Original article

Effect of litter, leaf cover and cover of basal internodes of the dominant species *Molinia caerulea* on seedling recruitment and established vegetation

Štěpán Janeček [a,b,*], Jan Lepš [a,c]

[a] *Department of Botany, Faculty of Biological Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic*
[b] *Institute of Botany, Academy of Science of the Czech Republic, Section of Plant Ecology, Dukelská 135, Třeboň-379 82, Czech Republic*
[c] *Institute of Entomology, Academy of Science of the Czech Republic, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic*

Abstract

The effects of litter removal, leaf cover of established plants and cover of basal internodes of a dominant species *Molinia caerulea* on seedling germination and the dynamics of established plants were studied in a field experiment in an oligotrophic wet meadow. Although the negative influence of litter on total seedling number and seedling species composition was non-significant, litter significantly affected the dynamics of the established vegetation and caused inhibition of total leaf cover development. The effects of total leaf cover of established plants on seedling establishment changed during the vegetation season. Whereas the effect of total leaf cover was positive at the start and in the middle of the vegetation season, at the end the total leaf cover negatively affected seedling establishment. Both total leaf cover and cover of basal internodes affected seedling composition. Effects of these two variables were statistically separable suggesting that they are based on different mechanisms. The response of seedling establishment to these factors was species specific and, consequently, our data support the hypothesis that that biotically generated spatial heterogeneity can promote species co-existence through the differentiation of species regeneration niches.

1. Introduction

Seedling germination and establishment are often the most critical phases of plant life. The requirements for germination and establishment were defined as the regeneration niche (Grubb, 1977). The main factors that determine establishment success in meadow communities can be divided into two groups. The first involves biotic factors such as litter production, leaf cover density and herbivory. The second group includes abiotic factors; mainly soil composition, temperature, humidity and light intensity. These two groups are closely related and their effects are hardly separable without an experimental approach.

The effects of individual factors differ among plant communities and the results of studies are also affected by the methods used (Xiong and Nillson, 1999). In meadows, the influence of established vegetation on seedlings can be divided into effects of individual layers by roots, litter, moss and leaves. In meadows dominated by tussock grasses, the layer of tussock bases formed by individual tillers has often a specific effect.

Root competition has a negative effect on seedling establishment in grasslands (Haugland and Tawfig, 2001; McKendrick, 1996) and, similarly, the effect of litter on seedling recruitment seems to be negative (Špačková and Lepš, 2004; Jensen and Gutenkunst, 2003; Xiong and Nillson, 1999). Both positive (Keizer et al., 1985; Ryser, 1993) and negative (Van Tooren, 1990; Špačková et al., 1998; Špačková and Lepš, 2004) effects of the moss layer on seedlings have been documented. The effects of leaf cover of established vegetation vary in similar ways. Ryser (1993) showed a positive effect of neighboring plants on conspecific seedlings thanks to protection against frost and/or drought. On the contrary, seed-

lings of *Reseda lutea* preferred microsites with low cover of established vegetation (Silvertown, 1981). The established vegetation and litter can also serve as a suitable habitat for seed predators (Reader, 1991). Although the effect of tussock bases can differ from the effect of leaf cover, these are usually not separated in the studies. One of the reasons is a strong spatial correlation between leaf and tussock base cover. Nevertheless, the tussock base layer has some specific characters different from the leaf layer, most notably the ability to mechanically exclude competitors (thanks to its density). On the other hand, it can provide a balanced microsite climate.

The highly specific conditions that enable seedling recruitment are often characterized as "safe site" (Harper, 1967). However, safe site conditions might be species specific conditions promoting recruitment of one species can be detrimental for another. This is one of the assumptions of Grubb's (1977) theory of maintenance of species diversity by differentiation of species regeneration niches.

The tussock base layer is well established in wet meadows dominated by *Molinia caerulea* or *Molinia arundinacea*. It is formed by the thick basal internodes of these species, which have a storage function (Taylor et al., 2001). In our study site, tussock bases of *M. caerulea* covered about 18% of the meadow surface, being a very important determinant of vegetation structure.

Many studies pointed to a deficiency of data on year to year variation in seedling recruitment (recently Špačková and Lepš, 2004). However, data on seasonal dynamics of seedling recruitment in meadows, and its relation to the dynamics of the established vegetation (primarily to leaf and tussock bases cover) are similarly needed (Ryser, 1993; Silvertown, 1981). In our experiment, we aimed to test the effects of litter on the seasonal dynamics of seedling recruitment and established vegetation. The second objective was to estimate and disentangle the effect of two aboveground layers, basal internodes and leaf cover, on seedling recruitment.

