

SENSITIVITY OF SEEDLING RECRUITMENT TO MOSS, LITTER AND DOMINANT REMOVAL IN AN OLIGOTROPHIC WET MEADOW

Iva Špačková¹⁾, Ivana Kotorová¹⁾ & Jan Lepš^{1,2)}

1) Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic

2) Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic; E-mail suspa@entu.cas.cz

Keywords: Analysis of deviance, Competition, Manipulative experiment, Regeneration niche, Redundancy analysis

Abstract: The effect of a dominant species, the litter layer, and the moss layer on seedlings and established vegetation was evaluated in two manipulative experiments in an oligotrophic wet meadow (*Molinion* with some features of *Violion caninae* according to phytosociological classification). In the first experiment, the dominant species (*Nardus stricta*), litter layer, and litter layer together with the moss layer were removed and the response of the established vegetation and seedlings were compared with a control. Results revealed that after one season there was no significant effect of the treatments on established vegetation, but seedling recruitment was significantly affected. The greatest increase of seedling recruitment for many species was observed in the plots with the moss layer removed. In the second experiment, seeds of *Selinum curvifolia* were sown into plots subjected to the following treatments: complete vegetation removal, mowing, mowing combined with removal of the moss layer, and an untreated control. The highest number of seedlings was found in plots with the vegetation removed, but the seedling recruitment was nearly as high in plots with the moss layer removed. Low numbers were found in mown plots and the lowest in the untreated control. The results show that seedling recruitment is more sensitive to competition than the established vegetation, at least over one season. This supports the idea of the importance of the regeneration niche for the maintenance of diversity in grassland communities.

INTRODUCTION

Competition is an important process shaping plant communities. According to TILMAN's (1993) hypothesis, the suppression of seedling recruitment is the dominant factor in the decrease of species diversity on productivity gradients. It is well known that seedling recruitment is usually more sensitive to the influence of competition than the established vegetation (e.g., RABOTNOV 1987, HILJER 1990, KŘENOVÁ & LEPŠ 1996); the differences are so striking that the term "regeneration niche" (GRUBB 1977) was developed to describe the specific requirements and sensitivities of the seedling stage. Vascular plant seedlings are not only influenced by other vascular plants. For example, during the establishment phase the moss layer plays an important role (PERTTULA 1941, KEIZER et al. 1985, VAN TOOREN 1988, 1990, DURING & VAN TOOREN 1990). In addition, the litter layer has been shown to influence seedling emergence and establishment (FACELLI & FACELLI 1993). GRIME (1979) considers persistent litter to be one of the features of the competitive strategy.

Oligotrophic species-rich meadows are among the rapidly vanishing communities of Central Europe. They are man-made communities that have been maintained by traditional management, i.e., mowing, for centuries (BAKKER 1989). Their species richness is often high; at a scale of one to several square meters they belong to the world's most diverse communities (KULL & ZOBEL 1991). Mechanisms that maintain their high species richness and prevent competitive exclusion are of fundamental research interest (KRAHULEC 1995). The importance of the regeneration niche (GRUBB 1977, HILLIER 1990), and species mobility (VAN DER MAAREL & SYKES 1993), are often taken into account to explain the phenomenon.

Recently, oligotrophic meadows have been considered to be uneconomical, and management is either intensified (fertilization), or the meadows are abandoned. Both these processes lead to an eventual loss of species diversity. The species-rich communities are replaced by communities dominated by a few strongly competitive species. One of the reasons for the decline in species diversity of abandoned meadows is probably inhibition of germination and early seedling mortality (e.g., KŘENOVÁ & LEPŠ 1996).

The aim of the present paper is to evaluate the importance of competition from a dominant species and from the moss layer, and the effects of litter on established plants and seedlings in an oligotrophic wet meadow. Despite numerous attempts to deduce competition from community patterns (KLIMEŠ 1995, WILSON 1995, REJMÁNEK & LEPŠ 1996), manipulative experiments seem to be the most reliable, although not the only, tool for demonstrating competition in natural communities (GOLDBERG 1995). Consequently, in our study, effects are demonstrated by a series of manipulative experiments, comprising the removal of a dominant species, removal of the moss layer, removal of the litter layer, and experimental sowing. Furthermore, we investigated the relationship between small-scale variability in plant composition and variation in seedling emergence. No attempt was made to determine the resources involved in the competition, and the effect on seedling counts might be through the trigger which makes a seed germinate. Consequently, as we are not able to assess proximate mechanisms, we use the term competition in a wide sense as any negative effect of one plant on another.

METHODS

Study site

This study was conducted in an oligotrophic species-rich meadow located 10 km south-east of České Budějovice, Czech Republic, 48°57' N, 14°36' E, 510 m a.s.l. Mean annual temperature is between 7 and 8 °C, and mean annual precipitation is 600–650 mm (SYROVÝ 1958). According to phytosociological classification the vegetation on the experimental plot belongs to the *Molinietum caeruleae* (*Molinion*) with some species indicating a transition to *Violion caninae* (KRAHULEC, pers. comm.). The community can be characterized by the following 2 × 2 m relevé (names of species are followed by estimates of percent cover); (vascular plant nomenclature follows ROTHMALER 1976, bryophyte nomenclature follows ZITTOVÁ et al. 1982):

Herb layer: cover 85%; Grasses: *Anthoxanthum odoratum* 2, *Agrostis canina* 6, *Briza media* 7, *Festuca rubra* 8, *Holcus lanatus* 5, *Molinia caerulea* 18, *Nardus stricta* 20, *Danthonia decumbens* 6. Other graminoids: *Carex hartmanii* 4, *C. leporina* 1, *C. panicea* 8, *C. umbrosa* 1, *Juncus effusus* 2, *Luzula multiflora* 1. Forbs: *Ajuga reptans* 3, *Cirsium palustre* 4, *Galium boreale* 1, *G. uliginosum* 2, *Lathyrus pratensis* 1, *Lysimachia vulgaris* 0.5, *Mentha arvensis* 0.1,

Myosotis palustris 3, *Pedicularis sylvatica* 0.2, *Plantago lanceolata* 0.1, *Potentilla erecta* 8, *Prunella vulgaris* 2, *Ranunculus auricomus* 0.5, *Succisa pratensis* 0.5.

Moss layer: 35%: *Aulacomnium palustre* 20, *Climacium dendroides* 2, *Hylocomium splendens* 10, *Rhytidiadelphus squarrosus* 5.

The average number of vascular plant species in 0.1×0.1 m plots was 6 ($n=400$), in 0.5×0.5 m plots 20 ($n=16$), and in 1×1 m plots 26 ($n=16$). Bryophyte cover varied widely and was estimated to average about 35%. Experimental plots (16 m^2 in total) contained more than 50 species in total (inclusive of 6 bryophyte species). The meadow was regularly mown until the early 1990s, but at present it is not subjected to any agricultural management. The amount of litter, estimated at the end of the growing period, was 155 g.m^{-2} . The standing crop was estimated in a neighbouring experiment (20 m apart) to be 400 g.m^{-2} .

