

## Effect of competition and soil quality on root topology of the perennial grass *Molinia caerulea*

Vliv kompetice a kvality půdy na topologii kořenů vytrvalé trávy *Molinia caerulea*

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Changes in root topology of the tussock perennial grass *Molinia caerulea* were studied in a pot experiment. The target species *M. caerulea* was grown alone and with *Holcus lanatus* or *Carex hartmanii* as a competitor. The root topology in three different soils (sand, humus rich soil and a mixture of both) was measured. Influence of competitive pressure on root topology was determined in terms of root biomass surrounding the target root. Whereas no simple significant changes in root topology due to soil quality were observed, an increase in competition pressure caused a shift of root topology towards a more herringbone structure. This shift was greatest in nutrient poor sand and least in humus-rich soil. In addition, an influence of individual competitors on topological changes in humus-rich soil was observed after excluding the effect of total root biomass.

**Key words:** *Carex hartmanii*, competition, *Holcus lanatus*, *Molinia caerulea*, root plasticity, topology, tussock grass

### Introduction

Due to the complexity of the soil environment, new plant below-ground traits, which affect resource exploitation and both biotic and abiotic interactions are still being discovered. It is known that one of the most important features of this complexity is resource heterogeneity (Jackson & Caldwell 1993, Ryel et al. 1996). This heterogeneity can affect the outcome of plant competition (Campbell et al. 1991, Fransen et al. 2001, Rajaniemi & Reynolds 2004, Janeček et al. 2004), due to differences in allocating to plant root biomass, foraging scale and rate. Furthermore, the ability of plants to utilize patches of nutrient rich soil can be modified by changes in root morphology (Arredondo & Johnson 1999, Šmilauerová & Šmilauer 2002), root physiology (Derner & Briske 1999) and co-operation with other organisms, especially mycorrhizal fungi and nitrogen-fixing bacteria (Šmilauerová 2001, Šmilauerová & Šmilauer 2002, Cruz et al. 2004).

Roots can accommodate to soil heterogeneity by changing their topology. The centripetal topological model based on root links was suggested by Werner & Smart (1973) for topological classification of channel networks. This concept was adopted by Fitter (1985, 1986, 1987) to describe plant root systems. The fundamental element in this model is the link; in the case of roots it is the segment of a root between two branching points or between the api-

cal meristem and the first branch. The topology of a root ranges in type from herringbone to dichotomous. Whereas a herringbone system is composed only of the main axis and its laterals, in a dichotomous system the new branches arise equally likely on each exterior link.

Simulation models of space exploration, root costs and transport efficiencies showed differences between both these extreme types of topology (Fitter 1987, Fitter et al. 1991). The herringbone system seems to explore the space more efficiently, but is costly and less transport-efficient. Although these models predict that a particular topology is well suited to a specific environment, experimental results are not consistent. The results of Fitter & Stickland (1991) and Taub & Goldberg (1996) support the prediction that nutrient-rich soils favour the dichotomous topology of dicots. In contrast, Arredondo & Johnson (1999) show the opposite effect of nutrients on root topology of grasses. A similar shift in root topology to a more herringbone structure in more fertile conditions is reported for *Luzula campestris*, but not in *Poa angustifolia* and *Plantago lanceolata* (Šmilauerová & Šmilauer 2002).

It is known that root competition can change nutrient uptake and root proliferation (Robinson et al. 1999, Robinson 2001). Although some parameters, such as the R/S ratio and root placement, are relatively frequently studied (Bliss et al. 2001, Fransen et al. 2001, Janeček et al. 2004), there is little understanding of the reaction of root topology to competition (Šmilauerová & Šmilauer 2002). Moreover, the findings of Šmilauerová & Šmilauer (2002) contradict the predictions of the centripetal topological model (Fitter et al. 1991).