2. Methods

2.1. Study site

The study plots were established on an oligotrophic, species-rich wet meadow 10 km southeast of České Budějovice, Czech Republic (48°57′N; 14°36′E; 510 m a.s.l.). The mean annual temperature ranges between 7 °C and 8 °C, and mean annual precipitation is 600–650 mm. The most dominant species is *M. caerulea*, which determines the structure of all of the community by its compact tussocks. It is late flowering (July, August) grass forming compact tussocks up to 30 cm in diameter, with flower stems up to 1.5 m tall. Plots were established in an abandoned part of the meadow, which had not been mown for several years before the start of the experiment, and where the dominance of *Molinia* was higher than in the mown part, reaching cover over 90% at the end of vegetation season. Other common species in this part include grasses *Holcus lanatus*, *Deschampsia caespitosa*, *Festuca rubra*, graminoids *Juncus effusus*, *Carex hartmanii* and forbs *Cirsium palustre*, *Achillea ptarmica*, *Angelica sylvestris*. The amount of litter in the abandoned part of the meadow ranged from 400 to 700 g m^{-2} in the middle of vegetation season. There are several concurrent studies running in the locality (Špačková and Lepš, 2004 and papers cited there), of them, Lepš (1999) provides detailed description of the community.

2.2. Experimental design

Experimental plots were established in April 1999. Five experimental plots (1 × 1 m), where the litter was removed, and five control plots were arranged in a block of 2 × 5 plots. Removal plots regularly alternate with control plots. The data were recorded in 0.5 × 0.5 m plots, subdivided into 25 (10 × 10 cm) subplots, located in the center of each 1 m^2 plots. We visually estimated cover of individual species, cover of basal internodes of the dominant species *M. caerulea* and recorded the number of individual seedlings of all species in each 10 × 10 cm subplot three times throughout the vegetation season. Data collection took 3 days. For simplification, each sampling period was designated by the middle day (April 20th, June 2nd, August 2nd).

2.3. Data analysis

Seedling composition and cover of adult plants were determined for the same plot three times, resulting in a repeated measures design (i.e. split-plot design with litter removal as the main plot factor and time as the within-plot factor). Changes in univariate characteristics (seedling number, number of seedling species, leaf cover of *M. caerulea*, leaf cover of others species, total leaf cover and basal cover of *M. caerulea*) were analyzed by repeated measurements ANOVA. Profile analysis (Von Ende, 2001) was used to test hypotheses about parallelism, levels and flatness between individual observation dates. Profile analysis is a type of post-hoc testing, tailored to the repeated measures design (similarly as multiple comparisons for one-way ANOVA). In the profile analysis, the levels test the differences in the average value over each tested period, flatness tests whether there is any change during the tested interval, and parallelism tests whether the changes over the interval are the same in all the groups (interaction between time and the main plot factor, tested separately for each interval). Within-subject repeated measures data were transformed for parallelism and flatness analyses to a set of contrasts (i.e. differences between two subsequent measurements) and were tested by *t*-tests. To test the hypotheses about levels (test of main effect), values of two adjacent dates were averaged and then the means were compared between groups (for details see Von Ende, 2001). Because two *t*-tests were established between three observation dates in profile analysis the Bonferroni adjustment of $\alpha' = 0.025$ was used in each individual test to maintain an overall $\alpha = 0.05$. Influences of total leaf cover of adult plants and cover of basal

internodes of *M. caerulea* on seedling number in small 10 × 10 cm plots were tested by general linear models. For both, repeated measures and general linear models, data on count and percentage were square-root and log-transformed, respectively, to improve normality and homoscedasticity.

Redundancy analysis (RDA, constrained ordination method based on linear species response, Lepš and Šmilauer, 2003) was used to analyze the multivariate data because the species composition of both established plants and seedlings in the plots was rather homogenous, litter as the main factor was categorical and the response of seedlings to the continuous predictors (cover of *M. caerulea*, total leaf cover) was expected to be linear. Plot identifiers (coded as dummy variables) were used as covariates, when the influence of litter on time changes in plant and seedling compositions was tested. Time was considered categorical variable (we created three dummy variables for three observation dates). Data in the whole 50 × 50 cm plots were used for those analyses. Split-plot permutation tests were used where split plots were the individual observations and the whole plot was the 50 × 50 cm plot. RDA was conducted with and without standardization by sample norm. RDA without standardization includes both the effects of total seedling number and seedling community composition, RDA with standardization takes into account the species proportions only.