Experiment 1

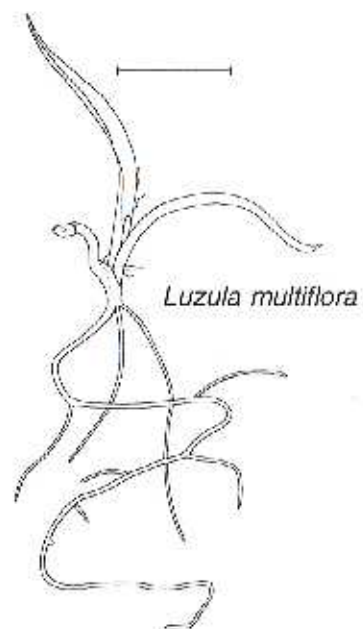
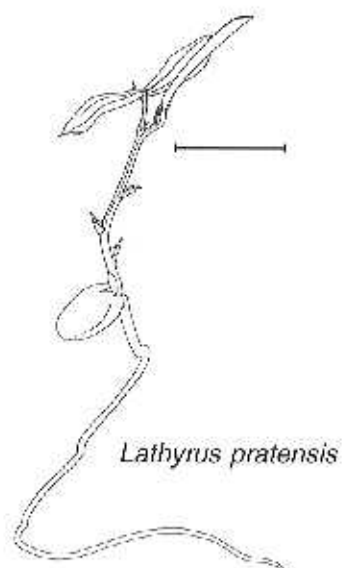
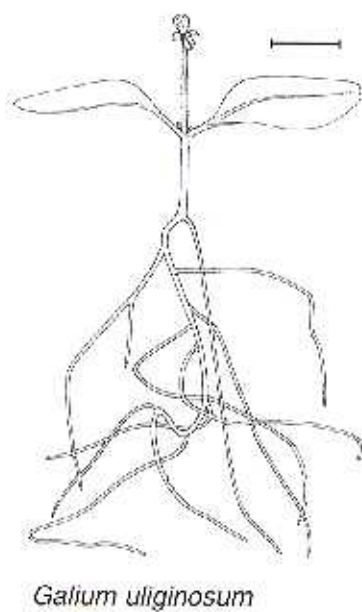
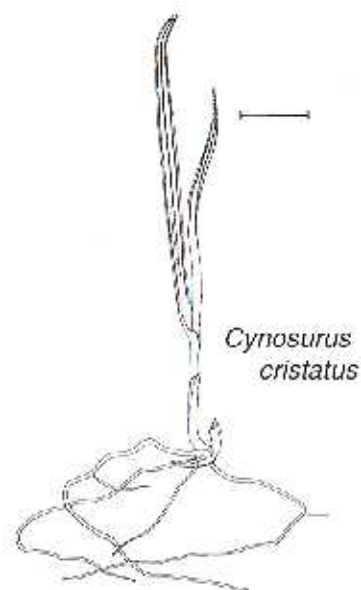
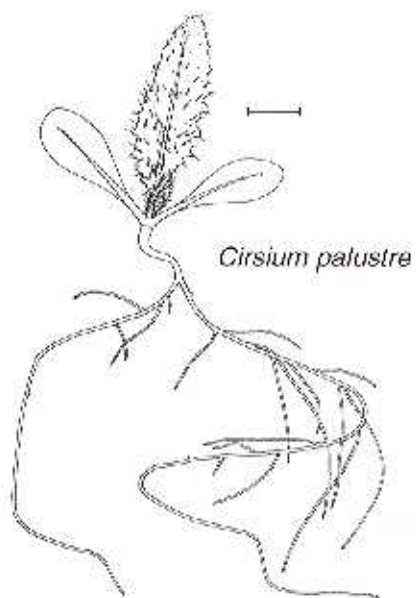
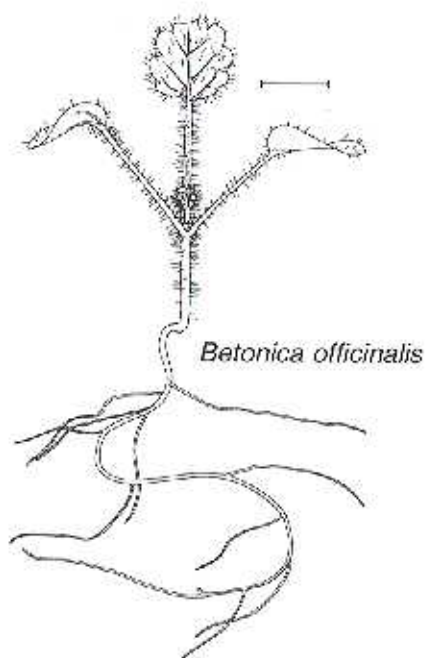
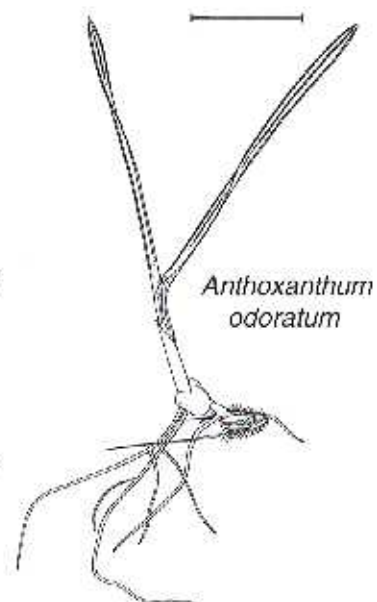
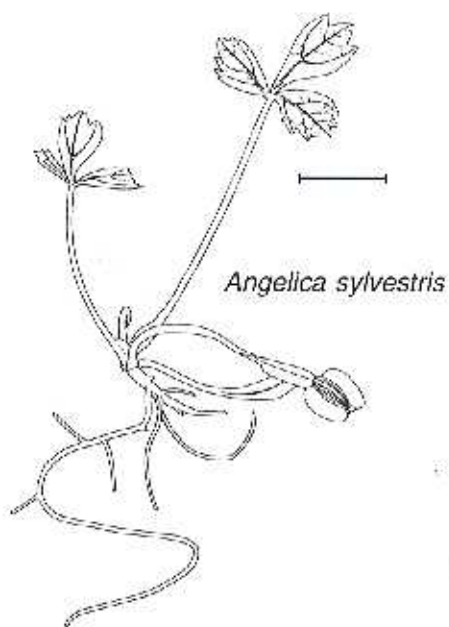
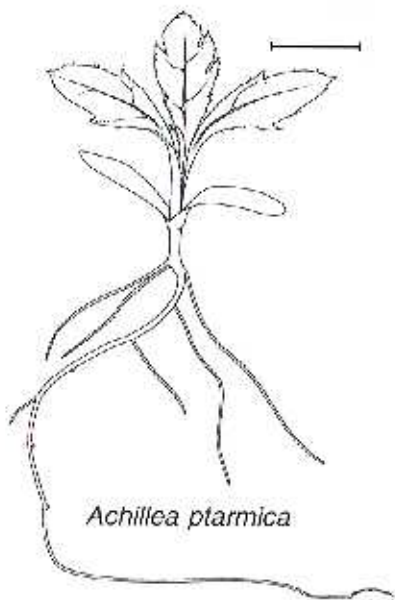
Experiment 1 was established in March 1994, shortly after snow melt, in four randomized complete blocks. Each block contained four treatments, i.e., (1) removal of litter, (2) removal of litter and bryophytes, (3) removal of the dominant species *Nardus stricta*, and a (4) control plot where the vegetation remained undisturbed. Each plot was 1×1 m square. The original cover of *Nardus stricta* was about 25%; its removal was very successful with nearly no regrowth. In the spring the removal causes only minor soil disturbance that is not visible in summer.

