# Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow

## Lepš, Jan

*Department of Botany, Faculty of Biological Sciences, University of South Bohemia, and Institute of Entomology,*
*Czech Academy of Sciences, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic;*
*Fax +4203845985; E-mail suspa@entu.cas.cz*

**Abstract.** In many species-rich hay meadows in Central Europe, the traditional extensive (low input, low output) management is no longer economical and meadows are either fertilized or abandoned. Both these practices lead to changes in species composition and usually to a loss in species diversity. The response of a species-rich meadow plant community to fertilization, mowing and removal of dominant species was studied in a manipulative factorial experiment over four years. Both species richness and seedling recruitment were positively influenced by mowing and to a lesser extent by removal of the dominant species, *Molinia caerulea,* and were negatively influenced by fertilization. Fertilization caused an immediate increase in community biomass. Response to removal of the dominant species was delayed by one season, continued over the whole period, and by the fourth year the biomass reached a similar value as in the plots with *Molinia* present. Changes in species composition were evaluated by RDA for repeated measurements. The best and only significant predictor of species response to fertilization was plant height. This shows that with increased nutrient availability, nutrient limitation weakens and competition for light becomes the decisive factor. Competition for light appears to be more asymmetric than competition for nutrients, and consequently, it is more likely to drive inferior species to extinction. This is, together with seedling recruitment limitations, the most important cause of a decrease in species richness under high nutrient levels.

**Keywords:** Coexistence; Mowing; Redundancy Analysis; Removal experiment; Species richness.

**Nomenclature:** Rothmaler (1976).

## Introduction

Species coexistence can be considered as a violation of the Competitive Exclusion Principle (Palmer 1994). This theory, often reformulated (see Palmer 1994) suggests that the number of coexisting populations should not be greater than the number of limiting resources. Plants compete for light, water and a few limiting nutrients. Despite this there are, for example, grassland communities with tens of species per m$^2$. How are species able to coexist and avoid competitive exclusion? How is

diversity maintained? These questions are central to an understanding of the population structure of ecological communities (e.g. Huston 1994; Palmer 1994).

Species diversity changes in predictable ways along many environmental gradients. In particular, the highest species diversity in grasslands is often found in the middle of soil fertility and disturbance intensity gradients (e.g. Grime 1979). In many cases an increase in fertility leads to a decrease in species richness (e.g. Mountford et al. 1993) and there are also many cases in which a cessation of disturbance leads to a decrease in species richness (Bakker 1989). Several models (e.g. Huston 1979; Tilman 1988) have been suggested to explain these phenomena. The positive effect of disturbance is usually explained by promoting non-equilibrium coexistence (preventing competitive exclusion - e.g. Huston 1979).

The effect of nutrients is more surprising - with more resources available some species are more likely to be driven to extinction than under a resource shortage. According to Grime (1979), the intensity of competition increases with soil fertility and decreases with stress. Tilman (1982, 1988), however, claimed that the intensity of competition is either independent of, or decreases with, resource availability. As was shown by Grace (1990), this contention is partly a consequence of differences in the definition of competition intensity (cf. Tilman 1987; Thompson 1987; Thompson & Grime 1988). It should be noted that declines in species richness at opposite ends of the gradients are also documented, i.e. species poor communities at extremely unproductive sites (Tilman & Pacala 1993, and references therein) and at high-disturbance sites (e.g. after overgrazing, e.g. Levin 1993). This phenomenon is not surprising and is sometimes trivial. However, why fewer species are able to coexist in more favourable conditions has no trivial explanation; increase in the size of individuals (Oksanen 1996) can only explain exclusion of species on small plots.

Many temperate zone meadows are anthropogenic communities, formed and maintained by mowing and/or grazing for many centuries. Many meadow types are extremely species-rich, for example Estonian dry

meadows have up to 63 species/m$^2$ (Kull & Zobel 1991). Oligotrophic wet meadows are also species-rich: in our study we regularly found more than 30 species/m$^2$ and more than 10 species/0.01 m$^2$. These meadows belong to the most endangered plant communities in Central Europe. The traditional extensive (low input, low output) management is no longer economical and the meadows are either fertilized or abandoned; this leads to changes in species composition and usually to a loss in species diversity. The expected cause of this loss is exclusion of competitively inferior species – many of which are of conservation interest, e.g., Křenová & Lepš (1996). Here, we investigate proximate causes of species disappearance after fertilization or cessation of mowing. Suggested mechanisms include both suppressed seedling recruitment and changes in competitive relationships among established plants (Tilman 1993; Křenová & Lepš 1996; Špačková et al. 1998).

Many generalizations about the observed patterns of community dependence on nutrient status and disturbance are based on observational data (Tilman & Pacala 1993). Experiments with nutrient additions have also been carried out (e.g. DiTommaso & Aarssen 1989 and references therein) in wet meadows (e.g. van Duren et al. 1997), sometimes with other treatments such as mowing or dominant removal (Gibson et al. 1993; Gurevitch & Unnasch 1989). Although experiments are needed in order to test mechanistic hypotheses (Goldberg 1995; Lepš 1995), experimental manipulations usually have side-effects and some manipulations are not feasible. Consequently, experimental evidence has to be combined with observational results. In Central Europe the biological characteristics of constituent species are often known. Comparisons of species' responses to experimental manipulations with their biological characteristics can shed light on the mechanisms of the response. Some hypotheses of species diversity stress the importance of the available species pool (Pärtel et al. 1996; Zobel 1997; Zobel & Liira 1997; Zobel et al. 1998). Through local manipulations we can guarantee that the species pool is identical and the plots differ in the manipulated factors only. It is, however, impossible to guarantee that all the species in the pool will be equally suited to various experimental conditions (e.g. to low and high nutrient conditions). Consequently, it is very difficult to experimentally test the 'species pool hypothesis' as formulated by Taylor et al. (1990, p. 247).

To test for the effects of stress, disturbance and competition on the structure of an oligotrophic wet meadow community I conducted a factorial experiment. Stress level was reduced by fertilization, disturbance (sensu Grime 1979) was performed by mowing and competition was manipulated by removal of the dominant species.

## Study site

The study site is a species-rich wet meadow 10 km southeast of České Budějovice, Czech Republic, 48°57'N, 14°36'E, at 510 m a.s.l. Mean annual temperature is 7.8 °C and mean annual precipitation is 620 mm (České Budějovice Meteorological Station). Traditional meadow management consisted of regular mowing, once or twice a year. This was stopped at the end of the 1980s and the meadow was not mown again until the start of the experiment in 1994. Phytosociologically, the vegetation belongs to the *Molinietum caeruleae* (*Molinion*) with some elements of the *Violion caninae*. The dominant species in a representative analysis of 100 m$^2$ in the meadow was *Molinia caerulea* (35% cover), followed by *Nardus stricta* (12%), *Festua rubra* (6%), *Potentilla erecta* (6%), *Carex panicea* (4%) and 70 other vascular and moss species.