Further testing of the influence of total leaf cover and cover of basal internodes of *M. caerulea* was performed by RDA analysis. Microsites data (10 × 10 plots) were used to separate the effect of *M. caerulea* internode cover and total leaf cover. Species data in all RDA analyses were $\log(x + 1)$ transformed. Analyses were performed using the CANOCO software (Ter Braak and Šmilauer, 2002).

3. Results

3.1. Effect of litter on seasonal development of established vegetation

Both standardized and non-standardized RDA analyses of cover values of all the species showed a significant effect of litter on established vegetation development (significant time by litter interactions, Table 1). Both the development of total leaf cover (Table 2) and the development of species composition were significantly affected by litter. Development of total leaf cover on plots without litter was faster and reached on average 88% in June (in contrast to plots with litter where the total cover was only 55%). In August, leaf cover was approximately equal in both groups (slightly above 90%, Fig. 1.). Interestingly, the response of leaf cover development for the dominant species *M. caerulea* differed from that of other plants. Litter affected negatively leaf cover of other species, but leaf cover of *M. caerulea* increased during the vegetation season and on August 2nd it was slightly higher in plots with litter present (Fig. 1; Table 2). Cover of basal internodes increased throughout the vegetation season. This increase was not caused by development of new basal internodes but by basal internode thickening (Janeček, unpublished data).

3.2. Effect of litter on the development of the seedling community through the vegetation season

Seedling number, number of seedling species and seedling composition changed during the vegetation season (Figs. 1 and 2; Tables 2 and 3). The numbers of seedlings and seedling species were lower in plots with litter, but this effect

Table 1

RDA analyses results performed on established vegetation data. Permutation (two lines for each test)—upper line: type of permutation on the whole plot level, lower line: type of permutation on split-plot level; % exp—percent of variability explained by all canonicalaxes; t1,t2,t3—time identifiers coded as three dummy variables; Plot ID—plot identifierscoded as 10 dummy variables. Nonstandardized/standardized-standardization by sample norm

Explanatory variables	Covariables	Permutation	% exp.	F trace	P trace
Nonstandardized					
Litter	t1,t2,t3	Freely, No	8.9	2.959	0.350
t1,t2,t3	Litter	No, Freely	12.9	2.144	**0.002**
t1*litter, t2*litter, t3*litter	t1,t2,t3, Plot ID	Freely, Freely	2.3	1.746	**0.026**
Standardized					
Litter	t1,t2,t3	Freely, No	9.6	3.015	0.360
t1,t2,t3	Litter	No, Freely	7.3	1.137	**0.002**
t1*litter, t2*litter, t3*litter	t1,t2,t3, Plot ID	Freely, Freely	2.6	1.679	**0.038**

Table 2

Influence of time and litter on univariate seedling and established plantscharacteristics, tested by repeated measures ANOVA. df-error degrees of freedom