In each 1 m^2 plot adult plant and bryophyte cover was visually estimated in August 1994. At that time, a new square (0.5×0.5 m) was marked out in the center of each plot and divided into 25 0.1×0.1 m subplots. In each subplot adult plant cover and numbers of seedlings were recorded. Seedlings were determined according to CSAPODY (1968), LHOTSKÁ & KROPÁČ (1985), and by comparing with seedlings grown from seed (Fig. 1).

Experiment 2

Experiment 2 was carried out on separate plots. To test germination and recruitment of *Selinum carvifolia*, seeds were sown experimentally into $0.5 \text{ m} \times 0.5 \text{ m}$ plots subjected to four treatments in four randomized complete blocks. *Selinum carvifolia* (*Daucaceae*) is a perennial plant, relatively common on plots adjacent to the experimental plots, with seeds 3–4 mm long, weighting about 1 mg. Preliminary laboratory tests showed good germinability, with a slight negative effect of chilling (about 60% without chilling, 50% with chilling). In each block, the following treatments were used: (1) control, (2) mowing with a sickle, (3) mowing and removal of the moss layer, and (4) all above ground vegetation along with roots removed by hand, thereby producing a gap. Seeds were collected in October 1994 in the same locality; treatments were established and seeds sown on March 24, 1995; 1500 seeds were sown in each $0.5 \text{ m} \times 0.5 \text{ m}$ plot. An additional block containing all the treatments was left unsown, to check for possible germination from the seed bank. (Results showed that germination from the seed bank was negligible and need not be taken into account and therefore this block was not used.)

Seedling censuses of experimental plots were conducted on June 22, August 14, and October 8, 1995. The seedlings were counted in the central $0.25 \text{ m} \times 0.25 \text{ m}$ of each plot to avoid edge effects. The 0.25×0.25 m squares were divided by a grid into 25 $0.05 \text{ m} \times 0.05 \text{ m}$ subplots to facilitate counting and reveal within plot variability.



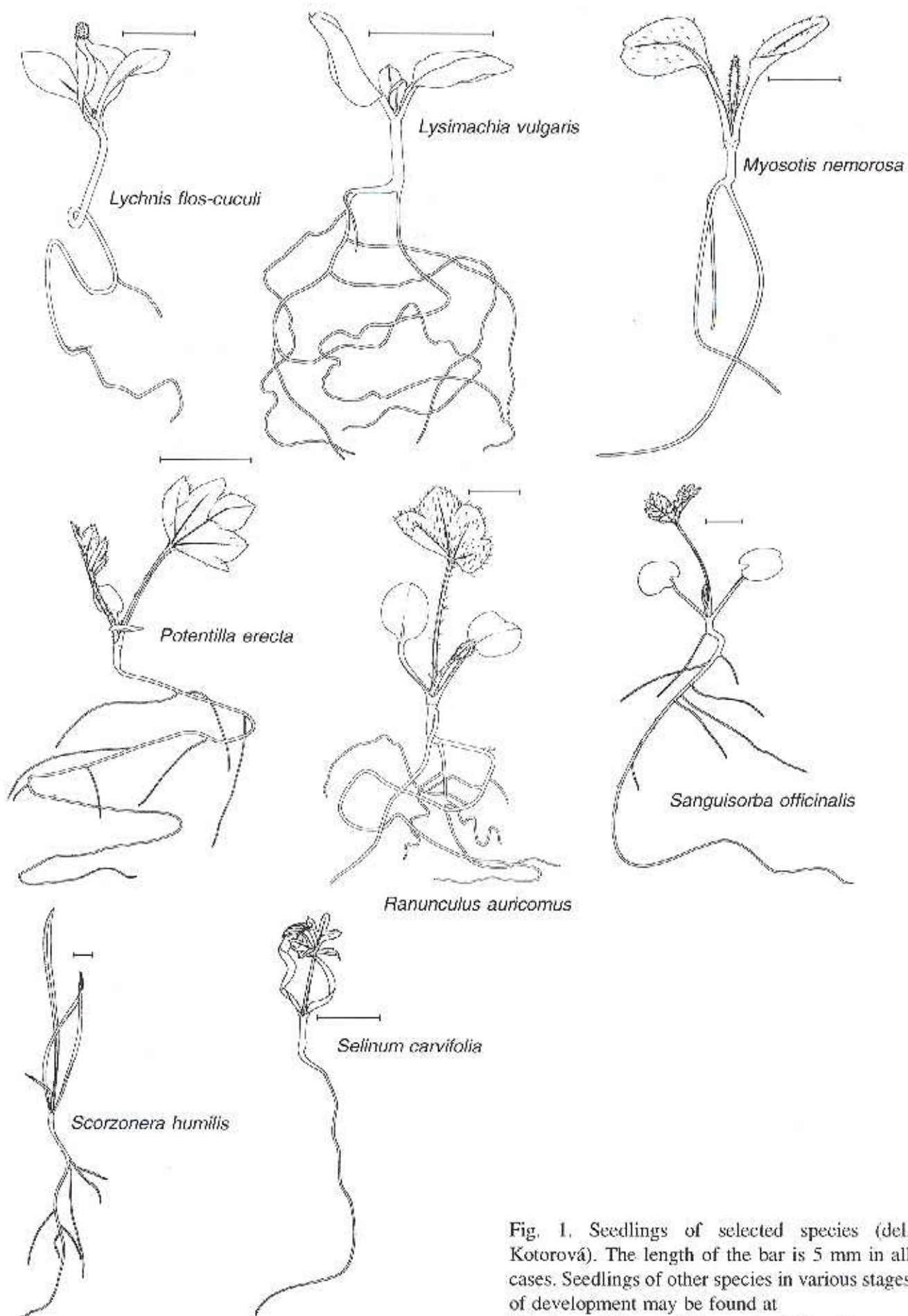


Fig. 1. Seedlings of selected species (del. Kotorová). The length of the bar is 5 mm in all cases. Seedlings of other species in various stages of development may be found at <http://www.bf.jcu.cz/tix/suspa/seedling.htm>

Table 1. Characteristics of the RDA analyses in experiment 1. ^a – Established vegetation or seedlings; ^b – First unconstrained axis; ^c – Variability in species data explained by the first axis (%); ^d – F-ratio on the first RDA axis; ^e – Significance of the first RDA axis estimated using the Monte Carlo permutation test.

