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The effect of environmental heterogenity on clonal behaviour of *Prunella vulgaris*

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Bakalářská práce

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Anotace:
The growth response of clonal species *Prunella vulgaris* to the surrounding vegetation and decreasing light quantity or quality was investigated in three manipulative experiments in the field and in the growth chamber conditions. The stolon orientation was analysed using methods of circular statistics.

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Prohlašuji, že jsem uvedenou práci vypracoval sám, s použitím uvedené literatury.
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Content

Abstract

I studied the growth forms and orientation of stolons of a clonal herb *Prunella vulgaris* in response to plant position in gap, identity of neighbouring graminoid species and light competition. *Prunella vulgaris* is a common species in Czech Republic, growing in various plant communities including wet meadows. It has a prostrate growth form with long aboveground stolons penetrating deep into the surrounding vegetation. I compared the growth characteristics, such as the stolon and internode length in a competitive environment of *Molinia caerulea, Juncus effusus* and *Nardus stricta* and in gaps in a manipulative field experiment. Two pot experiments studied the effect of reduced light and of low red/far red ratio (R/FR) on the plant growth characteristics. In the field and one of the pot experiments, I monitored stolon orientation in a treatment divided into two parts (competition/shaded or gap/unshaded). I used circular statistics to evaluate stolon orientation. Plants growing in tussocks of graminoids had longer internodes and stolons. Flowering was more frequent than in plants growing in the gaps. The effect of treatments on the other characteristics (i.e. the amount of stolons and leaves, the sum of the length of stolons) was not significant. In the pot experiment, the internodes were longer in low R/FR and low light intensity treatments. In addition, biomass, stolon and leaves number were lower and leaves were smaller. In the divided treatments, the mean angles and centres of gravity of stolon tips were oriented away from the vegetation or out of the shaded parts (except low R/FR treatment with random distribution of stolons). However, the length of the stolons was not significantly dependent on the stolon orientation. *Prunella vulgaris* seems to grow patchilly in competition friendly environments or favourable light regime and escapes from the more unfavourable conditions by prolonging its internodes. *Prunella vulgaris* prefers unfertilised plots with regular mowing or similar disturbance regime.

Introduction

The grasslands in general, and particularly meadows, are plant communities with amazing species richness in Europe. The meadows often contain more than 50 species per square meter (Kull & Zobel 1991). However, this richness is in many cases endangered by human influence. These man made communities have been preserved for a long time by extensive management, grazing and mowing. Recently, the extensive management tactics have become less economical, thus the meadows are either fertilised or often abandoned (Špačková et al. 1998). The biomass increase with dominance of a few strong competitors, and consequently the decrease of species diversity, is a result of intensive management and abandonement also leads to a decrease of species diversity. The highest species diversity is

frequently found in the middle of disturbance and soil fertility gradients (Lepš 1999; Grime 1979).

In these species rich meadows, 80% of the species are clonal (Klimeš et al. 1997). The interest in the study of clonal plants has increased in the last decade (de Kroon and van Gronendalen 1990; de Kroon and van Gronendalen 1997). The modularity is typical for all clonal plants. They are composed of repeating ramets, feeding sites with resource acquiring structures, and spacers, the connections between ramets (Oborny 1994). They have many advantages, for example the longevity, and communication skills between ramets, resulting in the support of the young ramet in establishing phase or in redistribution of the resources after one module's death and the foraging, as a consequence of the plastic response of the clone to its environment. Nevertheless, the disadvantages are also present, including the easy spread of pathogens within the clone, and the accumulation of somatic mutations or metabolic and construction costs (Klimešová et Klimeš 1997; Hutchings & Bradbury 1986; Klekowski 1997). The differences within the clonal plants are mainly in the architecture (determined by the structural blue print, onthogenic variation and environmental conditions (Huber et al. 1999)), i. e. in the shoot growth parameters: the intensity and angle of branching and stolon length (Herben 1996). These factors define the growth strategies "phalanx", typical representant is *Nardus stricta*, and "guerilla" type, the growth form of species *Fragaria vesca* or *Prunella vulgaris* (Lovett Doust 1981). Based on their clonal characters, two types of horizontal competition can be distinguished: the "founder control" or "dominance control" (Herben 1996).

In this study I have conducted field and laboratory manipulative experiments with *Prunella vulgaris*, one of the clonal herbs present in the oligotrophic wet meadows, to investigate the response of its clonal growth to the neighbouring vegetation. The experiments in the growth chamber serve as the verification of the relationship found in the field experiment.

The aims of this study were as follows: First, by transplanting *Prunella vulgaris* seedlings into different types of vegetation, I investigated the effect of both above-ground and under-ground competition on the stolon and internode lengths and on the investment to sexual reproduction. I investigated how the microsites differ in space and whether there is any difference among competitors of various species. Second, in the growth chamber experiment I estimated only the effect of the aboveground competition on the stolon and spacer lengths and on the biomass production of target species by the manipulation of the light accessibility and quality. Third, in both experiments I investigated the ability of *Prunella vulgaris* to differentiate between the more and less advantageous conditions by placing the new ramets preferentially into the more advantageous patches or giving them the ability to escape from the disadvantageous ones.

My predictions were: First, because of the asymmetry of the competition for light (Lepš 1999) the seedlings of *Prunella* will grow better in places with the vegetation removed. In bunches of graminoid species the stolon will be very long and less foliaged. There might be differences between the graminoid species, because of their different density. Second, both the light quantity and quality decrease will force the clone to the formation of long internodes in comparison with the internodes under the normal light conditions. In spite of the lower biomass production with the light quality decrease, the leaves will be larger to absorb the remaining light. Third, the stolons will be more oriented out of low light places and once established there, they will veer out of these conditions by changing their growth angle.

As the statistics to evaluate the data on a circular scale are not readily available (Aradóttir et al. 1997), one of the goals of this study was to prepare programs for use of these statistical methods based on their description in literature (Batschelet 1981; Zar 1996) and to use them in the evaluation of my experiments.

Material and Methods

Study species

The object of my studies was *Prunella vulgaris* L., a species belonging to a small genus in the family Lamiaceae. It has boreal, circumpolar distribution (Dostál 1989) (see App. 1) and occurs in many stands, for example in abandoned fields, pastures, lawns, along roads and paths, in open woodlands and on the borders of aquatic areas (Winn 1985; Bocher 1940; Schmid & Harper 1985; pers. obs.). *Prunella vulgaris* is a prostrate, annual to short lived perrenial herb (Winn 1991; Bocher 1940), (in our conditions mostly perennial) (pers. obs.), characterised by the *Fragaria vesca* type of clonal growth form (see Klimeš et al. 1997). The branching of *Prunella vulgaris* however, is monopodial with long internodes and fast clonal spreading. The typical "guerrilla" growth habit allows it to forage in a patchy environment (Schmid & Harper 1985; Schmid 1985b). The flowering individuals produce an erect stem with one terminal and several lateral inflorescences which flower later than the terminal inflorescence. Within an inflorescence flowers open basipetaly. Each flower is self compatible and contains four ovules, so the maximal number of nutlets per flower is four. They have no specialized means of dispersal and do not survive in the soil more than 1yr (Winn & Werner 1987). Their weight, and their success in emerging, is dependent on the length of time from pollination, and the growing season (Winn 1986). The flowers appear in June, and can be open more than one month and finish by seed dispersal in early November (pers. obs.; Winn & Gross1993). Schmid (1985a) claims that the reproduction of *Prunella vulgaris* is mainly by clonal growth and the establishment of seedlings is rare, but this result is in contrast with others (Winn & Werner 1987). In our study site Zelený (1999) documents

seedlings in tussocks of *Molinia,* but seedling survival was not studied. *Prunella vulgaris* is a weak competitor for light and it grew better after litter removal in locality Ohrazení (see below), it prefers mown unfertilized plots (Lepš 1999). *Prunella vulgaris* is mycorrhizal, VAM type (Titus & Lepš 2000; Streitwolf-Engel et al. 1997; Moora & Zobel 1996) and has 2n=28 (Dostál 1989).

Study sites

The field experiment was located in the locality Ohrazení. It is an oligotrophic wet meadow with high species richness, located 10 km south-east of České Budějovice, Czech Republic, 48° 59' N, 14° 36' E, 510 m a.s.l.. Mean annual precipitation is 600-650 mm and mean annual temperature is between 7°C and 8°C. According to phytosociological classification the vegetation belongs to the Molinion (Molinietum caeruleae), in the eastern part with some species characteristic to Violion caninae. The management of the locality was regular mowing (once or twice a year) since early 1990s (Špačková et al. 1998; Lepš 1999). In the locality Ohrazení the long term research have been conduced with publication outcomes (Lepš 1999; Petrů & Lepš 2000; Špačková et al. 1998; Titus & Lepš 2000; Kotorová & Lepš 1999) and several thesis.

The second part of the experiment was in the laboratory conditions in České Budějovice in a small growth chamber with light regime 12/12 h respectively 11/13 h with the temperature fluctuating between 20°C (night) to 28°C (day).

Experimental design

Field experiment

The *Prunella vulgaris* seeds were sown at the room temperature in mid April 1998. The field experiment was established 5 June 1998 in recently mown meadow with litter removed. I transplanted 120 jiffy pots with *Prunella vulgaris* seedlings to 20-1m^2 quadrats; each quadrat contained six treatments. The seedlings were transplanted into one of three bunches of graminoid species: *Nardus stricta, Juncus effusus* and *Molinia caerulea*, and into three types of gaps: square gaps (vegetation removed from 20cm × 20cm gap), natural gaps (place without the vegetation, among the bunches) and half-gaps (vegetation removed diagonally from half of the 20cm × 20cm square, seedling transplanted to the centre of the square, see App. 2). After three weeks, three dead seedlings were replaced by new ones. The number and length of stolons (in the half-gap also the orientation of stolons) and number of leaves on each stolon were measured, five times (18 August 1998 and 9 May, 31 May, 3 July and 12 August 1999), until the end of the experiment at the end of 1999. The litter was removed for the second time in April 1999.

Nine relevés 2m × 2m each with or without *Prunella vulgaris* were recorded in June 1999 around the locality Ohrazení to evaluate its local phytosociological behaviour.

Growth chamber experiment

The laboratory pot experiments consisted of two similar experiments. The first part was established on 19 November 1998 by transplanting 84 jiffy pots with seedlings of *Prunella vulgaris* into pots. After two weeks, I covered them with aluminium foil of varying shapes, decreasing the Photon Flux Density (PFD) (i.e. the total amount of light). The four treatments were: "A-f 1" (the entire pot shaded by foil with a 10cm × 10cm square), "A-f 3/4" (three-quarters of the seedlings shaded by foil), "A-f 1/2" (half of the seedlings shaded with a 10cm × 5cm rectangle) and "Control" (without foil). The experiment was arranged in a randomised block design. I measured the width of the first two completely developed leaves, the number of leaves on each stem, the length of the stolons and the number of leaves of each stolon. Stolons shorter than 0,5 cm were not measured. Two measurements were done on 17 December 1998 and 5 January 1999. The light regime was a 12 hour day length.