|	Litter			Time			Time*litter		
	df	F	P	df	F	P	df	F	P
Seedling number	8	1.978	0.197	16	43.142	**0.000**	16	2.566	0.108
Number of seedling species	8	3.150	0.114	16	25.029	**0.000**	16	1.128	0.348
Leaf cover of *M. caerulea*	8	0.119	0.739	16	244.236	**0.000**	16	10.665	**0.001**
Leaf cover of others species	8	2.019	0.193	16	0.6838	0.519	16	4.774	**0.024**
Total leaf cover	8	17.979	**0.003**	16	114.088	**0.000**	16	9.364	**0.002**
Cover of basal internodes of *M. caerulea*	8	0.1925	0.672	16	4.283	**0.032**	16	2.952	0.081
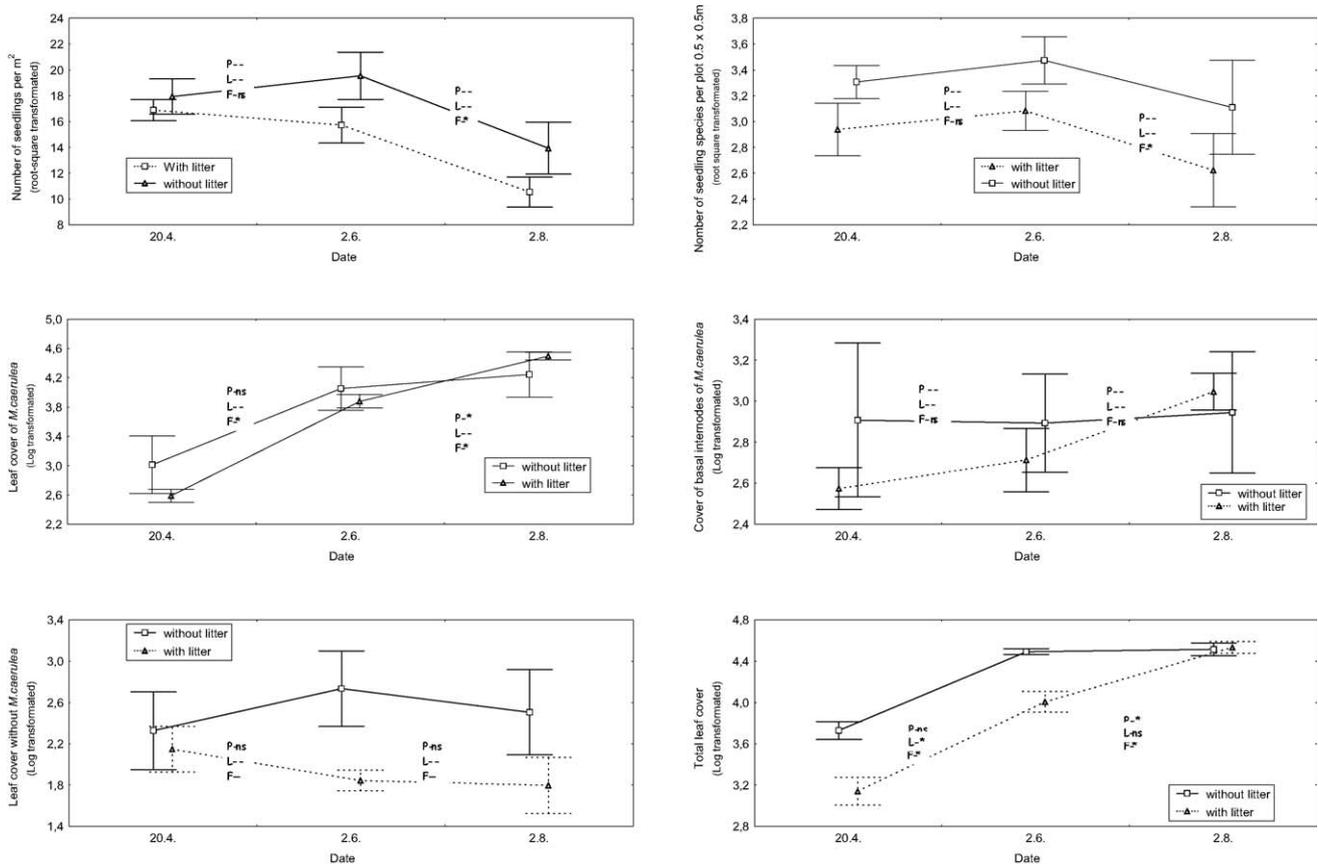
Fig. 1. Effect of litter on univariate characteristics of seedlings and established vegetation. Results of the profile analysis are indicated for each time interval: P—parallelism; L—levels; F—fleetness; * indicates $P < 0.05$ (after Bonferroni adjustment); -- indicates that the test was not performed due to a non-significant result in the repeated measurement test (see Table 2); ns—non-significant. Means and S.E. (whiskers) are displayed.

was not significant. Maximum seedling number per m² (395) was recorded in June in plots without litter. On the contrary minimum seedling number per m² (117) was recorded at the end of the vegetation season in August in plots with litter. A similar development was observed in number of seedlings
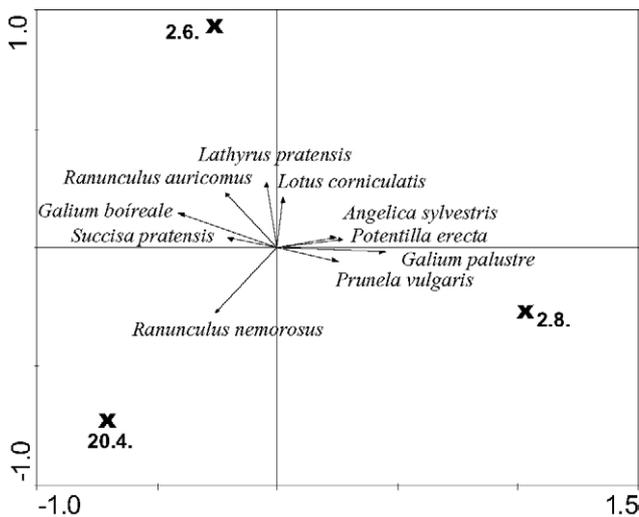

Fig. 2. Changes in species composition of seedlings on individual sampling dates. Results of standardized RDA, with time (coded as three dummy variables) as environmental variables, and litter presence as a covariable. Differences were highly significant ($F = 1.769$, $P = 0.002$).

species, with the maximum species number per plot (12) recorded in June in plots without litter and the minimum (7.2) in August in plots with litter (Fig. 1).