	Quadrat size [m]	Species data ^a	Envir. variables	Covariables	Standard-ization	Eigenval. 1-st axis	Eigenval. 4-th axis ^b	1-st axis variab. ^c	F^d	P^e
1	1×1	Establ.	Treatment	Block	N	0.082	0.286	14.0	1.46	0.69
2	1×1	Establ.	Treatment	Block	Y	0.101	0.253	17.1	1.85	0.60
3	0.1×0.1	Establ.	Treatment	Block	N	0.011	0.300	1.2	4.64	0.80
4	0.1×0.1	Establ.	Treatment	Block	Y	0.080	0.247	0.9	3.08	0.86
5	0.1×0.1	Seedl.	Treatment	Block	N	0.046	0.331	4.7	19.29	<0.01
6	0.1×0.1	Seedl.	Treatment	Block	Y	0.021	0.187	2.2	8.73	0.03
7	0.5×0.5	Seedl.	Treatment	Block	N	0.287	0.229	34.5	4.75	0.01
8	0.5×0.5	Seedl.	Treatment	Block	Y	0.121	0.215	15.5	1.65	0.54
9	0.1×0.1	Seedl.	Establ.	Block, Treat.	N	0.031	0.306	3.4	12.44	0.64

Data analysis

To evaluate the response of both particular species and total numbers of seedlings (i.e., univariate variables, in both Experiment 1 and 2) the analysis of deviance was used (McCULLAGH & NELDER 1989). This method was developed in the framework of generalized linear models (McCULLAGH & NELDER 1989). S-plus 3.0 (STATISTICAL SCIENCES 1995) package was used for calculations. This analysis allows for the use of variables with other than the normal distribution. The number of seedlings in quadrats were modeled as variables with a Poisson distribution.

For the evaluation of total community response constrained ordinations were used. Their use is also important from a statistical point of view, i.e., if many (univariate) analyses are performed, the probability of type I error equals the predetermined significance level in each test performed. This means that the probability of at least one type I error occurring is high and could lead to statistical 'fishing' when significant results are selected and interpreted. The significant result of the overall test provided by multivariate methods gives reliable evidence that there is an entire community response. For this reason we first present the results of the multivariate analysis and if these are significant the differences in response of particular species will be tested by univariate analyses. Owing to the nature of explanatory variables (treatment as a categorical variable) and relatively low heterogeneity of the compared plots, we used redundancy analysis (RDA, JONGMAN et al. 1987), in the program CANOCO 3.10 (TER BRAAK 1990). CANODRAW and CANOPOST (ŠMILAUER 1992) were used for graphical output. We used both RDA with and without standardization by sample norm. RDA without standardization reflects both differences in the sum of importance values of all the species (e.g., the total number of seedlings) and species proportions, while RDA with standardization reflects relative proportions of species only. The appropriate covariables were used to reflect the design of the experiment. The species that were subjected to experimental manipulations (i.e., *Nardus* and bryophytes) were made passive in order not to influence ordination results. In all cases, the significance of results was tested by the Monte Carlo test for the first canonical axis, with permutations reflecting the experimental design. In particular, when the analysis was performed on the 0.1 m × 0.1 m subplots, the experiment has a hierarchical design and the effect of treatment must be tested against whole plot variability

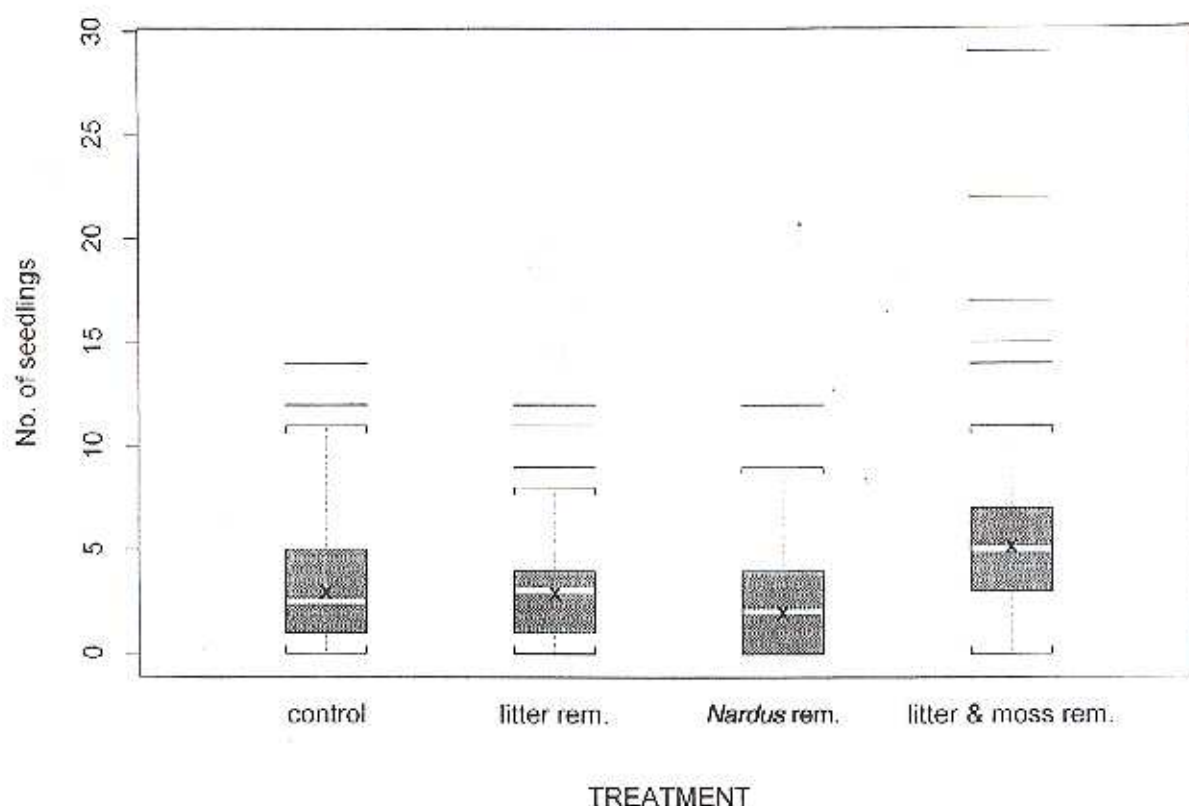


Fig. 2. Box and whisker plot of total numbers of seedlings in $0.1\text{ m} \times 0.1\text{ m}$ subplots of Experiment 1 for four treatments. The horizontal line in the interior of the box is located at the median of the data, \times is located at the mean. The height of the box is equal to interquartile distance (IQD). The whiskers (dotted lines) extend to extreme values of the data within a $1.5 \times \text{IQD}$ from appropriate quartile. Data points that fall outside the whiskers are indicated by horizontal lines.

among the $0.5\text{ m} \times 0.5\text{ m}$ plots rather than against that among the subplots. Consequently, all the $0.1\text{ m} \times 0.1\text{ m}$ subplots belonging to a single $0.5\text{ m} \times 0.5\text{ m}$ plot were kept together and randomly permuted as a block (permutations read from file option was used; a special program was designed to prepare the file). The particular multivariate analyses applied are numbered consecutively and summarized in Tab. 1. Subsequently they are referred to by their numbers.