In the second pot experiment, seeds were sown on 10 January 2000 and seedlings were transplanted into pots on 28 January 2000. In mid February I randomised all pots and covered the seedlings by two types of foil, one aluminium foil as in the last experiment and second green plastic foil changing the light quality by decreasing the R/FR ratio (ratio of red to far red light, Dong 1993) (with foil: R/FR = 70; without foil: R/FR = 180). The five treatments, again arranged in completely randomised block design, were: "A-f 1" (the entire pot shaded by aluminium foil with a 10cm × 10cm square), "A-f 1/2" (half of the seedlings shaded by aluminium foil with a 10cm × 5cm rectangle), "G-f 1" (the entire pot shaded by green plastic foil with a 10cm × 10cm square), "G-f 1/2" (half of the seedlings shaded by green plastic foil with a 10cm × 5cm rectangle) and "Control" (without foil). The width of the first two completely developed leaves, the length of the stolons, the number of leaves of each stolon and the angular orientation of each stolon in treatments "A-f 1/2" and "G-f 1/2" were measured twice, on 22 March and 14 April 2000. Stolons shorter than 0,5 cm were not measured. The light regime was 11 hours in the light and 13 hours in the dark. The experiment was completeled 18 April when the above-ground and below-ground biomass were harvested, dried and weighted with precision 0.01g on an analytic scale.

The seed germination was recorded prior to both experiments (both with seeds collected at locality Ohrazení in September 1998).

Data analysis

The data in the linear scale (ratio scale of Zar 1997) from both field and laboratory experiments (i.e. the number of stolons, their length, the number of flowers and leaves, the

width of the leaves, biomass weight and the mean internode length) were analysed using the standard statistical methods in the STATISTICA package (Anon 1996): ANOVA, including the Repeated measures model where needed. For the post hoc comparison between treatments, the Tukey honest significant difference HSD test was used.

In the case of the "Half treatment" in the field experiment and the "A-f 1/2" and "G-f 1/2" treatments in the pot experiment the methods of the circular statistics were used for the analyses of the angles of the stolons and their length (Batschelet 1981; Zar 1997). The angles from 1° to 180° signify the side without the vegetation in the field, and without any foil in the chamber, the angles from 181° to 360° (0°) are directed to the vegetation, or to a foil side of the treatment. The centroids, the centres of gravity, of each plant tips of stolons were calculated. The uniformity of distribution of the centroids around the circle was tested by the Rayleigh test (Batschelet 1981). I used Parametric one-sample second-order analysis of angles (Zar 1997) for testing the existence of the mean angle of the stolons, the tested null hypothesis was: There is no mean population direction of the stolon growth (i.e. $\rho=0$). The mean angle and centroid are not synonymous. The mean angle was computed using the frequencies of the stolon directions only (ignoring their lengths), the centroids are computed with the real length of the stolon in addition. The Angular linear correlation (Zar 1997) tested the (in)dependency of the length of stolons on the direction, i.e. angle of the clonal spreading of the stolons. All the statistical methods were programmed in the Visual Basic editor (Linke 1998). To test the hypothesis of the stolon growth preference of the side with or without the vegetation, i.e. green (aluminium) foil or the part without any foil, the One sample t-test and χ^2 test were used. For the t-test the angles were transformed from the circular scale to the linear scale. The only X coordinate of angles (the sine of angle of the each centroid, the negative values means the orientation to the vegetation or to the side with foil) were used. For χ^2 test, the preference for either side was used. The last question tested investigated the difference between vegetation and gap side (or the side with or without foil) in the stolon internode distance using ANOVA. The centroids, i.e. mean angles, were used, instead of all angles, to avoid the dependency of the measured angles. The angles recorded from the same individual are not independent (Cain 1989).

The ordination, PCA analysis in the statistical package CANOCO for Windows (ter Braak & Šmilauer 1998), was used as a presentation of the vegetation structure recorded at the form of the relevés in the locality Ohrazení and its surrounding.

The seed germination data were analysed simply by the arithmetic mean of the emerged seeds.

Results

The effects of different types of competitors

In the field transplant three different competitors and three different gaps were established. Both the clonal spreading and sexual reproduction of *Prunella* transplants are affected by the growth form and thickness of the neighbouring vegetation. The numbers of newly originated stolons are similar in all the treatments, and numbers of leaves do not differ among treatments. The differences in the sum of lengths of all stolons are close to significant (see Tab. 1). The individuals transplanted to the thick bunches of *Nardus*, less thick bunches of *Molinia* and in the "Square gap" posses the highest length of the longest stolon ($F=5,785$; $p=0,000111$, Fig. 1). and also highest mean length of stolons ($F=7,85$; $p=3\times10^{-6}$) (Fig. 2). The difference in the mean internode length is also significant ($F=9,13$; $p=3\times10^{-6}$) (Fig. 3), (Tab. 1). The individuals in bunches of graminoid competitors have longer stolons but also the internodes are longer than in the gaps treatments, i.e. the number of leaves is nearly the same in all treatments. The longest stolons with the longest internodes exist in the *Nardus* treatment, on the second extremity the "Half gap" treatment occurs. However, the three graminoid competitors did not differ (even in tests with gap treatments removed) in any morphological characteristic of clonal growth. The tendency to differ is possible to see in Fig. 2 and Fig. 3.

Tab. 1

The table of results form the field experiment in Ohrazení 1998 - 1999. Effects of treatments on the particular morphological and clonal growth characteristics of *Prunella vulgaris*. The interaction of the treatment with time is also presented. p are the significance levels in repeated measurement ANOVA.

Question Are there any differences between the treatments in:	Answer	p the main effect	p the interaction with time	Graphic presentation
-the number of fertile stolons	yes	**0,043**	-	
-the number of all stolons	no	0,403	0,088	
-the length of the longest stolon	yes	**0,0001**	**0,0016**	Fig. 1
-the sum of the lengths of stolons	no	0,083	0,097	
-the number of the leaves of each stolon	no	0,293	0,773	
-the mean stolon length	yes	**3×10^{-6}**	**7×10^{-5}**	Fig. 2
-the mean internode length	yes	**1×10^{-6}**	**0,0057**	Fig. 3

The first pot experiment was slightly different from the preceding one. The aluminium foil to simulate the lower availability of the light in the vegetation (the light quantity, but not the quality yet) was established. The important role of the light quantity could be seen in all the ANOVA results (Tab. 2), the treatment most affected in the negative sense was the most shaded one ("A-f 1"). But the differences in other treatments were also significant. The width of the two completely developed leaves was the highest in the "control" and decreased with shading ($F=16,87$; $p=1\times10^{-6}$) (Fig. 4), as well as the number of stolons ($F=14,35$; $p=0,0004$) (Fig. 5). This results at the differences in the sum of the length of stolons ($F=5,66$; $p=0,0016$) and the total number of the leaves ($F=16,14$; $p=0,0003$). The longest stolons were observed in the treatments "Control" and "A-f 1/2" ($F=5,09$; $p=0,0031$). The differences were found at the mean stolon length ($F=4,61$; $p=0,0054$) and at the longest mean internode length ($F=3,21$; $p=0,0281$). The longest internodes were observed in the treatment "A-f 1/2" (Fig. 6).

Tab. 2

The table of results form the pot experiment in 1998 - 1999. Different shapes of the aluminium foil influence on the target species and the interaction with time are showed. p are the significance levels in repeated measurement ANOVA.

Question Are there any differences between the treatments in:	Answer	p the main effect	p the interaction with time	Graphic presentation
-the width of two completely developed leaves	yes	**1×10^{-6}**	**1×10^{-6}**	Fig. 4
-the number of all stolons	yes	**4×10^{-4}**	**1×10^{-6}**	Fig. 5
-the length of the longest stolon	yes	**0,0031**	**2×10^{-5}**	
-the sum of the lengths of stolons	yes	**0,0016**	**5×10^{-5}**	
-the number of the leaves of each stolon	yes	**3×10^{-4}**	**1×10^{-6}**	
-the mean stolon length	yes	**0,0054**	**6×10^{-5}**	
-the mean internode length	yes	**0,0281**	**1×10^{-4}**	Fig. 6

In the second pot experiment, I changed not only the quantity but also the quality of light by the green foil changing R/FR ratio. Big differences ($F>40,88$; $p=1\times10^{-6}$) in both underground and above ground biomass were found (Fig. 7). All treatments except "A-f 1/2" and "G-f 1/2" are significantly different (Tukey HSD test). The width of the two completely developed leaves was significantly lower in the treatments with decreased light quantity and quality, "A-f 1" and "G-f 1", and the treatment "G-f 1/2" has the biggest ones (Fig. 8). The

treatments differed in the number of stolons ($F=122,89$; $p=1\times10^{-6}$), consequently in their sum of length ($F=3,32$; $p=0,015$) and also in the number of leaves ($F=12,2$; $p=1\times10^{-6}$). The longest stolons of all the treatments, except the "A-f 1" ones, have the similar length. The mean stolon length did not differ among the treatments. These results imply the significant difference in the mean internode length ($F=2,505$; $p=0,0497$) and the Fig. 9 shows that the treatment with green square foil "G-f 1" has the longest internodes. (See Tab. 3)

Tab. 3

The table of results form the pot experiment in March and April 2000. The effect of foil decreasing PFD or R/FR and control and their interaction with time are compared. p are the significance levels in repeated measurement ANOVA.

Question Are there differences between the treatments in:	Answer	p the main effect	p the interaction with time	Graphic presentation
-the weight of the above ground biomass	Yes	**1×10^{-6}**	-	Fig. 7
-the weight of the under ground biomass	Yes	**1×10^{-6}**	-	
-the width of two completely developed leaves	Yes	**1×10^{-6}**	**6×10^{-6}**	Fig. 8
-the number of all stolons	Yes	**1×10^{-6}**	**1×10^{-6}**	
-the length of the longest stolon	No	0,0961	**0,033**	
-the sum of the lengths of stolons	Yes	**0,0150**	**0,035**	
-the number of the leaves of each stolon	Yes	**1×10^{-6}**	**2×10^{-4}**	
-the mean stolon length	No	0,2604	0,084	
-the mean internode length	Yes	**0,0497***	0,291	Fig. 9

* in this case the covariable "Block" was used

Angular analysis

This part of experiment analyses the treatments "Half gap", "G-f 1/2" and "A-f 1/2" in both transplant and pot experiments.

Uniformity of distribution of the stolons

In the field experiment the centroids were not distributed uniformly around the circle ($p< 0,02$) except the result of measurement on 31 May where the null hypothesis was not rejected. The non uniform distribution of the centroids is shown at Fig.10. In both treatments in growth chamber the hypothesis of the uniformity was not rejected (see Tab. 4).

Tab. 4

The Rayleigh test of the uniform distribution of centroids around the circle. The significant treatments have non uniform distribution of centroids.

Date	treatment	z	critical value of Rayleigh's z	p	Graphic presentation
9 May 1999	"Half gap"	4,31	2,941	**< 0,02**	
31 May 1999	"Half gap"	2,86	2,941	$0,05 < p < 0,1$	
3 July 1999	"Half gap"	5,54	2,941	**< 0,005**	Fig. 10
12 August 1999	"Half gap"	5,51	2,941	**< 0,005**	
22 March 2000	"G-f 1/2"	1,75	2,956	$0,1 < p < 0,2$	
22 March 2000	"A-f 1/2"	2,25	2,956	$0,1 < p < 0,2$	
14 April 2000	"G-f 1/2"	0,89	2,956	$0,2 < p < 0,5$	
14 April 2000	"A-f 1/2"	2,47	2,956	$0,05 < p < 0,1$	

Parametric one-sample second-order analysis of angles

In the field experiment each measurement have the mean angle which is pointed to the space without the vegetation (see Tab. 5). The experiment in the growth chamber is divided into two different results. The treatments "A-f 1/2" have significant mean angle, on the other hand the treatment with decreased light quality "G-f 1/2" did not have it (Tab. 5). Although, the mean angles did not exist, the centroids, computed with the real stolon length, exist in all treatments and are, of course, different from the mean angles (Tab. 6). Their distributions in the three different treatments is seen in the Fig. 10, Fig.11 and Fig.12.