## Methods

### Experimental design

Treatments were established in a 4-m$^2$ quadrat factorial design (n = 24) in three contiguous complete blocks in 1994. The treatments were fertilization, mowing and removal of the dominant species (*Molinia caerulea*). Fertilization included the application of 65 g/m$^2$ of commercial NPK fertilizer: 12% N (nitrate and ammonium), 19% P (as P$_2$O$_5$) and 19% K (as K$_2$O), 50 g/m$^2$ in autumn and 15 g/m$^2$ in spring (from 1997 the total dosage was applied in spring). Mowing was in late June or early July using a scythe and the biomass was removed. *Molinia caerulea* individuals were manually removed using a screwdriver in April 1995 with a minimum of soil disturbance. New individuals were removed annually.

### Sampling

Plots were sampled in the growing season (June, July) each year, starting in 1994. Note that initial sampling was conducted before the first experimental manipulation in order to have baseline data for each plot. The cover of all vascular species, the moss layer and litter was visually estimated in the central 1 m$^2$ of the 2 m × 2 m plot. From 1996, seedlings were counted in the central 0.5 m × 0.5 m using a continuous grid of 25 0.1 m × 0.1 m subplots. Starting in 1995, the biomass in the central 0.5 m × 0.5 m of the mown plots was clipped before mowing, sorted into species, oven-dried and weighed. Biomass determinations were not possible in unmown plots.

On the sunny days of March 10 and March 24, 1995, soil surface temperatures were measured.

## Data analysis

Data are in the form of repeated measurements; the same plot was sampled four times for cover and three times for biomass. For univariate characteristics (number of species, biomass) the corresponding repeated-measurements ANOVA-models were used (von Ende 1993). For species composition, I used Redundancy Analysis (RDA) in the CANOCO package (ter Braak 1990) with the Monte Carlo permutation test. Programs CanoDraw and CanoPost (Šmilauer 1992, ter Braak & Šmilauer 1998) were used for graphical presentations of ordination results (not shown here).

RDA, a method based on a linear species response, was used because species composition in the plots was rather homogeneous and the explanatory variables were categorical. Because *Molinia* cover was manipulated, it was passive in the analyses. By using various combinations of explanatory (environmental in CANOCO terminology) variables and covariables in RDA, together with the appropriate permutation scheme in the Monte Carlo test, we are able to construct tests analogous to the testing of significance of particular terms in ANOVA models (including repeated measures). See ter Braak & Šmilauer (1998) for details of permutation tests. In ANOVA, all the effects are tested simultaneously. In CANOCO, a separate analysis is used to test for each effect. When covariables are used in CANOCO, their effect is first eliminated and the residual variation is then related to the explanatory variables (comparable with covariates in ANCOVA). As the data form repeated observations that include the baseline (before treatment) measurements, the interaction of treatment and time is of greatest interest and corresponds to the effect of the experimental manipulation. When we test for the interaction, the plot identifiers (coded as many dummy variables) are used as covariables. In this way we subtract the average (over years) of each plot, and the changes in the particular plot only are analysed. Values of time were 0, 1, 2, 3 for the years 1994 - 1997, respectively. This corresponds to a model where the plots of various treatments do not differ in 1994 and the linear increase in difference is fitted by the analysis (this approach is analogous to single degree polynomial contrasts rather than ordinary effect testing in repeated measurement ANOVA).

Species scores on the constrained axis of analyses, where time*treatment was the only explanatory variable and the other factors were covariables, were considered characteristic of the species response to the treatment. Then the following biological characteristics of species were tested as possible predictors of this response:
1. Species height, taken as the middle of the range given in the local flora (Dostál 1989); 2. Presence of arbuscular mycorrhizae (AM), based on data from Grime et al. (1988) and from the ecological flora database (Fitter & Peat 1994); 3. Relative growth rate (RGR) of seedlings (based on Grime et al. 1988).

As I expected that species similar to *Molinia* would benefit most from *Molinia* removal, I also used a fourth (ordinal) variable, deviation of a species from *Molinia*, for predicting the effects of *Molinia* removal. Similarity 1 was assigned to graminoids taller than 50 cm, 2 to broad-leaved graminoids smaller than 50 cm, 3 to narrow-leaved graminoids smaller than 50 cm, and 4 to forbs. Spearman correlation was used for analysis of the relationship of this value with the RDA score of *Molinia* removal.

The numbers of seedlings in the 0.5 m × 0.5 m seedling plots were analysed for a single year, 1996.

Both non-standardized and standardized by sample norm RDA were used. Non-standardized analyses investigate if there is any effect of treatment on absolute values (e.g. seedling counts). Standardized analyses show the effect on species proportions: in the case of seedlings significant results of standardized analysis may be interpreted that there is a differential response of seedling recruitment between various species. The standardized and non-standardized analyses differ particularly when the sum of species values in a sample (or sample norm) fluctuates in a wide range.

The competitive response (CR) of the rest of the community (Goldberg 1990) was quantified by the ratio of community biomass without *Molinia* in the control plots, and community biomass in the corresponding *Molinia* removal plot in a given block, i.e.

$$CR = (Total - \textit{Molinia in control})/(Total - \textit{Molinia in removal}) \quad (1)$$

The value of the remainder of the community in a *Molinia* removal plot is very close to total biomass, as *Molinia* was removed. However, because the removal was never perfect the biomass of survivors have to be subtracted from the total. Values of CR close to 1 correspond to no effect of competition and the lower the value the more pronounced the effect of competition is. However, in all the interpretations we have to keep in mind that *Molinia* is not only manipulated, but it is also subject to competition from the rest of the community.

## Results

The *Molinia* removal was very successful. As each tiller was carefully and separately removed before the onset of the growing season, there were no visible gaps in the plots in the first season after removal, and in the next season no signs of disturbance caused by this removal were detectable.

## Total biomass

The following results refer only to the mown plots, for which biomass data were available. Changes in total biomass (Fig. 1) show that the community responded immediately to fertilization ($P<0.01$ in repeated measures ANOVA). However, there was no response to *Molinia* removal in the first season – biomass of the rest of the community was roughly the same in removal and control plots (total biomass was higher in control plots). This means that the remaining species did not increase their above-ground biomass when released from *Molinia* competition during the first season. However, biomass in the removal plots increased with time (significant effect of removal*time interaction, $P<0.05$), and by the third season it reached a level similar to control plot total biomass. This shows that the empty space was filled by the remaining species to a level similar to the biomass that the dominant species had attained before removal.