In the majority of analyses, the categorical explaining variable with four categories was used, corresponding to three binary explaining variables. Consequently, only the first three axes were constrained (i.e., corresponding to variability explained by experimental treatment). To compare the explained and unexplained variability, we also report the eigenvalue corresponding to the fourth (i.e., the first unconstrained) axis. If more environmental variables were used (Analysis 9), hybrid analysis with only the first three axes constrained was performed. Consequently, in all the analyses, the fourth axis was unconstrained and the corresponding eigenvalue reflects the variability unexplained by the model.

In experiment 2 the data were subjected to two analyses. First, repeated measures ANOVA was applied to the log transformed numbers of seedlings. In this case, the plot factor in the analysis corresponds to the differences in numbers of seedlings and the plot \times time interaction to differences in rates of change. Although some new seedlings appeared after the first census, the number of seedling decreased and we could consider the interaction term as characteristic of differences in survival rate. The second analysis used analysis of deviance. We first tested the differences in number of seedlings on the first date (number of seedlings modeled as a

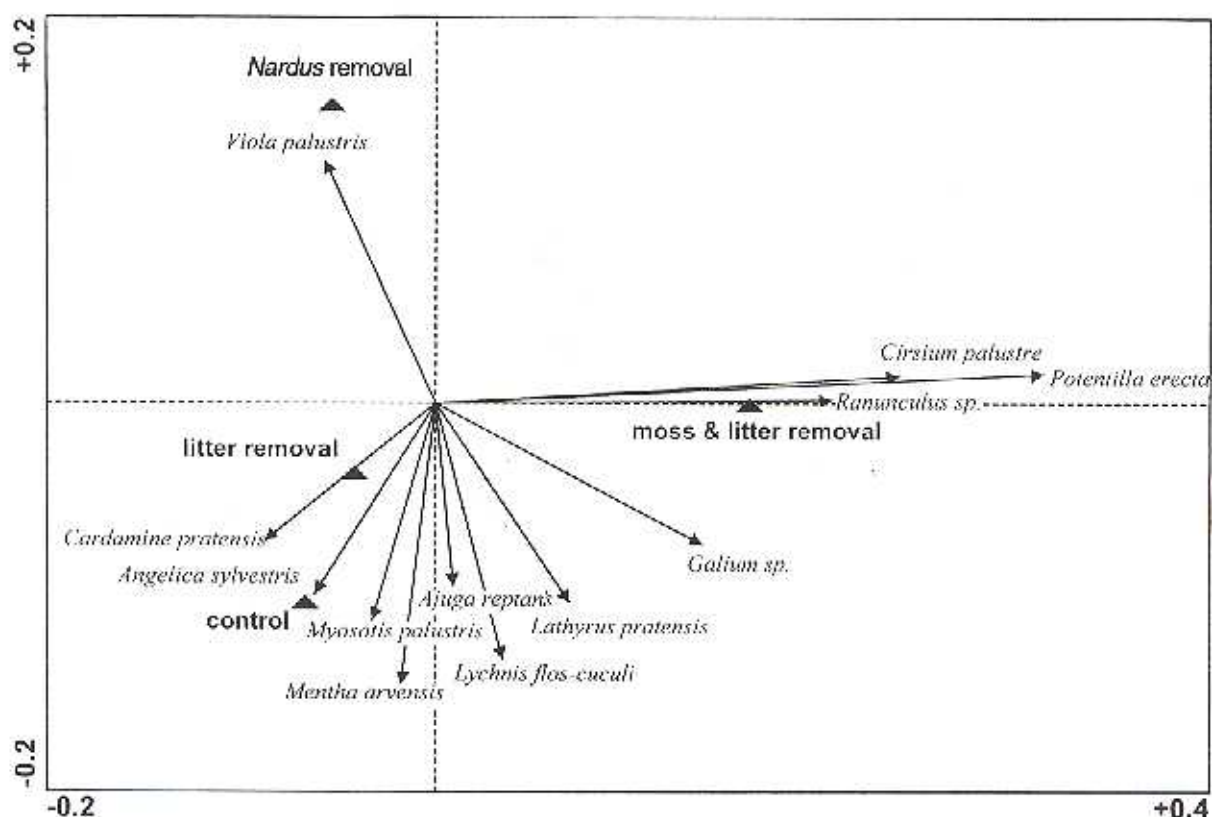


Fig. 3. Results of the RDA analysis of seedlings (Analysis 5) in experiment 1. The horizontal and vertical axes are the first and the second RDA axes respectively. The first axis is highly significant ($P < 0.01$).

Poisson variable) and then survival between dates modeled as a binomial variable (number of surviving seedlings from the number of all the seedlings in the plot).

RESULTS

Experiment 1

Response of the established plant community to experimental treatments

No differences in plant community composition were found with respect to treatment, regardless of the type of analysis used, in both the 1 m² and 0.01 m² plots (Analyses 1, 2, 3, and 4). This means that the established species either do not respond, or the response is too slow to be observed within the short time frame after manipulation.

Response of seedlings to experimental treatments

The total number of seedlings differs significantly among treatments (analysis of deviance, $P < 0.05$), with the highest numbers found in plots with the litter and moss layer removed (Fig. 2). Only removal of both litter and moss leads to a significant increase in the number of seedlings. In addition, the highly significant results of the unstandardized RDA, both for the whole plots (Analysis 5, Fig. 3) and for the 0.1 m × 0.1 m subplots (Analysis 7), show that there was a clear seedling response to experimental treatments. Again, the largest difference could be found between the combined moss and litter removal and the remaining treatments, which caused the differentiation on the first axis. Differences between the untreated control and plots with litter removal only were very small. Of the differences revealed by