3.3. Effect of total leaf cover and cover of basal internodes of M. caerulea on seedlings

The effect of total leaf cover (TLC) of established vegetation on seedling number changed during the season (significant time × TLC interaction, Table 4). Whereas in April and June, the effect was positive, the effect was negative in August. Seedling species composition was affected significantly by both leaf cover and cover of *M. caerulea* basal internodes (CBI) in the microsites (10 × 10 cm) and this effect changed through the vegetation season (Table 5). TLC and CBI explained different parts of the variability at the start and end of the vegetation season (Table 6). Part of the explained variability was shared between CBI and TLC only in the middle of the vegetation season (June) (Figs. 3–5, Table 6). The explanatory power of TLC decreased while that of CBI increased during the season (Figs. 3–5, Table 6). Relationships between CBI, TLC and individual seedling species also changed during the vegetation season (Figs. 3–5). Increasingly seedlings of most species were not found in plots with high TLC. This effect was probably caused by increasing total leaf cover. Only seedlings of *A. sylvestris* were positively cor-

Table 3
RDA analyses results performed on seedling data. Permutation (two lines for each test)—upper line: type of permutation on the whole plot level, lower line: type of permutation on split-plot level; % exp—percentage of variability explained by all canonical axes; t1,t2,t3—time identifierscoded as three dummy variables; Plot ID—plot identifiers coded as 10 dummy variables. Nonstandardized/standardized-standardization by sample norm

Explanatory variables	Covariables	Permutation	% exp. trace	*F* trace	*P* trace
Nonstandardized					
Litter	t1,t2,t3	Freely, No	4.7	1.649	0.790
t1,t2,t3	Litter	No, Freely	22	3.899	**0.002**
t1*litter, t2*litter, t3*litter	t1,t2,t3, Plot ID	Freely, Freely	1.8	0.856	0.630
Standardized					
Litter	t1,t2,t3	Freely, No	3.4	1.051	0.950
t1,t2,t3	Litter	No, Freely	11.6	1.769	**0.002**
t1*litter, t2*litter, t3*litter	t1,t2,t3, Plot ID	Freely, Freely	1.6	0.587	0.928

related with TLC and even with CBI at the end of vegetation season in August. The highly significant results of the standardized RDA (Table 5) confirmed that different species preferred different microsites for their species recruitment.

4. Discussion

Špačková and Lepš (2004) on the same study site did not find any effect of litter removal on established vegetation over a 4 year experiment. In contrast, we observed the effect of litter on changes in plant composition in a single vegetation season. Litter also affected development of total leaf cover, leaf cover of *M. caerulea* and leaf cover of other species. Moreover we found that, in contrast to other species, *M. caerulea* was able to increase its leaf cover faster in the second half of the vegetation season on plots with litter and so compensate for thinner leaf cover at the start of the vegetation

Table 4
Results of the GLM analysis, testing the effects of time, total leafcover (TLC), cover of basal internodes of *M. caerulea* (CBI) and interactionsof TLC and CBI with time on the number of seedlings in 10 × 10 cm plots. Plot identifiers were used as a random factor, all the tested effects were fixed. Error df = 741

	df (effect)	*F*	*P*
Time	2	4.374	**0.013**
TLC	1	4.670	**0.031**
CBI	1	3.754	0.053
Time*TLC	2	5.321	**0.005**
Time*CBI	2	1.426	0.241

season on these plots. Unlike Špačková and Lepš (2004), we used an unmown part of the meadow, which has both a higher amount of litter and also a higher representation of *M. caerulea*. This comparison suggests that, in unmown meadows with high dominance of *M. caerulea*, litter can inhibit the development of a mature plant community throughout a vegetation season.

In contrast to mature vegetation, there was no significant effect of litter on seedlings. This result is in contrast to other studies (Bosy and Reader, 1995; Facelli and Facelli, 1993; Fowler, 1988), which have shown a negative effect of litter on seedling establishment. Špačková and Lepš (2004) found in the same study site (but on the mown part) only a shared negative effect of moss and litter on seedling recruitment. The absence of a significant effect on seedling recruitment can be also caused by the small number of replications; litter removal was the main plot factor, consequently with a low error degrees of freedom. Accordingly, in all of the cases, removal increased (albeit non-significantly) seedling recruitment. In contrast, the effects of foliage and basal internode cover were based on their variation in split plots, which provided a stronger test.