In attempting to quantify the competitive response, the fact that *Molinia* biomass was also influenced by the other experimental treatments should be kept in mind. In particular, relative representation of *Molinia* decreases in (mown) fertilized plots.
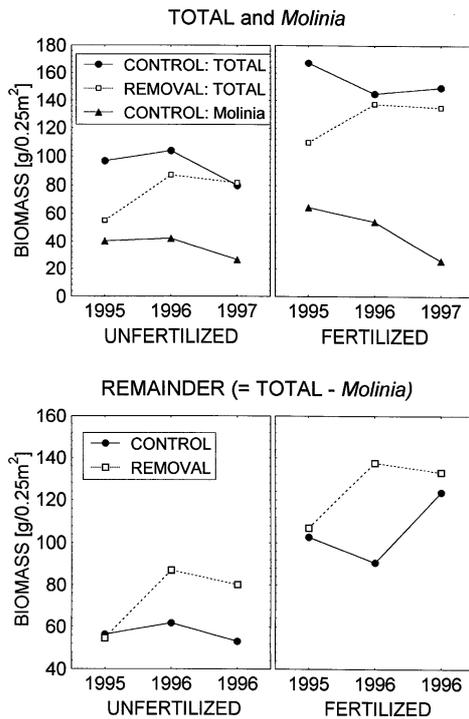


**Fig. 1.** Changes in biomass (g dry wt/0.25m² plot) in the mown plots only. Total biomass and biomass of *Molinia* in control plots (above), and biomass of the remainder (= species other than *Molinia*, below). The biomass of *Molinia* in removal plots was very low, so it is not displayed separately. The remainder is total – *Molinia* in both removal and control plots; in removal plots, it is nearly identical with the total.
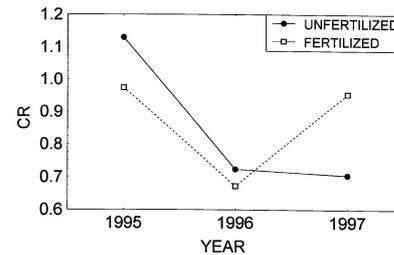


**Fig. 2.** Competitive response (see text) in nutrient-poor and fertilized plots.
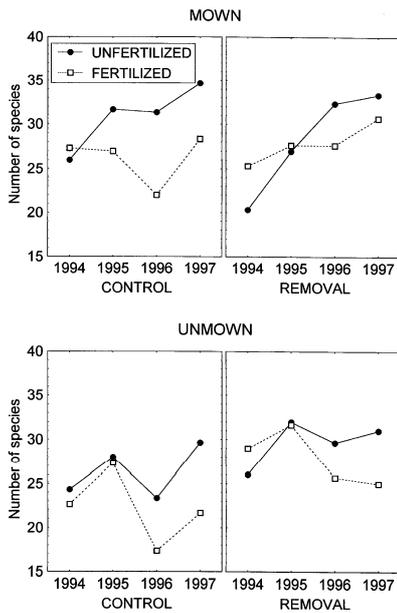
There was no difference in competitive response between fertilized and unfertilized plots in 1995 and 1996 (Fig. 2). The plots started to differ in 1997 when the competitive effect of *Molinia* in fertilized plots decreased; the difference is caused by a decrease in *Molinia* relative representation. Under fertilization, *Molinia* was not a superior competitor and decreased.

## Species richness

Data on species richness were analysed by univariate repeated measures ANOVA (Table 1). For all treatments the time-interaction term was significant (P< 0.01), with the highest sum of squares (i.e. highest variability accounted for) for fertilization. Mowing and removal had positive and fertilization negative effects on the development of species richness (Fig. 3). Highly significant (P <0.001) first order single degree polynomial contrasts for mowing and fertilization show that the differences caused by these treatments increased with time (Fig. 4). The effect of fertilization was strongest, followed by the effect of mowing. *Molinia*-removal increased the number of species in mown plots only.

**Table 1.** Table of repeated-measures ANOVA of species numbers in 1-m² plots. The effects are: M =mowing, F = fertilization, R = *Molinia* removal, Y =year (the repeated measures factor), * is for interaction. The significant effects ($P <0.05$) are printed in bold; $P = 0.000$ means $P <0.0005$.

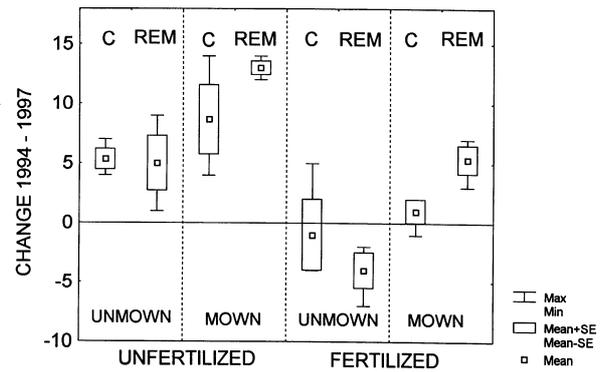| Factor | Effect | | Error | | | |
|---|---|---|---|---|---|---|
| | df | MS | df | MS | F | P |
| M | 1 | 75.26 | 16 | 28.63 | 2.629 | 0.124 |
| **F** | **1** | **184.26** | **16** | **28.63** | **6.437** | **0.022** |
| R | 1 | 94.01 | 16 | 28.63 | 3.284 | 0.089 |
| **Y** | **3** | **103.76** | **48** | **6.31** | **16.455** | **0.000** |
| M*F | 1 | 0.84 | 16 | 28.63 | 0.029 | 0.866 |
| **M*R** | **1** | **147.51** | **16** | **28.63** | **5.153** | **0.037** |
| F*R | 1 | 65.01 | 16 | 28.63 | 2.271 | 0.151 |
| **M*Y** | **3** | **65.95** | **48** | **6.31** | **10.460** | **0.000** |
| **F*Y** | **3** | **87.18** | **48** | **6.31** | **13.825** | **0.000** |
| **R*Y** | **3** | **31.93** | **48** | **6.31** | **5.063** | **0.004** |
| M*F*R | 1 | 6.51 | 16 | 28.63 | 0.227 | 0.640 |
| M*F*Y | 3 | 9.09 | 48 | 6.31 | 1.442 | 0.242 |
| M*R*Y | 3 | 10.20 | 48 | 6.31 | 1.618 | 0.197 |
| F*R*Y | 3 | 0.59 | 48 | 6.31 | 0.094 | 0.963 |
| M*F*R*Y | 3 | 2.32 | 48 | 6.31 | 0.367 | 0.777 |

**Fig. 3.** Mean number of species/1m² over time under various treatments.



**Fig. 4.** Change in number of species between 1994 and 1997. Mean value ± standard error (box) and maximum and minimum (whiskers) are shown. C = control, REM = removal plots.

## Species composition based on cover estimates

As the vegetation was closed, with a cover close to 100%, the total of cover values do not differ little between plots and consequently the results of standardized and non-standardized analyses are very similar (Table 2). RDA analyses (Table 2) show that all the treatments had significant effects on species composition. The most pronounced effect was fertilization (analyses C3 and C3st in Table 2), whereas the effect of *Molinia* removal was relatively small. *Lathyrus pratensis, Festuca rubra* and *F. pratensis* were the species most promoted by fertilization and mosses, *Anthoxanthum odoratum* and sedges were among the most suppressed. *Prunella vulgaris* performed best in mown unfertilized plots, whereas *Angelica sylvestris* increased most in unmown fertilized plots.

As expected, Spearman correlation between species deviating from *Molinia* and response to *Molinia* removal was negative, i.e. species similar to *Molinia* (*Holcus lanatus* and *Festuca pratensis*) increased the most after *Molinia* removal, but the relationship was not significant (Spearman correlation $= -0.150$, $P > 0.10$, $n = 48$). When compared by a one-tailed $t$-test, the broad-leaved graminoids taller than 50 cm (i.e. species most similar to *Molinia*) increased in cover more than the other species ($t = 1.77$, df $= 46$, $P = 0.041$). The use of a one-tailed test is justified, because the most similar species were expected *a priori* to fill up the empty space after *Molinia* removal. However, the relationship is not very strong. Besides broad-leaved tall graminoids, *Prunella vulgaris* and *Myosotis nemorosa* completely dissimilar to *Molinia*, also increased.

