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Community and individual level consequences of competition in an oligotrophic wet meadow: two manipulative experiments

MAGISTERSKÁ PRÁCE

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Prohlašuji, že jsem uvedenou práci vypracovala samostatně, s použitím uvedené literatury.

V Českých Budějovicích, 25. 8. 1998 ....Špačková..........

General introduction:

Submitted master thesis is presented in form of two independent scientific papers.

It is composed of two manipulative removal experiments conducted under field conditions in an oligotrophic species rich wet meadow (*Molinion*). Both experiments were dealing with competitive processes in a plant community. Responses to experimental treatments were followed for four years in the first experiment, respective for three years in the second experiment.

In the first experiment community consequences of competition were examined. The response of whole community to experimental treatments (i.e., removal of a dominant species, litter and moss layer) was tested using multivariate analyses. The response was evaluated separately for established vegetation and for seedlings. Possible factors, which may affect the establishment of seedlings, are discussed with regard to the differentiation of regeneration niche and the maintenance of species diversity in temperate grassland with implications for restoration management practices.

Unlike the first experiment, the second part of presented study concerns the evaluation of competitive effects of whole community experienced by selected target individuals of studied species (*Succisa pratensis*). The influence of above-ground and below-ground competition on two nutrient levels on target performance is examined. The response of roots and shoots of target plants to experimental treatments is assessed separately. An attempt was made to compare obtained results with other studies and put it into the relationship with a current debate in plant ecology - whether the competition intensity changes along a habitat productivity gradient.

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The effect of dominant species, litter layer and moss layer on seedlings and established vegetation

Abstract:

The effect of a dominant species, the litter layer and the moss layer on seedlings and established vegetation was studied in a four year manipulative experiment conducted in an oligotrophic wet meadow. The dominant grass species (*Nardus stricta*), litter layer, and litter layer together with the moss layer were removed and the community response of established plants and seedlings was tested by multifactorial analyses. Within four years, no significant effect of the treatments on established vegetation was found. On the contrary, species composition of seedling community and number of seedlings were affected significantly, mainly by the moss and litter removal treatment. A prevailing negative effect of the moss layer was found in this study. The effect of other treatments was negligible. In addition, the character of changes in established and seedling community over years is assessed. Again, no changes in established community were found, on the contrary of the seedling community where both numbers and species composition changed over years. The results obtained are discussed with respect to the importance of regeneration niche and the maintenance of species diversity in oligotrophic wet meadows.

Nomenclature: nomenclature of vascular plants follows Rothmaler (1976), nomenclature of bryophytes follows Zitová et al. (1982).

Introduction:

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 and Zobel 1991). Recently, oligotrophic meadows have been considered to be uneconomical, and their management is either intensified (fertilization), or the meadows are abandoned. Both these processes lead to an eventual loss of species diversity and the species rich communities are replaced by communities dominated by a few strongly competitive species.

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 and Sykes 1993), are often taken into account to explain the phenomenon.

The differentiation of the regeneration niche is influenced by many factors. Among them, the presence and character of the bryophyte layer (van Tooren 1988, Winn 1985, Ryser 1993, Keizer, van Tooren and During 1985), the litter layer (Facelli and Facelli 1993, Goldberg and Werner 1983), and of the openings in the vegetation turf (Goldberg and Werner 1983, Caruso 1969, McConnaughay and Bazzaz 1987) are most often mentioned.

Manipulative experiments conducted under natural conditions are one of the most reliable methods used to explain the processes and patterns shaping the plant communities (Aarsen and Epp 1990, Goldberg 1995). The most common neighbor manipulation approach in the field involves the removal of various component(s) of the vegetation (Aarsen and Epp 1990). Although numerous factors may confound the interpretation of results in a manipulative experiment, it is possible to eliminate some of these problems (Goldberg 1995). The confounding factors may include indirect effects of treatments on soil moisture content and/or nutrient levels, and on the activities of predators and decomposers (Aarsen and Epp 1990). Another question is the timing of experimental perturbations and recording of responses, including the problem of short term experiments (Goldberg 1995). Also, one well known problem is the trade-off between the soil disturbance caused by removal of neighboring vegetation with roots and the decomposition of root fragments left in the soil when only shoots of plants are removed. The impact of this artifact differs among various communities (Goldberg 1995, Wilson and Tilman 1993).

The aim of this study is to evaluate the importance of competition from a dominant species and from the moss layer, and the effects of litter on established plant community and on the seedlings in an oligotrophic wet meadow. In a manipulative removal experiment, effects of treatments on seedlings and adult plants were investigated over four years. Additionally, the relationship between small-scale variability in established plant community species composition and seedling emergence was analyzed. Finally, an attempt was made to determine the character of changes in seedling and established vegetation over time.

Methods:

Study site:

The study site is located in an oligotrophic species rich wet meadow 10 km southeast of České Budějovice, South Bohemia (latitude 48° 57' N, longitude 14° 36' E, altitude approximately 510 m). Mean annual temperature is between 7 and 8 °C, mean annual precipitation is 600 – 650 mm (Syrový 1958).

The vegetation of the study site is typical of middle European species rich wet lowland meadows. According to phytosociological classification it belongs to the *Molinietum caeruleae* (*Molinion*) with some species indicating a transition to *Violion caninae* in drier parts of the meadow (Krahulec, pers. comm).

The vegetation is dominated by two perennial grasses (*Molinia caerulea, Nardus stricta*). Other common graminoids are *Anthoxanthum odoratum, Agrostis canina,Briza media, Festuca rubra, Holcus lanatus, Daltonia decumbens*, and a number of sedges, including, but not limited to *Carex panicea, C. palescens, C. leporina* and *C. hartmanii*. The most common herbs are *Myosotis palustris, Potentilla erecta, Prunella vulgaris, Lathyrus pratensis, Cirsium palustre, Galium uliginosum,* and *Lysimachia vulgaris*. During the four years of study, a remarkable increase in the occurrence of some of the rare species (*Dactylorhiza majalis*) was noticed, probably due to disturbances caused by researchers.

All plant species occurring on the study site are native, except for *Epilobium adenocaulum.*

The average number of vascular plant species in a 1x1m plots was 26 (including 8 grass species, 4 sedges and 14 forbs). The experimental plots contained 6 bryophyte species, all of them typical for this class of meadow (*Aulacomnium palustre, Climacium dendroides, Hylocomium splendens, Rhytidiadelphus squarrosus,* and *Pseudocscleropodium purum*).

The total cover was estimated to be about 82%. The average cover of *Nardus stricta* was 25%. Bryophyte cover varied widely and was estimated to average about 35%.

The meadow was regularly mown until the early 1990s , but at present it is not subjected to any agricultural management.

Experimental design:

Experimental plots were established in March 1994 shortly after snow melt. Plots 1x1m square each were set up in a randomized complete block design, with each of the four blocks containing the following treatments: (1) a control plot where vegetation remained undisturbed, (2) litter removal (3) removal of the dominant species (*Nardus stricta*) and (4) litter and bryophyte removal. Mosses and the dominant grass were removed by careful hand weeding, in attempt to minimize soil disturbances. However, despite the effort, removal of *Nardus* (partly with roots) led to minor soil disturbances, which were not visible during summer recording. The removal of *Nardus* was very successful with nearly no regrowth. Removal of mosses did not cause any noticeable disturbances of the soil surface.

During the summer 1994 in the middle of each plot new 0.5 x 0.5 m square was marked out and wire rods were inserted into the soil in the corners of each square. A wooden sampling frame with openings fitting into the wire rods was used, thereby improving precision of square placement each year. The sampling frame was divided by strings into a grid of squares 10x10 cm each. The coverage of established plant species were estimated and the numbers of seedlings were recorded in every 10x10 cm square. As seedlings were claimed plant individuals grown from seeds before reaching their first winter season.

Species` identities were determined according to Csapody (1968), Lhotská & Kropáč (1985), and by comparing with seedlings grown from seed in a laboratory.

The experiment was reestablished every spring and censused were conducted every summer in the mid-season (beginning of July).

Statistical analysis:

For the evaluation of total community response multivariate analyses - with constrained ordinations were used. Because treatment was considered as a categorical variable with relatively low heterogeneity of the compared plots (thus linear response model), redundancy analysis was used (RDA, Jongman et al. 1987), in the program CANOCO 3.10 (ter Braak 1990). CANODRAW and CANOPOST (Šmilauer 1992) were used for graphical output. Both, RDA with and without standardization by sample norm were used. RDA without standardization determines both differences in the total numbers of seedlings and species proportions, while RDA with standardization reflects relative proportions of species only. The appropriate covariables were used according the design of the experiment. The species that were subjected to experimental manipulations (i.e., *Nardus* and bryophytes) were made passive in order to not influence ordination results. In all cases, the significance of results was tested by the Monte Carlo test for first canonical axis, with permutations reflecting the experimental design.

If there were significant differences in the entire community response, further testing was performed to evaluate the response of both particular species and total number of seedlings. For this purpose analysis of variance - repeated measures test was performed, respective for data from the first year of the experiment, analysis of deviance in S-plus 3.0 (STATISTICAL SCIENCES 1995) package (McCullagh and Nelder 1989) was used to evaluate the response of particular seedling species to experimental treatments. This analysis allows for the use of variables with other than normal distribution. (In this case the number of seedlings in quadrates were modeled as variables with a Poisson distribution.)

The relationship of seedlings to established vegetation was tested by RDA, with the species composition of established vegetation as explaining variables while block and treatment structure were used as covariables. In this configuration only the relationship of seedlings to local vegetation is analyzed.

To measure the changes in seedling community composition over the four experimental years , CANOCO program was used again. The differences in number of seedlings between years and eventual changes in numbers of established and seedling species found in 10x10cm squares during the four years of the experiment were tested by ANOVA repeated measures.

Results:

Response of the established plant community to experimental treatments

No differences were observed in community composition of established plants in any of the four years of the experiment with respect to treatment. Neither of the analyses used (RDA with and without standardization) revealed significant results (Analyses 1 - 5 in Table 1). The difference in community species composition between the first and last year of the experiment was assessed in Analysis 6. Due to the character of the data, special treatment was required for analysis. Instead of conducting the test with 400 covariables (all 10x10 cm squares), the covers of particular species in each square for year 1994 were subtracted from that of year 1997 and only the resulting differences were analyzed. Nevertheless, no change in community species composition was found (Analysis 6, Table 1).

Response of seedlings to experimental treatments

On the contrary, species composition of seedling community and numbers of seedlings differed significantly.

Analyzing the response of seedling community by multifactorial analysis a clear change was observed in species composition with regard to experimental treatments. When tested by unstandardized RDA (Analysis 16. Table 1), the outcomes were highly significant. The results obtained by standardized RDA (Analysis 17, Table 1) also showed significant differences in seedling community composition, although with a slightly lower significance level. This is due to the fact that a standardized analysis evaluates differences in the proportions of species only (unlike a RDA without standardization which reflects both, the differences in the total number of seedlings and seedling species proportions.) The significant result of standardized RDA reveals that species proportions were not constant among treatments and that there were differences, albeit small, among species in their response to particular treatments. The distribution of species is shown in Fig.1. Most of the seedling species show a tendency to occur in plots where mosses and litter were removed. On the contrary, no species was found to tend to grow in *Nardus* removal plots. Furthermore, a similarity in species composition between control plots and litter removal plots was found.

Testing the seedling response to experimental treatments, all RDA analyses (with only one exception -Analysis 13). revealed significant results. The summary of all RDA tests performed is in Table 1.

Results of Analysis of variance confirmed those of RDA.

The total number of seedlings changed significantly among treatments when tested by analysis of variance (ANOVA repeated measures, $P<0.01$, Table 2). The highest number of seedlings was found in plots with moss/litter removal treatment. The smallest amount of seedlings was recorded in plots with *Nardus* removed, followed by litter removal treatment and control plots (Fig. 2). However, pronounced differences were found only between plots without bryophyte and litter layer and the plots without *Nardus*, the remaining treatments differed only slightly.

When the dependence for particular years was examined, only two of the tests performed showed significant changes in seedling numbers (Table 2).

The response of total number of seedlings and of particular species to the treatments was tested by analysis of deviance for the data from 1994. The numbers of seedlings differed significantly among treatments ($P<0.01$). Equally, the results showed certain differences in particular species occurrence. In 1994, the three species with the most abundant seedlings, i.e., *Cirsium palustre, Potentilla erecta and Ranunculus sp.*, showed statistically significant responses to experimental treatments (analysis of deviance, $P<0.05$), with the highest seedling numbers in plots with the litter and moss layer removed. The abundance of another species (seedlings of *Galium sp., Myosotis nemorosa* and *Cardamine pratensis*) also differed significantly among treatments. Seedlings of Galium (most of them belonging to *Galium uliginosum*) were infrequent in plots with *Nardus* removed ($P<0.05$). Seedlings of this species were usually observed in *Nardus* tussocks. Seedlings of *Myosotis palustris* responded similarly to those of *Galium* ($P<0.05$). The highest number of *Cardamine pratensis* seedlings were found in untreated plots ($P<0.05$). Differences for other species were not significant.

Response of seedling species to the composition of established plant community

Regarding data from the first experimental year, the overall relationship of seedlings to established vegetation was analyzed by RDA, using species composition of established vegetation as the explaining variable and the block and treatment structure as covariables. In this configuration the influence of both the block and treatment are removed and only the relationship of seedlings to local vegetation is analyzed. The result of the RDA was non-significant (Analysis 7 Table 1) and no relationship was found. However, due to so many predictors (i.e., every single established species), the test is very weak. When forward selection of variables was used (all variables which explaining power was significant at $\alpha=0.05$ were selected), the following five species were chosen for further testing: *Anthoxanthum odoratum*, *Cirsium palustre*, *Prunella vulgaris*, *Succisa pratensis* and *Viola palustris*. The resulting RDA was highly significant ($P<0.01$). However, the real significance is unknown because the best predictors were chosen from a large pool of possibilities.

Changes in established and seedling community over years

Because no response of adult plants to the treatments was found, no attempt was made to value the changes in their species community composition among years.

The species composition of seedlings tested by both standardized and unstandardized RDA, varied significantly between years (Analyses 18 and 19, Table 1). The distribution of species in years is shown in Fig. 4.