In the glasshouse experiment reported here, root parameters (topological and dimensional) of *Molinia caerulea* were studied in three different soils and three competition treatments: no interspecific competition (only intra-specific competition), or competition with one of two other meadow plant species (*Carex hartmanii* or *Holcus lanatus*). The aim was to answer the following questions: (1) Are the root parameters affected by the soil in which they grow? (2) Are the root parameters affected by the identity of the competitor and by the biomass of its roots?

## Materials and methods

### *Species*

Individuals of the species studied were collected from an oligotrophic meadow at Ohrazení, which is 10 km SE of České Budějovice, Czech Republic, 48°57'N, 14°38'E, at 530 m a.s.l. The mean annual precipitation and mean annual temperatures are 600–650 mm and 7.8 °C, respectively.

The roots of *Molinia caerulea* (L.) Moench, a dominant species in several vegetation types (Taylor et al. 2001) can reach a depth of more than 80 cm (Jefferies 1915, 1916). It forms a vegetation matrix of dense tussocks at the study site. *Holcus lanatus* L. is a tufted grass, which is able to increase in cover when *M. caerulea* is removed (Lepš 1999 and unpublished data). *Carex hartmanii* Cajander is a rhizomatous sedge, which penetrates the vegetation by means of its rhizomes, which may be longer than 0.5 m (personal observation).

### *Experimental design and procedure*

The pot experiment was primarily established to study the influence of soil heterogeneity and competition on the growth of the target species, which was measured in terms of

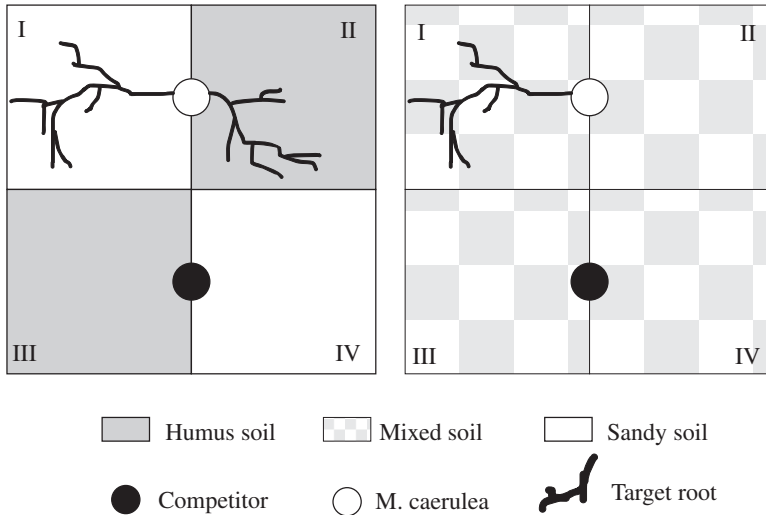


Fig. 1. – The experimental design. Both heterogeneous (left) and homogenous (right) treatments were performed in square  $19 \times 19$  pots. I, II, III, IV – sector numbers. Open circle – the position where the standard unit of *Molinia caerulea* was planted. Closed circle – the position where the standard unit of competitor (*Holcus lanatus* or *Carex hartmanii*) was planted. In the no-competition treatments the competitor place remained empty.

above- and below-ground production (Janeček et al. 2004). However, it was realized that changes in root morphology could provide further insights into the mechanisms of root competition.