**Table 2.** Results of the RDA analyses of cover estimates (data centered by species) in 1m × 1m plots. Standardization (St) means standardization by sample norm (Y = yes, N = no). Expl. var. = Explanatory variables; Covar. = Covariables; % ax 1 = % species variability explained by axis 1 – measure of the explanatory power of the explanatory variables; $r$ ax 1 = species-environment correlation on axis 1. $F = F$-ratio statistics for the test on the trace. $P$ = corresponding probability value obtained by the Monte Carlo permutation test (499 permutations, i.e. Type I error probability in testing the hypothesis that the effect of all the explanatory variables is zero). Yr = serial year number; M = mowing; F = fertilization; R = *Molinia* removal; PlotID = identifier of each plot; * = interaction.

| Anal. | Expl. var. | Covar. | St | % ax 1 | $r$ ax 1 | $F$ | $P$ |
|---|---|---|---|---|---|---|---|
| C1 | Yr, Yr*M, Yr*F, Yr*R | PlotID | N | 16.0 | 0.862 | 5.38 | 0.002 |
| C1st | Yr, Yr*M, Yr*F, Yr*R | PlotID | Y | 17.9 | 0.874 | 5.93 | 0.002 |
| C2 | Yr*M, Yr*F, Yr*R | Yr, PlotID | N | 7.0 | 0.834 | 2.76 | 0.002 |
| C2st | Yr*M, Yr*F, Yr*R | Yr, PlotID | Y | 7.1 | 0.869 | 2.71 | 0.002 |
| C3 | Yr*F | Yr,Yr*M, Yr*R, PlotID | N | 6.1 | 0.824 | 4.40 | 0.002 |
| C3st | Yr*F | r,Yr*M, Yr*R, PlotID | Y | 6.1 | 0.858 | 4.45 | 0.002 |
| C4 | Yr*M | Yr,Yr*F, Yr*R, PlotID | N | 3.5 | 0.683 | 2.50 | 0.002 |
| C4st | Yr*M | Yr,Yr*F, Yr*R, PlotID | Y | 3.5 | 0.679 | 2.44 | 0.002 |
| C5 | Yr*R | Yr,Yr*M, Yr*F, PlotID | N | 2.0 | 0.458 | 1.37 | 0.040 |
| C5st | Yr*R | Yr,Yr*M, Yr*F, PlotID | Y | 1.8 | 0.595 | 1.23 | 0.048 |

Null hypotheses of the tests for particular analyses are similar for corresponding non-standardized and standardized analyses, related to cover, and relative cover respectively:

C1: there are no directional changes in species composition, neither common to all the treatments, nor specific for particular treatments (corresponds to the test of all within-subject effects in repeated measures ANOVA).

C2: The temporal trend in species composition is independent of the treatments.

C3 (C4, C5): Fertilization (mowing, removal, respectively) has no effect on the temporal changes in species composition (corresponds to the tests of particular terms in repeated measures ANOVA).
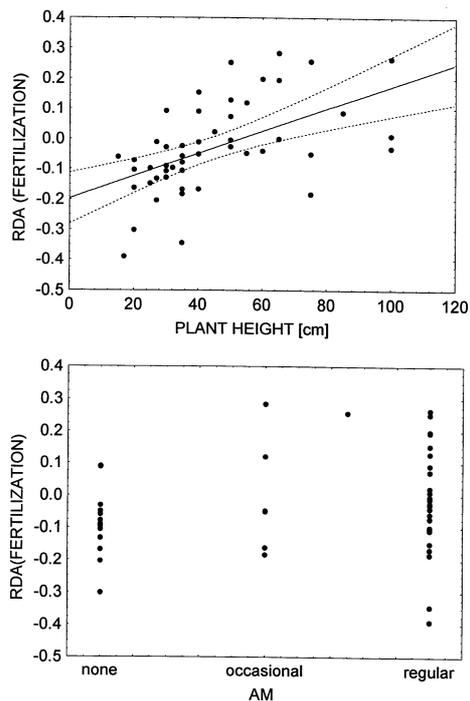
**Fig.5 . a.** Regression of species response to fertilization expressed as RDA score on plant height (from Dostál 1989); equation: $RDA(FERT) = -0.1965 + 0.0037 \cdot HEIGHT$ (cm), $r=0.542, P<0.01$ . **b.** Relationship between presence of mycorrhiza and species response to fertilization; ANOVA, $P>0.10$. Mycorrhiza categories: (1) none; (2) occasional: roots either mycorrhizal or non-mycorrhizal; (3) regular: roots always mycorrhizal (data from Grime et al. 1988 and Fitter & Peat 1994).

It seems that these species were suppressed by the persistent litter of *Molinia*. None of the other biological characteristics of the species used were able to predict the reaction to mowing and *Molinia* removal. Response to fertilization is best predicted by plant height: taller plants gain from fertilization, whereas shorter plants are suppressed. There is no difference in response to fertilization between species that differ in the presence of mycorrhiza (Fig. 5).

### Species composition based on species biomass

The analysis of species composition based on plant biomass in the mown plots only produced similar results in terms of importance of experimental treatments (Table 3). Again, the differences between standardized and non-standardized analyses are small. As the number of plots was low and the number of species high, while baseline data are missing, the power of the test is low and some results are not significant (removal). Nevertheless, some species increased their biomass after *Molinia* removal. This can be clearly seen for species
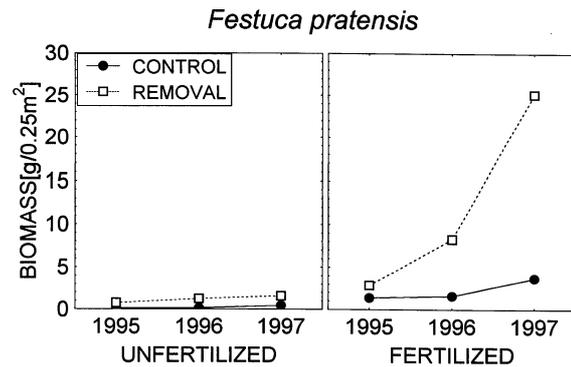


**Fig. 6.** Response of *Festuca pratensis* biomass to *Molinia* removal in mown plots.

similar to *Molinia*, for example, *Festuca pratensis* which has about the same height and is also a broad-leaved grass (Fig. 6). For this species, all terms of great interest in repeated measures ANOVA (time * removal, time * fertilization, time * fertilization * removal) were significant ($P<0.05$). *Festuca pratensis* increased with fertilization and also with *Molinia* removal and the combined effect of fertilization and removal was more than additive (Fig. 6). However, because *Festuca pratensis* was selected *a posteriori* from a large species pool, the results of statistical testing have to be considered with caution.