Also the total number of seedlings computed by ANOVA differ significantly ($P<0.01$) among years. The highest amount of seedlings was found in 1995. It differed considerably in comparison to those found in 1994, 1996 and 1997, which were approximately the same (Fig. 3). The effect of a treatment on seedling numbers tend to change in years (i.e., the year x treatment interaction was on the significance limit, ANOVA, $P=0.06$, Fig. 5).

The changes in numbers of species found

No changes were found in established species numbers recorded in 10x10cm squares. Neither the treatment or the year had any effect on the species numbers in the squares.

On the contrary the same test performed with seedling species numbers data revealed significant results. The number of seedling species changed between years, with the highest amount of species found in 1995 ($P<0.05$, Fig. 6). The change was also noted among treatments ($P<0.01$, Fig. 6), with the highest species numbers found in plots subjected to moss/litter removal treatment type whereas the lowest number of species was found in plots with *Nardus* removed. The treatment x year interaction was also significant (P<0.05, Fig. 6). (All tests were performed using ANOVA repeated measures, Table 3).

Discussion:

A portion of the experiment (the first year results) was previously published (Špačková, Kotorová and Lepš 1998). The outcomes of the following years confirmed the results of the first.

Even after four experimental years no significant changes in species composition of the established plant community were found. This is most likely due to the fact that neither of the removal treatments are capable of influencing adult individuals in a considerable way.

The litter layer present on the experimental plots was composed mostly of grass stems and a compact layer was not created. In some studies where the effect of litter layer was found to be an important factor influencing the plant community, the litter created a dense, compact mat, often composed of rosette types of plants (Facelli and Facelli 1993).

Although the moss layer was often shown to influence plant individuals during their seedling stage (van Tooren 1988, Ryser 1993, Rabotnov 1969, Keizer, van Tooren and During 1985, Equiha and Usher 1993), only few experiments were found in which bryophytes affected established plants (Sohlberg and Bliss 1986, Malmer, Svensson and Wallen 1994, Svensson 1995). However, these experiments were conducted under extreme conditions (high-arctic meadow and peatbogs), and thus cannot be compared fully with the studied community of this experiment.

Many experiments show the competitive effect of a dominant plant species on the rest of the community (Gurevitch and Unnasch 1989, Fowler 1981). In our case, the removal of the dominant species did not have any remarkable effect on the species composition of the established plant community. This can probably be attributed to the low competitive ability of *Nardus stricta,* or the relatively low cover of this species in the plots (the average cover was 25%).

It is not likely that the changes in the community composition are slower than the duration of the experiment. Experiments are generally conducted in a much shorter time period. Goldberg and Barton (1992) found 62% of the experiments investigated to be performed in one year or even less. Considering experiments which measured population response, the longest experiment found was conducted over three years. Only two experiments tested whole community response using multivariate analyses and both found a significant effects on composition of the community, and both of them were conducted only during one year (Goldberg and Barton 1992).

Despite a lack of response from the established community, plants were clearly affected in their seedling stages, mainly by moss/litter removal treatment. This is in agreement with conclusions from other studies, including those from the same locality (Špačková, Kotorová and Lepš 1998, Kotorová and Lepš in press) as well as those from other study sites (van Tooren 1988, Ryser 1993, Rabotnov 1969, Keizer, van Tooren and During 1985, Equiha and Usher 1993).

The response of seedlings to moss removal in the studied community was generally positive, although a few species responded differently (*Myosotis nemorosa, Cardamine pratensis*). Both, positive (e.g. Keizer, vanTooren and During 1985, Ryser 1993) and negative effects (e.g. Keizer, van Tooren and During 1985, van Tooren 1988) of moss layer on seedling appearance are documented in many studies. The literature shows that under favorable conditions such as greater habitat productivity or sufficient water supply, competition by neighboring vegetation largely determines the establishment of seedlings, while with decreasing productivity or in communities with temporal desiccation the protective role of the moss layer is more important (Ryser 1990).

This study was not designed to reveal the mechanisms of interactions between the moss layer and seedlings. In addition to direct competitive effects, the mechanisms most often considered are lack of light under dense bryophyte turf, changes in red/ far red ratio, temperature or air and soil humidity. Mechanical effects („seed trap„), or indirect biotic effects (predation) may equally play a role (Keizer, van Tooren and During 1985). The allelopathic effects on the germination are also reported from several studies (Brown 1967). Unfortunately, data obtained in this study do not enable distinction between these mechanisms.

The seedling appearance was not affected considerably by other treatments.

Unlike dry grassland settings (Rusch and Fernández-Palacios 1995) we did not find a pronounced relationship between the established vegetation and seedling composition.

The number of seedlings was approximately the same in 1994, 1996 and 1997, whereas the seedling appearance in 1995 was considerably higher. The majority of experiments dealing with seedling germination and establishment do not involve data from more than one year. In two of three studies found, the same pattern of fluctuation of seedling appearance over years is confirmed. Rabotnov (1967) and Rapp and Rabinowitz (1972) report accordingly the roughly equal numbers of seedlings becoming established in „most„ of the years with peaks and sinks occurring every few seasons. Ryser (1993) in a two year experiment demonstrates a fluctuation in establishment success of seedlings. The possible reasons for these variations are most likely the weather conditions or the presence of pathogens and predators (Rabotnov 1967).

When testing possible changes in species numbers occurring in experimental plots, again, no differences were found within the established community. On the contrary, seedling species numbers changed among treatments and years, and the year x treatment interaction was also significant. It is a bit surprising, that pronounced changes in the seedling community did not cause any response in species composition of established plant community, even after four years. The possible explanation for this may be that although experimental treatments (mainly moss removal) can enhance the seedling germination and early survival, the disturbances performed are not strong enough to ensure later survival of seedlings. This could be supported by conclusion of McConnaughay and Bazzaz (1987). They found that while survivorship was greater in larger gaps only for two small seeded species, the probability of reaching reproductive maturity increased with gap size for all species regardless of seed size. Similarly Krahulec (1995) found that studies of spatiotemporal processes in temporal grasslands done in the past two decades show „uncoupling„ of the fine scale and large scale processes.

In conclusion, we can say that a plant community is very sensitive to different effects during its seedling stage. Various factors effect the seedling recruitment. Although their relative importance still needs to be investigated, the presence and character of the moss layer is of the considerable importance.

These factors cause the small scale spatial and temporal variation in neighboring vegetation and thus they contribute to differentiation of regeneration niche and the maintenance of species diversity. In Central Europe, the abandonment of traditional management practices (both, the use of fertilizers, and meadow abandonment) leads to a decline of species diversity and loss of competitively weak species, probably because of limitations to differentiation of regeneration niche.

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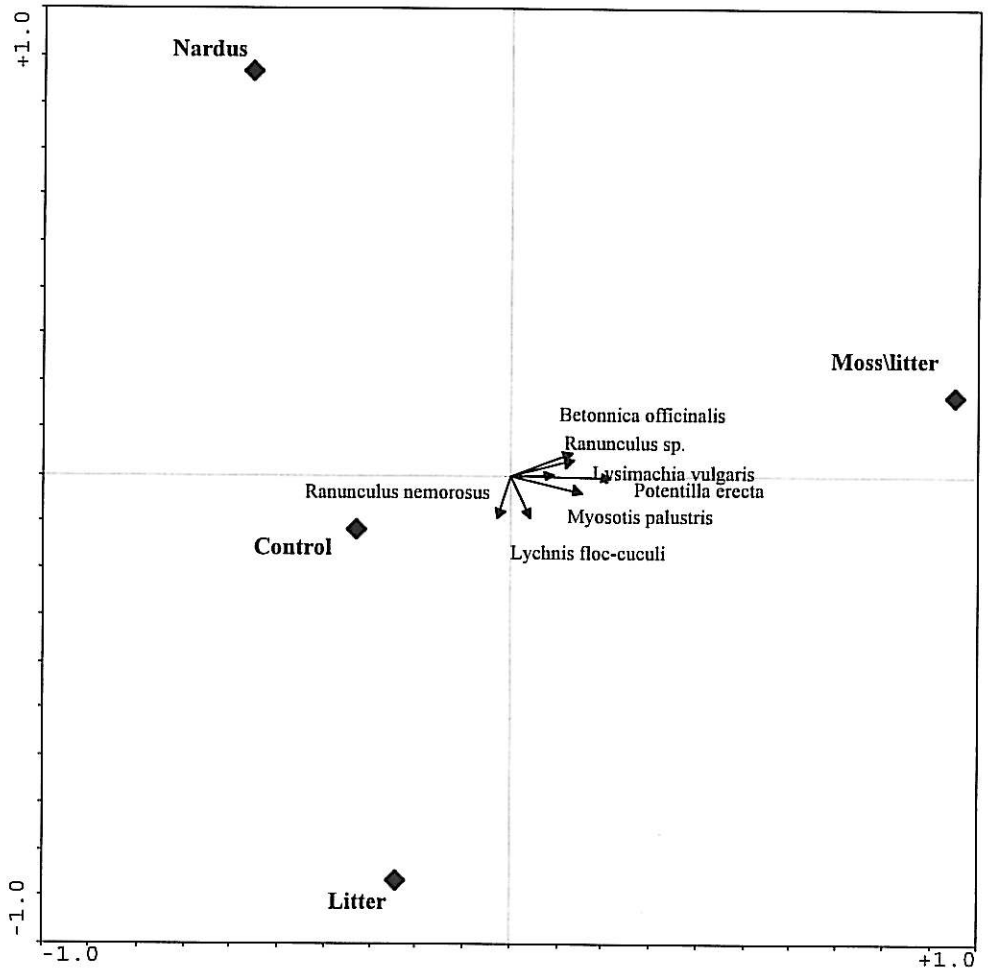

Fig.1:
Result of the RDA - Analysis 16. Distribution of seedling species in plots subjected to different removal treatments.

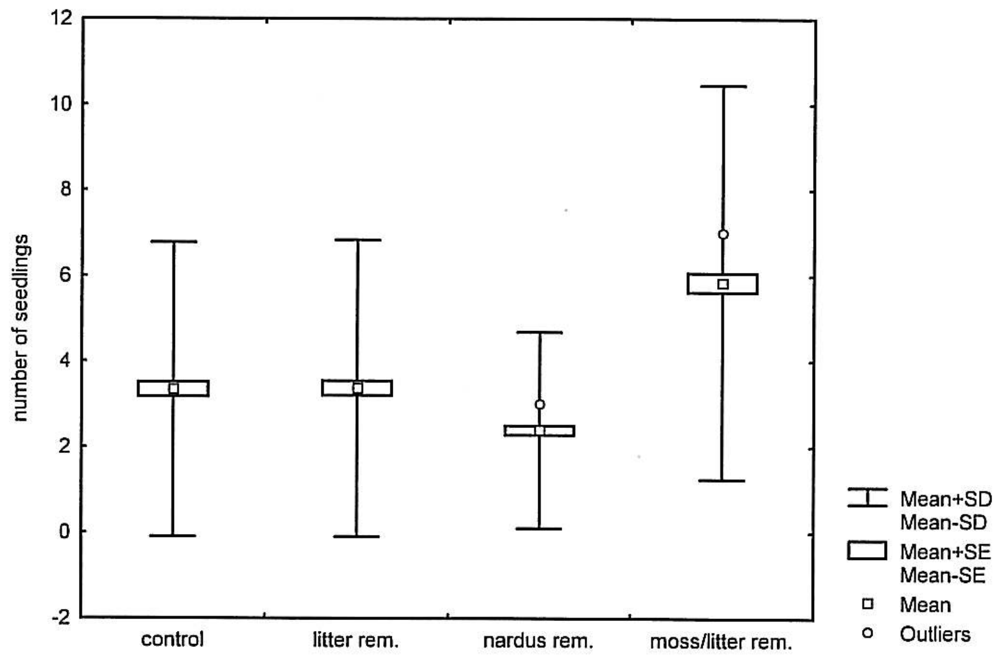

Fig. 2:
Box and Whisker plot - effect of experimental removal treatments on numbers of seedlings found in 10x10 cm subplots.

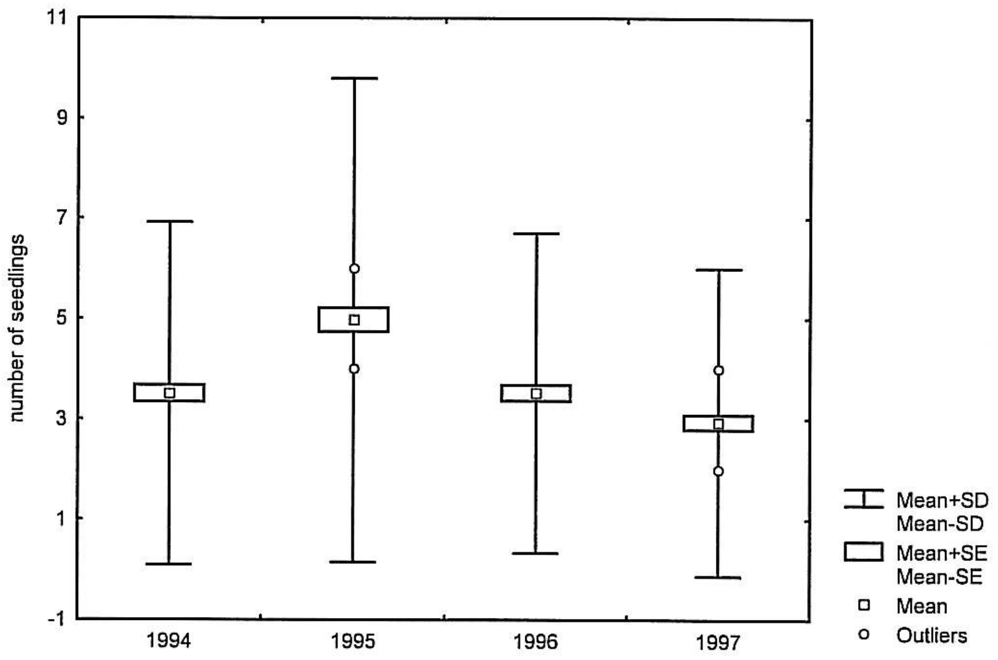

Fig. 3:
Box and Whisker plot - differences in number of seedlings found in 10x10 cm subplots during the course of the experiment.