Angular – linear correlation

In none measurement neither positive nor negative correlation between the stolons growth direction and their real length or mean internode length were obtained. There is no dependency of the length on the angle of dispersion.

Preference of the side

Despite this, some preferences of the stolon growth orientation were observed. In both experiments, in all measurements, except the treatment "G-f 1/2" on 14 April 2000, centroids have significant preference ($p<0,05$) for the positive values, i.e. for the side without the vegetation or without shading (see Tab. 7, Fig. 10 and Fig. 12). This test is probably stronger than the previous one.

Tab. 5

The existence of mean angles and their corresponding values, the results of Parametric one-sample second-order analysis of angles using F criterion.

Date	Treatment	F criterion	f	Mean angle (if it exists)
9 May 1999	"Half gap"	**6,95**	3,98	113° 47'
31 May 1999	"Half gap"	**5,93**	3,89	121° 50'
3 July 1999	"Half gap"	**19,96**	3,89	122° 45'
12 August 1999	"Half gap"	**7,05**	3,89	119° 40'
22 March 2000	"G-f 1/2"	0,96	3,59	
22 March 2000	"A-f 1/2"	**4,17**	3,59	118° 04'
14 April 2000	"G-f 1/2"	0,58	3,59	
14 April 2000	"A-f 1/2"	**4,08**	3,59	105° 34'

Tab. 6

A comparison of values of mean angles and centroids and the length of centroids in the divided treatments ("Half-gap", "A-f 1/2" and "G-f 1/2") in the field and pot experiments.

Date	Treatment	Mean angle (if it exists)	Centroid	Centroid length (cm)	Distribution of centroids
9 May 1999	"Half gap"	113° 47'	110° 24'	3,24	
31 May 1999	"Half gap"	121° 50'	102° 52'	3,06	
3 July 1999	"Half gap"	122° 45'	127° 36'	4,85	Fig. 10
12 August 1999	"Half gap"	119° 40'	115° 07'	4,39	
22 March 2000	"G-f 1/2"		96° 44'	16,71	
22 March 2000	"A-f 1/2"	118° 04'	98° 41'	17,00	
14 April 2000	"G-f 1/2"		39° 34'	42,95	Fig. 11
14 April 2000	"A-f 1/2"	105° 34'	73° 11'	42,35	Fig. 12

Tab. 7

The result table of the centroid side preference. Significant value means the centroid orientation to the 1°-180° half of the circle. Used method: One sample t-test.

Date	treatment	t-value	P
9 May 1999	"Half gap"	2,853974	**0,007404**
31 May 1999	"Half gap"	4,216942	**0,000173**
3 July 1999	"Half gap"	3,868623	**0,000471**
12 August 1999	"Half gap"	3,515978	**0,001264**
22 March 2000	"G-f 1/2"	2,343548	**0,024293**
22 March 2000	"A-f 1/2"	2,184945	**0,034966**
14 April 2000	"G-f 1/2"	1,081133	0,286278
14 April 2000	"A-f 1/2"	2,512065	**0,016251**

The number of the centroids pointed to the side without the vegetation is significantly greater in three measurements in the field experiment (Fig. 10). The second measurement is close to significant (Tab. 8). The nearly significant results are also in the pot experiment in all treatments (comp. Fig. 12) except the treatment "G-f 1/2" at 14 April 2000 (Fig. 11) (see Tab. 8).

Tab. 8

The preferences in centroid direction. The result of χ^2 test, significant treatments have greater part of centroids pointed out of the vegetation.

Date	Treatment	χ^2	p
9 May 1999	"Half gap"	5,333	**0,020928**
31 May 1999	"Half gap"	3,571	0,058791
3 July 1999	"Half gap"	5,857	**0,015519**
12 August 1999	"Half gap"	5,857	**0,015519**
22 March 2000	"G-f 1/2"	3,556	0,059336
22 March 2000	"A-f 1/2"	3,556	0,059336
14 April 2000	"G-f 1/2"	2,000	0,157309
14 April 2000	"A-f 1/2"	3,556	0,059336

Internode length

There was no significant difference in the internode length between the vegetation and gap side or the side with and without any foil. The only nearly significant result was in the

treatment "G-f 1/2" at 14 April 2000 where to the side with the green foil were oriented the stolons with longer internodes (p=0,0741).

The seed emergence

In the 1998 the emergence of seeds was 46% after two weeks. The same seeds in January 2000 had only 28% emergence after two weeks; it increased to 49,5% after 50 days.

The vegetation and the management

The PCA of the species composition of the plots in the surroundings of the locality Ohrazení is shown at the Fig. 15. In these sites the species *Mentha arvensis* or *Sanguisorba officinalis* are positively correlated with the *Prunella* species, the negative correlation is with the species *Molinia caerulea, Myosotis nemorosa, Galium uliginosum* or *Nardus stricta*. The negative correlation with the species *Potentila erecta* is surprising, and might be caused by the low number of recorded relevés. The positive correlation between *Mentha arvensis* and *Prunella vulgaris* might be due to the fact that both species are able to colonize disturbed plots (Lepš pers.comm.).

The occurrence of *Prunella vulgaris* is also affected by management. The results based on unpublished data from the field experiment of Lepš (1999) where three treatments, i.e. mowing, fertilization and removing of the dominant species *Molinia caerulea*, were combined in a factorial design, show significant effect of mowing and fertilization (both $F>87,00$; $p=1\times10^{-6}$) on its occurrence. The removing of the species *Molinia caerulea* did not have significant effect (p=0,12). *Prunella vulgaris* prefers mown unfertilized plots (Fig. 13).

Discussion

Many species have short living spacers and place their ramets far away from the mother plant (de Kroon & van Groenendael 1990). This is also the case with *Prunella vulgaris*. In the graminoid treatments, *Prunella* takes on a growth form with long stolons penetrating deep into the vegetation. This type could be seen in the treatment *Nardus,* where the neighbouring grass *Nardus stricta* has very dense root and shoot system like a cushion where the establishment gaps are missing and *Prunella* can not root there. It could be compared to *Elymus lanceolatus* which forms long stolons as a response to the dense root system of *Agropyron desertorum* (Huber-Sannwald et al. 1998). Another example is *Hydrocotyle bonariensis* which forms in the patches of grass long stolons veering away and establishing preferentially out of the vegetation. In the grass bunches, it has increased the length of internode and decreased branching because of low availability of nutrients there

(Evans & Cain 1995). Nevertheless, these results were found not only in the treatment *Nardus*. The similarity of the response of *Prunella* species to the graminoid neighbours correspond to the Goldberg's theory of the equivalence of the competitors, that all bunchgrasses may have equivalent competitive effect on the target plant (Goldberg & Werner 1983).

Contrary to the bunches, in the gaps *Prunella vulgaris* has a more condensed growth with short stolons and more dense foliage. It could be because of lack of aboveground competition in the non occupied space. (The difference in the "Natural gap" was probably caused by higher retention of water there and the last measurement at the treatment "Square gap" had increased stolon length because of high defoliation by animals.) The low nutrient availability could be a result of the decreased nutrient level by the competitive strong neighbour (Huber-Sannwald et al. 1998) so in the places without vegetation the nutrient availability is higher. The high level of nitrogen (the potential source of nutrients could be the remnant roots of the removed vegetation) induce the decrease of the cytokinin synthesis and consecutive decrease of apical dominance. This is the cause of increased branching, i. e. shortage of spacers (Hutchings & Bradbury 1986). In addition, similar results as Schmid and Harper (1985), were found in my studies. In the bunches, *Prunella* is flowering more frequently, contrary to the treatments with sparse vegetation cover where *Prunella vulgaris* use preferentially vegetative growth.

Prunella vulgaris is a typical representative of "guerilla" type clonal growth. Nevertheless, it is able to produce short internodes which are at variance with the growth type. If the long internodes are normal for this species (Schmid & Harper 1985), *Prunella* could by active growth response shorten the internode length in favourable conditions, the response typical for foraging plants. The passive growth response is branching (Cain 1994) and is very frequent in clonal plants (Piqueras et al. 1999). In spite of some authors characterising foraging as an escape of plant from the unfavourable patches rather than the plant's capacity to exploit the rich one (Herben 1996), the similar results with other species were found in many studies (Evans & Cain 1995; Alpert 1999; Huber-Sannwald et al. 1998; Dong & de Kroon 1994). The common definition of foraging in clonal plants is that plants can exploit favourable and avoid unfavourable portions of their habitat by changing their growth response, for example by decrease of stolon length or increasing branching (Oborny & Cain 1997; Klimešová 1997; Skálová & Krahulec 1992). In poor conditions, the plants have a few long spacers and try to escape. On the contrary, in favourable conditions the plants have numerous short spacers (de Kroon & Schieving 1990; Huber-Sannwald et al. 1998; Cain 1994). To prove that a plant is foraging, it is necessary to measure number of daughter ramets, the length and the direction of stolons (Cain 1994). The fact of decreased stolon length itself is not sufficient to prove that a plant forages. There are many foraging plants, for

example *Hydrocotyle bonariensis* (Evans & Cain 1995), *Trientalis europea* (Piqueras et al. 1999), and Schmid (1985b) stays that *Prunella vulgaris* is able to forage and to discriminate between the low and high quality habitat. My results support this hypothesis.

Internode length difference may be also caused by changing the light quality and quantity (Evans & Cain 1995). That is why I have changed both parameters in two manipulative experiments in a growth chamber. The light quantity was decreased by the aluminium foil and the light quality was changed by green foil absorbing red and transmitting far-red, comparable to plant coverage at the natural conditions (Leeflang 1999). It was the simulation of the vegetation layer and the simulation of the competition for the light. (Of course, the total light quantity was also decreased by the green foil, even if not so much as by the aluminium foil.)

The drastic quantity deficiency of light, the treatment "A-f 1", decrease practically all life factors, such as, elongation of the stolons, the width of the leaves or the amount of the produced under-ground biomass. It was probably caused by the reduced or nearly stopped photosynthesis, resulting in the lack of energy.

The lower quantity deficiency of light had lighter and weaker effect on the target plant. The stolons were long, but not numerous and the branching was minimal as in the other studies of *Potentilla reptans, Trifolium repens* and *Glechoma hederacea* species (Huber et al. 1999; Kemball et al. 1992). The plant size decreased with low Photon Flux Density (PFD) (also in the study of (Winn & Evans 1991)).

There are some studies that have concentrated on the effect of changing R/FR ratio on the shoot growth parameters (Skálová & Vosátka 1998; Skálová & Krahulec 1992; Leeflang 1999). In the first two (Skálová & Vosátka 1998; Skálová & Krahulec 1992) the biomass and number of tillers of species *Festuca rubra* decreased with low R/FR ratio. In addition to the decrease of above-ground biomass, the decrease of under-ground biomass was observed also in my experiment. Leeflang (1999) analysed the R/FR response in spacer length of six species, but without finding any remarkable differences. Probably, these plants are not able to avoid the neighbouring vegetation on the basis of perception of light quality. Contrary to this study I found increase of the internode length especially in the treatment with square green foil – "G-f 1". If we take into account produced biomass, it is, in comparison to the control, the great difference. Thus the plants growing under low R/FR conditions, limiting their energetic resources, invest large part of the remaining energy to the escape from these unfavourable conditions (Comp. Fig. 7 and Fig. 9).