### Seedling recruitment

Seedling recruitment was evaluated on the basis of seedling counts in the $0.25m^2$ plots in 1996. For the total number of seedlings all the main effects were significant ($P<0.05$), with mowing and *Molinia* removal having positive and fertilization negative effects on the total numbers of seedlings (Fig. 7, Table 4). Similarly, fertilization had negative and *Molinia* removal positive effects on the number of seedling species. This expected result is based simply on the increase in number of seedlings. However, there is a strong removal * mowing interaction effect on the number of seedling species: *Molinia* removal had almost no effect in mown plots, but caused a pronounced increase in the number of species in unmown plots (a similar, but nonsignificant interaction is also found for seedling number). This is probably caused by persistent litter of *Molinia*, its effect is very pronounced in unmown plots; but in mown plots the amount of litter is small.

The response of seedling species composition evaluated by RDA was also significant (Table 5), with more pronounced treatment effects found in non-standardized analyses. Note that only one out of eight analyses is displayed, analysis S1 in Table 5, showing the general pattern of response to all the three treatments projected into a two-dimensional plain. The general pattern is

**Table 3.** RDA analyses of biomass data in 0.5m × 0.5m plots. Only mown plots were analysed. Data are centered by species. Standardization (St) means standardization by sample norm (Y =yes, N =no). Expl. var. =explanatory variables; C ovar. =covaria bles. % ax 1 =percent of species variability explained by the first axis, i.e. a measure of the explanatory power of explanatory variables. $r$ ax 1 =species-environment correlation on the first axis. $F = F$-ratio statistics for the overall test. $P$ =corresponding probability value obtained by the Monte Carlo permutation test, 499 random permutations (i.e.Type I error probability in testing the hypothesis that the effect of all the explanatory variables is zero). F =fertilization, R = *Molinia* removal, PlotID =identifier of each plot. * =interaction between terms. The corresponding null hypotheses are analogous to those in C2 (B1), C3 (B2) and C5 (B3), again applied either to biomass or standardized biomass. Significant analyses ($P$ <0.05) are in bold.

| Anal. | Expl. var | Covar. | St | % ax 1 | $r$ ax 1 | $F$ | $P$ |
|---|---|---|---|---|---|---|---|
| **B1** | **Yr*R** | **Yr, PlotID** | **N** | **14.8** | **0.727** | **2.35** | **0.012** |
| | **Yr*F** | | | | | | |
| **B1st** | **Yr*R** | **Yr, PlotID** | **Y** | **13.0** | **0.759** | **1.94** | **0.026** |
| | **Yr*F** | | | | | | |
| **B2** | **Yr*F** | **Yr, Yr*R, PlotID** | **N** | **15.1** | **0.719** | **3.74** | **0.002** |
| **B2st** | **Yr*F** | **Yr, Yr*R, PlotID** | **Y** | **11.6** | **0.759** | **2.75** | **0.006** |
| B3 | Yr*R | Yr, Yr*F, PlotID | N | 4.4 | 0.507 | 0.971 | 0.504 |
| B3st | Yr*R | Yr, Yr*F, PlotID | Y | 5.1 | 0.572 | 1.133 | 0.480 |

**Table 4.** ANOVA of the total numbers of seedlings and numbers of seedling species in 0.5 m × 0.5 m quadrats. Effects are: M =mowing, F =fertilization, R = *Molinia* removal, * = interaction. Significant effects ($P$ <0.05) in bold. $P$ =0.000 means $P$ <0.0005.
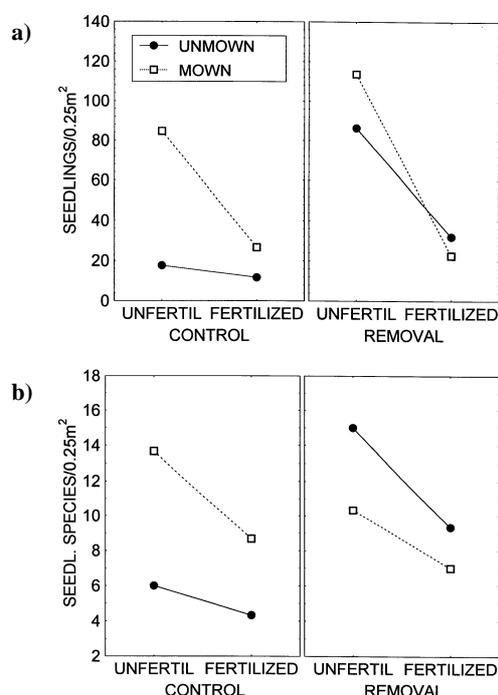
Number of seedlings

| Source | df | MS | $F$ | $P$ |
|---|---|---|---|---|
| **M** | **1** | **3750.00** | **4.551** | **0.049** |
| **F** | **1** | **16432.67** | **19.942** | **0.000** |
| **R** | **1** | **4873.50** | **5.914** | **0.027** |
| M*F | 1 | 2948.17 | 3.578 | 0.077 |
| M*R | 1 | 1536.00 | 1.864 | 0.191 |
| F*R | 1 | 2480.67 | 3.010 | 0.102 |
| M*F*R | 1 | 88.17 | 0.107 | 0.748 |
| Error | 16 | 824.04 | | |

Number of seedling species

| Source | df | MS | $F$ | $P$ |
|---|---|---|---|---|
| M | 1 | 9.38 | 1.679 | 0.213 |
| **F** | **1** | **92.04** | **16.485** | **0.001** |
| **R** | **1** | **30.38** | **5.440** | **0.033** |
| M*F | 1 | 0.38 | 0.067 | 0.799 |
| **M*R** | **1** | **135.38** | **24.246** | **0.000** |
| F*R | 1 | 2.04 | 0.366 | 0.554 |
| M*F*R | 1 | 12.04 | 2.157 | 0.161 |
| Error | 16 | 5.58 | | |

affected mainly by the most pronounced response, i.e. by the response to fertilization.

The response of a species to a certain treatment is best described by its score on the constrained axis of partial analysis, with single treatment used as explanatory variable and others as covariables (analyses S2, S3 and S4, both standardized and non-standardized). The response to fertilization was striking, with nearly all the species being influenced negatively (including those showing an increase as adults, such as *Lathyrus pratensis*). It seems that seedlings of all species were similarly suppressed by fertilization, so that the result of the standardized analysis is not significant. Seedling numbers for the majority of species were positively influenced by mowing (*Potentilla erecta, Selinum carvifolia, Lathyrus pratensis*), but some species are negatively influenced (*Galium uliginosum, Sanguisorba officinalis, Betonica officinalis*). However, the negative effect is not pronounced. The significant results of RDA standardized by sample norm reveal that the species respond differently to mowing. In comparison with fertilization, the effect of mowing was less pronounced, but more discriminating among species. *Molinia* removal had a positive effect on the majority of species (e.g. *Potentilla erecta, Betonica officinalis*), but a slightly negative effect on *Cirsium palustre*. The number of seedlings in the quadrats was positively correlated with moss layer cover ($r=0.77$, $n=24$, $P<0.01$) and negatively correlated with estimated litter cover (Fig. 8). However, neither litter nor moss layers were manipulated directly and they were both influenced by the experimental



**Fig.7. a.** Total numbers of seedlings/0.25m$^2$ under various treatments in 1996. All main effects are significant (Table 4). **b.** Numbers of seedling species/0.25m$^2$ under various treatments in 1996. Effects of fertilization, removal, and removal* mowing are significant (Table 4).

