms. – *J. Ecol.* **87**: 609–619.
- El-Shatnawi, M. K. J. & Makhadmeh, I. M. (2001): Eco-physiology of the plant-rhizosphere system. – *J. Agron. Crop Sci.* **187**: 1–9.
- Fitter, A.; Hodge, A. & Robinson, D. (2000): Plant response to patchy soils. In: Hutchings, M. J.; John, E. A. & Stewart A. J. A. (eds.): The ecological consequences of environmental heterogeneity. pp. 71–90. – Blackwell, Oxford.
- Fransen, B. & De Kroon, H. (2001): Long-term disadvantages of selective root placement: root proliferation and shoot biomass of two perennial grass species in a 2-year experiment. – *J. Ecol.* **89**: 711–722.
- Fransen, B.; De Kroon, H. & Berendse, F. (1998): Root morphological plasticity and nutrient acquisition of per-

- ennial grass species from habitats of different nutrient availability. – *Oecologia* **115**: 351–358.
- Fransen, B.; Blijenberg, J. & De Kroon, H. (1999): Root morphological and physiological plasticity of perennial grass species and the exploitation of spatial and temporal heterogeneous nutrient patches. – *Plant Soil* **211**: 179–189.
- Fransen, B.; De Kroon, H. & Berendse, F. (2001): Soil nutrient heterogeneity alters competition between two perennial grass species. – *Ecology* **82**: 2534–2546.
- Gibson, D. J.; Connolly, J.; Hartnett, D. C. & Weidenhamer, J. D. (1999): Designs for greenhouse studies of interactions between plants. – *J. Ecol.* **87**: 1–16.
- Goldberg, D. E. & Landa, K. (1991): Competitive effect and response: hierarchies and correlated traits in the early stages of competition. – *J. Ecol.* **79**: 1013–1030.
- Gross, K. L.; Peters, A. & Pregitzer, K. S. (1993): Fine root growth and demographic responses to nutrient patches in four old-field plant species. – *Oecologia* **95**: 61–64.
- Humphrey, L. D. & Pyke, D. A. (1997): Clonal foraging in perennial wheatgrasses: a strategy for exploiting patchy soil nutrients. – *J. Ecol.* **85**: 601–610.
- Humphrey, L. D. & Pyke, D. A. (1998): Demographic and growth responses of a guerrilla and a phalanx perennial grass in competitive mixtures. – *J. Ecol.* **86**: 854–865.
- Jackson, R. B. & Caldwell, M. M. (1993): The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. – *Ecology* **74**: 612–614.
- Kleijn, D. & Van Groenendael, J. M. (1999): The exploitation of heterogeneity by a clonal plant in habitats with contrasting productivity levels. – *J. Ecol.* **87**: 873–884.
- Lepš, J. (1999): Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. – *J. Vegetat. Sci.* **10**: 219–230.
- Lovett Doust, L. (1981): Population dynamics and local specialization in a clonal perennial *Ranunculus repens*. I. The dynamics of ramets in contrasting habitats. – *J. Ecol.* **69**: 743–755.
- Pickett, S. T. A.; Cadenasso, M. L. & Jones, C. G. (2000): Generation of heterogeneity by organisms: creation, maintenance and transformation. In: Hutchings, M. J., John, E. A. & Stewart A. J. A. (eds.): *The ecological consequences of environmental heterogeneity*. pp. 33–52. – Blackwell, Oxford.
- Robinson, D. (1994): The responses of plants to non-uniform supplies of nutrients. – *New Phytol.* **127**: 635–674.
- Ryel, R. J.; Caldwell, M. M. & Manwaring, J. H. (1996): Temporal dynamics of soil spatial heterogeneity in sagebrush-wheatgrass steppe during a growing season. – *Plant Soil* **184**: 299–309.
- Salemaa, M. & Sievänen, R. (2002): The effect of apical dominance on the branching architecture of *Arctostaphylos uva-ursi* in four contrasting environments. – *Flora* **197**: 429–442.
- Schwinning, S. & Weiner, J. (1998): Mechanisms determining the degree of size asymmetry in competition among plants. – *Oecologia* **113**: 447–455.
- Taylor, K.; Rowland, A. P. & Jones, H. E. (2001): *Molinia caerulea* L. Moench. – *J. Ecol.* **89**: 126–144.
- Veresoglou, D. S. & Fitter, A. H. (1984): Spatial and temporal patterns of growth and nutrient uptake of five co-existing grasses. – *J. Ecol.* **72**: 259–272.
- Weiner, J.; Wright, D. B. & Castro, S. (1997): Symmetry of below-ground competition between *Kochia scoparia* individuals. – *Oikos* **79**: 85–91.
- Wijesinghe, D. K. & Whigham, D. F. (2001): Nutrient foraging in woodland herbs: a comparison of three species of *Uvularia*, Liliaceae, with contrasting belowground morphologies. – *Amer. J. Bot.* **88**: 1071–1079.
- Wijesinghe, D. K.; John, E. A.; Beurskens, S. & Hutchings, M. J. (2001): Root system size and precision in nutrient foraging: responses to spatial pattern of nutrient supply in six herbaceous species. – *J. Ecol.* **89**: 972–983.