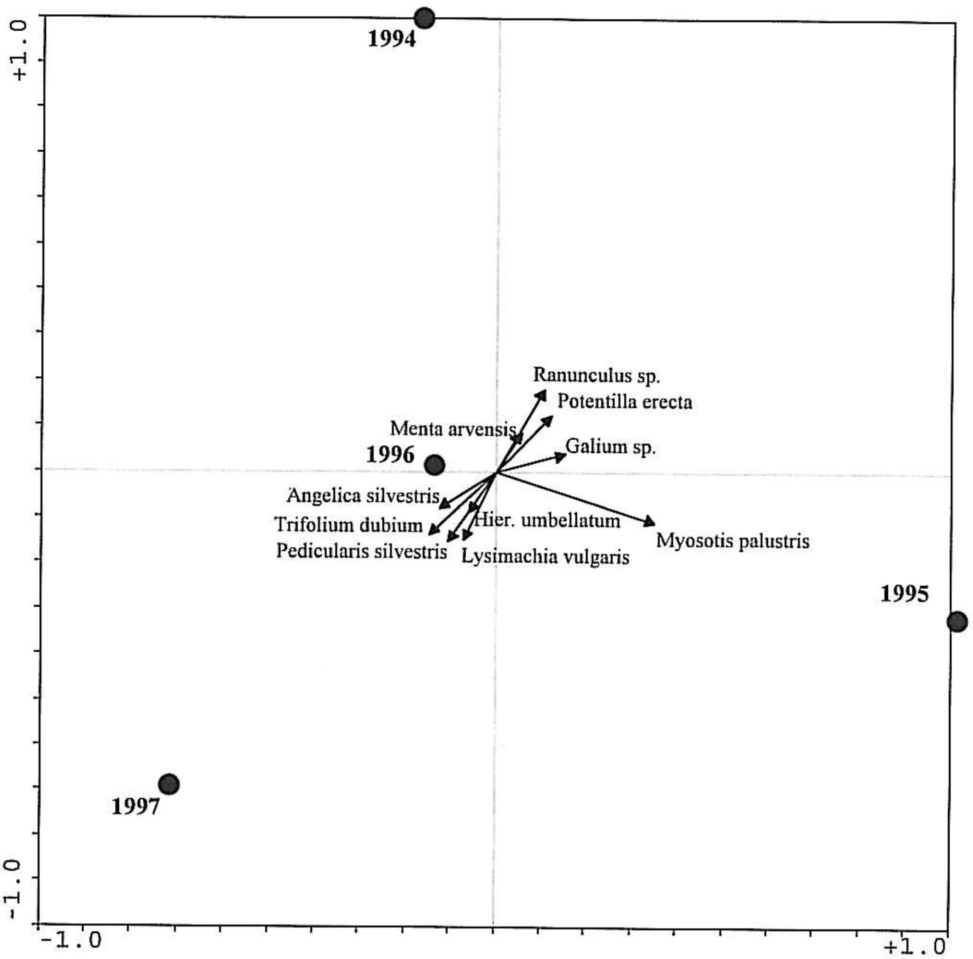

Fig. 3:
Results of the RDA - Analysis 18. Distribution of seedling species found in different years.

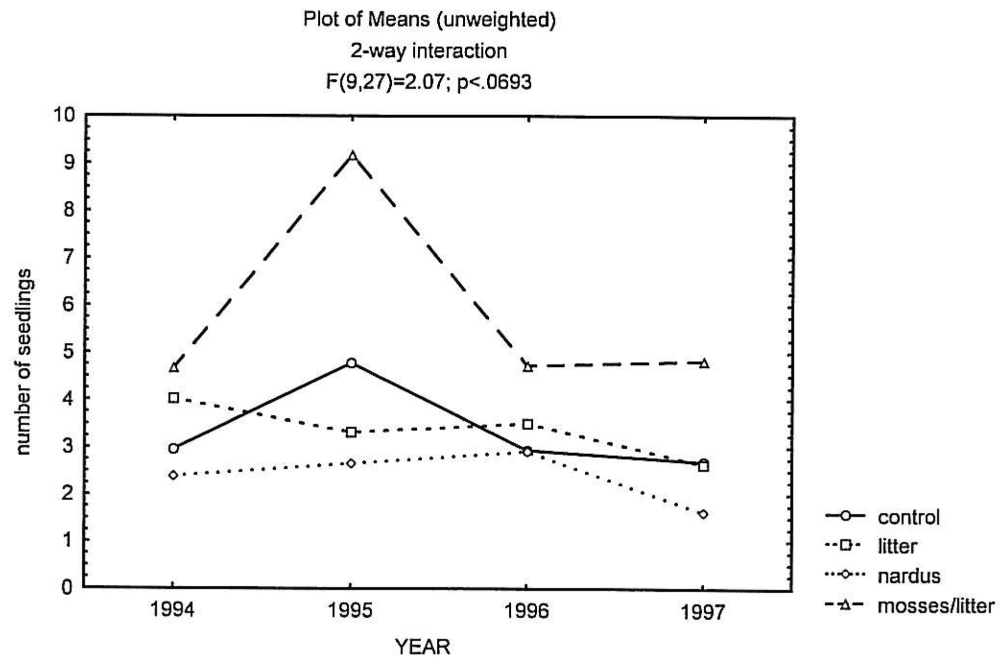

Fig. 5:
Numbers of seedlings in 10x10 cm subplots over years in different treatments.

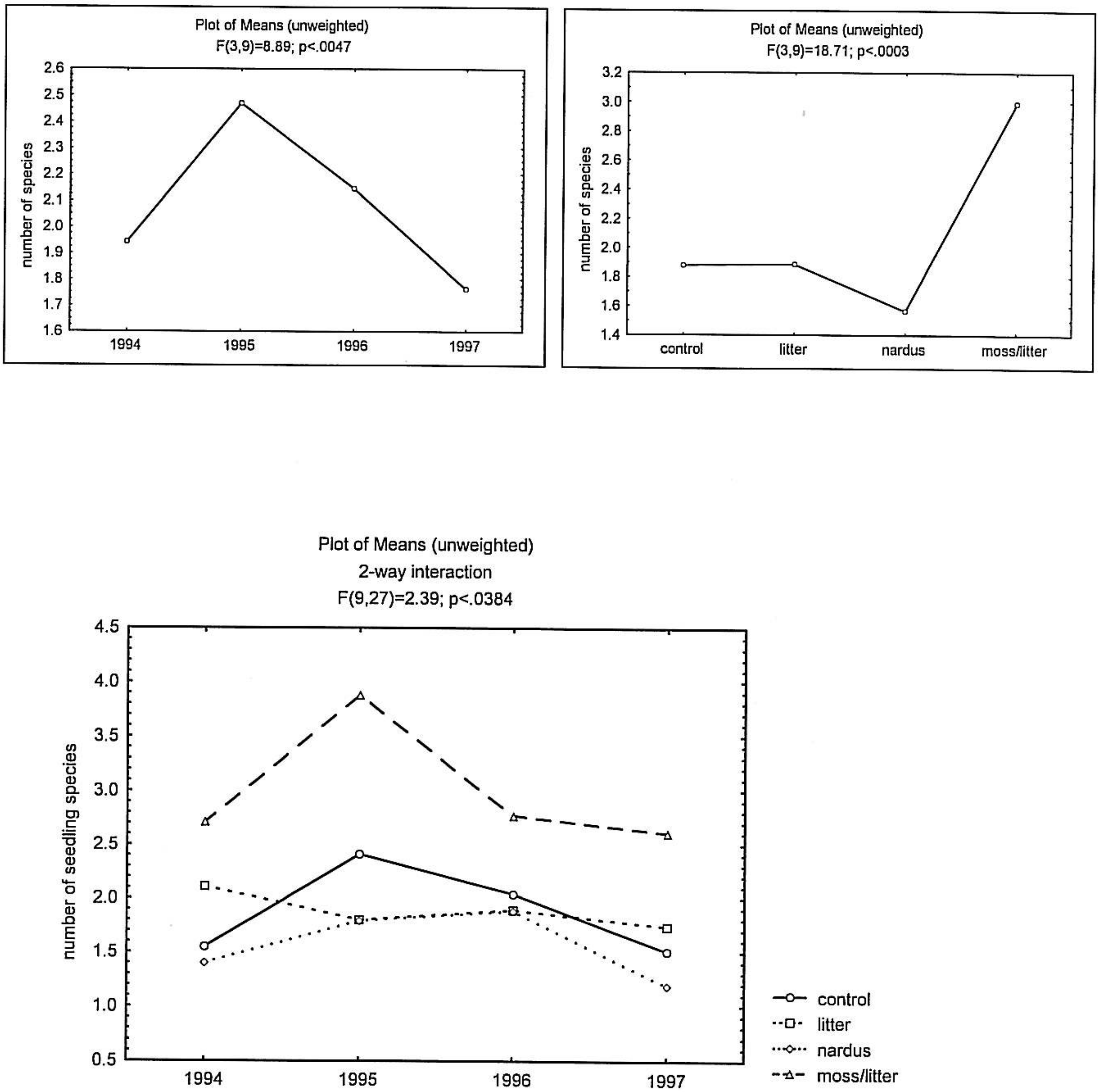

Fig 6:
Changes in seedling species numbers found in 10x10 cm subplots. Differences are shown for removal treatments and years (main effects) and for treatment x year interaction.

Analysis #	Standard.	Species data	Year	Env. variable	Covariable	r 1-st axis	% expl. 1-st axis	F-ratio	P
1	N	est.plants	94	treatment	block	0.011	1.2	4.64	0.80
2	Y	est.plants	94	treatment	block	0.080	0.9	3.08	0.86
3	N	est.plants	95	treatment	block	0.011	1.1	4.45	0.68
4	N	est.plants	96	treatment	block	0.009	1.0	3.94	0.80
5	N	est.plants	97	treatment	block	0.404	1.7	6.67	0.72
6	N	est.plants	diff. 94-97	treatment	block	0.324	0.9	3.40	0.93
7	N	seedlings	94	est.plants	block, treat.	0.031	3.4	12.44	0.64
8	N	seedlings	94	treatment	block	0.046	4.7	19.29	0.01
9	Y	seedlings	94	treatment	block	0.021	2.2	8.73	0.03
10	Y	seedlings	95	treatment	block	0.028	2.4	9.75	0.01
11	N	seedlings	95	treatment	block	0.088	9.4	40.79	0.01
12	N	seedlings	96	treatment	block	0.030	3.1	12.39	0.01
13	Y	seedlings	96	treatment	block	0.020	2.1	8.61	0.22
14	Y	seedlings	97	treatment	block	0.488	1.9	7.78	0.01
15	N	seedlings	97	treatment	block	0.482	3.5	14.46	0.01
16	N	seedlings	94-97	treatment	block, year	0.350	2.1	28.91	0.00
17	Y	seedings	94-97	treatment	block, year	0.388	2.3	36.65	0.01
18	N	seedlings	94-97	year	block, treat.	0.430	3.0	49.00	0.01
19	Y	seedlings	94-97	year	block, treat.	0.430	2.3	37.24	0.01
20	N	seedlings	94-97	year, treat.	block	0.470	4.4	44.60	0.00
21	Y	seedlings	94-97	year, treat.	block	0.466	3.4	55.95	0.01

Table 1:
Summary of performed RDA analyses with results. Standard. - no standardization or standardization by sample norm. Species data -seedlings or established species. Env. variable - enviromental variable. r 1-st axis - species-enviroment correlation on the first axis. % expl. 1-st axis - percent of species variability explained by the first axis, measure of the explanatory power of enviromental variables. F-ratio - the F-ratio statistics for the overall test. P - significance of the first RDA axis estimated using the Monte Carlo permutation test. For Anal. 6 the difference between numbers of seedlings recorded in 1994 and those recorded in 1997 was analyzed.

Year	Effect	MS error	F	P<
1994	treatment	68.6	1.5	0.26
1994	block	9.5	0.8	0.49
1994	tr. x block	9.5	7.1	0.001
1995	treatment	104.5	8.2	0.01
1995	block	14.0	9.4	0.001
1995	tr. x block	14.0	7.4	0.001
1996	treatment	25.3	2.8	0.09
1996	block	9.2	1.8	0.13
1996	tr. x block	9.2	2.7	0.01
1997	treatment	21.24	8.5	0.01
1997	block	7.5	4.2	0.01
1997	tr. x block	7.5	2.7	0.01
94-97	treatment	53.1	16.5	0.001
94-97	block	13.4	6.5	0.001
94-97	year	33.9	8.9	0.01
94-97	tr. x block	13.4	3.9	0.001
94-97	tr. x year	55.6	2.1	0.06
94-97	bl. x year	9.1	3.7	0.001
94-97	tr.x bl.x year	9.1	6.1	0.001

Table 2:
Summary of ANOVA results. The effect of treatment on number of seedlings in 10x10 cm subplots.

	Effect	MS error	F	P<
established plants	treatment	13.6	0.4	0.78
	block	3.7	6.9	0.001
	year	12.4	2.4	0.13
	tr. x block	3.7	3.6	0.001
	tr. x year	5.2	0.7	0.67
	bl. x year	2.1	6.1	0.001
	tr.x bl.x year	2.1	2.6	0.001
seedlings	treatment	8.3	18.7	0.001
	block	2.2	6.9	0.001
	year	4.1	8.8	0.01
	tr. x block	2.2	3.7	0.001
	tr. x year	4.2	2.3	0.05
	bl. x year	1.5	2.6	0.01
	tr.x bl.x year	1.5	2.7	0.001

Table 3:
The effect of treatment on the number of established and seedling species in 10x10 cm subplots. Results of ANOVA repeated measures.

