



The effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris* L.

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Abstract

We studied the response of a clonal herb, *Prunella vulgaris*, to its position in a gap, the identity of neighbouring graminoid species, and simulation of competition for light. The growth characteristics, such as stolon length, internode length and number of stolons were recorded in competitive environments with graminoid bunches of *Molinia caerulea*, *Juncus effusus* and *Nardus stricta* and in different types of 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 both field and pot experiments we monitored stolon orientation in a treatment divided into two parts (competition/shaded or gap/unshaded). Methods of circular statistics were used to evaluate stolon orientation. The graminoid bunches had equivalent effects on plant vegetative growth – plants had longer stolons and internodes than plants growing in gaps. The effects of treatments on other characteristics (amounts of stolons and leaves) were not significant. In divided treatment, plants responded by accumulation of stolons and leaves in vegetation removed part, and avoided the vegetated part. In the pot experiments the plant biomass and stolon number decreased in low R/FR and in low irradiance treatments, but the internodes in low R/FR were 26% longer compared to the control. Centroids were uniformly distributed in divided low R/FR treatment contrary to low irradiance treatment where they showed preference for unshaded part. No dependency of stolon length on its orientation was found in divided treatments of both experiments. *Prunella vulgaris* in heterogeneous environment distinguished favourable and less favourable conditions and produced more stolons with shorter internodes under favourable conditions. This resulted in concentration of resource acquiring structures in favourable patches.

Introduction

European anthropogenic meadows are plant communities with remarkable species richness, often containing more than 50 species/m² (Kull and Zobel 1991). These human created communities have been maintained for a long time by extensive management, such as grazing and mowing. However, their species richness is in many cases endangered because the extensive management techniques have become uneconomical and meadows are either fertilised or abandoned (Špačková et al. 1998). These impacts

generally result in dominance by a few strong competitors, increased biomass and decreased species diversity.

Many theories have been coined to explain the ability of species to avoid competitive exclusion in these diverse systems (Palmer 1994). The majority of meadow species are clonal (Klimeš et al. 1997) and understanding clonal growth is one of the clues to explain species coexistence in species rich meadows. We investigated the ecological behaviour of one of their constituent clonal species, *Prunella vulgaris*.

Generally clonal plants are composed of repeating ramets, which are feeding sites with resource acquiring structures, and spacers, the connections between ramets (Oborny 1994). Differences between clonal plants are mainly architectural, i.e., in shoot growth parameters, which include intensity and angle of branching and stolon length. Within the species, differences in plant architecture are caused both by competition for light and nutrient availability. In *Prunella vulgaris* light and nutrient distributions may also influence the resource allocation to the vegetative and generative growth (Schmid and Harper 1985). Another parameter that may change plant growth is character of a competitor. Huber-Sannwald et al. (1998) found root density to be important for stolon placement. In graminoid competitors a degree of bunch density may be also important.

Clonal plants have been shown to be able to modify their growth in a way that increases the placement of resource acquiring structures in more favourable places, and this behaviour has been called foraging. This could be achieved either by producing shorter spacers, or by higher branching in favourable conditions. de Kroon and Hutchings (1995) have shown, that although both of these modification could increase the proportion of resource acquiring structures in favourable places, the increased branching is also consistent with simple increased growth under favourable conditions, and consequently, it is not unequivocal support for the foraging. If a plant's nearest neighbourhood is heterogeneous then selective placement of new ramets into favourable parts of the surrounding is another foraging method. This could be achieved by modifying the direction of newly produced stolons.

In the grasslands the prostrate species are subjected to a strong competition for light, usually stronger than competition for nutrients. Foliage of taller species decreases the light intensity and change the R/FR ratio, which results in reduced photosynthesis and consequently the amount of plant resources (Winn and Evans 1991).

A plant could allocate its limited resources either to the clonal growth, or to the generative reproduction. The tradeoff between allocation into either vegetative spread or generative reproduction is usually modified by the environment, with vegetative spread being favored in less competitive environment (Caswell 1985; Eriksson 1997), whereas seed production can be seen as an escape in space or time.

We conducted field and laboratory manipulative experiments with *P. vulgaris*, to investigate the response of its clonal growth to surrounding conditions. We aimed to see, whether the changes in species morphology are consistent with the foraging behaviour. More specifically, our aims were: 1. To test the effect of graminoid competitor species on clonal growth and sexual reproduction of *P. vulgaris*. This was tested in a field transplant experiment. 2. To determine the effect of changes in light quality and quantity on the plant morphology and growth in a pot experiment. 3. To investigate in both experiments the ability of *P. vulgaris* to differentiate between more and less advantageous conditions in its nearest surrounding by the selective placement of new ramets into more favourable conditions.