The effect by leaf cover of established vegetation on seedlings varied throughout the vegetation season. During spring and early summer, leaf cover was positively correlated with seedling numbers (suggesting a protection against desiccation), but in late summer, the correlation was negative, probably due to an increasing effect of competition for light. Other studies revealed both negative and positive effects. The negative relation of *R. lutea* seedlings to microsites of dense leaf

Table 5
RDA analyses results performed on seedling data, testing the effect of total leaf cover (TLC), cover of basal internodes of *M. caerulea* (CBI) and time. Permutation (two lines for each test)—upper line: type of permutation on the whole plot level, lower line: type of permutation on split-plot level; Def. by cov.—permutation in blocks defined by covariables, % exp—percent of explained variability by all canonical axes. t1,t2,t3—time identifiers coded as three dummy variables; Plot ID—plot identifiers coded as 10 dummy variables. Nonstandardized/standardized-standardization bysample norm

Explanatory variables	Covariables	Permutation	% exp. trace	*F* trace	*P* trace
Nonstandardized					
TLC, CBI	t1,t2,t3 Plot ID	Freely, No	4.8	23.757	**0.002**
TLC*t1, TLC*t2, TLC*t3, CBI*t1, CBI*t2, CBI*t3	Plot ID, TLC, CBI, t1,t2,t3	Def. by cov.	0.9	2.343	**0.012**
Standardized					
TLC, CBI	t1,t2,t3 Plot ID	Freely, No	3.7	16.802	**0.002**
TLC*t1, TLC*t2, TLC*t3, CBI*t1, CBI*t2, CBI*t3	Plot ID, TLC, CBI, t1,t2,t3	Def. by cov.	0.9	2.148	**0.004**

Table 6

Results of non-standardized RDA analyses. Separation of total leaf cover (TLC) and cover of basalinternodes of *M. caerulea* (CBI) effects on seedling data for individual dates. Note that only in June the effect of both (i.e. CBI, TLC) is considerably higher than both the partial effects, suggesting shared effect of the two explanatory variables; at the beginning and end of the season, the two effects seem to be independent

Explanatory variables	Covariable	Explained variability (%)	F	P
April 20th				
TLC	CBI	6.6	17.799	**0.002**
CBI	TLC	2.6	7.149	**0.002**
CBI, TLC		9.1	12.365	**0.002**
June 2nd				
TLC	CBI	4.6	12.475	**0.002**
CBI	TLC	2.7	7.284	**0.002**
CBI, TLC		8.7	11.716	**0.002**
August 2nd				
TLC	CBI	0.8	2.056	**0.044**
CBI	TLC	4.7	12.388	**0.002**
CBI, TLC		5.6	7.284	**0.002**

cover was demonstrated by Silvertown (1981). On the other hand the positive effect of vegetation shelter on *Primula veris* and *Arabis hirsuta* seedlings was described by Ryser (1993). Likewise Fowler (1988) showed that safe sites for seedling survival can be near neighboring plants.

Variation partitioning in seedling data sets showed that it is possible to separate the effect of leaf cover from that of the basal internode layer of *M. caerulea*. The ability of leaf cover to explain the variability in the seedling data decreased as the

Fig. 3. Results of non-standardized RDA analysis. Relation of seedling species to total leaf cover (TLC) and cover of basal internodes of *M. caerulea* (CBI) for the April 20th sample.
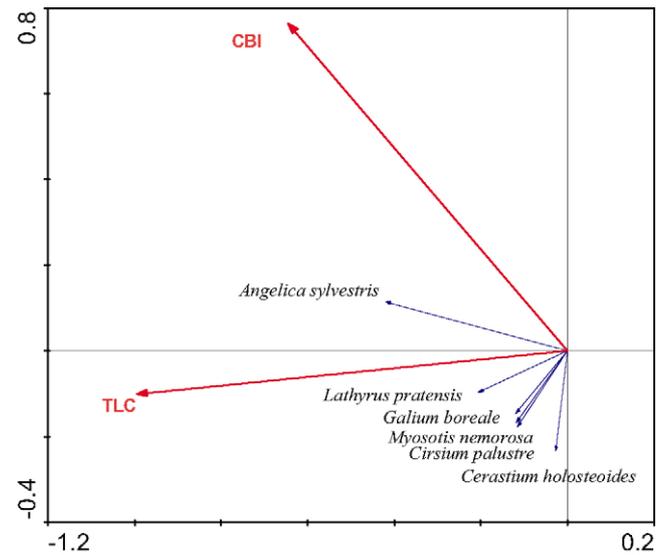