Few studies have used the circular analyses because it poses some problems (Cain 1989). The non uniformity of the centroid distribution in the field treatment "Half-gap" can have two possible causes. The cumulation of the great number of stolons in certain sector of a circle, or the existence of not numerous but very long stolons in this sector of a circle. As

could be seen in the Figure 14 the majority of stolons preferred the stripped part of the treatment and consequently they have there the mean angle. This preference is not necessary due to high nutrient availability in the vegetation removed part or due to the low R/FR ratio in the other side. It could be simply because of the mechanic obstruction to the penetration into the vegetation, and/or this response may be caused by root interaction between *Prunella vulgaris* and the neighbouring species (comp. Huber-Sannwald 1998). However stolons cumulate in the stripped part of the experiment.

The situation in the pot experiment was slightly different. From the results it is not possible to say that the distribution of the centroids is not uniform, but in the treatment "A-f 1/2" the mean angle exists, thus there is some preference for the side. The plants respond to the half light availability by great accumulation of the stolons in the side without the foil. On the contrary, the treatment "G-f 1/2" did not have the mean angle and also the preference of the side does not exist there. The low R/FR ratio did not defend to the stolon to growth there. Although the decrease of R/FR ratio, contrary to the low light availability, did not affect the stolon growth angle, it did affect the internode length in the same way the aluminium foil or vegetation have done, i.e. lenghtening of internodes.

The question arises: Is *Prunella vulgaris* able to exhibit resource partitioning? The existence of physical connection between ramets does not itself prove that there is a functional relationship between them. In addition, (de Kroon & van Groenendael 1990) claim that the transport between ramets is restricted by the typical vascular organisation in Labiateae. Nevertheless my results found the foraging capacity in the species *Prunella vulgaris* that implies the usefulness of the nutrient transport. This discrepancy needs further investigation in further manipulative experiments.

Sexual reproduction and even limited recruitment from seeds is important for many clonal species (Price & Marshall 1999). For *Prunella vulgaris* it is the way to escape from places with high competition. The graminoid species, especially *Nardus stricta*, represent the strong competitors for many herb species. In these conditions *Prunella vulgaris* use flowering, i. e. sexual reproduction, to survive and spread by seeds out of the unfavourable conditions within the bunches.

The effects of the treatment type on the clonal growth characteristics of different plant organization levels are summarised in the Tab. 9.

Prunella vulgaris is a widely distributed herb present in many habitats. According to my results this species prefers mown (mowing decrease the asymmetry in the competition for light (Lepš 1999)) and unfertilised habitats with the lower competition (Schmid 1985a).

What is the role of clonal behaviour of *Prunella vulgaris* in the natural conditions of the oligotrophic wet meadow community? For this weak competitor, the identity of its graminoid competitor is probably not important. To survive and persist in the grassland plant

community, it needs some type of disturbance forming gaps in the turf. This can be attained by grazing or cutting of the vegetation. On the other hand, the unsuitable form of the management is fertilization inducing the increasing amount of biomass of a few strongly competitive species. This species is prosperous in heterogenous species rich environment with particular disturbance regime.

Two approaches were conduced to study the effects of neighbouring vegetation on clonal growth characteristics of *Prunella vulgaris*. *Prunella* takes penetrating guerilla type of growth in the presence of any graminoid competitor, but in the absence of it, its growth is more condensed with shorter internodes. Also the simulations of the competition for light effect by two types of foil decreasing the light quality or quantity have the similar effect like the vegetation cover has. Furthermore, it seems that *Prunella* can distinguish between favourable and unfavourable patches in the heterogenous environment and is able to exploit the favourable ones and escape from the poor ones by changing the internode length. Thus *Prunella vulgaris* has the foraging capacity, however, I was not able to show its capacity to avoid the unfavourable patches by changing the growth direction of the stolons. By elongation of internodes *Prunella* minimises the costs necessary to grow in unfavourable conditions.

Clonal growth is an important characteristic of the species present in the meadow community. The large spatial mobility of species at the same time is one of the main mechanism for species coexistence there (Herben et al. 1994).

Tab. 9

The summarising table of the competitor and foil influence on the clonal growth characteristics in different levels of clonal growth of *Prunella vulgaris*.

Level	Factor investigated	Foil	Graminoid competitor
Organ	width of leaves	little decrease	Unknown
	sum of leaves	decrease	None
	internode length	little lengthen (expect treatment "A-f 1")	Lengthen
Stolon	sum of stolons	decrease	None
	mean stolon length	none (expect "A-f 1")	Lengthen
Plant	Biomass	decrease	Unknown
	Flowering	unknown	increase of flowering stem

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Figures

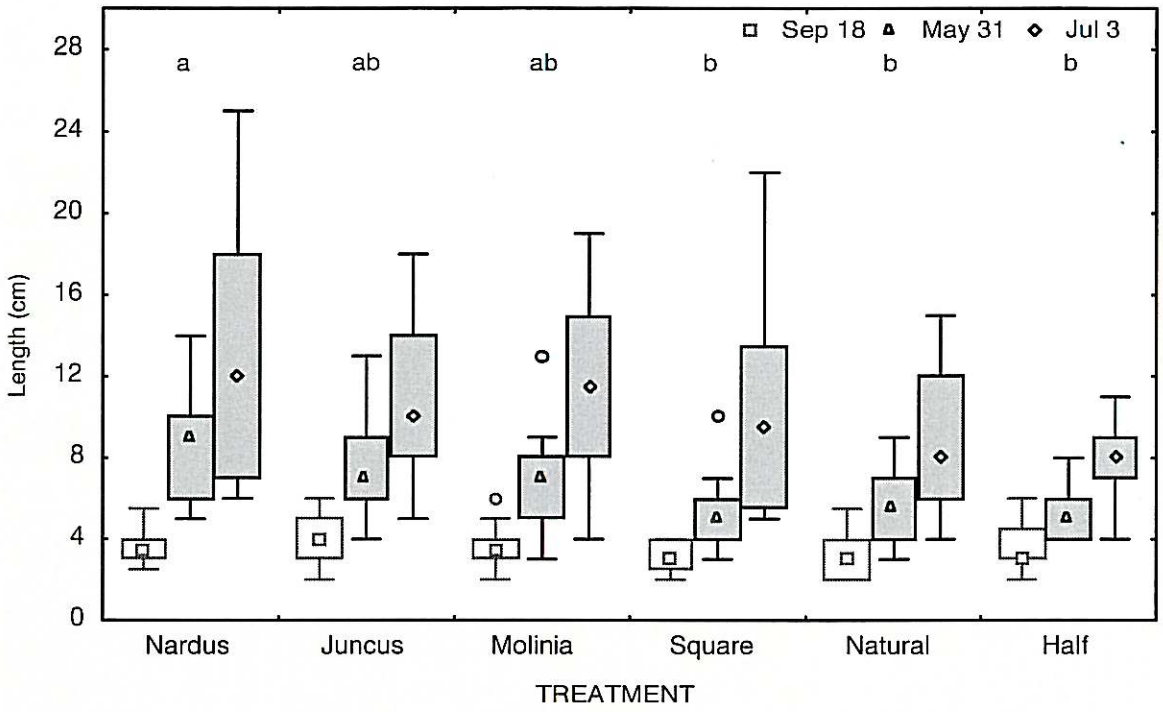


Figure 1

Effect of the treatment type on the formation of the longest stolon. ANOVA, Multiple comparison of three measurements in Ohrazení. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges (p>0,05) for the measurement on 3 July 1999 (Tukey HSD test). Treatments: Nardus = *Nardus stricta*, Juncus = *Juncus effusus*, Molinia = *Molinia caerulea*, Square = Square gap, Natural = Natural gap and Half = Half gap.

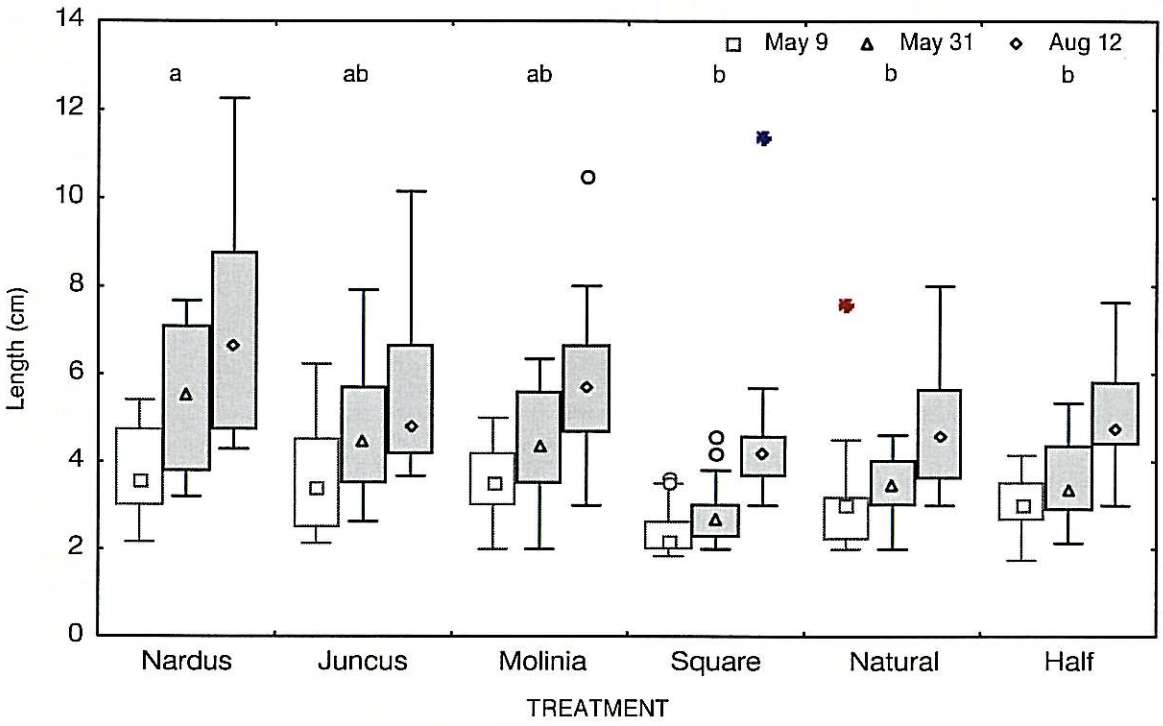


Figure 2

Effect of the treatment type on the mean stolon length. ANOVA, Multiple comparison of three measurements in Ohrazení. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the measurement on 3 July 1999 (Tukey HSD test). Treatments: Nardus = *Nardus stricta*, Juncus = *Juncus effusus*, Molinia = *Molinia caerulea*, Square = Square gap, Natural = Natural gap and Half = Half gap.