The effect of shoot and root competition and nutrient enrichment on a studied species (*Succisa pratensis*)

Abstract:

The effects of above-ground and below-ground competition on plant performance of studied species (*Succisa pratensis*) was investigated in a three year manipulative fertilization experiment. Established individuals of studied species were set up in a 3x2 factorial design with competition level and nutrient level as factors. Levels of „competition" treatment were as follows: (1) trenching - no competition, (2) clipping - root competition only and (3) untreated control - full competition. A common NPK fertilizer was applied. The response of both above-ground and below-ground parts of plants to the experimental treatments was examined. The existence of competition was proved. Although the relative importance of root and shoot competition could not be evaluated precisely, shoot competition showed to be of considerable importance in comparison with other studies found. Total competition intensity did not vary with nutrient level. The results of the experiment support Tilman`s rather than Grime`s competition theory. Remarkable differences in the response of above-ground and below-ground parts of plants were found, which emphasizes the need of experiments dealing with below-ground processes and root systems of plants.

Introduction:

Competition holds a central place in plant ecology theory. Attempts to explain various aspects of this subject have been made in many field or greenhouse studies (Goldberg and Barton, 1992). Despite these attempts, the role competition plays in structuring natural communities and the mechanisms involved remain unresolved.

A debate has recently developed, that has become of particular importance to plant ecologists. The issue is whether the intensity of competition varies as a function of habitat productivity. Two contrasting hypotheses concerning this relationship are currently discussed. The first is that increasing habitat productivity results in high growth rates and large amount of biomass, which is followed by increasing intensity of competition for both light and soil resources (Grime 1979, Keddy 1989). The second hypothesis predicts that root and shoot competition is negatively correlated, therefore with increasing standing crop competition for light becomes more important, but competition for below-ground resources declines. Thus, total competition intensity remains constant across a productivity gradient (Tilman, 1982).

Many experiments trying to resolve this problem reveal conflicting results supporting both theories (e.g. Gurevitch 1986, Gurevitch and Unnasch 1989 vs. Reader et al. 1994, Wilson and Tilman 1991, Wilson and Tilman 1993). One of the reasons for this failure is the confusion in defining competition intensity (Grace 1993). Competition intensity can be measured either as an absolute or as a relative reduction in yield. Some studies have demonstrated that results can differ when the competition intensity is expressed in both of these ways, as a relative and as an absolute. While relative intensity of competition was found to be constant across an experimental gradient, thus supporting the second theory, absolute intensity of competition was greatest when soil fertility was high, thus confirming the first theory (Campbell and Grime 1992, Turkington, Klein and Chanway 1993). The relative intensity of competition was suggested to be a more proper measure of expressing the intensity of competition (Grace 1995).

Some of the experiments dealing with plant competition involve the separation of both effects - competition for light and competition for nutrients. First attempts were conducted in a number of pot experiments (e.g. Donald 1958). Many experiments were also conducted under a simple crop-weed community (Wilson 1988).

Recently, attempts have been made to distinguish these two components under natural conditions. For the purpose of controlling below-ground competition the method known as trenching is usually used. It has been most commonly used in forest studies (Aarsen and Epp 1990). In grassland communities, a modification of this method consisting in inserting plastic or steel tubes vertically into the soil around a target plant is predominantly used for the same purpose (Peltzer, Wilson and Gerry 1998, Wilson and Tilman 1991, Snaydon and Howe 1986, Marti 1994, Grubb, Ford and Rochefort 1997, Cook and Ratcliff 1984). For restricting above-ground competition, various methods (e.g. the use of herbicides, clipping neighboring vegetation, or tying it back) are applied.

Although the influence of both components of competition on plant performance is often examined, only few studies take into account the response of both roots and shoots. The majority of the experiments measures the response of aboveground parts only. However, some experiments (Eagles 1971) imply that the presumption of corresponding responses of aboveground and below-ground parts of a plant should not be taken for granted.

The aim of this experiment was (1) to test the validity of one of the two conflicting hypotheses concerning the intensity of competition across a productivity gradient, and (2) to determine whether the response to experimental treatments is the same for above-ground and below-ground parts of a plant.

Methods:

The second experiment was established in June 1995 on the study site Ohrazení, 10 km southwest of České Budějovice. See page 3 for more details about the locality .

Sixty established individuals of studied species - *Succisa pratensis* (Dipsacaceae) - were chosen. *Succisa pratensis* is a rosette-forming herb with a root system composed of spreading, rather superficial roots. It represents a species typical to relatively unproductive damp pastures and ungrazed grassland. Its abundance is decreasing as result of drainage and high fertilizer input (Grime, Hodgson and Hunt 1987). More information can be found in Adams (1995).

The experiment was set up in ten blocks, with 6 individuals of *Succisa pratensis* in each of them. Within each block experimental treatments were randomly assigned to plants. The design of the experiment was 3x2 factorial in which the factors were (1) two levels of nutrient enrichment (fertilized and unfertilized) and (2) three competition levels (full competition, underground competition only and no competition). A commercial NPK fertilizer was applied according to the instructions from the producer at the beginning of every vegetation season. 15 g of NPK was added per plot. The levels of competition were as follows: (1) untreated control (full competition), (2) the vegetation within the 25cm radius of the target plant was repeatedly clipped and removed (shoot competition absent, present only root competition), and (3) trenching (both root and shoot competition absent). In trenched plots the root competition was controlled by surrounding the target individual by a polyethylene tube inserted into the soil (50 cm diameter, 30 cm deep). Shoot competition was excluded by hand pulling of the vegetation inside the tube. To prevent the ponding of water, the upper part of the tubes was level with the ground. The vegetation recovering inside the tubes was pulled periodically throughout the vegetation season to maintain the removal.

The numbers of leaves and tillers were counted at the beginning and the end of the vegetation season (June - September). At the end of the season, the numbers of flowers, flowering stems and the height of the plants were also recorded. After the third year of the experiment, the above-ground parts of all of the plants were collected. The leaf areas were measured and dry aboveground biomass of each plant was weighted. Moreover, the underground parts of 18 plants (3 blocks) were extracted and the root length, underground biomass and total biomass were determined also. Image Analyzer was used for measuring both leaf area and root length. Intensity of competition was measured as the suppression of target appearance in presence of both roots and shoots of neighboring vegetation or in presence of roots of neighbors only. Total competition intensity (CI_T), shoot competition (CI_S) and root competition (CI_R) were calculated as

$$CI_T = (B_{Tr} - B_{Co})/B_{Tr}$$

$$CI_R = (B_{Tr} - B_{Cl})/B_{Tr}$$

where B_{Tr}, B_{Cl} and B_{Co} is target biomass of trenched, clipped and control plants. Aboveground competition intensity was assumed to be the difference between CI_T and CI_R, so that CI_S was calculated as

$$CI_S = CI_T - CI_R$$

CI was counted separately for fertilized and unfertilized plants, and for shoots, roots and total biomass.

For statistical analyses, data were subjected to two-way ANOVA (biomass, leaf area, root length and competition intensity), or to repeated measures ANOVA with two trial factors - season and year (number of leaves, shoots, flowering stems, flowers and plant height). The correlation between biomass, leaf area, and root length and other morphological characters was analysed.

Results:

To assess the reliability of traits recorded over three seasons, their correlation with biomass, leaf area and root length of plants subjected to experimental treatments was analyzed. Only the data collected in autumn 1997 could be used.

All of the traits measured were significantly correlated with total and above-ground biomass. Except for plant height, all of the traits were correlated with below-ground biomass and the leaf areas of the experimental plants. Only the numbers of leaves, tillers and flowering stems were significantly correlated with root lengths of measured individuals. The relationship between root length and number of flowers was on the significance limit ($P=0.05$). From the summary of the tests performed (Table 1) it is evident that the number of leaves of an experimental individual was most closely associated with variables such as biomass, leaf area or root length. Hence it was used as a dependent variable in most of the tests in which these traits could not be used.

Leaf area:

The leaf area size is significantly affected by experimental treatments. The factor influencing experimental plants is the „level of competition„ (ANOVA, $P<0.01$). Individuals completely released from competition or those affected by root competition only had considerably larger leaf area than those subjected to full competition (Fig. 1).

Unlike the competition level, the leaf area size is not significantly affected by the nutrient level ($P=0.19$), although the leaf area of fertilized plants is larger (Fig. 2).

Furthermore, the effect of the nutrient enrichment differs with the „level of competition„ factor, i.e., the nutrient enrichment x competition level interaction is statistically significant ($P<0.01$, Fig. 3). The lowest leaf area was measured on control plants - both fertilized and unfertilized. Considerably enlarged leaf area in comparison with the control treatment was found in those plants released from shoot competition. Within these, slightly larger leaf area was detected on unfertilized plants. While the size of the leaf area increased in fertilized plants when bellow-ground competition was also prevented, unfertilized plants clearly showed a decrease in leaf area size.

Root length:

The results of the analyses testing the root length are analogical to those of leaf areas, although their significances are not so high.

As before, the root length is influenced by „competition level„ treatment type ($P<0.05$, Fig. 1) and the enhancement of soil nutrients does not affect the plants ($P=0.23$). Unlike the preceding results, the nutrient enrichment x competition level interaction is not significant ($P<0.12$, Fig. 2). However, it should be noted, that the root length was measured in only 18 plants and thus the test is very weak.

In comparison with the full competition treatment, more developed root system was found in trenched plots. Although the response of plants growing in presence of roots of neighbors was closely associated with the response of plants without neighbors when leaf area was analyzed, the opposite is true for root length test. In this case, the root length did not differ between control and root competition treatment.

Even though the competition x nutrient level interaction did not reveal statistically significant results, certain trend can be detected from Fig. 3. When released from above-ground competition, no reaction of either fertilized or unfertilized plants was found. On the contrary, when released from root competition, pronounced changes, especially within fertilized individuals, were revealed.

Longer root length in the absence of competition is due to substantially higher number of smaller side roots, which are responsible for nutrient uptake (Fig.4).

Biomass

The amount of above-ground biomass differs significantly among treatments ($P<0.01$), and again, the nutrient level does not significantly affect the plants. The competition x nutrient level interaction did not reveal significant results either.

According to root biomass analysis performed, no changes were found with respect to the experimental treatment. Neither of the factors tested nor their interaction revealed significant results. However, the response of root biomass to competition level treatment was on the significance limit ($P=0.052$).

The processes occurring aboveground are different from those, taking place in below-ground parts of the plants. While the shoot weight increased accordingly in both fertilized and unfertilized plots when shoot competition was restricted, the reaction of plants depended upon the nutrient level when competition was further lowered. Subsequently, in fertilized plants a further increase of aboveground biomass was found, while unfertilized individuals showed a decrease. The changes described were found when analysing root biomass as well, but here the differences in response of fertilized and unfertilized plants were detected when shoot competition was controlled (Fig. 5).

Significant changes in total biomass were detected among competition level treatments only ($P=0.05$). The amount of total biomass was not affected by the presence of soil nutrients ($P=0.89$). Equally, both fertilized and unfertilized plants showed good consiliency in their response to competition level treatments (competition level x nutrient level interaction, $P=0.85$). The maximal biomass was found in trenched plants. A continuous decline of biomass was found in clipped and control plants (Fig. 6). The results of tests are reported in Table 2.

Repeated measures:

Analysing the data from all three years of the experiment, the number of leaves of experimental plants differ significantly among competition level treatments ($P<0.01$), between the beginning and the end of a season ($P<0.01$) and between years ($P<0.01$). The complete result of this analysis is presented in Table 3.

The lowest leaf number was found in control plants, the highest in plants growing in the absence of competition. As before, the numbers were lower in unfertilized plants compared with the fertilized ones, but the results of the test were not significant. The number of leaves was lowest in the first year of the experiment, with a continuous increase in the following two years. Not surprisingly, the numbers of leaves were higher in the autumn than in the spring.

Also, some of the interactions analyzed revealed significant results (Fig. 7-Fig. 11). Clearly, the importance of competition level was proved to change during the course of the experiment (competition level x year - Fig. 7 and competition level x year x season interactions were highly significant). On the other hand, neither nutrient level x year (Fig. 8), or nutrient level x season interaction revealed significant results. This means that the effect of nutrient addition on plant performance was negligible. However, nutrient level x season x year interaction was significant ($P<0.05$). The detailed picture of changes occurring within years is shown in Fig. 9 and Fig. 10. The competition x nutrient level interaction is not significant, although a certain trend was found implying that the relative importance of shoot and root competition changes with nutrient level ($P= 0.08$, Fig. 11).

When analyses of other plant attributes - number of tillers, flowering stems, flowers and the height of plants - were performed, less significant results were found (Table 4). Within them, the most pronounced differences were found among competition treatments and among years. Also the competition x nutrient level and the competition level x year interactions showed significant results often.

The plant trait found to be most often influenced by experimental treatments was the number of shoots. The least affected trait was the height of the plants.

Competition intensity

The intensity of competition does not vary with the amount of nutrients present. Nevertheless, the competition was found to be less intense in fertilized plots. No differences among shoot, root and total competition intensity were found either.

When different source of data (i.e., shoot, root or total biomass) was used for calculation of competition intensity, resulting values showed a tendency to differ ($P=0.08$). This was confirmed by significant source x type of competition intensity (i.e., root, shoot or total competition intensity) interaction ($P<0.05$, Fig. 12). Above-ground and below-ground parts of plants (source of data) differed completely in the pattern of their response to the intensity of above-ground and below-ground competition. When separate analyses for shoot, root and total CI were performed, the values of CI_S and CI_T showed a tendency to differ in dependency on the source of data used. On the contrary, the intensity of root competition was found to be the same when counted from root, shoot or total biomass.

The difference in CI values calculated using different sources of data can be found especially in fertilized plots (nutrient level x source interaction; P=0.08, Fig. 13). For more details about the source x type of competition intensity x nutrient level relationship see Fig. 14.

Nutrient enrichment does not affect the way in which different parts of a plant reflect root, shoot and total competition intensity (nonsignificant nutrient level x source interaction).

Discussion

Leaf area, root length, biomass

When examining the relationship between leaf area, root length, and biomass of plants and experimental treatments, analyses were based on the data set from summer 1997. This means that only 60, respective 18 data points were available for analyses.

Generally the plants responded to competition level treatment.

Although they were generally larger when fertilized, the plants did not show a significant response to nutrient enrichment.

It is evident from Fig. S1.STG that above-ground and below-ground parts of plants responded differently to the experimental treatments. While the changes in shoot biomass and leaf area were observed when the plant was released from above-ground competition, the root biomass and root length did not show an increase until bellow-ground competition was restricted. This leads to the conclusion that the presence of competition for light determines a large part of the development of aboveground parts of the plants, and similarly, the root system reflects the intensity of competition for nutrients. This hypothesis is supported by Eagles (1971) who found similar differences in the response of above-ground and below-ground parts of plants. No other paper where the response of both roots and shoots of a target plant to competition treatments was examined was found.