Fig. 4. Results of non-standardized RDA analysis. Relation of seedling species to total leaf cover (TLC) and cover of basal internodes of *M. caerulea* (CBI) for the June 2nd sample.

cover on the meadow became more closed. Concurrently, the explanatory power of *M. caerulea* basal internode cover increased. Whereas dense leaf cover had a negative effect on the seedlings at the end of the vegetation season, tufts of *M. caerulea*, represented by cover of basal internodes provided suitable conditions for seedlings of some species (especially *A. sylvestris*). Therefore, basal internode layer created a spe-
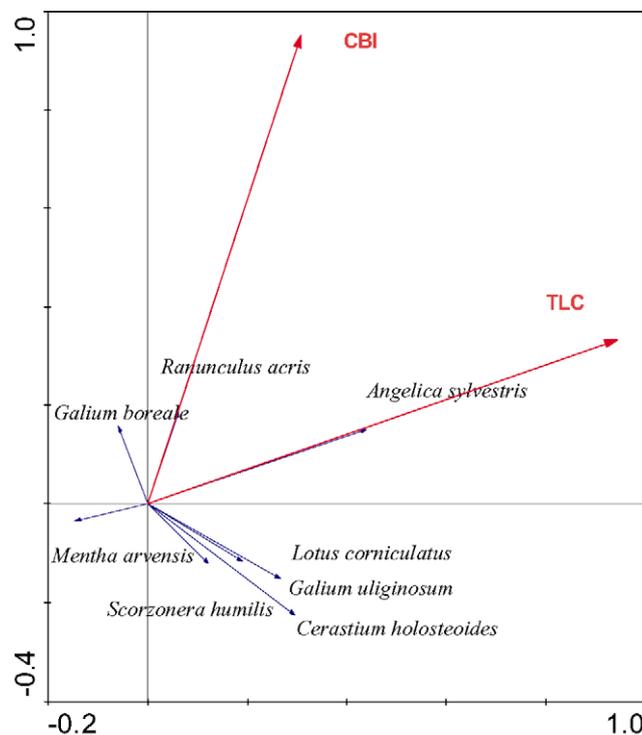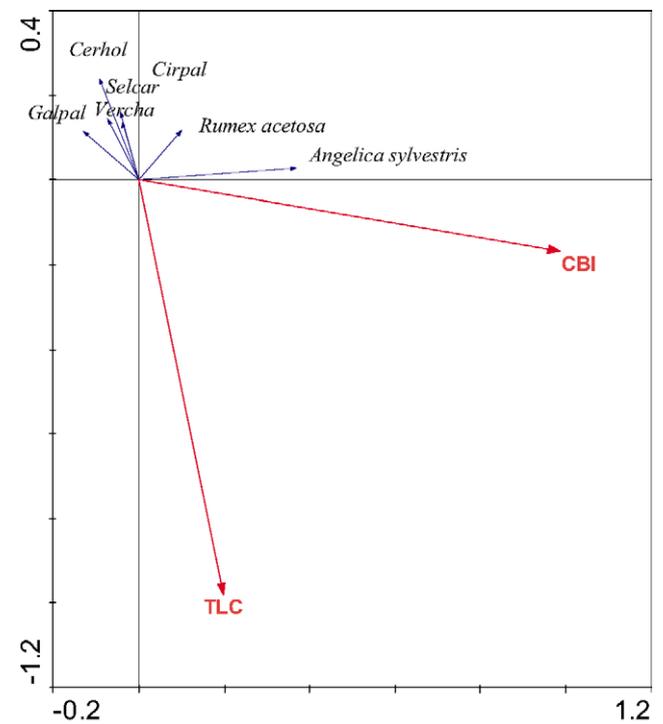

Fig. 5. Results of non-standardized RDA analysis. Relation of seedling species to total leaf cover (TLC) and cover of basal internodes of *M. caerulea* (CBI) for the August 2nd sample. Abbrevations of seedling species names: *Cirpal-Cirsium palustre; Selcar-Selinum carvifolia; Vercha-Veronica chamaedris; Galpal-Galium palustre; Cerhol-Cerastium holosteoides.*

cific microhabitat for seedling recruitment. The central part of a tuft is formed by a dense layer of basal internodes and is raised above the surface. However, the densest cover of leaves is on the circumference of the tuft. This part of the tuft is probably also influenced the most by *M. caerulea* litter. The fact that each of *Molinia* litter, leaf cover and cover of basal internodes affects the seedling germination differently, enables many possible combinations of their joint effects. This suggests potential for differentiation of microsites. These factors in combination with large interannual variation of weather and corresponding variation of seedling recruitment (Špačková and Lepš, 2004) can support the species co-existence through the regeneration niches differentiation (Grubb, 1977).