Square plastic pots,  $19 \times 19$  cm and 15 cm deep were divided between two treatments, heterogeneous (19 pots analysed) and homogenous (20 pots); see Table 1 for details. The pots assigned to the heterogeneous treatment were divided vertically into four sectors. The two diagonal parts contained humus rich soil and the other two sand. There was no barrier between the sectors so the roots could grow freely in the whole pot (Fig. 1). The soil parameters measured at the end of the experiment in the sandy soil sector were: N total  $< 0.2$  g/kg, P total  $< 6$  mg/kg, pH 6.04, and in humus-rich sector: N total 12.5 g/kg, P total 120 mg/kg, pH 5.47. Both of these soils were mixed together in the homogeneous treatment. Standard pieces of *M. caerulea*, *C. hartmanii* and *H. lanatus* were transplanted into the pots at the end of April 2001. The pots were watered with tap water when needed. Because of the strong effect of genotype in grass (Pecháčková 1999) each standard unit of *M. caerulea* was taken from a different tussock, which possibly resulted in each standard unit being from a different genotype (Janeček 2005). The transplanted standard units were of similar weight and consisted of two interconnected basal internodes of *M. caerulea*, two closely interconnected tillers of *C. hartmanii* (forming a small tussock), or one tiller of *H. lanatus*. Single standard units of each species (*M. caerulea* and a competitor) were grown in each pot in the competition treatment. *Molinia caerulea* was grown with either *C. hartmanii* or *H. lanatus* as the competitor (Fig. 1). There was only one plant of *M. caerulea* per pot in the no-competition treatment.

Table 1. – Number of replicates (N) and the biomass and root characteristics of *Molinia caerulea* in individual soil types and competition treatments. Mean is followed by standard deviation (in brackets). CTHL – competition treatment with *Holcus lanatus*; CTCH – competition treatment with *Carex hartmanii*; NCT – no-competition treatment. ILL – the average length of interior links, ELL – the average length of exterior links,  $\mu$  (magnitude) – the number of root tips, as well as two topological indexes. Explanation of topological parameters: Log(Pe)/Log( $\mu$ ) and DBI is given in the Material and methods.

	Sandy soil sector			Mixed soil sector			Humus soil sector		
	CTHL	CTCH	NCT	CTHL	CTCH	NCT	CTHL	CTCH	NCT
N	6	7	6	5	7	8	6	7	6
Root dry biomass of competitor in target sector (g)	0.026 (0.032)	1.268 (0.628)	–	0.170 (0.138)	1.616 (0.612)	–	0.036 (0.037)	2.882 (1.077)	–
Root dry biomass of <i>M. caerulea</i> in target sector (g)	0.133 (0.104)	0.203 (0.114)	0.266 (0.099)	0.183 (0.102)	0.168 (0.067)	0.245 (0.059)	0.330 (0.282)	0.299 (0.219)	0.337 (0.072)
ILL (mm)	3.883 (1.560)	4.843 (3.617)	3.767 (1.122)	3.100 (0.381)	3.571 (0.509)	2.900 (0.393)	3.033 (0.314)	4.057 (1.536)	3.433 (0.729)
ELL (mm)	6.400 (2.940)	7.229 (2.076)	6.683 (1.728)	4.760 (0.404)	5.414 (1.202)	4.325 (0.752)	4.617 (1.067)	6.871 (2.304)	5.117 (0.838)
$\mu$	312.3 (294.7)	43.0 (26.6)	302.8 (136.8)	412.8 (135.5)	94.1 (45.7)	516.1 (242.9)	609.7 (427.4)	60.9 (47.8)	523.7 (372.0)
Log(Pe)/Log( $\mu$ )	1.635 (0.067)	1.782 (0.035)	1.633 (0.045)	1.648 (0.030)	1.729 (0.044)	1.604 (0.066)	1.617 (0.086)	1.761 (0.061)	1.637 (0.047)
DBI	0.234 (0.112)	0.735 (0.216)	0.214 (0.110)	0.210 (0.069)	0.513 (0.192)	0.157 (0.110)	0.198 (0.186)	0.703 (0.295)	0.199 (0.105)

Each pot was divided into four sectors, at the end of the experiment in the middle of August 2001 (see Fig. 1). One root growing from basal internode of *M. caerulea* was randomly selected from sector I in the homogenous treatment and sectors I (sandy soil) and II (humus soil) in the heterogeneous treatment (Fig. 1). The remaining root biomass was harvested separately for each sector and species. The roots were mostly still attached to the above-ground parts. The unattached roots were identified according to their colour and structure, which differ slightly among the species.