The effect of nutrient enrichment tends to change with respect to competition level treatment, even though the differences are not significant in most of the analyses performed. In previous analyses, no differences between trenched and clipped plants (when aboveground biomass and leaf area were tested), and between clipped and control plants (when roots were examined) were demonstrated. When the amount of nutrients present was taken into account, contradictory trends in plant appearance were found between these treatments. The biomass, leaf area, and root length of fertilized plants showed an increase when a relevant competition level was restricted, whereas a decline was detected when nutrient level was low.

I am aware of no other comparable studies that have examined similar problem or have found similar results. A possible explanation for this paradoxical phenomenon may be the competition for space, as described in Yodzis (1986). Plants tend to fill any free space available before other plants do so, in order that the uptake of resources from other plants is prevented. Because the amount of soil nutrients is a factor that limits the growth of a plant, when nutrients are available, growth of both, above- and bellow-ground parts is enabled. However, when the amount of soil nutrients is low, only growth of either the shoot or the root can be realized. Thus, when competition for light is absent (i.e., no neighboring plants are present) unfertilized individuals show an increase in above-ground biomass but the growth of roots is suppressed or shows a decline, and when no neighboring roots are present, experimental individuals show an increase in bellow-ground parts to the detriment of shoot performance. This implies that the presence of nutrients and below-ground processes are probably more important than the results of this experiment suggest.

Number of leaves, stems, flowers, flowering stems, and the height of the plants

When analyses of the data recorded within three years of the experiment were carried out, a more complex and reliable picture describing the changes occurring during the course of the experiment was obtained.

Unfortunately, the character of data collected does not enable to derive any generally acceptable conclusions concerning the character of the competitive processes occurring, since only above-ground attributes were examined. Preceding results show that the response of above-ground parts of the plant cannot be applied to bellow-ground parts also (Fig. ..).

In spite of that, the pattern of influence of root and shoot competition on shoot performance was confirmed, as well as the lack of response to nutrient addition and the minor importance of the competition x nutrient level interaction. The mode of the response to experimental treatments that was obtained for biomass (Fig. 5) and discussed above was detected only in the last year of the experiment (Fig. 7).

The changes occurring during the course of the experiment were investigated. Between the beginning and the end of vegetation season, pronounced changes were found mainly in the first year of the experiment (Fig. 11). This can be due to the fact, that the main changes following the establishment of the treatments occurred only in the first year. However, this is not confirmed by the other results of the experiment.

On the contrary, within years, the differences between fertilized and unfertilized plants tended to increase (Fig. „16„). The relative importance of competition level treatments is also changing throughout the years. The role of root competition increases gradually and reaches the highest point in the last year (Fig. 7). However, when a distinction between fertilized and unfertilized individuals was made, this was true for fertilized plants only (Fig. 11).

This probably shows that the biomass accumulation is limited by nitrogen availability even after three years of fertilization and that the increasing amount of nutrients causes increasing difference between no competition treatment and root competition treatment, which is seemingly revealed as increasing importance of root competition. Again, it supports the idea of that below-ground competition is underestimated.

The intensity of competition

The total intensity of competition was not found to vary with habitat productivity, which would support Tilman`s hypothesis. However, if this is true, the intensity of root and shoot competition should change along this gradient (Wilson and Tilman 1991, Wilson and Tilman 1993), which was not confirmed.

When assessing the intensity of competition, the variability of results in relation to the source of data used for its calculation should be noted. This means that different components of competition intensity are reflected differently in above-ground and below-ground parts of a plant. However, this is true only for total and above-ground competition, where changes in both of them are reflected in shoot appearance, but not in the root system of a plant. The below-ground competition intensity is reflected in both roots and shoots, although the extent seems to be higher in below-ground parts of a plant. One possible mechanism as to how root competition affects above-ground parts of a plant may be the change in light availability. Tilman (1984) reports that resource addition caused the decline of light penetrating the soil surface from 70% in untreated vegetation to 4% in fertilized plots. No studies that I am aware of evaluated both competition for light and nutrient intensities in above-ground and below-ground parts of plants.

Relative importance of root and shoot competition

The relative importance of root and shoot competition is often discussed in the literature (e.g.

Eagles 1971, Belcher, Keddy and Twolan-Strutt 1995, Snaydon and Howe 1986, Wilson 1988).

The higher importance of both components root (Snaydon and Howe 1986, Eagles 1971) and shoot competition (Gibson 1988, Grubb, Ford and Rochefort 1997) is reported. Nevertheless, studies in which root competition was found to be more important are prevailing (Wilson 1988).

The interpretation of the relative importance of above- and below-ground competition is based on the assumption that the effects of above- and below-ground competition are purely additive, so that the difference in performance of plants grown with all neighbors and those grown with only the roots of neighbors is caused by above-ground competition. In a review of pot experiments dealing with above-ground and below-ground competition both positive interactions (the effect of full competition is greater than the sum of their separate effects) and negative interactions between above- and below-ground competition were reported (Wilson 1988). These interaction were suggested to occur relatively rarely. More than half of the interactions were found to be negative (Wilson 1988). New designs are required to test whether such interactions occur in natural vegetation (Wilson and Tilman 1991).

If negative interactions occurred, the importance of root competition was underestimated in this experiment.

Although in the study presented, it is not possible to reach final conclusion, and although the importance of root competition is probably underestimated, it seems that the role of competition for light is more pronounced than in most of the studies found.

In summary, the results obtained demonstrate, that competition importance does not change along a productivity gradient and that Tilman`s rather than Grime`s theory is supported. The role of shoot competition is more pronounced than other studies found it to be. The response of aboveground parts of plants to competition differs considerably from that of below-ground. Because the conclusions reported in the majority of studies are based on the response of only above-ground parts, experiments dealing with root systems are needed for a better understanding of the nature of competitive processes.

Limitations of the experimental design

A significant part of the results is based on a relatively small sample size. Below-ground parts of only three experimental blocks were dug out. Except for root length and root biomass tests, all total biomass and all competition intensity analyses were performed using this limited data set. Thus the significance of the relationships is underestimated and many analyses which revealed the P to be close to the five percent limit would reveal significant results if the sample size was larger.

The results showed not to respond to nutrient addition. Unfortunately, no measurements were made which would evaluate the exact amount of nutrients really available for plant growth. Especially in oligotrophic habitats, the nutrients may be strongly immobilized by inorganic adsorption and lost through leaching processes (DiTommaso and Aarsen 1989). The activity of decomposers may also considerably confound the interpretation of fertilization experiments (Pastor et al. 1987). The amount of nutrients available for plants may be affected also by the decomposing roots from removed neighboring vegetation, which is often mentioned in literature (Aarsen and Epp 1990, Goldberg, Turkington and Olswig-Whittaker 1995, Goldberg 1995).

Also, no measurements of light availability were made, thus the results showing the importance of shoot competition cannot be compared properly with other studies.

The method used for restriction of above-ground competition might have caused changes in below-ground competitive ability of neighboring vegetation.

Another misinterpretation of results may be caused by changes in water drainage in trenched plots (Aarsen and Epp 1990).

And, finally, the shoot competition intensity was assumed to be the subtraction of total and root CI. The interaction between root and shoot competition was assumed not to exist. This is, however, only an assumption. For precisely evaluating the importance of shoot competition, a fourth treatment where root competition would be restricted and only shoot competition would occur is necessary. This is difficult to establish under field conditions, although a few attempts have been made. For controlling shoot competition, glass divisions were used in a box experiment (Eagles 1971). and tubes of reflective aluminum were placed around seedlings in a sward for the same purpose (Snaydon and Howe 1986).

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Poděkování:

Přeji Šuspovi, aby ho v případě, že na Papuu nakonec doopravdy odcestuje, nesežrali domorodci, protože to by byla věčná škoda. Dík patří paní Šimkové i ostatním na ÚMBRu, protože byli tolerantní, když jsem jim při měření listových ploch zabírala místo v jejich laboratoři. A v neposlední řadě bych chtěla poděkovat všem na této fakultě za to, že jsou tak

ŠÍLENÍ!

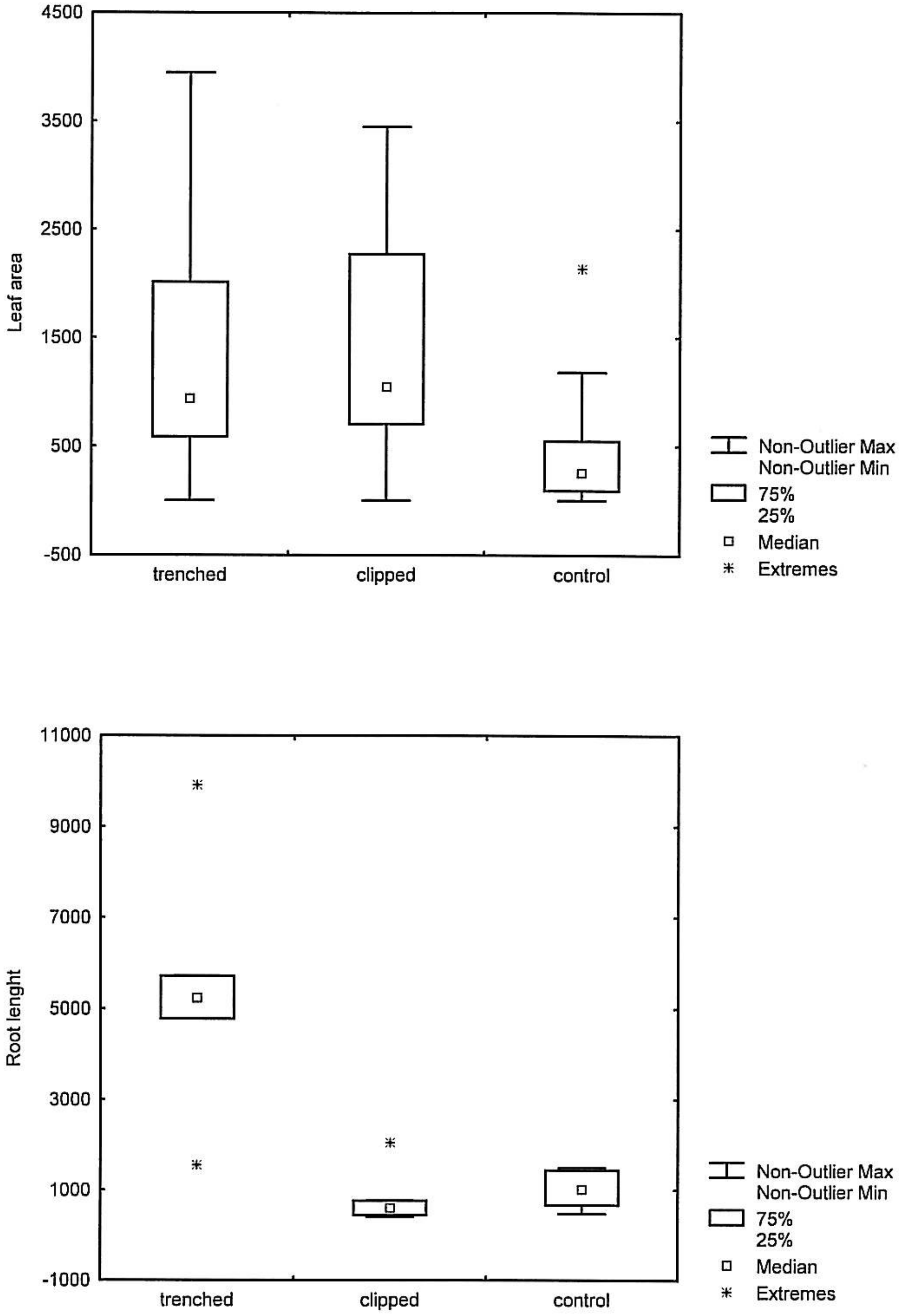


Fig. 1:
Box and whisker plots of leaf area size and root length of plants in different competition treatments (trenched - no competition, clipped - root competition, control - full competition).

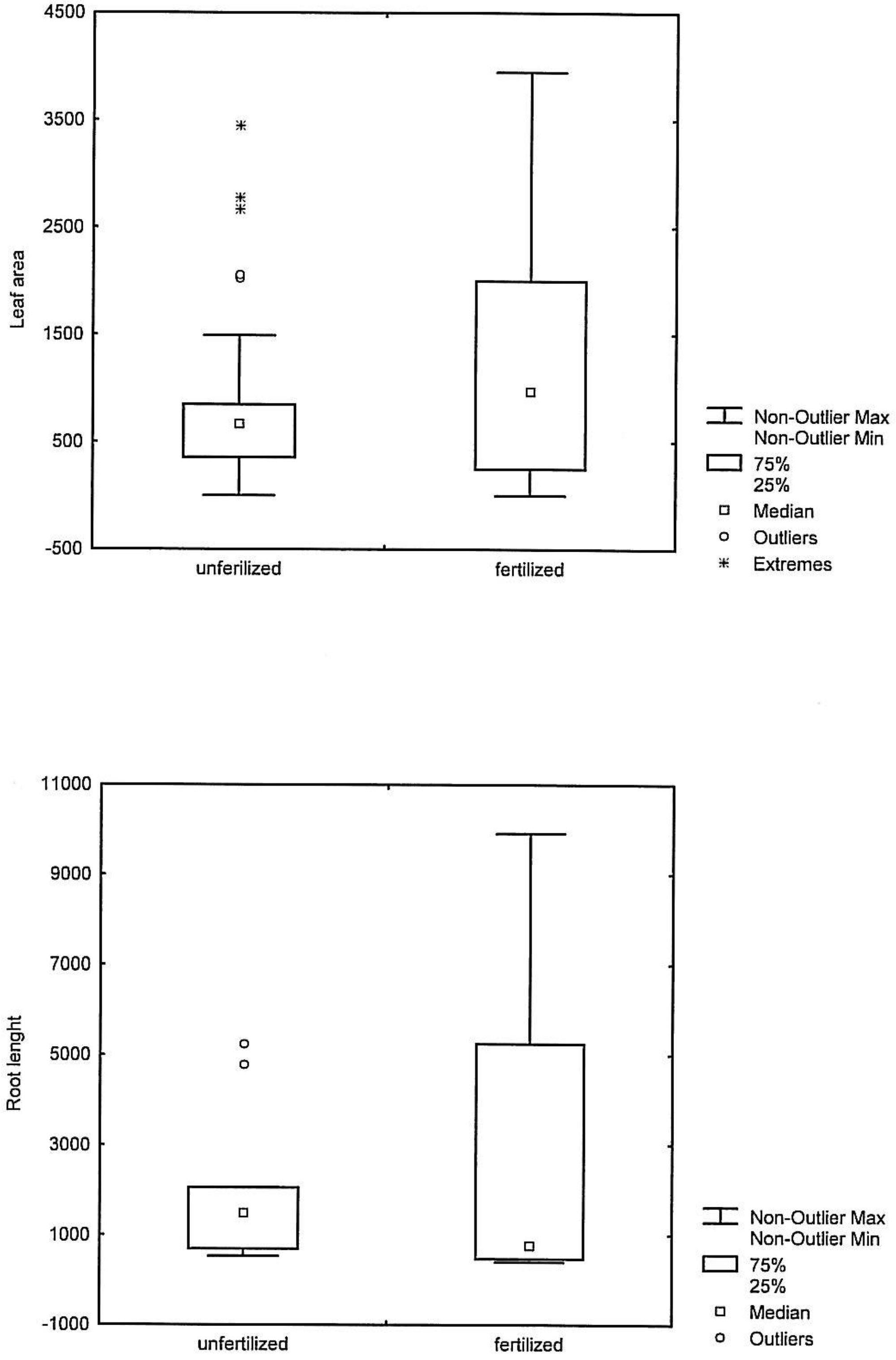


Fig. 2:
Box and whisker plots of leaf area size and root length of plants in plots with different nutrient levels.