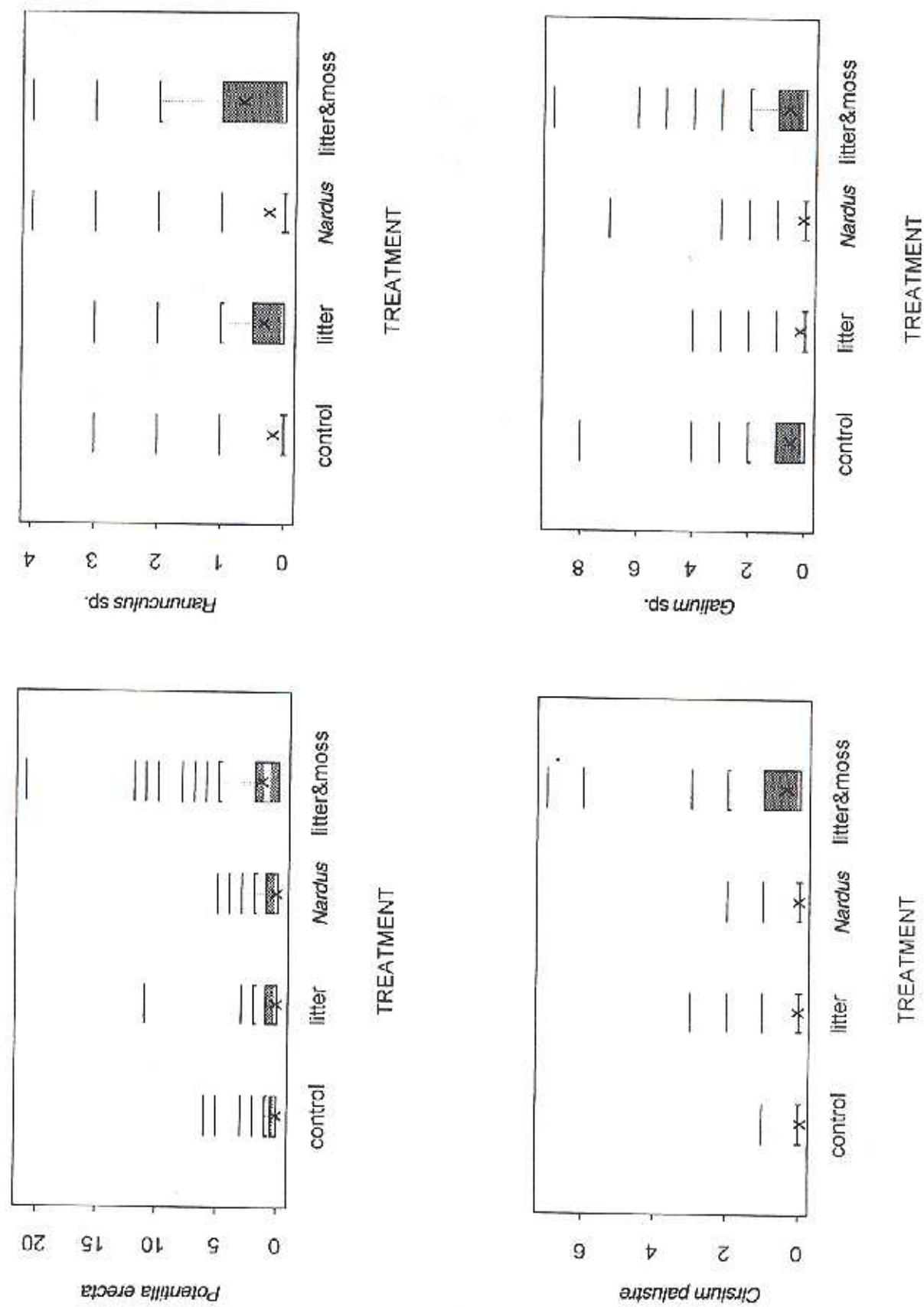


Fig. 4. Box and whisker plots of numbers of seedlings of the common species in 0.1 m x 0.1 m subplots of Experiment 1, for four treatments. For further details see Fig. 2.

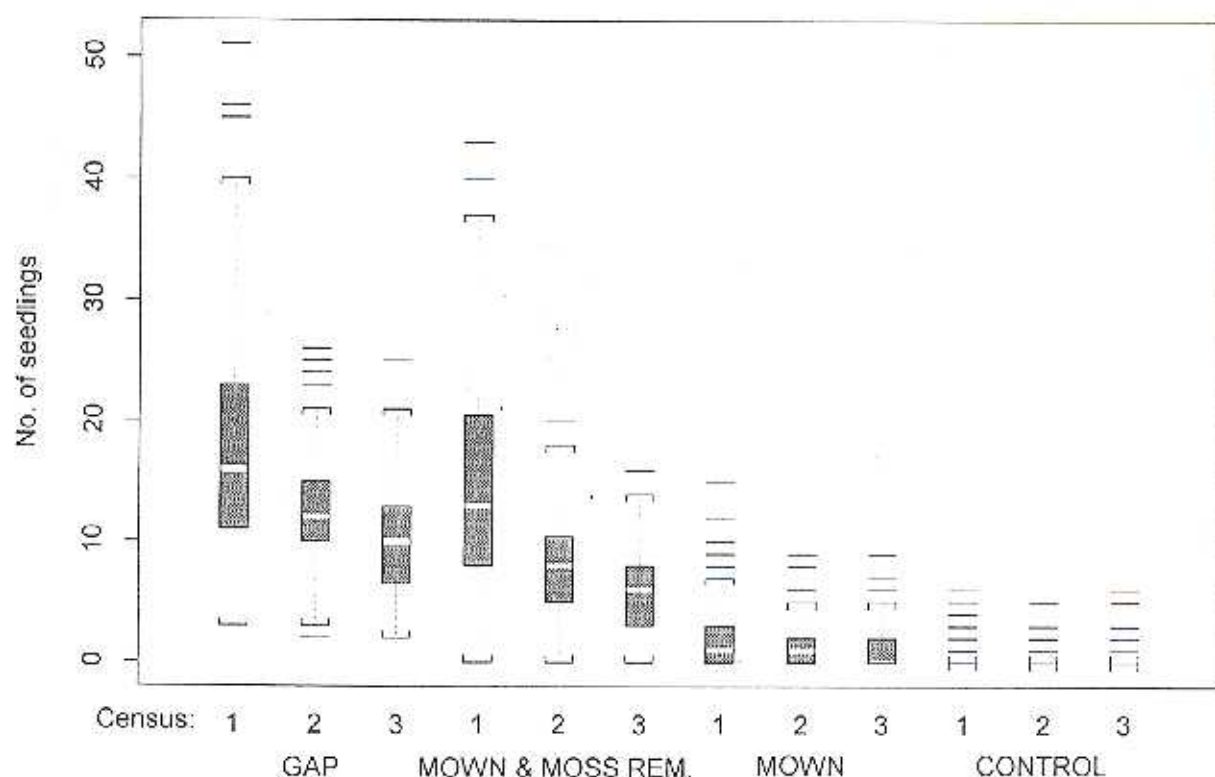


Fig. 5. Box and whisker plots of numbers of *Selinum* seedlings in 0.05 m \times 0.05 m plots in Experiment 2, for four treatments and changing with the serial number of census. Monitoring dates are: Census 1 – June 22; Census 2 – August 14; Census 3 – October 8. For the meaning of symbols see Fig. 2.

standardized RDA (Analyses 6 and 8), significant results were obtained for 0.1 m \times 0.1 m subplots only; moreover, differences are smaller than in the unstandardized analysis. Standardized analysis evaluates differences in the proportions of species. The significant result shows that species proportions were not constant among treatments. This reveals that there were differences, albeit small, among species in their response to particular treatments.