Separated roots were spread on a glass plate and their images were scanned using a flat-bed scanner with a resolution of 300 dpi. Root parameters, recorded in the image files, were evaluated using ROOTARCH software (P. Šmilauer, unpublished). Each root system can be seen as a branching structure, where each link is a segment of the root either between two consecutive branching points (interior link), or between branching point and terminal meristem (exterior link). Following parameters were used: ILL – the average length of interior links, ELL – the average length of exterior links,  $\mu$  (magnitude) – the number of root tips, and two topological indexes: Log(Pe)/Log( $\mu$ ) (Fitter 1996), where Pe is the sum of the number of links in all paths from any exterior link to the root base and  $\mu$  is magnitude and DBI – dichotomous branching index (Šmilauerová & Šmilauer 2002). Both of the topological indices increase with a shift of the root architecture from a dichotomous to a herringbone structure and seem to be independent of root size (Fitter 1996, Šmilauerová & Šmilauer 2002). The advantage of the dichotomous branching index (DBI) is that its values are between 0 (fully dichotomous) and 1 (fully herringbone) (see Šmilauerová & Šmilauer 2002)

### Data analysis

Because of the possible dependence of two roots from one plant in the heterogeneous treatment and independence between roots from the mixed soil and both sand and humus rich soil treatments three t-tests were performed (one for dependent and two for independent samples) to analyse differences between soil types. A Bonferroni correction:  $\alpha_{\text{used}} = \alpha_{\text{nominal}} / 3$  (three t-tests) was used to keep the probability of Type I error at the nominal significance level. In effect, all P values from individual t-tests were multiplied by 3.

The influence of root biomass on the studied parameters was analysed using linear regression. Root biomass from the sector where a given root was taken was used. Analysis of the competitor effect on root parameters in individual soil types was performed by ANCOVA, where the identity of competitor was the grouping factor and root biomass in the corresponding sector the covariate. The aim of these analyses was to detect competitor effects, which are independent of root productivity in individual competition treatments. Data were analysed using the program STATISTICA 7.0 (Anon. 1996).

### Results

Roots of *M. caerulea* showed high plasticity in their topology. The dichotomous branching index (DBI) ranged from 0.05 to 1 (mean 0.36). Means of ELL and ILL in all root systems were 5.72 mm and 3.63 mm, respectively. The mean number of exterior links (magnitude) was 311.5. The detailed information on root biomass and topological parameters in individual treatments are given in Table 1 and Janeček et al. (2004).

There appeared to be only one significant effect of soil quality on the root characteristics (Table 2): The average exterior link length was significantly larger in sand (6.8 mm) than in mixed soil (4.8 mm). In contrast the root biomass of the competitor in the sector of the target root was an important factor determining root architecture and number of exterior links (magnitude) (Table 3). In all soil types, root structure became more herringbone branched as root biomass increased. Moreover, the regression slope decreased in the order: sand – mixed – humus-rich soil. Likewise, the explained variability ( $R^2$ ) decreased in this sequence (Fig. 2). The regressions were non-significant when root biomass of *M. caerulea* was used and the results were similar when sum of both root biomass of the competitor *M. caerulea* was used.

Root biomass of the competitor negatively affected root magnitude. The most negative regression slope was for plants grown in mixed soil. A significant positive effect of root biomass on average length of interior links was detected in the mixed soil (Table 3).

There were significant effects of the competitor on the average exterior length (ANCOVA adjusted means: without competitor = 4.01, with *H. lanatus* = 3.54 and with *C. hartmanii* = 9,05) and DBI index (ANCOVA adjusted means: without competitor = 0.11, with *H. lanatus* = 0.11 and with *C. hartmanii* = 0.88) in humus-rich soil when total root biomass was used as a covariate to search for specific competitor effects on root parameters (Table 4).