**Table 5.** RDA analyses of seedling counts in 0.5m × 0.5m plots. Data are centered by species and either no standardization by samples was applied or data were standardized by sample norm (Y =yes, N =no). Expl. var. =explanatory variables; Covar. =covariables. % ax 1 =percent of species variability explained by the first axis, i.e. a measure of the explanatory power of explanatory variables. *r* ax 1 =species-environment correlation on the first axis. *F*-r = *F*-ratio statistics for the overall test. *P* =corresponding probability value obtained by the Monte Carlo permutation test, 499 random permutations (i.e., Type I error probability in testing the hypothesis that the effect of the explanatory variables is zero). M =mowing, F =fertilization, R = *Molinia* removal, Bl =block identifier. * =interaction between terms. The tests correspond to the test of the overall model (S1) and to tests of particular terms (S2 - S4) in three-way ANOVA without interactions. The non-standardized analyses test for differences in absolute seedling numbers, the standardized ones in relative species representation. Significant analyses (*P* <0.05) are in bold.

| Anal. | Expl. var | Covar. | St | % ax 1 | *r* ax 1 | *F*-r | *P* |
|-------|-----------|--------|----|--------|----------|-------|-----|
| **S1** | **F, R, M** | **Bl** | **N** | **30.0** | **0.800** | **3.242** | **0.002** |
| S1st | F, R, M | Bl | Y | 12.8 | 0.814 | 1.445 | 0.084 |
| **S2** | **F** | **Bl, M, R** | **N** | **19.0** | **0.680** | **4.210** | **0.002** |
| S2st | F | Bl, M, R | Y | 5.7 | 0.523 | 1.081 | 0.384 |
| S3 | R | Bl, F,M | N | 7.0 | 0.404 | 1.504 | 0.156 |
| S3st | R | Bl, F, M | Y | 4.5 | 0.535 | 0.935 | 0.454 |
| **S4** | **M** | **Bl, F, R** | **N** | **12.9** | **0.536** | **2.962** | **0.014** |
| **S4st** | **M** | **Bl, F, R** | **Y** | **10.1** | **0.736** | **2.248** | **0.030** |

manipulations. The moss layer was very low in fertilized plots (both mown and unmown) and increased with mowing, in unfertilized plots (both effects and interaction significant with *P*<0.01) litter decreased with mowing and with *Molinia* removal (*P*<0.01).

Mowing resulted in an increase of the soil surface temperature on both sunny spring days, March 10 from 1.6 °C to 2.2 °C, March 24 from 4.9 °C to 7.2 °C, fertilization and removal had no major effect.
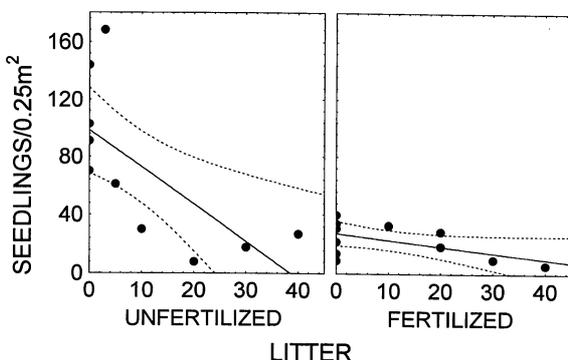


**Fig. 8.** Relationship between numbers of seedlings and estimated litter cover (%) in 1996, separately for unfertilized and fertilized plots. In the general linear model, both the main effects (litter, fertilization) and their interactions are highly significant (*P* <0.01).

## Discussion

In field experiments we must be aware of treatment side-effects. For example, the removal of a plant population inevitably leads to two confounding effects: (1) other nearby populations and soil (including organisms therein) 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, as most of the roots were removed and in view of the relatively slow mineralization rate, we can consider the nutrient addition due to release from decomposing roots as unimportant in our experiment. Similarly, Wilson & Tilman (1993) in their study based on a removal experiment concluded that "This suggests that very little of increase in transplant growth associated with dead neighbors was caused by neighbor root decomposition and nutrient release", even though they killed the neighbours with herbicide and did not remove them. We cannot completely avoid disturbing the other populations. Nevertheless, removal was done very carefully, tiller by tiller, and before the start of the growing season, so that interference was minimized.

Response to *Molinia* removal was detectable from the second season after removal, and eventually the increase in biomass of the rest of the community was approximately the same as the amount of *Molinia* biomass originally removed. The delayed response to removal urges caution in our interpretation of any lack of response to removal as a lack of competition, unless we are confident enough that the time scale was sufficient for the response to occur (compare the duration of published experiments in the review of Goldberg & Barton 1992). It seems that the vacant space after *Molinia* removal was filled preferentially by species with a similar physiognomy (*Festuca pratensis, Holcus lanatus*), but also species most affected by the persistent litter of *Molinia* (*Prunella vulgaris*) increased. Nevertheless, the response of most species is roughly the same and consequently the changes in total species composition after removal are not pronounced; this corresponds to the equivalence of the competitors hypothesis (Goldberg & Werner 1983). However, Herben et al. (1997) have shown that the specificity of the response increases at a smaller scale.

In a similar study conducted in an old-field community Gurevitch & Unnasch (1989) found more pronounced effects of dominant removal. In particular, in their case dominant (*Dactylis glomerata*) removal prevented the decline of species richness caused by nutrient additions and the increase in species richness was more

pronounced than in our experiment. The difference is probably caused by the differences in life-history strategy of the dominant (Grime et al. 1988): whereas *Dactylis glomerata* in the old-field is classified as intermediate between C-S-R and a competitor (and the genotypes of productive soils exhibit traits of a competitive strategy), *Molinia caerulea* is characterized as a stress-tolerant competitor, well adapted to infertile soils. Probably, increase in competitive strength with increasing fertility is much higher for *Dactylis* than for *Molinia*, with consequences for community richness. Also, the *Dactylis* biomass formed more than 50 % of the community biomass, whereas for *Molinia* it was less than 40 % in our experiment. Moreover, in our case other competitive grasses (e.g. *Holcus lanatus*) were able to fill up the empty space and outcompete the subordinate species.

Mowing proved to promote species richness in our plots, as was also found in many published studies (e.g. Bakker 1989; Collins et al. 1998). By mowing the tall plants are removed disproportionately more (compare Grime et al. 1987) and asymmetry in competition for light is highly reduced, at least for some time. Weak competitors for light, such as the creeping *Prunella vulgaris*, need regular mowing. Mowing also reduces the amount of litter, increases spring temperatures and promotes seedling germination. Mowing is a type of disturbance that only forms infrequent small gaps (by a missed stroke of the scythe), but it probably increases the effect of already existing gaps. Gaps at the scale of several to tens of cm$^2$ in unmown meadows are not suitable for seedling germination as they are highly shaded and soon covered by litter. However, after mowing and the removal of biomass these small gaps form suitable seedling habitats (Podolská, Křenová, pers. comm.). Regular mowing was a disturbance regime applied in these meadows for decades and perhaps centuries. During this time, the species composition stabilized. Any recent change in disturbance regime might be expected to cause a species loss by changing the competitive equilibria leading to exclusion of certain species; the only possibility to compensate for this loss is establishment by new species.