On a per species basis, the results of analyses of deviance correspond to multivariate analyses. The three species with abundant seedlings, i.e., *Cirsium palustre*, *Potentilla erecta* and *Ranunculus* sp., differed significantly among treatments (analysis of deviance, $P < 0.05$, Fig. 4), with the highest seedling abundance occurring in plots with the litter and moss layer removed. *Galium* (the vast majority of them belonging to *G. uliginosum*) were infrequent in the treatment with *Nardus* removal ($P < 0.05$). This corresponds to the fact that seedlings of this species were usually only observed in *Nardus* tussocks. *Myosotis nemorosa* was also infrequent in plots from which *Nardus* had been removed ($P < 0.05$). Differences were also significant for *Cardamine pratensis* (analysis of deviance, $P < 0.01$), with the highest seedling abundance found in untreated controls. Differences for other species were not significant.

Relationship of seedling abundance to established vegetation

The overall relationship of seedlings to established vegetation was analyzed by RDA (Analysis 9), with the species composition of established vegetation explaining variables and the block and treatment structure used as covariables. In this configuration the influence of both block and treatment are removed, and only the relationship of seedlings to local vegetation is analyzed. The results of the RDA were non-significant. However, due to so many predictors

(i.e., all the established species were predictors), the test is very weak. When forward selection of variables was used (i.e., the variables were selected when their explaining power was significant at $\alpha=0.05$), the following five species were selected: *Anthoxanthum odoratum*, *Cirsium palustre*, *Prunella vulgaris*, *Succisa pratensis*, and *Viola palustris*. The resulting RDA was highly significant ($P < 0.01$). However, it should be noted that the real significance (i.e., the real probability of type I error) is unknown because the best predictors were selected from a large pool of possible predictors. Further relationships were tested by analysis of deviance with block and treatment as covariables again. First, the selected species (*Anthoxanthum odoratum*, *Cirsium palustre*, *Prunella vulgaris*, *Succisa pratensis*, *Viola palustris*) were used as predictors for the total number of seedlings in a square. This analysis showed that regression coefficients for each of the species were positive. It seems that at least some of the species selected as predictors often grow in gaps within the plots, as the seedling do. On the other hand, the tussock grasses and sedges either separately or as total cover, do not show a significant influence on either total seedling number or on seedling abundance of particular species. However, for several species the best predictor for their seedlings was conspecific cover. This was true particularly for short species with relatively heavy seeds (according to GRIME et al. 1988), such as *Prunella vulgaris* (the positive relationship between established plant cover and number of seedlings was significant, $P < 0.0001$), *Viola palustris* ($P < 0.0001$), *Ajuga reptans* ($P < 0.0001$), *Galium* sp. ($P = 0.019$), and *Myosotis nemorosa* ($P < 0.001$). In contrast, the relationship was not significant for *Cirsium palustre*, a tall species with plumed seeds.

Experiment 2

The results of the sowing experiment support those of Experiment 1. The majority of *Selinum carvifolia* seedlings appeared before the first census was conducted with only a few appearing later. Although differences in seedling number between censuses principally reflect mortality, the appearance of new seedlings cannot be ruled out. Differences between numbers of seedlings in various treatments were highly significant ($P < 0.01$, for all analyses). The highest number of seedlings were found in plots with cut sod (gaps), but nearly as many seedlings were found in mown plots with the moss layer removed (Fig. 5). Mowing without moss layer removal increased the number of seedlings slightly in comparison to the control, but the number is considerably lower than that with the moss layer removed. This again shows the importance of moss in influencing seedling recruitment. Neither the time \times treatment in the repeated measures analysis, nor the direct testing for survival by analysis of deviance was significant ($P > 0.05$ in all cases). This shows that the ratios of surviving seedlings in various treatments remained fairly constant.

DISCUSSION

Our results reveal that the response of established plants and seedlings to particular treatments are very different. The lack of response in the established vegetation is probably due to the response time being longer than that of the seedlings. In any case, the results clearly show that competition by mosses is an important factor influencing seedling germination. Seedling regeneration has been shown to be an important factor affecting community composition in a number of studies ranging from experimental to theoretical (e.g. KEIZER et al. 1985, HILLIER 1990, TILMAN 1993, LAVOREL & CHESSON 1995).

In field experiments we must be aware of treatment side-effects. For example, the removal of a plant population inevitably leads to the two following confounding effects: (1) other nearby populations are disturbed and/or (2) remnant roots of the removed population remain in the soil and act as a potential source of nutrients. There is a trade-off between these two effects, i.e., the more thoroughly we attempt to remove all the roots, the greater the disturbance to other populations. However, decaying roots have been shown to be an unimportant nutrient addition (WILSON & TILMAN 1993), and therefore, the impact of these two confounding effects is acceptable.

In our experiment the response to moss removal was positive for several common species. A few species, however, showed a negative response to removal of the moss layer (e.g., *Myosotis nemorosa*, *Cardamine pratensis*). Two explanations for the latter effect are possible: (1) the moss layer may prevent their desiccation, or (2) it is an artifact of the manipulation, i.e., moss removal lead to seed removal, or harmed the seedlings of these species. Although the former possibility is more probable, our data do not provide unequivocal evidence to select between them. Provided that our results are not an artifact caused by moss removal this would support the regeneration niche differentiation hypothesis of species coexistence (e.g., GRUBB 1977, LAVOREL & CHESSON 1995).

This study was not designed to reveal the mechanisms of interactions between moss layer and seedlings. The mechanisms influencing germination most often considered are lack of light under the bryophyte mat, changed red/far-red ratio, mechanical prevention of seeds reaching the soil layer, and allelopathic effects (see VAN TOOREN 1990, DURING & VAN TOOREN 1990). Our data do not enable us to differentiate between these mechanisms. The lack of light may also be critical for seedling survival after germination. Experiment 1 does not enable us to separate the effect on germination from the effect on seedling survival. However, the results of Experiment 2 indicate that the effect on germination was probably larger than the effect on establishment.

Unlike in dry grassland (RUSCH & FERNÁNDEZ-PALACIOS 1995), we did not find a pronounced relationship between the established vegetation and seedling composition. However, as expected, the seedling density of barochoric species, particularly the short ones, was positively correlated with cover of conspecific adults.

Both protective (e.g. RYSER 1990) and inhibitive (KEIZER et al. 1985, RABOTNOV 1987: 115, VAN TOOREN 1990) roles of moss for seedling germination in grassland communities have been reported. It seems that the protective role is more important in dry grasslands (RYSER 1990) or in communities with temporal desiccation like dunes or desert crusts (DURING & VAN TOOREN 1990). Also, a moss mat was shown to provide protection against seed predation (VAN TOOREN 1988). The inhibitive role is probably more important in wet meadows (the reduction in the number of seedlings in our wet meadow is higher (by up to 30%) than that reported by VAN TOOREN 1990 for chalk grassland). Competitive effects upon the established vegetation is reported from *Sphagnum* dominated peat-bogs (MALMER et al. 1994, SVENSSON 1995), although peat bogs are not directly comparable to meadow conditions. The effect of the moss layer on the vascular plant changes from the seed to the seedling stage. RABOTNOV (1987: 115) and KEIZER et al. (1985) report positive effects of moss removal on germination and early survival. However, later survival was better where the moss was not removed. Our results show that the negative effect of the moss layer is significant to germination or early survival, whereas the effect on the survival of older seedlings is less clear.