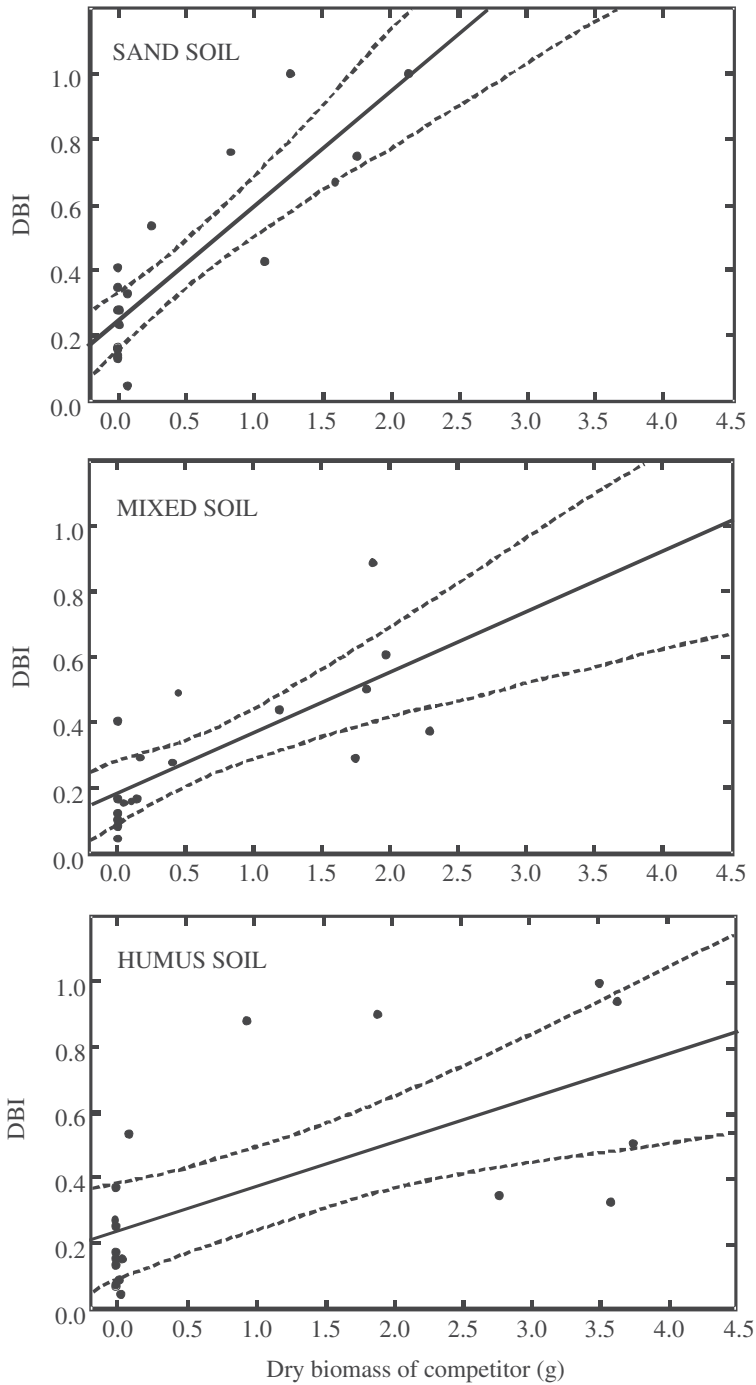


Fig. 2. – Dependence of the dichotomous branching index (DBI) on root biomass in individual soils. Statistical analyses are given in Table 3. Sandy soil:  $y = 0.245 + 0.353x$ ,  $R^2 = 0.75$ . Mixed soil:  $y = 0.184 + 0.185x$ ,  $R^2 = 0.54$ . Humus soil:  $y = 0.239 + 0.135x$ ,  $R^2 = 0.42$ . DBI ranges from 0 for completely dichotomously branched to 1 for herringbone-style branched roots.