There was no difference between the competitive response (CR) to *Molinia* under low and high nutrient levels during the first two years after removal (i.e. before the amount of *Molinia* changed considerably in fertilized control plots). We can conclude that the competitive effect of *Molinia* on the rest of the community is roughly the same under low and high nutrient levels; this result is consistent with many other published results (Wilson & Tilman 1993 and references therein). Note, that our formula for CR is equivalent to the formula of Wilson & Tilman (1993); in our case, the target is the community affected by a single species, in their case the target is an individual affected by a community.

It should be noted that CR and similar measures of competition do not measure the intensity of competition but only the response of the target, in this case the rest of the community. CR-values depend not only on the intensity of competition, but also on the (a)symmetry of competition. Thus, we cannot conclude that there is no difference in competitive intensity between low and high nutrient environments. In any competition experiment, the target individual is not the only affected, but the competing counterpart is also affected. Both, the ability to affect the competitor and the ability to withstand the effect of competitor depend on the nutrient status. To estimate the competition intensity (whatever definition we accept), we must estimate not only the effect of species (element) A on species (element) B, but also the effect of species B on species A. In our case, we are missing the estimate of the competition effect of surrounding vegetation on *Molinia.*

In a long-term experiment, the quantity of the manipulated species also changes in control plots, particularly in factorial experiments where other treatments are also present. The CR should be interpreted as the effect of competition exhibited by the amount of *Molinia* present in the respective non-removal plots.

It was shown by Keddy et al. (1997) that under high nutrient levels competitive asymmetry increases. Why? With an increase in nutrients, community nutrient limitations weaken considerably. As a consequence, (aboveground) biomass increases. This leads to increased intensity of competition for light (similar results were obtained by Goldberg & Miller 1990 in an annual dominated 1st-yr old-field community). The fact that plant height is the best predictor of species response to fertilization supports this explanation. Similar reasons were presented by Tilman & Pacala (1993). Similarly we found in a previous study (Pyšek & Lepš 1991) that the weed species with the strongest positive response to fertilization were *Apera spica-venti* (the tallest weed species) and *Galium aparine* (a species able to reach considerable height by climbing). Competition for light is probably more asymmetric than competition for nutrients. It is much easier to monopolize light than to monopolize nutrients (Huston & DeAngelis 1994; Weiner & Thomas 1986). Moreover, nutrients are more patchily distributed and occur in three dimensions, whereas light, which can be captured by the tallest plants, occurs more or less in two dimensions. To monopolize light, it is enough to get a sufficient amount of biomass above the other plants. To monopolize nutrients, the complete three-dimensional space should be filled with roots.

The above discussion can be used to explain the humped back pattern of maximal species richness at intermediate fertility (Al-Mufti et al. 1977; Grime 1979).

At the left side of the hump (i.e. unproductive soils), biomass is low and competition for light is not so important. The decisive factor is competition for soil resources (water, nutrients) and this competition increases with decreasing levels of resources. Similarly, Wilson & Tilman (1991, 1993) have shown that root competition is relatively more important at lower levels of soil nutrients. In very infertile soils, the decrease in the number of species can also be caused by the inability of species to grow under very low water or nutrient conditions. With increasing soil productivity, competition for nutrients becomes less important and the importance of competition for light increases. This leads to an increasing asymmetry in competition and eventually to a decrease in competitively inferior species. It should be noted that this explanation is, as is the humped back model, based on mechanisms in grasslands. In multilayer forest communities the situation is more complicated.

This 'theory' also provides a testable prediction: in the very unproductive environment, where the addition of nutrients increases the number of species, the characteristics related to nutrient competition should be good predictors of response to fertilization. For example, the release from nutrient stress should be more important for non-mycorrhizal and facultatively mycorrhizal species and those species should respond more positively than species adapted to acquire nutrients through obligate mycorrhizal symbiosis. On the other hand, where the addition of nutrients causes a decrease in species richness, the ability of a species to compete for light (plant height) is the best predictor of species response. This is confirmed in our experiment and is in good agreement with the model of Huston & DeAngelis (1994). Also, in concordance with the 'theory', in our plot where the fertilization decreased the number of species, AM presence was not related to species response. It should be noted, that the **presence** of AM, as extracted from Fitter & Peat (1994), need not necessarily correspond to species **dependence** on AM. Nevertheless, our more detailed study of AM at the locality (Titus & Lepš subm.) suggests that AM is not a good predictor of species response to fertilization; rather, the level of AM colonization is influenced in some species by fertilization.

However, the above factors are not the only ones. Species mobility (see Herben et al. 1993; van der Maarel & Sykes 1993, 1997) requires continuous seedling recruitment. This phenomenon is suppressed under highly productive conditions, probably by direct shading by the above-ground biomass and by the effect of litter; the recruitment is also influenced by the moss layer. As neither the litter nor the moss layer were manipulated in this study, it is difficult to separate those effects. We

have found a positive correlation (over all treatments) between the number of seedlings and the moss layer and a negative correlation between number of seedlings and cover of litter. Parallel studies (Špačková et al. 1998; Kotorová & Lepš 1999) have shown that both removal of moss and removal of litter have positive effects on seedling recruitment. Consequently, the positive correlation of seedling number and moss layer is probably a consequence of similar responses of these two variables to the experimental manipulations, not a consequence of causal relationship. As litter has also been shown to have negative effects (Špačková et al. 1998; Kotorová & Lepš 1999), the negative correlation is in good agreement with manipulative experiments, and probably reflects a causal relationship. The negative slope of the regression lines in Fig. 8, and the difference in regression lines between fertilized and unfertilized plots suggests that both the effect of litter and direct shading by living plant biomass play a role in seedling recruitment. The results of standardized analyses of seedling counts (Table 5) show that the response differs among factors; the response to mowing differs considerably among species, whereas fertilization suppressed the seedling recruitment of all species. The number of seedlings found in a plot results from the number of seeds in the plot and their germination and establishment. Our treatments affected both the seed availability and conditions for seedling recruitment. That is probably why the number of seedlings of *Betonica officinalis* and *Sanguisorba officinalis* was negatively influenced by mowing, whereas the manipulative experiment with sown seeds of those species (Kotorová & Lepš 1999) has shown a positive effect of mowing on seedling recruitment. Both species are late flowering species, and the number of seeds produced is considerably reduced by mowing in late June or early July. The differential response of seedling recruitment to mowing is in agreement with the hypothesis that environmental heterogeneity can promote species coexistence through its effect on the recruitment process (Grubb 1977).