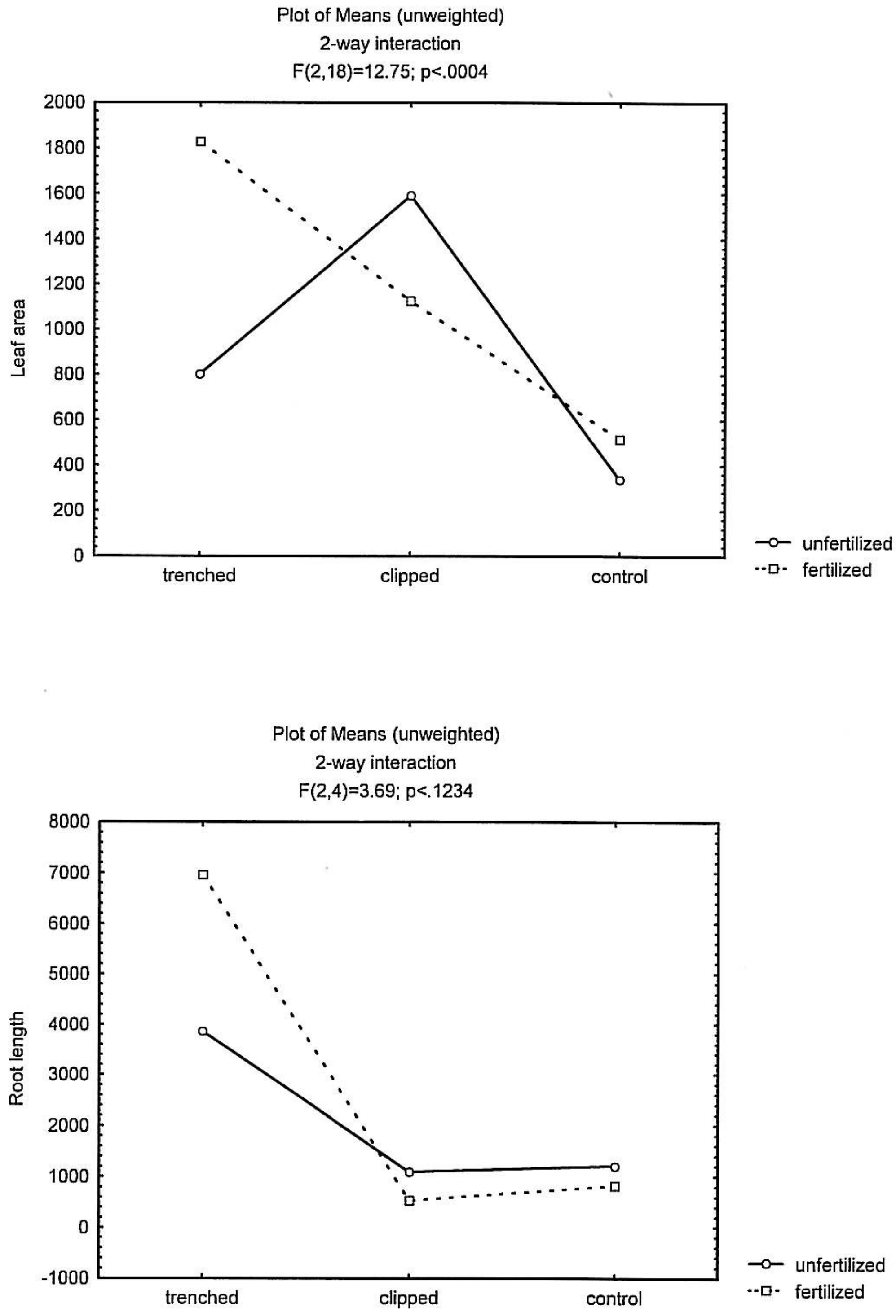
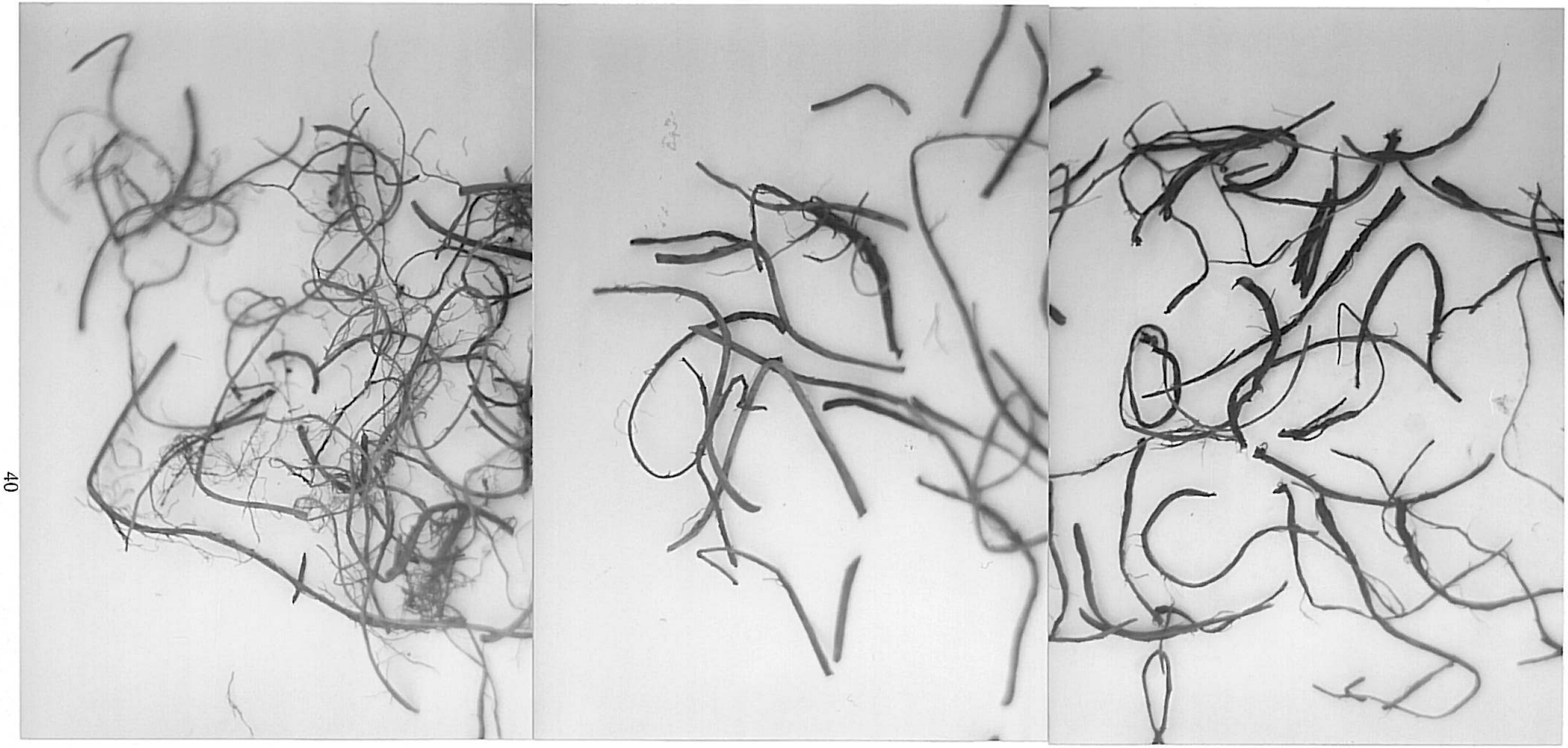
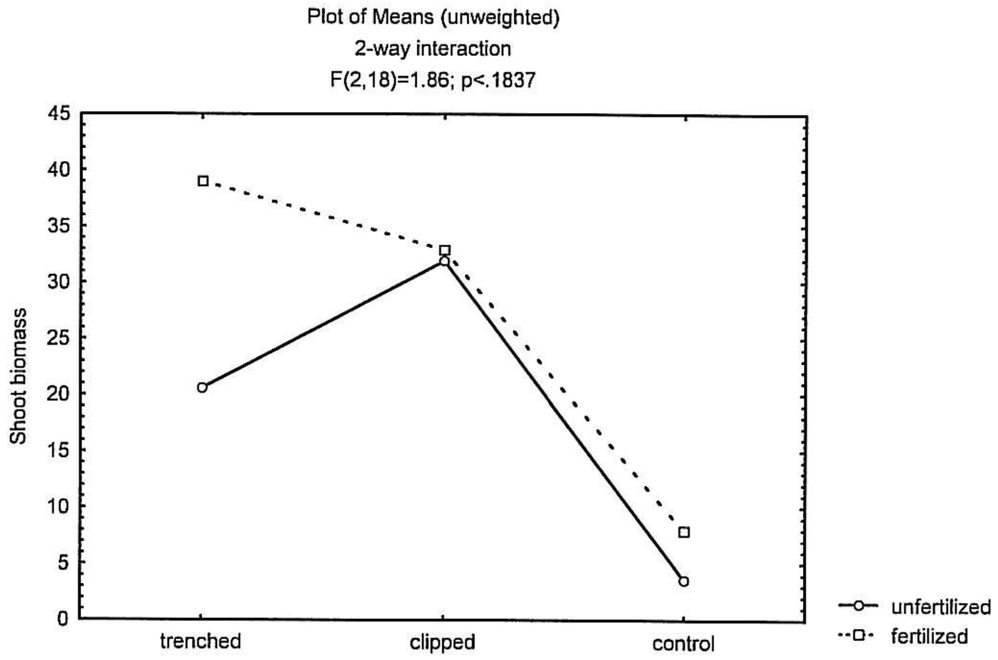


Fig. 3:
Plots of means - leaf area size and root length of plants in dependency on competition and nutrient level treatments analyzed by two-way ANOVA - competition level x nutrient level interaction.



Trenched Clipped Control

Fig. 4:
Roots of plants growing in trenched, clipped and control plots.



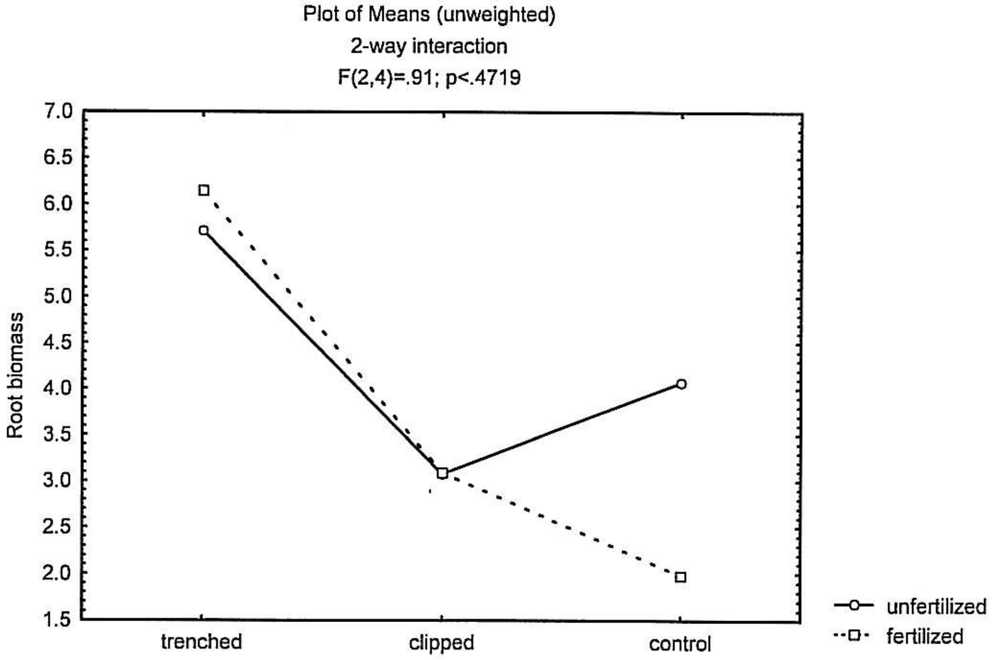


Fig. 5:
Plot of means - the amount of shoot and root biomass in dependency on competition and nutrient level treatments analyzed by two-way ANOVA - competition level x nutrient level interaction.