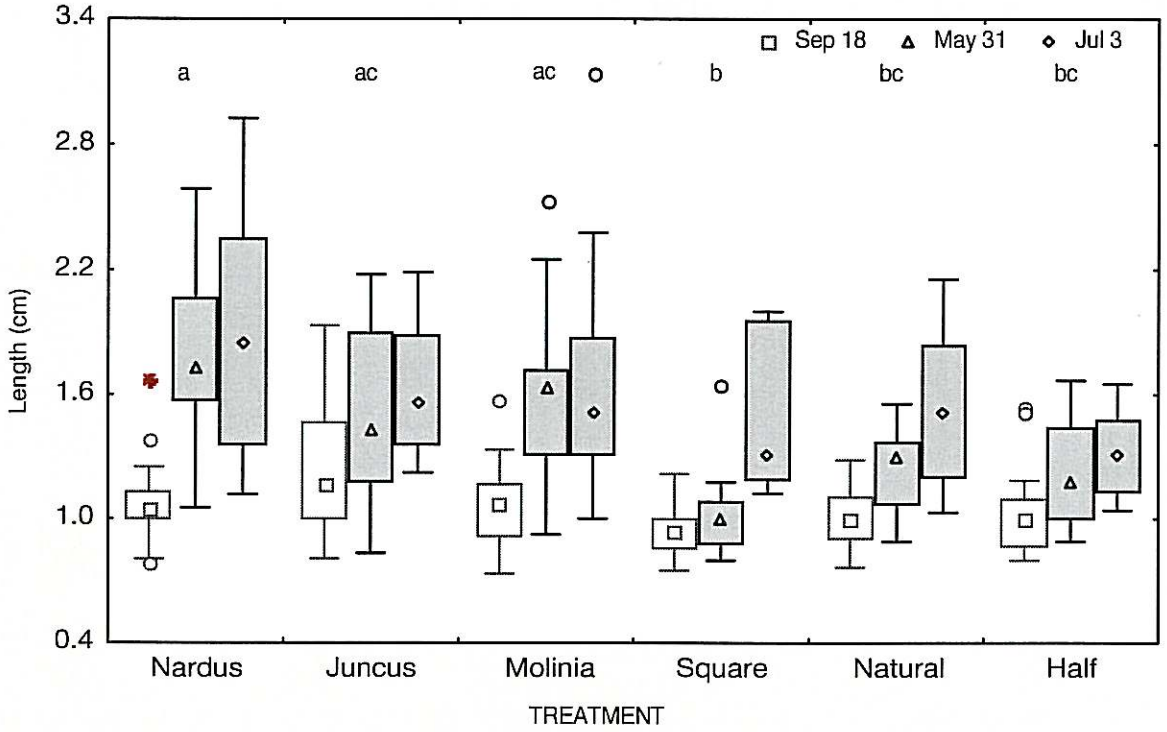


Figure 3

The treatment effect on the *Prunella* mean internode length. ANOVA, Multiple comparison of three measurements in Ohrazení. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges (p>0,05) for the measurement on 3 July 1999 (Tukey HSD test). Treatments: Nardus = *Nardus stricta*, Juncus = *Juncus effusus*, Molinia = *Molinia caerulea*, Square = Square gap, Natural = Natural gap and Half = Half gap.

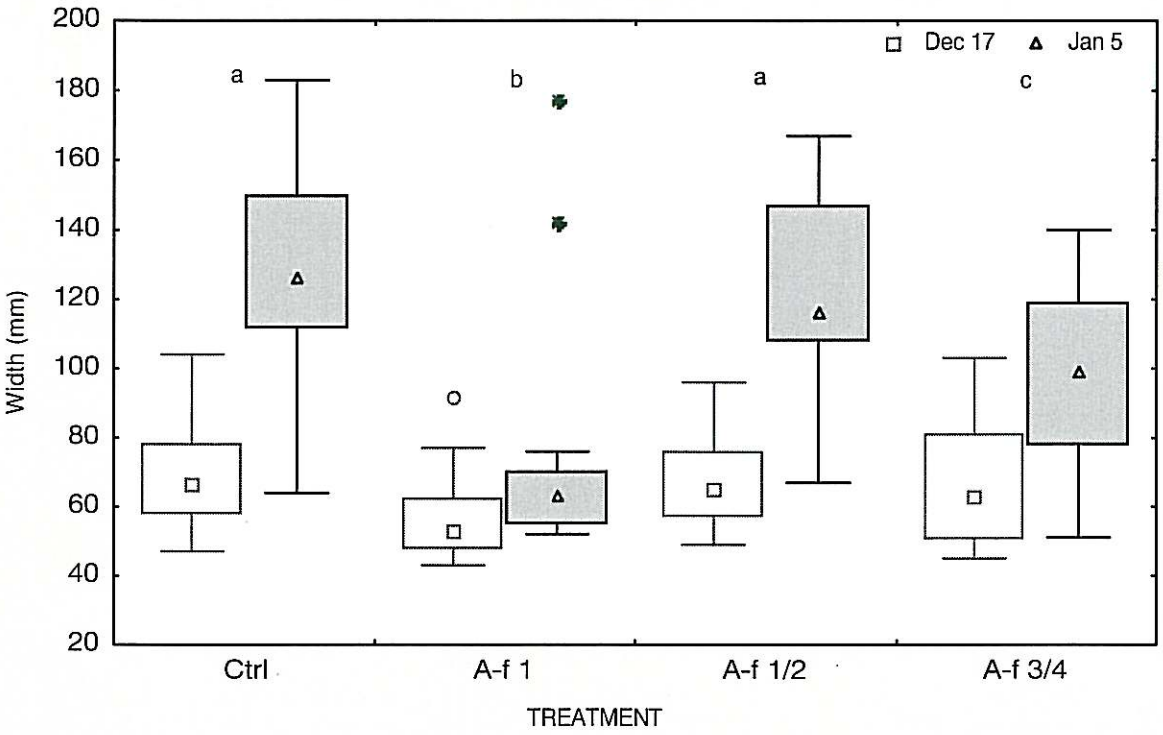


Figure 4

Affection of the width of two completely developed leaves by the shading of the target plant by different foil shapes. ANOVA, Multiple comparison of the growth chamber experiment in 1998 - 1999. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the measurement on 5 January 1999 (Tukey HSD test). Treatments: Ctrl = Control, A-f 1 = Aluminium square foil, A-f 1/2 = Aluminium foil shading half of the pot, A-f 3/4 = Aluminium foil shading 3/4 of the pot.

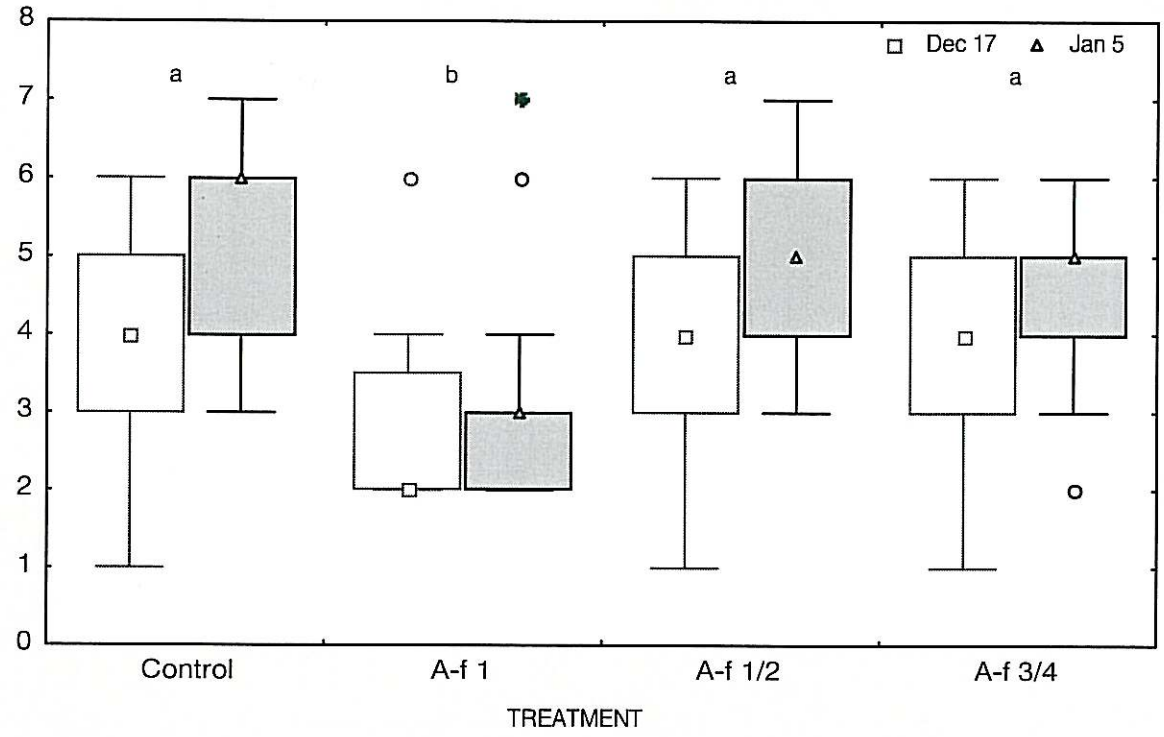


Figure 5

The number of all stolons developed by differently shaded plant. ANOVA, Multiple comparison of the growth chamber experiment in 1998 - 1999. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the measurement on 5 January 1999 (Tukey HSD test). Treatments: Ctrl = Control, A-f 1 = Aluminium square foil, A-f 1/2 = Aluminium foil shading half of the pot, A-f 3/4 = Aluminium foil shading 3/4 of the pot.

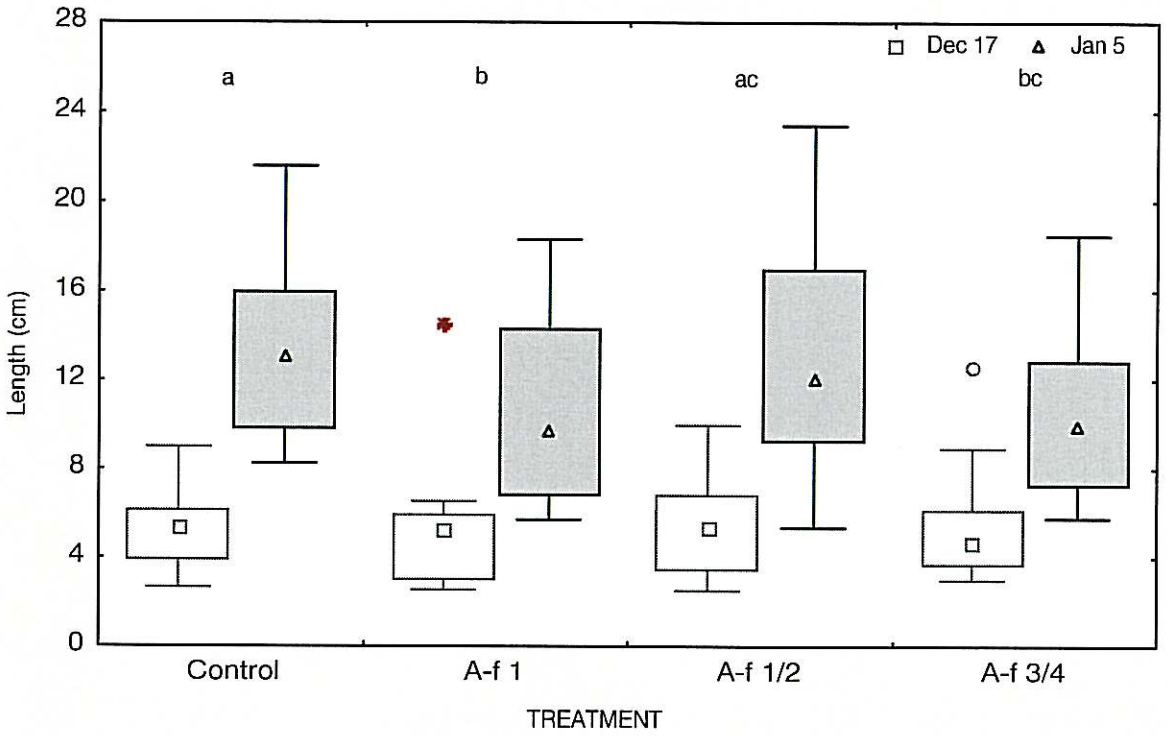


Figure 6

The mean internode length of target plants. ANOVA, Multiple comparison, growth chamber 1998 - 1999. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the measurement on 5 January 1999 (Tukey HSD test). Treatments: Ctrl = Control, A-f 1 = Aluminium square foil, A-f 1/2 = Aluminium foil shading half of the pot, A-f 3/4 = Aluminium foil shading 3/4 of the pot.