These results correspond to the findings of Kupferschmid et al. (2000), who showed that tussocks of *M. arundinacea* created unfavorable microsites for germination of *A. hirsuta*, but they supported seedling survival. Analogs to our results for *A. sylvestris*, Kupferschmid et al. (2000) described better germination of another umbellifer *Daucus carota* on tussocks of *M. arundinacea* in abandoned plots. Likewise Clarke and Davison (2001) did not find any obvious effect of grass tussocks removal on seedling emergence and survival.

In agreement with many previous studies (Jensen and Gutenkunst, 2003; Bullock et al., 1995; Pons and van der Toorn, 1988; Gross, 1984; Grime et al., 1981) our study showed that "safe site" is highly species specific. It supports the idea that biotically generated spatial heterogeneity can promote species co-existence through the differentiation of species regeneration niches.

Acknowledgements

References

Bosy, J.L., Reader, R.J., 1995. Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. Funct. Ecol. 9, 635–639.

Bullock, J.M., Hill, C.B., Silvertown, J., Sutton, M., 1995. Gap colonisation as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. Oikos 72, 273–282.

Clarke, P.J., Davison, E.A., 2001. Experiments on the mechanism of tree and shrub establishment in temperate grassy woodlands. Austral Ecol. 26, 400–412.

Facelli, J.M., Facelli, E., 1993. Interactions after death: plant litter controls priority effects in successional plant community. Oecologia 95, 277–282.

Fowler, N.L., 1988. What is a safe site? neighbor, litter, germination date, and patch effects. Ecology 69, 947–961.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M., Shaw, S., 1981. A comparitive study of germination characteristics in a local flora. J. Ecol. 69, 1017–1059.

Gross, K.L., 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. J. Ecol. 72, 369–387.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.

Harper, J.L., 1967. A Darwinian approach to plant ecology. J. Ecol. 55, 247–270.

Haugland, E., Tawfig, M., 2001. Root and shoot competition between established grass species and newly sown seedlings during spring growth. Grass Forage Sci. 56, 193–199.

Jensen, K., Gutenkunst, K., 2003. Effects of litter on establishment of grassland species: the role of seed size and successional status. Basic Appl. Ecol. 4, 579–587.

Keizer, P.J., van Tooren, B.F., During, H.J., 1985. Effect of briophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. J. Ecol. 73, 493–504.

Kupferschmid, A.D., Stampfli, A., Newbery, D.M., 2000. Dispersal and microsite limitation in an abandoned grassland of the southern prealps. Folia Geobot. 35, 125–141.

McKendrick, S.L., 1996. The effects of fertilizer and root competition on seedlings of *Orchis morio* and *Dactylorhiza fuchsii* in chalk and clay soil. New Phytol. 134, 335–342.

Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

Pons, T.L., van der Torn, J., 1988. Establishment of *Plantago lanceolata* L. and *Plantago major* L. among grass. Oecology 75, 394–399.

Reader, R.J., 1991. Control of seedling emergence by ground cover: a potential mechanism involving seed predation. Can. J. Bot. 69, 2084–2087.

Ryser, P., 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. J. Veg. Sci. 4, 195–202.

Silvertown, J.W., 1981. Micro-spatial heterogeneity and seedling demography in species-rich grassland. New Phytol. 88, 117–128.

Špačková, I., Kotorová, I., Lepš, J., 1998. Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotropphic wet meadow. Folia Geobot. 33, 17–30.

Špačková, I., Lepš, J., 2004. Variability of seedling recruitment under dominant, moss, and litter removal over four years. Folia Geobot. 29, 41–55.

Taylor, K., Rowland, A.P., Jones, H.E., 2001. *Molinia caerulea* (L.) Moench. J. Ecol. 89, 126–144.

Ter Braak, C.F.J., Šmilauer, P., 2002. CANOCO reference manual and CanoDraw for user's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.

Xiong, S., Nillson, C., 1999. The effect of plant litter on vegetation: a meta-analysis. J. Ecol. 87, 984–994.

Van Tooren, B.F., 1990. Effects of bryophyte layer on the emergence of seedlings of chalk grassland species. Acta Oecol. 11, 15–163.

Von Ende, C.N., 2001. Repeated-measures analysis: Growth and other time dependent measures. In: Scheiner, S., Gurevitch, I. (Eds.), The Design and Analysis of Ecological Experiments. Oxford University Press, pp. 134–157.