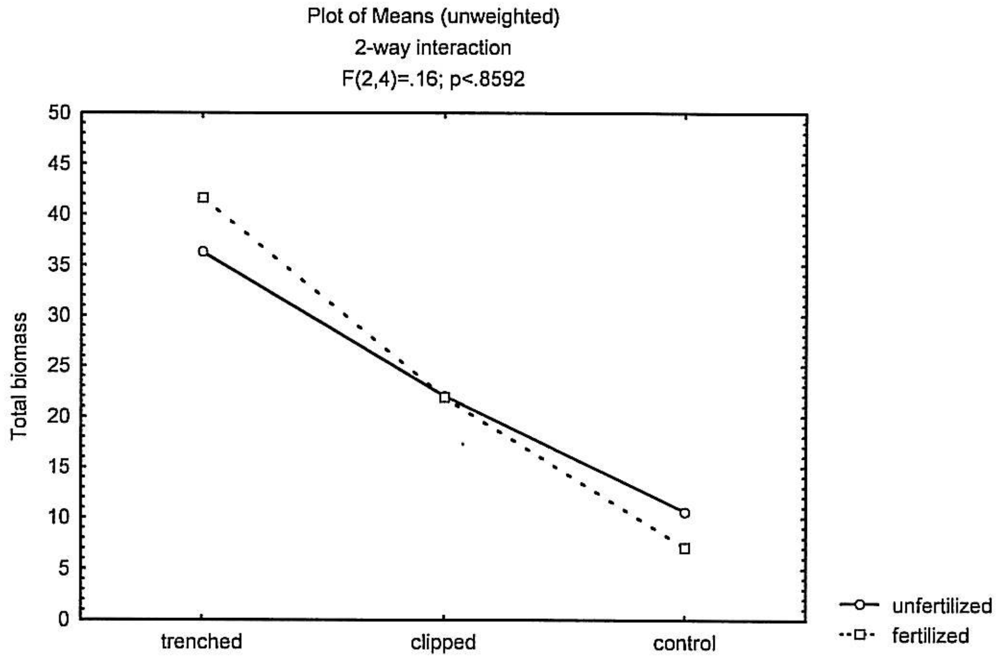


Fig. 6:
Plot of means - the amount of total biomass in dependency on competition and nutrient level treatments analyzed by two-way ANOVA - competition level x nutrient level interaction.

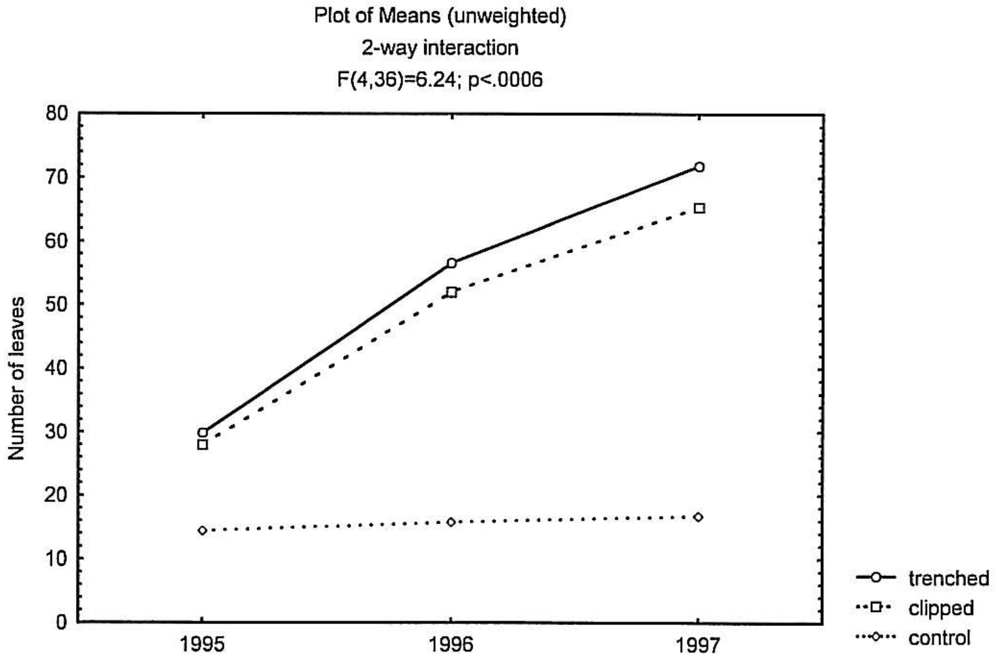


Fig. 7:
Plot of means - changes in number of leaves of experimental plants in plots with different competition level treatment over years; competition x year interaction.

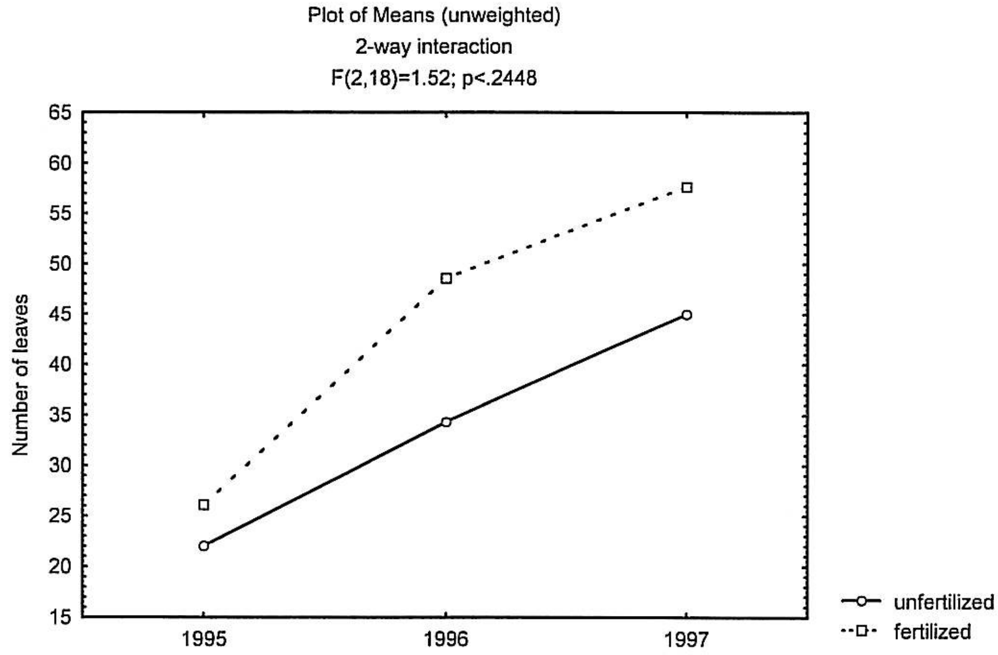


Fig. 8:
Plot of means - changes in number of leaves of experimental plants in plots with different nutrient level over years; nutrient level x year interaction.

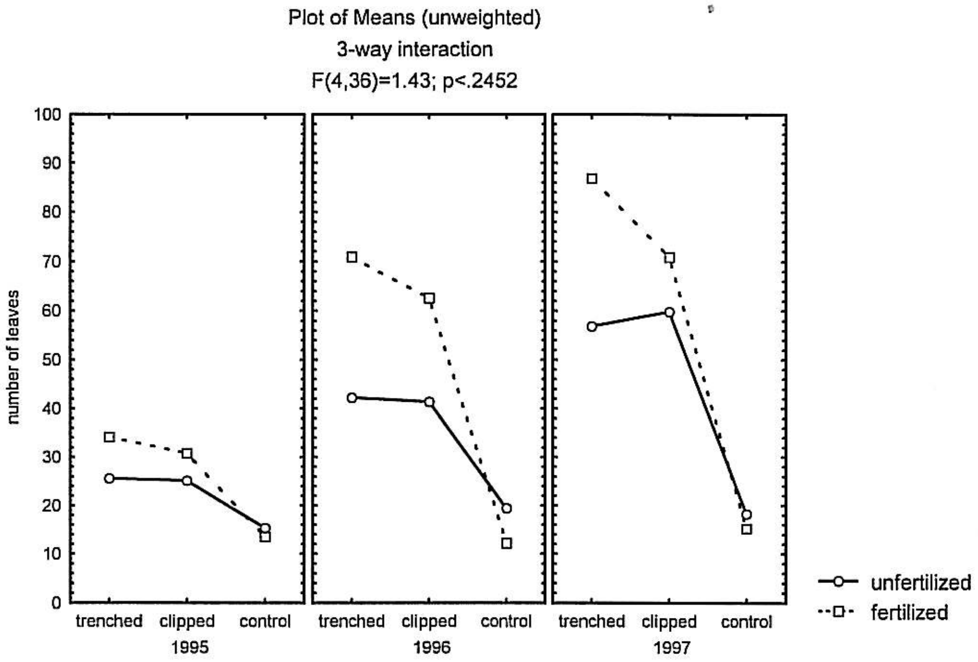


Fig. 9:
Plot of means - changes in number of leaves of experimental plants in plots with different competition and nutrient level treatments over three years of experiment - result of competition x nutrient level x year interaction.

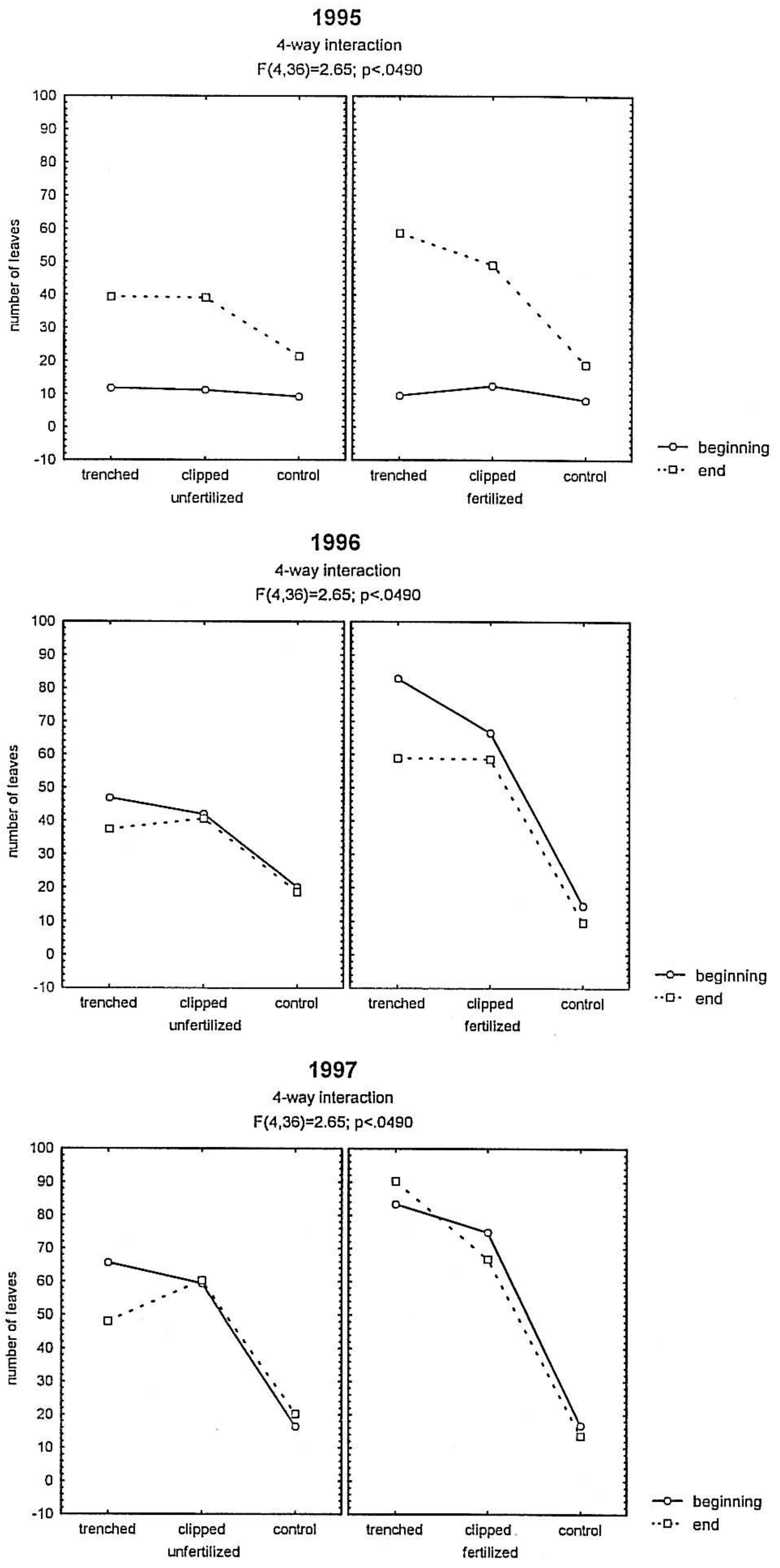


Fig. 10:
Plot of means - changes in number of leaves during the course of the experiment. Competition level x nutrient level x year x season interaction.

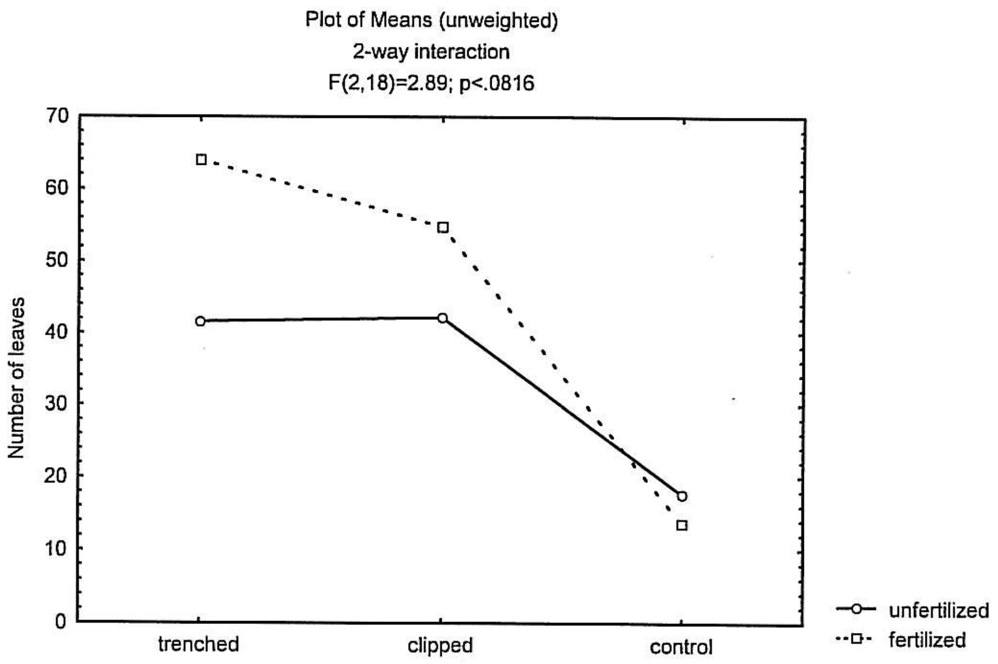


Fig. 11:
Plot of means - changes of number of leaves of experimental plants subjected to different competition and nutrient treatments. Mean values of number of leaves for all three years of the experiment are figured.