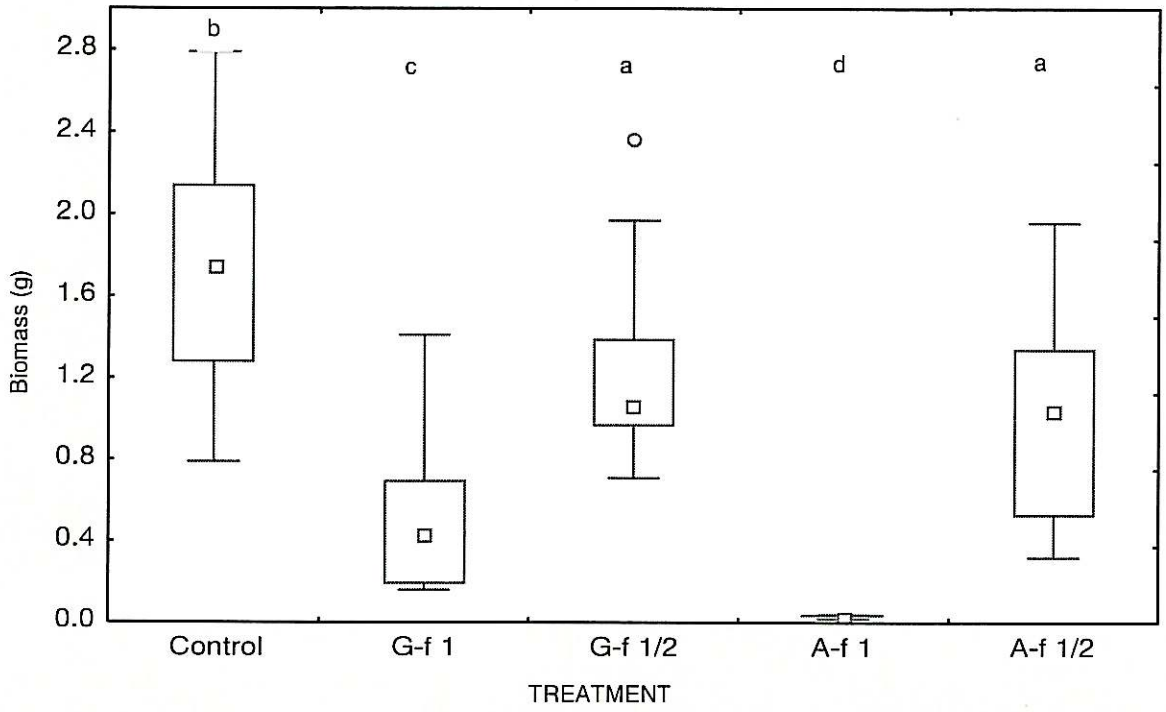


Figure 7

The amount of the above-ground biomass of target plants. ANOVA, growth chamber 2000. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the harvesting date measurement (Tukey HSD test). Treatments: Ctrl = Control, G-f 1/2 = Green foil shading half of the pot, G-f 1 = Green square foil shading all the pot, A-f 1 = Aluminium square foil, A-f 1/2 = Aluminium foil shading half of the pot.

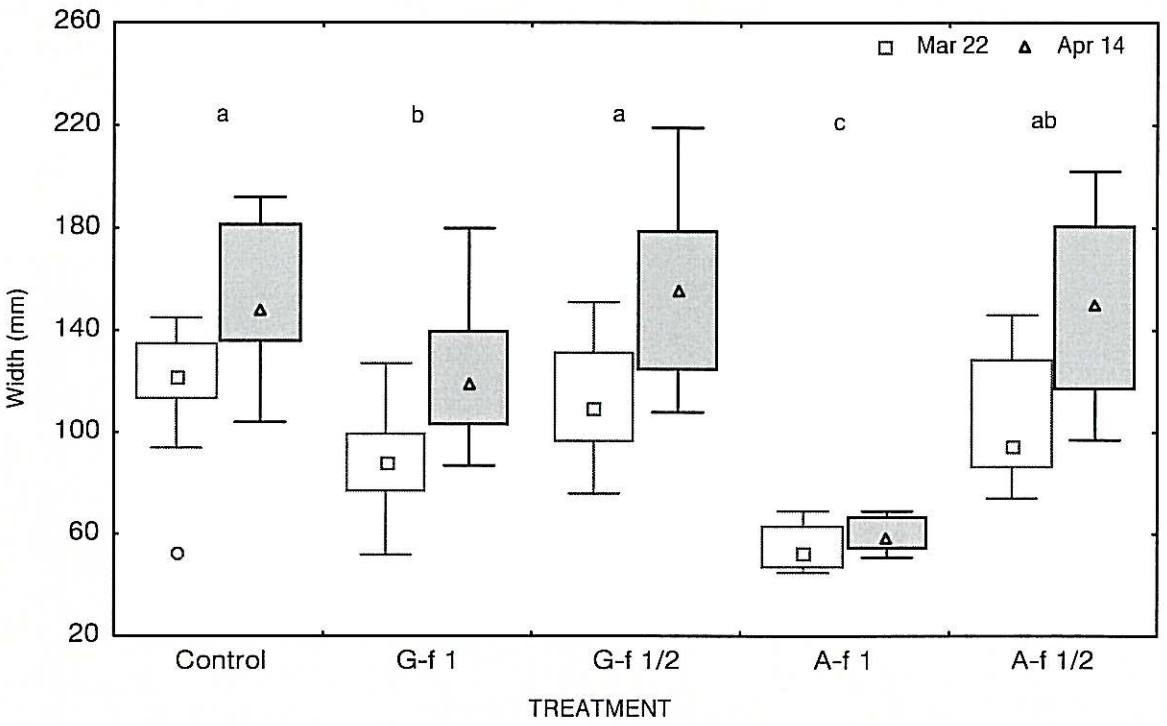


Figure 8

Effect of the different foil shading on the width of two completely developed leaves. ANOVA, growth chamber 2000. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the second measurement (Tukey HSD test). Treatments: Ctrl = Control, G-f 1/2 = Green foil shading half of the pot, G-f 1 = Green square foil shading all the pot, A-f 1 = Aluminium square foil, A-f 1/2 = Aluminium foil shading half of the pot.

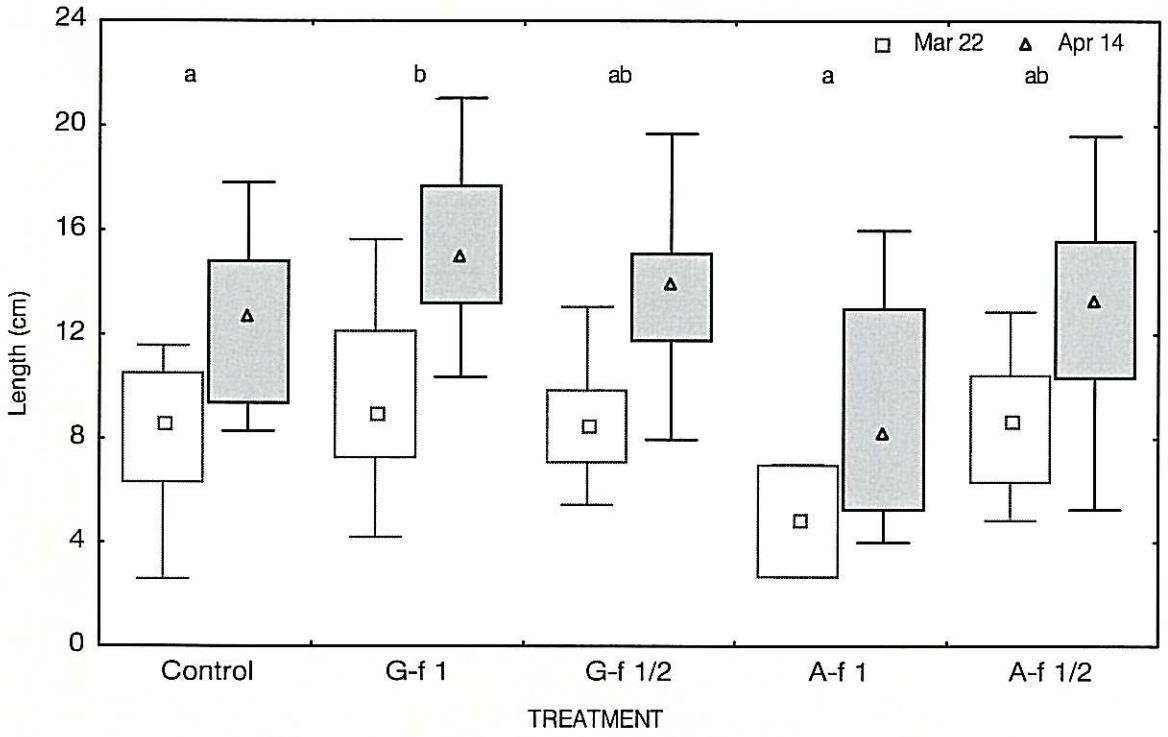


Figure 9

Effect of the different foil shading on the mean internode length. ANOVA, growth chamber 2000. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. The identical letters on the top of figure correspond to the non significant ranges ($p>0,05$) for the second measurement (Tukey HSD test). Treatments: Ctrl = Control, G-f 1/2 = Green foil shading half of the pot, G-f 1 = Green square foil shading all the pot, A-f 1 = Aluminium square foil, A-f 1/2 = Aluminium foil shading half of the pot.