Table 2. – Differences in the root parameters of *Molinia caerulea* in the different soils. Three t-tests were performed for each parameter. Whereas the sand × humus soil difference was tested using t-test for dependent samples, the other two contrasts were tested using t-test for independent samples. Correction for Type I error was performed by Bonferroni adjustment (P in table = P corresponding with t statistics in brackets × 3). ILL – the average length of interior links, ELL – the average length of exterior links,  $\mu$  (magnitude) – the number of root tips, as well as two topological indexes. Explanation of topological parameters: Log(Pe)/Log( $\mu$ ) and DBI is given in the Material and methods.

	ILL	ELL	$\mu$	Log(Pe)/Log( $\mu$ )	DBI
Sand × humus soil	ns (1.20)	ns (1.87)	ns (2.20)	ns (0.72)	ns (0.41)
Sand × mixed soil	ns (1.87)	0.002 (3.69)	ns (1.76)	ns (1.18)	ns (1.44)
Humus × mixed soil	ns (1.32)	ns (1.71)	ns (0.36)	ns (0.67)	ns (1.03)

Table 3. – Linear regressions of the effect of the measured parameters on root biomass of the competitor in individual soils. The P-value is followed by the F-ratio statistic (in brackets). Superscript + associated with the significance value means a positive effect of total root biomass on parameter studied, superscript – means a negative effect. ILL – the average length of interior links, ELL – the average length of exterior links,  $\mu$  (magnitude) – the number of root tips, as well as two topological indexes. Explanation of topological parameters: Log(Pe)/Log( $\mu$ ) and DBI is given in the Material and methods.

	ILL	ELL	$\mu$	Log(Pe)/Log( $\mu$ )	DBI
Sand soil	ns (0.35)	ns (0.41)	0.018 <sup>–</sup> (6.85)	< 0.0001 <sup>+</sup> (26.61)	< 0.0001 <sup>+</sup> (50.50)
Mixed soil	0.001 <sup>+</sup> (15.69)	ns (3.06)	0.001 <sup>–</sup> (17.03)	0.002 <sup>+</sup> (13.22)	0.001 <sup>+</sup> (19.81)
Humus soil	ns (2.90)	ns (2.54)	0.010 <sup>–</sup> (8.50)	0.005 <sup>+</sup> (10.41)	0.003 <sup>+</sup> (12.28)

Table 4. – ANCOVA analyses of the effect of different competitors (*Carex hartmanii*, *Holcus lanatus* and no-competitor) on the measured parameters of *Molinia caerulea*. Total root biomass in target soil sector was used as a covariate in order to exclude the effect of different root productivities in the individual treatments. The P-value is followed by the F-ratio statistic (in brackets) and corresponds to the competitor identity effect. ILL – the average length of interior links, ELL – the average length of exterior links,  $\mu$  (magnitude) – the number of root tips, as well as two topological indexes. Explanation of topological parameters: Log(Pe)/Log( $\mu$ ) and DBI is given in the Material and methods.

	ILL	ELL	$\mu$	Log(Pe)/Log( $\mu$ )	DBI
Sand soil	ns (0.40)	ns (0.10)	ns (0.59)	ns (2.28)	ns (2.11)
Mixed soil	ns (0.37)	ns (1.12)	ns (1.66)	ns (3.10)	ns (1.71)
Humus soil	ns (0.34)	0.038 (4.11)	ns (1.41)	ns (3.35)	0.039 (4.05)

## Discussion

Of the several parameters tested in *Molinia caerulea*, the difference in average length of exterior links between roots growing in sand and in mixed soil was the only significant effect of soil quality. Nevertheless the reaction to competition was largest in nutrient-poor sand and smallest in humus-rich soil, indicating that the root reaction depends on soil quality. This is in agreement with some studies, which did not detect any influence of soil fertility on root parameters in grasses (Fitter & Stickland 1991, Taub & Goldberg 1996, Šmilauerová & Šmilauer 2002). On the other hand Arrendo & Johnson (1999) have shown that root topology of three grasses shifted from a herringbone to a dichotomous structure in a low nutrient environment. Dawson et al. (2003) obtained similar results for *Festuca ovina*. However, the response of *Lolium perenne* in the same study was in the opposite direction, which agrees with the model of Fitter et al. (1991). Generally, our results, together with the previously mentioned studies, suggest that changes in grasses' root topology along a fertility gradient need not (in contrast to dicots) follow theoretical predictions (Fitter et al. 1991) and increase dichotomous branching in nutrient-rich soils (Fitter & Stickland 1991, Taub & Goldberg 1996).