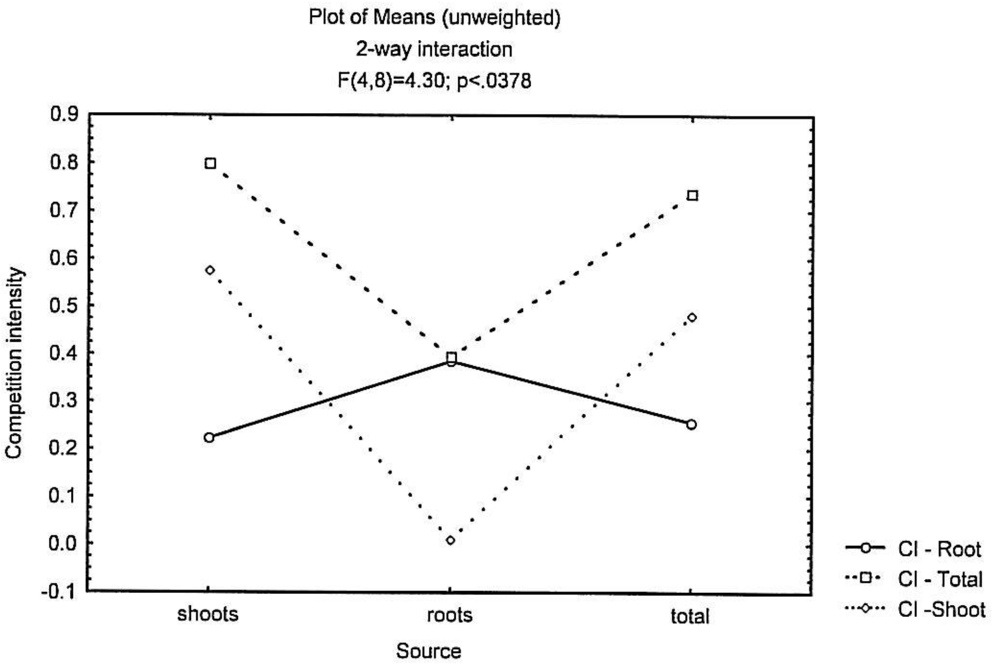


Fig. 12:
Plot of means - source of data x type of CI interaction. Root competition intensity (CI - root), total competition intensity (CI - total) and shoot competition intensity (CI - shoot) were calculated using above-ground biomass (source - shoots), below-ground biomass (source - roots) and total biomass (source - total).

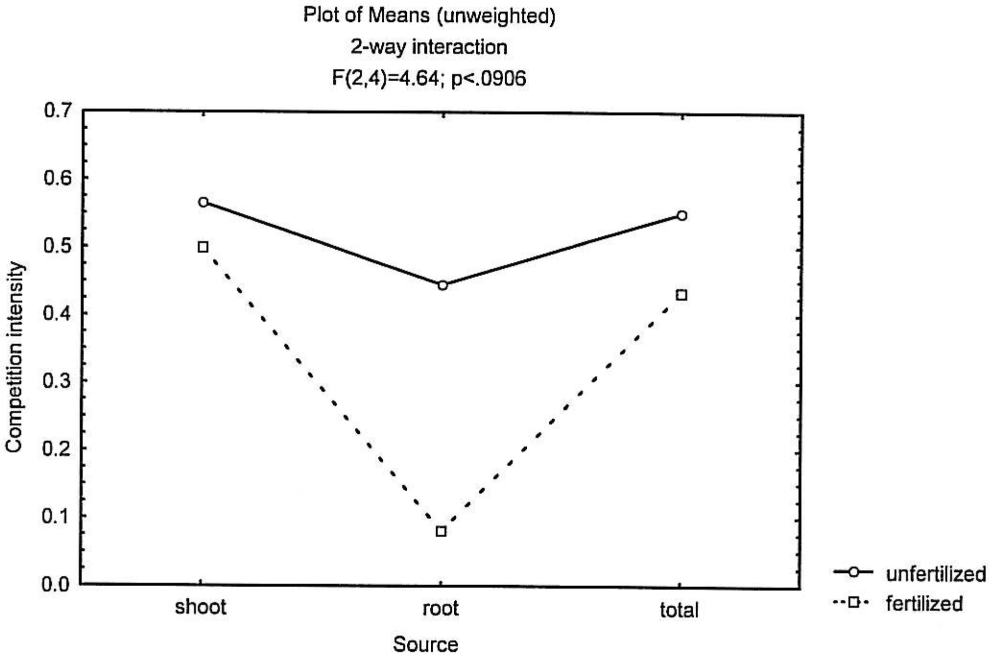


Fig. 13:
Plot of means - changes in competition intensity in dependency on nutrient level and source of data used for calculation; source x nutrient level interaction.
Above-ground biomass (shoot), below-ground biomass (root), or total biomass (total) was used for calculation of competition intensity.

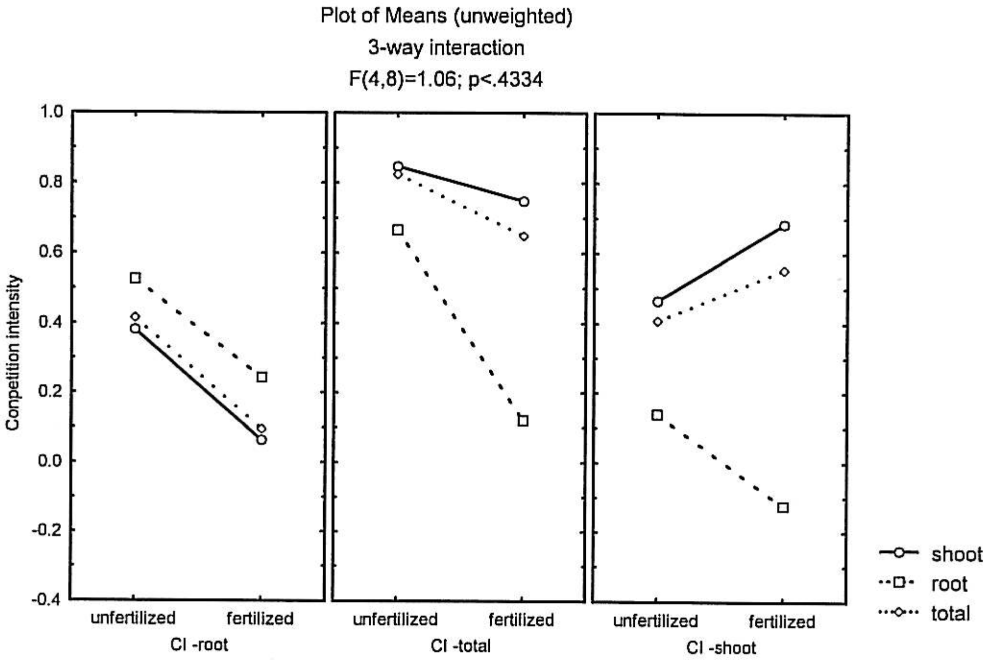


Fig. 14:
Plot of means - changes in different types of competition intensity (CI root, CI total and CI shoot) in dependency on nutrient level (fertilized, unfertilized) and source of data used for calculation (line pattern : shoot - above-ground biomass, root - below-ground biomass, total - total biomass).

Correlation matrix
Marked correlations are significant at p < .05

	root length	leaf area	aboveground biomass	belowground biomass	total biomass
number of leaves	0.8126	0.8227	0.7229	0.7771	0.7528
	p=.000	p=.000	p=.001	p=.000	p=.000
number of shoots	0.8126	0.6734	0.6867	0.7503	0.7167
	p=.000	p=.002	p=.002	p=.000	p=.001
number of flow. stems	0.7201	0.6056	0.7568	0.765	0.7818
	p=.001	p=.008	p=.000	p=.000	p=.000
number of flowers	0.4681	0.6615	0.8055	0.5654	0.7995
	p=.050	p=.003	p=.000	p=.014	p=.000
plant height	0.0474	0.1093	0.5936	0.124	0.5509
	p=.852	p=.666	p=.009	p=.624	p=.018

Table 1:
Results of correlation analysis of destructive and non-destructive variables.

LEAF AREA

Effect	df Effect	MS Effect	df Error	MS Error	F	p-level
1	9	2410188	0	0		
2	1	909462.813	9	466718.156	1.94863391	0.19621
3 *	2	5527017.5	18	427456.625	12.9300079	0.00033
12	9	466718.156	0	0		
13	18	427456.625	0	0		
23 *	2	2794362	18	219129.063	12.7521296	0.000355
123	18	219129.063	0	0		

ROOT LENGTH

Effect	df Effect	MS Effect	df Error	MS Error	F	p-level
1	2	1603143.5	0	0		
2	1	2333520	2	815828.75	2.86030626	0.23286
3 *	2	40558436	4	2965693	13.6758718	0.016278
12	2	815828.75	0	0		
13	4	2965693	0	0		
23	2	6393879	4	1730763	3.69425464	0.123363
123	4	1730763	0	0		

Table 2:
Results of two-way ANOVA for leaf area, root length, above-ground biomass, below-ground biomass and total biomass. Effects: 1- block, 2- nutrient level, 3- competition level. Significant results are marked by *.

ABOVE-GROUND BIOMASS

Effect	df Effect	MS Effect	df Error	MS Error	F	p-level
1	9	615.034363	0	0		
2	1	942.005127	9	303.033661	3.1085825	0.111712
3 *	2	4312.35254	18	267.159637	16.1414814	0.000097
12	9	303.033661	0	0		
13	18	267.159637	0	0		
23	2	430.12793	18	230.68396	1.8645767	0.183682
123	18	230.68396	0	0		

BELOW-GROUND BIOMASS

Effect	df Effect	MS Effect	df Error	MS Error	F	p-level
1	2	7.18580008	0	0		
2	1	1.35575557	2	0.32308888	4.19623089	0.177064
3	2	16.5360661	4	2.45116663	6.74620247	0.05229
12	2	0.32308888	0	0		
13	4	2.45116663	0	0		
23	2	2.74962211	4	3.01695561	0.91138971	0.47191
123	4	3.01695561	0	0		

TOTAL BIOMASS

Effect	df Effect	MS Effect	df Error	MS Error	F	p-level
1	2	21.1458721	0	0		
2	1	1.3393389	2	60.7602386	0.02204302	0.89559
3 *	2	1366.16199	4	195.563385	6.98577595	0.049539
12	2	60.7602386	0	0		
13	4	195.563385	0	0		
23	2	29.6010723	4	187.778473	0.15763827	0.859217
123	4	187.778473	0	0		

Table 2 - continuation:
Results of two-way ANOVA for leaf area, root length, above-ground biomass, below-ground biomass and total biomass. Effects: 1- block, 2- nutrient level, 3- competition level. Significant results are marked by *.

NUMBER OF LEAVES 1995-1997

Effect	df Effect	MS Effect	df Error	MS Error	F	p-level
1	9	5714.917	0	0		
2	1	9620.336	9	2389.385	4.02628	0.075747
3 *	2	49349.23	18	3057.841	16.13859	0.000097
4 *	2	22866.63	18	1405.482	16.2696	0.000092
5 *	1	2662.336	9	279.5213	9.524627	0.013009
12	9	2389.385	0	0		
13	18	3057.841	0	0		
23	2	5357.145	18	1853.518	2.890258	0.081557
14	18	1405.482				
24	2	890.3111	18	584.5364	1.523106	0.244843
34 *	4	4826.079	36	773.2057	6.24165	0.000638
15	9	279.5213	0	0		
25	1	43.40278	9	137.9213	0.314692	0.588507
35	2	195.0778	18	74.53148	2.617388	0.100509
45 *	2	11015.51	18	145.6315	75.63963	0.000000
123	18	1853.518	0	0		
124	18	584.5364				
134	36	773.2057				
234	4	633.9319	36	444.4813	1.426229	0.245152
125	9	137.9213	0	0		
135	18	74.53148	0	0		
235	2	471.7444	18	177.4574	2.658353	0.097375
145	18	145.6315				
245 *	2	614.7444	18	167.6982	3.66578	0.046184
345 *	4	1208.465	36	120.8819	9.99707	0.000015
1234	36	444.4813				
1235	18	177.4574	0	0		
1245	18	167.6982				
1345	36	120.8819				
2345 *	4	409.5236	36	154.5607	2.649598	0.048958
12345	36	154.5607				

Table 3:
Results of repeated measures ANOVA for number of leaves recorded over three years of the experiment. Effects: 1- block, 2 - nutrient level, 3- competition level, 4- year, 5- season (difference between the beginning and the end of vegetation season). Significant reults are marked by *.

	nutrient level	competition level	season	year	nutrient x competition	competition x season	competition x year	season x year	nutrient x competition x season	compet. x season x year
number of shoots	0.22	< 0.001	< 0.01	<0.001	0.089	< 0.001	< 0.001	< 0.10	< 0.01	< 0.01
number of flow. stems	0.085	< 0.001		< 0.001	< 0.05		< 0.001			
number of flowers	< 0.05	< 0.001		0.56	< 0.05		> 0.10			
plant height	0.31	< 0.01		<0.001	> 0.10		> 0.10			

Table 4:
Summary of Repeated measures ANOVA results for number of shoots, flowering stems, flowers and for height of plants.
P for all main effects and for some of the interactions (those revealing $P < 0.10$ at least in one of the tests performed) is presented.