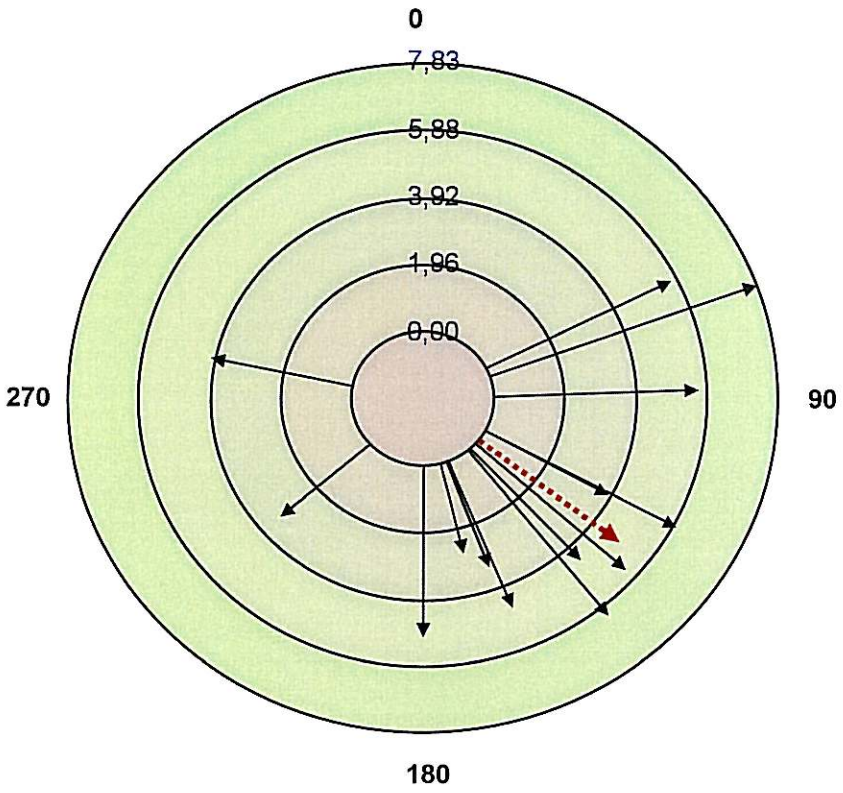


Figure 10

Distribution of the centroids in the treatment "Half gap".

The red arrow is the mean angle.

The part from 0° to 180° is the stripped part of the treatment.

Ohrazení, 3 July 1999.

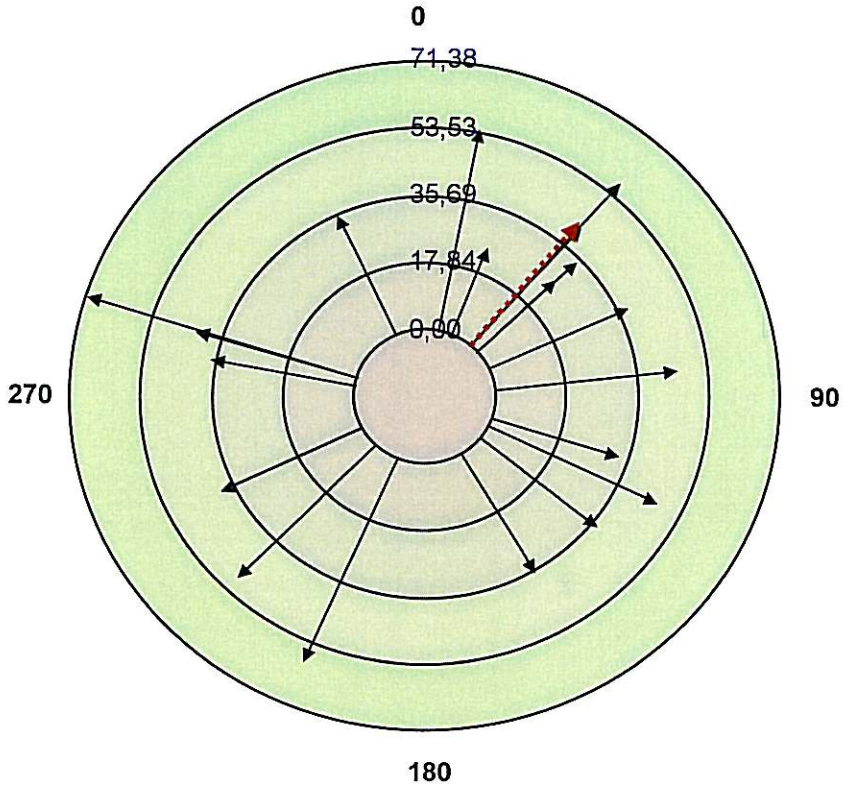


Figure 11

Distribution of the centroids in the treatment "G-f 1/2".

The red arrow is the mean angle.

The part from 0° to 180° is the part without foil.

Growth chamber, 14 April 2000.

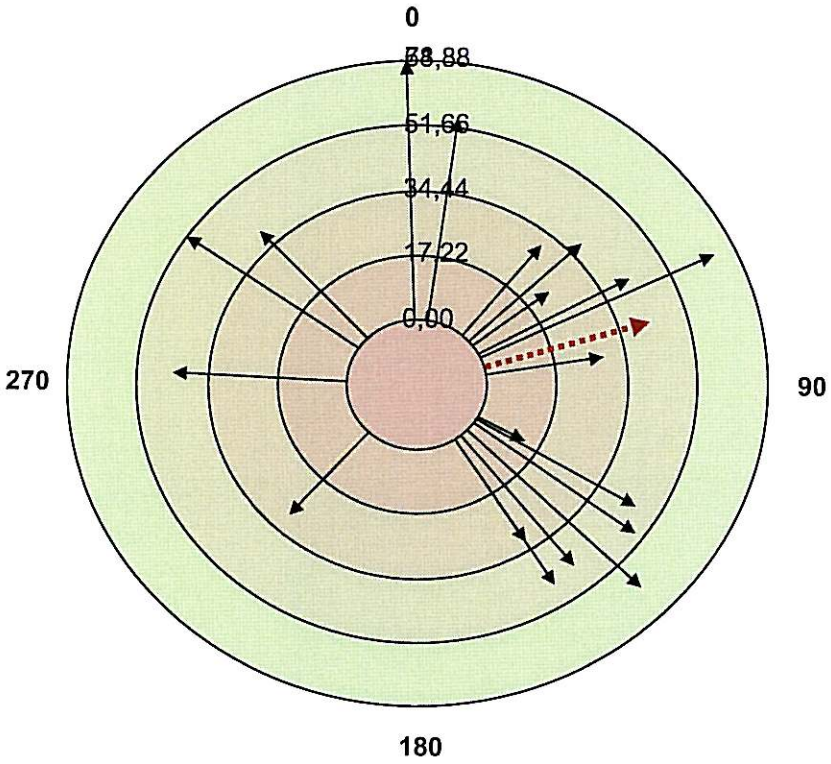


Figure 12

Distribution of the centroids in the treatment "A-f 1/2".

The red arrow is the mean angle.

The part from 0° to 180° is the part without foil.

Growth chamber, 14 April 2000.

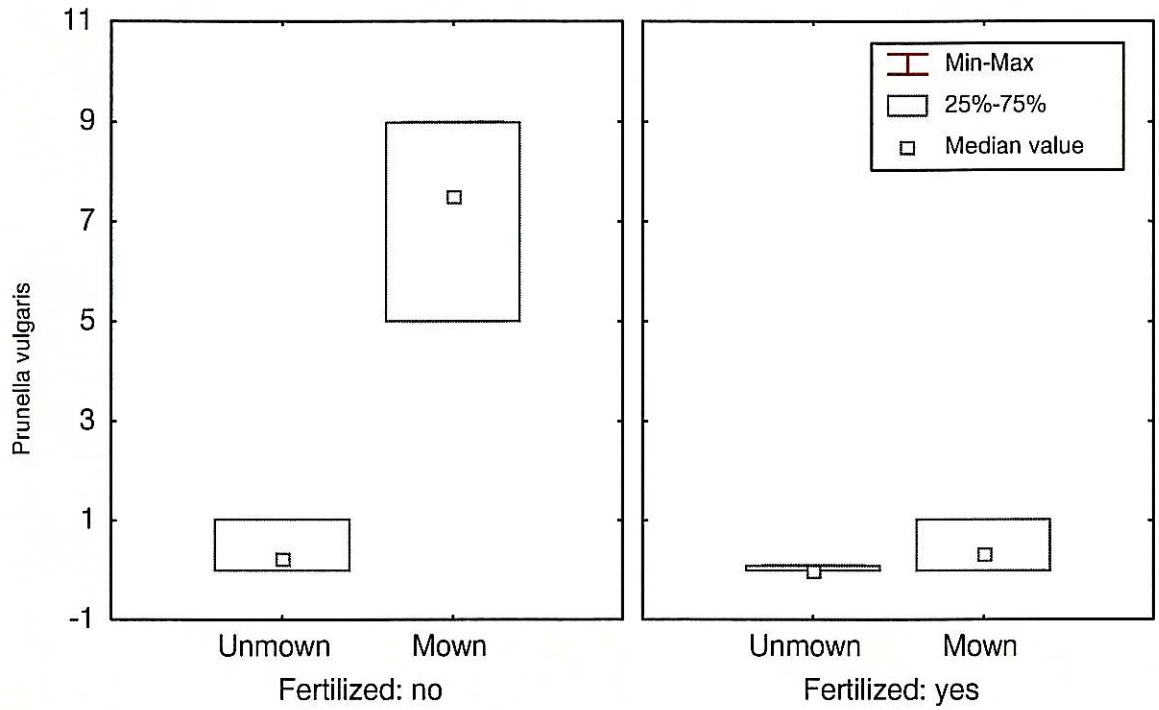


Figure 13

The occurrence of species *Prunella vulgaris* in the plots with different type of management. This species prefers mown unfertilised plots. ANOVA, Ohrazení 1998, unpublished data from Lepš.

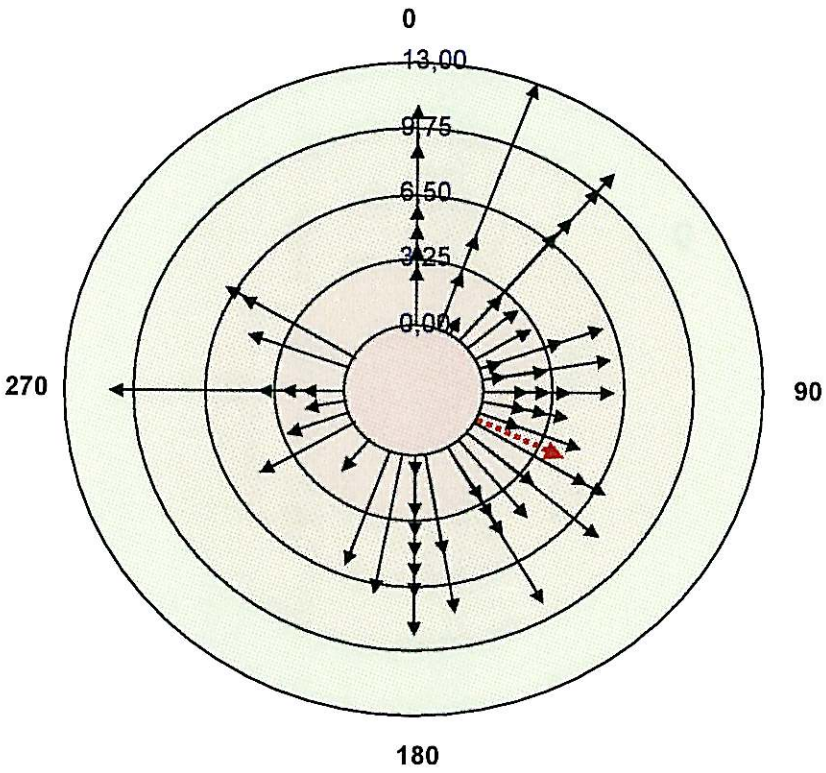


Figure 14

Distribution of all stolon directions in the treatment "Half gap".

The red arrow is the mean angle.

The part from 0° to 180° is the stripped part of the treatment.

Ohrazení, 12 September 1999.