The species diversity of a community changes as a result of (clonal) growth, the death of established plants and the recruitment of new individuals. Any change in environmental conditions affects all three of them. For example, soil productivity affects the relative importance of competition for soil resources and light, and by this the asymmetry of competition. Increasing asymmetry increases the chances of driving a species to local extinction. With increasing productivity, the amount of litter also increases and both living biomass and litter suppress recruitment. For the resulting diversity, not only total recruitment suppression and the death rate of established plants, but also the selectivity of those processes is important: a high death rate of established plants

resulting from strong competition, need not decrease the diversity, if all the populations are equally affected. On the contrary, weaker but highly asymmetric competition will lead to local extinction of some species and a decrease in diversity. The relative importance of competition for established plants and seedling recruitment limitations differs among biotopes; nevertheless, it seems that both mechanisms play an important role in the decrease of species diversity with an increase in productivity and with the cessation of mowing.

## References

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-792.

Bakker, J.P. 1989. *Nature management by grazing and cutting.* Kluwer Academic Publishing, Dordrecht.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745-747.

DiTommaso, A. & Aarssen, L.W. 1989. Resource manipulation in natural vegetation. *Vegetatio* 84: 9-29.

Dostál, J. 1989. *Nová květena ČSSR.* [*New Flora of Czechoslovakia.*] Academia, Praha.

Fitter, A.H. & Peat, H.J. 1994. The ecological flora database. *J. Ecol.* 82: 415-425.

Gibson, D.J., Seastedt, T.R. & Briggs, J.M. 1993. Management practices in tallgrass prairie: large- and small-scale experimental effects on species composition. *J. Appl. Ecol.* 30: 247-255.

Goldberg, D.E. 1990. Components of resource competition in plant communities. In: Grace, J.B. & Tilman, D. (eds.) *Perspectives on plant competition.* pp. 27-49. Academic Press, San Diego, CA.

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: 511-518.

Goldberg, D.E. & Barton, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.* 139: 771-801.

Goldberg, D.E. & Miller, T.E. 1990. Effects of different resource additions on species diversity in an annual plant community. *Ecology* 71: 213-225.

Goldberg, D.E. & Werner, P.A. 1983. Equivalence of competitors in plant communities, a null hypothesis and a field experimental approach. *Am. J. Bot.* 70: 1098-1104.

Grace, J.B. 1990. On the relationship between plant traits and competitive ability. In: Grace, J.B. & Tilman, D. (eds.): *Perspectives on plant competition,* pp. 51-65. Academic Press, San Diego, CA.

Grime, J.P. 1979. *Plant strategies and vegetation processes.* Wiley, Chichester.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. *Comparative plant ecology.* Unwin Hyman, London.

Grime, J.P., Mackey, J.M.L., Hillier, S.H. & Read, D.J. 1987. Floristic diversity in model system using experimental microcosms. *Nature* 328: 420-422.

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

Gurevitch, J. & Unnasch, R.S. 1989. Experimental removal of a dominant species at two levels of soil fertility. *Can. J. Bot.* 67: 3470-3477.

Herben, T., Krahulec, F., Hadincová, V., & Kovářová, M. 1993. Small scale spatial dynamics of plant species in a grassland community during six years. *J. Veg. Sci.* 4: 171-178.

Herben, T., Krahulec, F., Hadincová, V. & Pecháčková, S. 1997. Fine-scale species interactions of clonal plants in a mountain grassland: a removal experiment. *Oikos* 78: 299-310.

Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.

Huston, M.A. 1994. *Biological diversity - the coexistence of species on changing landscapes.* Cambridge University Press, Cambridge.

Huston, M.A. & DeAngelis, D.L. 1994. Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.* 144: 954-977.

Keddy, P., Twolan-Strutt, L. & Shipley, B. 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. *Oikos* 80: 253-256.

Kotorová, I. & Lepš, J. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *J. Veg. Sci.* 10: 175-186. (This issue.)

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: 715-719.

Lepš, J. 1995. Variance deficit is not reliable evidence for niche limitation. *Folia Geobot. Phytotax.* 30: 455-459.

Levin, S.A. 1993. Grazing theory and rangeland management. *Ecol. Appl.* 3: 1.

Mountford, J.O., Lakhani, K.H. & Kirkham, F.W. 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *J. Appl. Ecol.* 30: 321-332.

Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artifact due to plot size? *J. Ecol.* 84:293-295.

Palmer, M.W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobot. Phytotax.* 29: 511-530.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. 1996. The species pool and its relation to species richness - evidence from Estonian plant communities. *Oikos* 75: 111-117.

Pyšek, P. & Lepš, J. 1991. Response of a weed community to nitrogen fertilizer: a multivariate analysis. *J. Veg. Sci.* 2: 237-244.

Rothmaler, W. 1976. *Exkursionsflora für die Gebiete der DDR und der BRD.* Kritischer Band. Volk und Wissen, Berlin.

Šmilauer, P. 1992. *CANODRAW users guide v. 3.0.* Microcomputer Power, Ithaca, NY.

Špačková, I., Kotorová, I. & Lepš, J. 1998. Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotrophic wet meadow. *Folia Geobot.* 33: 17-30.

Taylor, D.R., Aarssen, L.W. & Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58: 239-250.

ter Braak, C.J.F. 1990. *CANOCO - a FORTRAN program for CANOnical Comunity Ordination by [partial] [detrended] [canonical] corespondence analysis and redundancy analysis, version 3.10.* Microcomputer Power, Ithaca, NY.

ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO Release 4. Reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination.* Microcomputer Power, Ithaca, NY.

Thompson, K. 1987. The resource ratio hypothesis and the meaning of competition. *Funct. Ecol.* 2: 114-116.

Thompson, K. & Grime, J.P. 1988. Competition reconsidered - A reply to Tilman. *Funct. Ecol.* 2: 114-116.

Tilman, D. 1982. *Resource competition and community structure.* Princeton University Press, Princeton, NJ.

Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. *Funct. Ecol.* 1: 304-315.

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities.* Princeton University Press, Princeton, NJ.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.

Tilman, D. & Pacala, S. 1993. The maintenance of species richness in plant communities. In: Ricklefs, R.E. & Schluter, D. (eds.) *Species diversity in ecological communities,* pp. 13-25, University of Chicago Press, Chicago, IL.

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 der Maarel, E. & Sykes, M.T. 1997. Rates of small-scale species mobility in alvar limestone grassland. *J. Veg. Sci.* 8: 199-208.

van Duren, I.C., Pegtel, D.M., Aerts, B.A. & Inberg, J.A. 1997. Nutrient supply in undrained and drained *Calthion* meadows. *J. Veg. Sci.* 8: 829-838.

von Ende, C.N. 1993. Repeated measures analysis: Growth and other time-dependent measures. In: Scheiner, S.M. & Gurevitch, J. (ed.) *Design and analysis of ecological experiments,* pp. 113-117. Chapman and Hall, New York, NY.

Weiner, J. & Thomas, S.C. 1986. Size variability and competition in plant monocultures. *Oikos* 47: 211-222.

Wilson, S.D. & Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72: 1050-1065.

Wilson, S.D. & Tilman, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74: 599-611.

Zobel, K. & Liira, J. 1997. A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities. *Oikos* 80: 325-332.

Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends Ecol. Evol.* 12: 266-269.

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci.* 1: 55-66