However we need to point out that the comparison of the roots from one plant, which is a compound of two interconnected tillers of the same genotype (humus × sandy soil comparison in our analyses), can differ from that of the roots of separated individuals of a different genotype (sand vs. mixed soil and humus vs. mixed soil comparisons in our analyses). Whereas in the first comparison only the effect of soil environment on root properties was observed, in the second it was the phenotypic variability including the influence of genotypes. From the physiological point of view the integration between tillers can affect root development due to nutrient, assimilate and signal transport. Each root can be specialized for a different assignment (labour division hypothesis, Stuefer et al. 1996)

Whereas there was no effect of competition on root placement in nutrient rich patches (Janeček et al. 2004), a clear effect of competition on root topology of *Molinia caerulea* was found. This finding is in agreement with the theory, which predicts that a herringbone structure is more advantageous in a competitive environment as it minimizes intraplant and probably also interplant competition (Fitter et al. 1991). On the other hand, Šmilauerová & Šmilauer (2002) found no effect of root competition in the grass *Poa angustifolia* and *Plantago lanceolata* even exhibited the opposite response. If high root topological plasticity in *M. caerulea* is considered to be an adaptation to competition, then there are two possible advantages of this adaptation for tussock grasses: (1) The roots can respond to a high root density below the tussock. (2) Due to the extension of the main axes, the herringbone structure seems to be an adaptation to root foraging; an increase in competition results in an increased effort to search for new rich patches with lower competition. Root foraging can be extremely useful for tussock “phalanx” grasses (in contrast to “guerilla” plants), which are not able to move when nearby soil resources are depleted (for phalanx-guerilla growth forms see Lovett-Doust 1981).

The fact that root topology was not affected by soil quality (differing considerably in nutrient content), whereas it changed with root biomass in the soil, suggests that *M. caerulea* does not perceive competition only through a decrease in nutrient content (indirect competition). The growth response to amount of biomass may be a response to space limitation (McConnaughay & Bazzaz, 1992) and/or other signals can play an important role in root development (Gruntman & Novoplatsky 2004, Falik et al. 2003).



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## Souhrn

Změny v topologii kořenového systému jsou zajímavou reakcí rostliny jak na úživnost substrátu, tak přítomnost kompetitora. V této práci byl pomocí nádobového experimentu studován vliv kompetice a kvality substrátu na kořenovou topologii trsnatého druhu *Molinia caerulea*. Rostliny *M. caerulea* byly pěstovány samostatně nebo v kompetici ve třech typech substrátu lišících se úživností. Jako kompetitoři byly použity oddenkaté traviny *Holcus lanatus* nebo *Carex hartmanii*. Z každé varianty (typ kompetice a substrátu) byla analyzována topologie jednotlivých kořenů *M. caerulea*. Intenzita kompetice byla vyjádřena jako kořenová biomasa kompetitora obklopující analyzovaný kořen. Zatímco nebyl zaznamenán žádný samostatný vliv typu půdy na kořenovou topologii, zvýšená kompetice způsobila posun kořenové topologie směrem od dichotomického větvení ke struktuře "rybí kostry". Tento posun byl nejvýraznější v písku a nejmenší v živinami bohatém substrátu. Navíc byl zaznamenán specifický vliv jednotlivých kompetitorů na topologické změny v živinami bohatém substrátu po vyloučení efektu celkové kořenové biomasy.

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