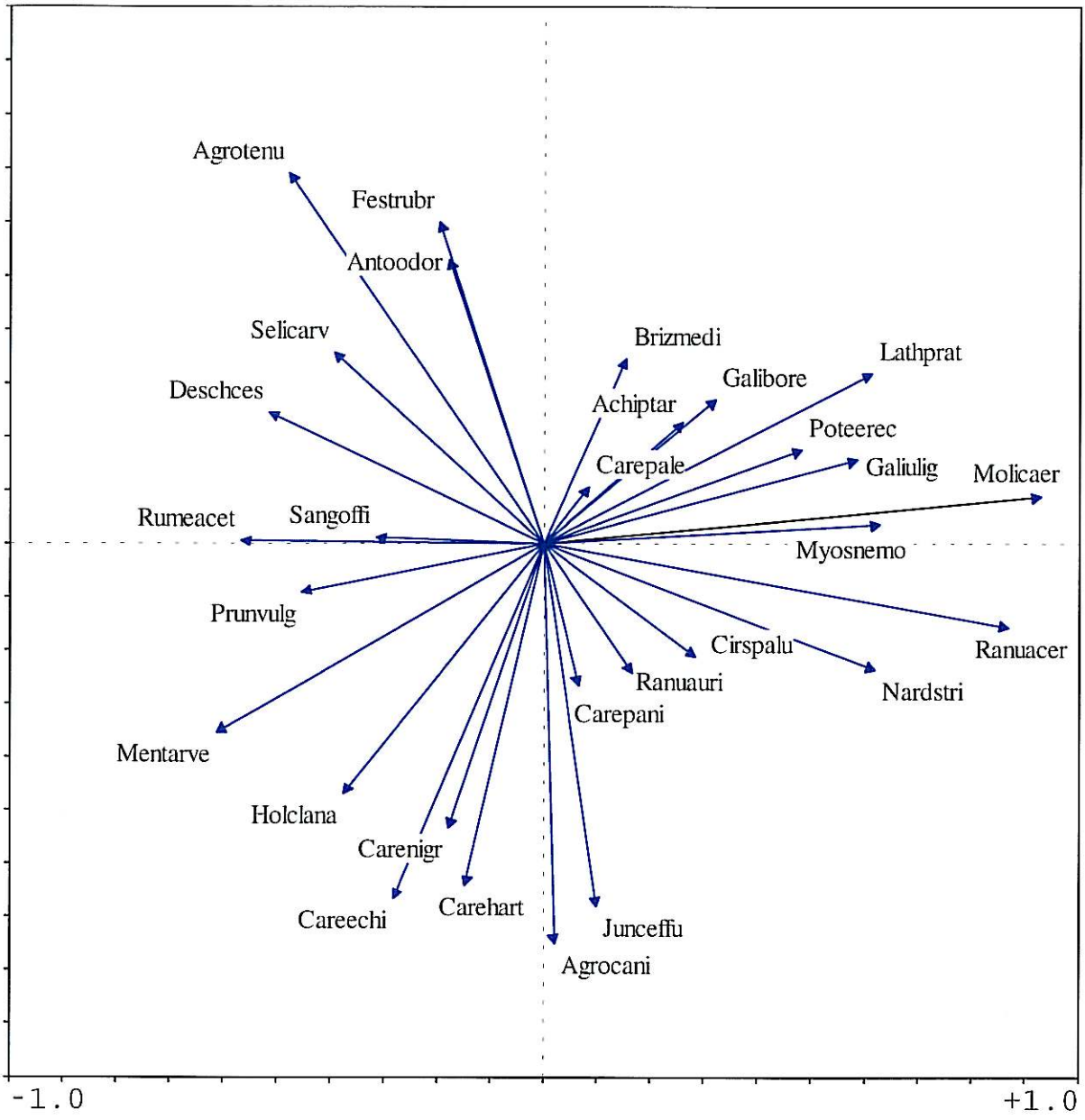


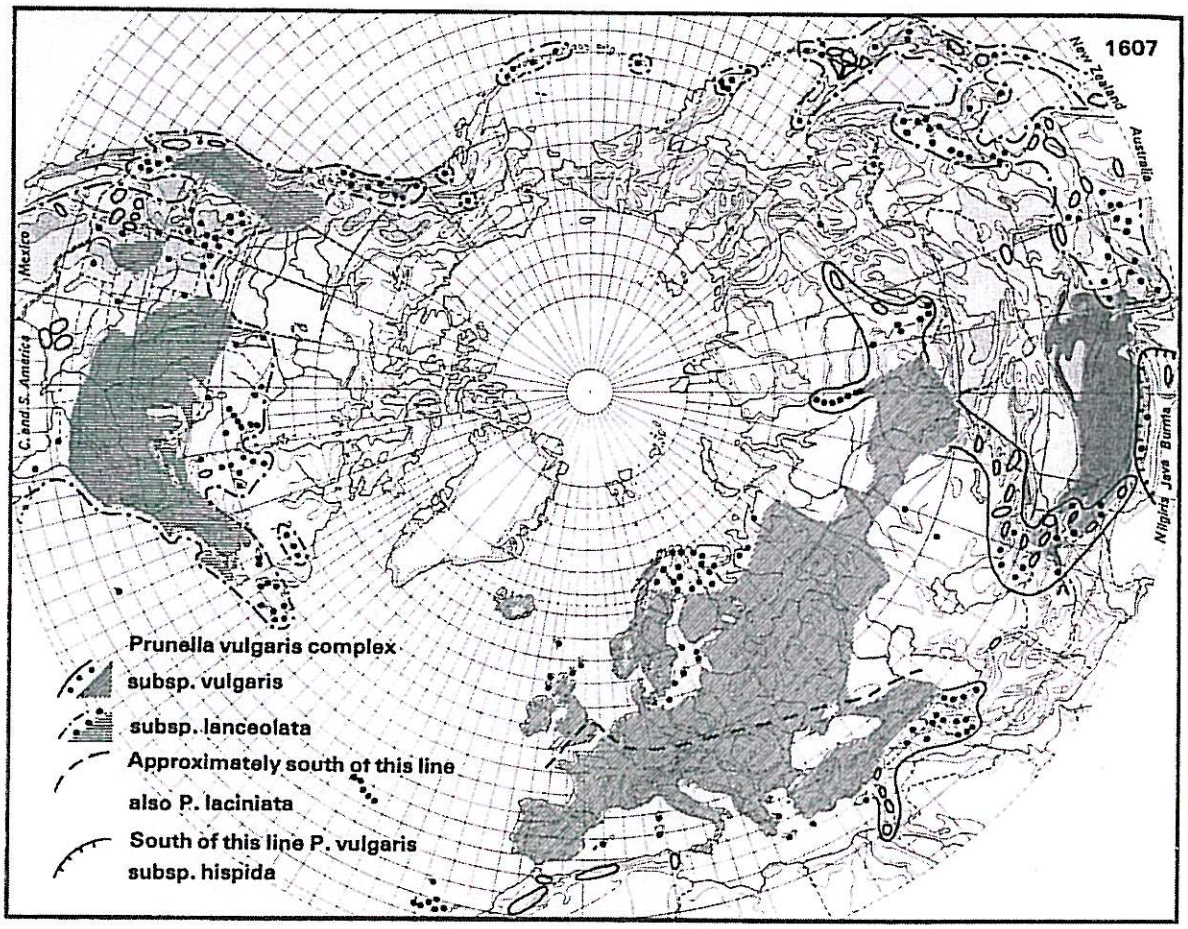
Figure 15

Result of ordination analysis (PCA) represented as a biplot showing the species composition of vegetation in the nearest neighbourhood of the locality Ohrazení. The species occurring in less than three samples were omitted. The list of abbreviations is in App. 3.

Appendixes

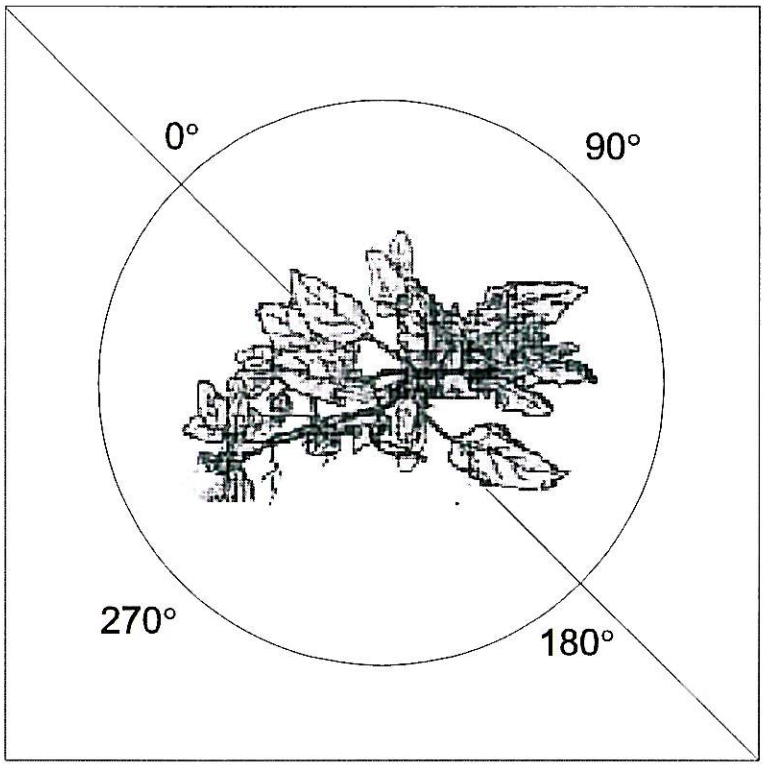
Appendix 1

The area of distribution of species *Prunella vulgaris* in the north hemisphere; (Hultén & Fries 1986)



Appendix 2

The position of the seedling in the treatment "Half-gap". The part from 0° to 180° is stripped, the part from 180° to 360° of treatment include the vegetation.



Appendix 3

List of species abbreviations and full names used in ordination diagram (Fig.15).

abbreviation	correct name	abbreviation	correct name
Agrocani	Agrostis canina L.	Holclana	Holcus lanatus L.
Agrotenu	Agrostis tenuis Sibth.	Junceffu	Juncus effusus L.
Achiptar	Achilea ptarmica L.	Lathprat	Lathyrus pratensis L.
Antoodor	Antoxanthum odoratum L.	Mentarve	Mentha arvensis L.
Brizmedi	Briza media L.	Molicaer	Molinia caerulea (L.)
Careechi	Carex echinata Murray		Moench
Carehart	Carex hartmanii Cajand.	Myosnemo	Myosotis nemorosa Besser
Carenigr	Carex nigra (L.) Reichard	Nardstri	Nardus stricta L.
Carepani	Carex panicea L.	Poteerec	Potentilla erecta (L.)
Carepale	Carex pallescens L.		Räuschel
Cirspalu	Cirsium palustre (L.) Scop.	Prunvulg	Prunella vulgaris L.
Deschces	Deschampsia cespitosa (L.) Beauv.	Ranuacer	Ranunculus acer L.

Festrubr	Festuca rubra L.	Ranuauri	Ranunculus auricomus L.
Sangoffi	Sanguisorba officinalis L.	Rumeacet	Rumex acetosa
Galibore	Galium boreale L.	Selicarv	Selinum carvifolia (L.) L.
Galiulig	Galium uliginosum L.		

Appendix 4

Photo 1: The "Nardus" treatment, September 1999

Photo 2: The "Square gap" treatment, September 1999