In Central Europe, the abandonment of traditional management practices leads to a considerable decline in species diversity (e.g., KŘENOVÁ & LEPŠ 1996). The cause for this decline is both management intensification, including an increased use of fertilizers, and meadow abandonment where the strongly competitively species take over. In agreement with TILMAN (1993), our results show that seedling germination is a process very sensitive to various factors and limitations to germination may be partly responsible for the decline of species diversity.

Acknowledgments: This research was supported by the Grant Agency of the Czech Republic (grant GA ČR 204/96/0522) and Mattoni Award for Biodiversity and Conservation (I.K.). Thanks are due to František Krahulec for phytosociological advice and Jon Titus and Petr Pyšek for helpful comments and linguistic help. The paper benefited from comments of three anonymous reviewers.

REFERENCES

- BAKKER J.P. (1989): *Nature management by grazing and cutting*. Kluwer Acad. Publ., Dordrecht.
- CSAPODY V. (1968): *Keimlingsbestimmungsbuch der Dikotyledonen*. Akadémiai Kiadó, Budapest.
- DURING H.J. & VAN TOOREN B.F. (1990): Bryophyte interactions with other plants. *Bot. J. Linn. Soc.* 104: 79–98.
- FACELLI J.M. & FACELLI E. (1993): Interactions after death: plant litter controls priority effect in a successional plant community. *Oecologia* 95: 277–282.
- GOLDBERG D. (1995): Generating and testing predictions about community structure: which theory is relevant and can it be tested with observational data? *Folia Geobot. Phytotax.* 30: 511–519.
- GRIME J.P. (1979): *Plant strategies and vegetation processes*. Wiley & Sons, Chichester.
- GRIME J.P., HODGSON J.G. & HUNT R. (1988). *Comparative plant ecology*. Unwin Hyman, London.
- GRUBB P.J. (1977): The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107–145.
- HILLIER S.H. (1990): Gaps, seed banks and plant species diversity in calcareous grassland. In: HILLIER S.H., WALTON D.W.H. & WELLS D.A. (eds.), *Calcareous grasslands – Ecology and management*. Bluntingham Books, Bluntingham, Huntingdon, pp. 57–66.
- JONGMAN R.H., TER BRAAK C.J.F. & VAN TONGHEREN O.F.R. (1987): *Data analysis in community and landscape ecology*. Pudoc, Wageningen.
- KEIZER P.J., VAN TOOREN B.F. & DURING H.J. (1985): Effects of bryophytes on seedling emergence and establishment of short lived forbs in chalk grassland. *J. Ecol.* 73: 493–504.
- KLIMŠ L. (1995): Small-scale distribution of species richness in a grassland (Bílé Karpaty Mts., Czech Republic). *Folia Geobot. Phytotax.* 30: 499–510.
- KRAHULEC F. (1995): Species coexistence in temperate grasslands. *Folia Geobot. Phytotax.* 30: 113–117.
- KŘENOVÁ Z. & LEPŠ J. (1996): Regeneration of a *Gentiana pneumonanthe* population in an oligotrophic wet meadow. *J. Veg. Sci.* 7: 107–112.
- KULL K. & ZOBEL M. (1991): High species richness in an Estonian wooded meadow. *J. Veg. Sci.* 2: 711–714.
- LAVOREL S. & CHESSON P. (1995): How species with different regeneration niches coexist in patchy habitats with local disturbances. *Oikos* 74: 103–114.
- LHOTSKÁ M. & KROPÁČ Z. (1985): *Atlas semen, plodů a klíčnic rostlin (Atlas of seeds, fruits and seedlings)*. SPN, Praha.
- MALMER N., SVENSSON B. & WALLÉN B. (1994): Interaction between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobot. Phytotax.* 29: 483–496.
- MCCULLAGH P. & NELDER J.A. (1989): *Generalized linear models*. Ed. 2. Chapman and Hall, London.
- PERTTULA U. (1941): Untersuchungen über die generative und vegetative Vermehrung der Blütenpflanzen in den Wald-, Hainwiesen- und Hainfelsen-Vegetation. *Ann. Acad. Sci. Fenn. Ser. A.* 58: 1–388.
- RABOTNOV T.A. (1987): *Eksperimental'naya fitotsenologiya (Experimental phytocoenology)*. Publ. House of Moscow University, Moscow.
- REJMÁNEK M. & LEPŠ J. (1996): Interspecific associations can reveal competition: *Cirsium vulgare* and *Arctostaphylos patula* in a clearcut succession. *Oikos* 76: 161–168.

- ROTJEMALER W. (1976): *Exkursionsflora für die Gebiete der DDR und der BRD. Kritischer Band*. Volk und Wissen, Berlin.
- RUSCH G. & FERNÁNDEZ-PALACIOS J.M. (1995): The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. *J. Veg. Sci.* 6: 417–427.
- RYSER P. (1990): Influence of gaps and neighbouring plants on seedling establishment in limestone grassland. Experimental field studies in northern Switzerland. *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* 104: 1–71.
- STATISTICAL SCIENCES (1995): *S-Plus Guide to statistical and mathematical analysis, version 3.3*. StatSci, Seattle.
- SVENSSON B.M. (1995): Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. *Oikos* 74: 205–212.
- SYROVÝ S. (1958): *Atlas podnebí Československé republiky (Atlas of the climate of Czechoslovak Republic)*. Ústřední Geodet. Kartogr. Ústav, Praha.
- ŠMILAUER P. (1992): *CANODRAW users guide v. 3.0*. Microcomputer Power, Ithaca.
- TER BRAAK C.J.F. (1990): *CANOCO – a FORTRAN program for CANONICAL Community Ordination by [partial] [detrended] [canonical] correspondence analysis and redundancy analysis, version 3.10*. Microcomputer Power, Ithaca, NY.
- TILMAN D. (1993): Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179–2191.
- VAN DER MAAREL E. & SYKES M.T. (1993): Small scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *J. Veg. Sci.* 4: 179–188.
- VAN TOOREN B.F. (1988): The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. *Oikos* 53: 41–48.
- VAN TOOREN B.F. (1990): Effect of bryophyte layer on the emergence of seedlings of chalk grassland species. *Acta Oecol.* 11: 155–163.
- WILSON J.B. (1995): Testing for community structure: a Bayesian approach. *Folia Geobot. Phytotax.* 30: 461–469.
- WILSON S.D. & TILMAN D. (1993): Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74: 599–611.
- ZITTOVÁ J., VÁŇA J. & HERBEN T. (1982): Mechorosty/Bryophytes. In: NEUHAUSLOVÁ Z. & KOUBEK J. (eds.), *Seznam vyšších rostlin, mechorostů a lišejníků střední Evropy, užitých v bance geobotanických dat BÚ ČSAV (List of names of higher plants used in a database of geobotanical data of Institute of Botany, ČSAV)*, BÚ ČSAV, Průhonice, pp. 134–178.

Received 7 February 1997, revision received 12 May 1997, accepted 21 July 1997