Material and methods

Study species

Prunella vulgaris L. (Lamiaceae) is a prostrate, annual to perennial hemicryptophyte herb, at our study site mostly perennial that occurs in many habitats (Böcher (1940) and Winn and Werner (1987), Schmid and Harper (1985); pers. obs.). It is characterised by the *Fragaria vesca* type of clonal growth form according to the classification of Klimeš et al. (1997) and has monopodial branching with long internodes, typical for the guerrilla growth habit (Lovett Doust 1981; Schmid 1985b). An erect flowering stem has one terminal and several lateral inflorescences appearing in June. Flowers can remain open more than one month; seed dispersal is finished in early November (pers. obs.; Winn and Gross (1993)). The relative importance of clonal growth and sexual reproduction varies. According to Schmid (1985a), reproduction of *P. vulgaris* is mainly by clonal growth and seedling establishment is rare, whereas Winn and Werner (1987) found seedling regeneration to be important. At our study site, Zelený (1999) documented seedlings of *P. vulgaris* in bunches of *Molinia*, but their survival was not studied. According to Lepš (1999) *Prunella vulgaris* is a weak competitor for light, its growth is inhibited by litter layer, and it prefers mown and unfertilised plots. Titus and Lepš (2000) found *Prunella vulgaris* to be mycorrhizal at the study site. Streitwolf-Engel et al. (1997, 2001) demonstrated that various AM fungi species can affect differently the clonal characteristics of *Prunella vulgaris*.

Study site

The field experiment was conducted in an oligotrophic wet meadow with high species richness in Ohrazení, 10 km southeast of České Budějovice, Czech Republic, 48°59' N, 14°36' E, 510 m a.s.l., and complemented other studies carried out there (Lepš (1999) and references therein). Mean annual precipitation is 600–650 mm and mean annual temperature is 7.8 °C. The vegetation belongs to the Molinion type. The meadow has been regularly mown (once to twice a year) since the early 1990s.

The second part of this study was conducted in a simple growth facility with regulated day length (fluorescent tubes Polyflux XL F36W/830, GE Lighting, the photon flux rate was 95 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ PhAR).

Experimental design

Field experiment

The field experiment was established 5 June 1998 in recently mown meadow with litter removed. We transplanted 120 *P. vulgaris* seedlings (~ 2 cm tall) in starter ("Jiffy") pots to 20–1 m² quadrats. The experimental design of one quadrat is shown in Figure 1. Each quadrat contained six microsites (treatments). These consisted of three types of gaps: "Square gap" (both above ground and below ground vegetation removed from a 20 cm \times 20 cm square), "Natural gap" (place without vegetation among the bunches) and "Half gap" (above ground and below ground vegetation removed diagonally from half of the 20 cm \times 20 cm square, seedling transplanted to the centre of the square), and three graminoid species: *Nardus stricta*, *Juncus effusus* and *Molinia caerulea*. Our graminoid species differ mainly in the bunch structure, i.e., density of tillers. *Nardus stricta* forms the most compact bunch with tillers close to each other and fine, dense, but relatively short leaves. *Molinia caerulea* and *Juncus effusus* have less dense shoot systems, but have taller shoots. The number and length of stolons (in the "Half-gap" also the orientation of stolons) and number of leaves on each stolon were recorded five times (18 August 1998 and 9 May, 31 May, 3 July and 12 August 1999). The presence of flowers in 1999 was recorded on 12 August. In all treatments litter was removed for the second time in April 1999.

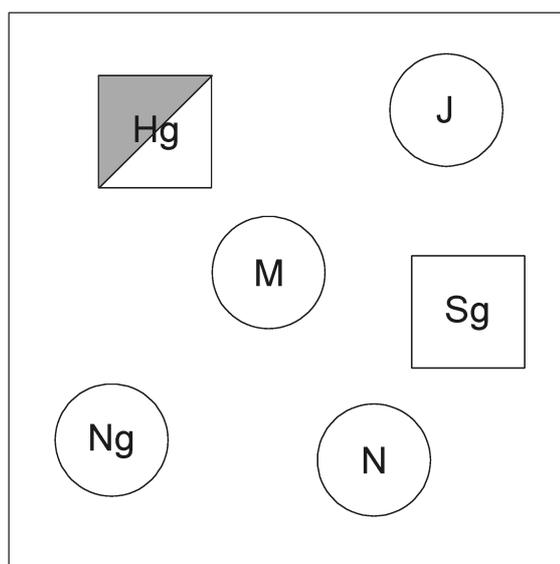


Figure 1. Experimental design within the quadrats. Each quadrat contained six treatments: N = *Nardus stricta*, J = *Juncus effusus*, M = *Molinia caerulea*, Sg = Square gap, Ng = Natural gap and Hg = Half gap. For explanation see the text.

Pot experiments

The pot experiments consisted of two similar parts. The first part was established on 19 November 1998 by transplanting 84 starter pots with a ~ 2 cm seedling of *P. vulgaris* into 10 cm \times 10 cm pots. After two weeks, we covered the pots with aluminium foil of varying shapes ~ 6 cm above the soil surface thereby 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 10 cm \times 10 cm square of foil), "A-f 3/4" (three-quarters of the pot shaded by foil), "A-f 1/2" (half of the pot shaded by a 10 cm \times 5 cm foil rectangle) and "Control" (without foil). In the partially shaded treatments, the seedlings were positioned at the edge of the foil. The experiment was arranged in a randomised block design. The size of the first two completely developed leaves as a distance of tips of the leaves, number of leaves on each stem, stolon length, and the number of leaves of each stolon were recorded twice (17 December 1998 and 5 January 1999). Stolons shorter than 0.5 cm were not measured. The light regime was a 12 h 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 we covered the seedlings with two types of foil, aluminium foil as in the first experiment and green plastic foil to

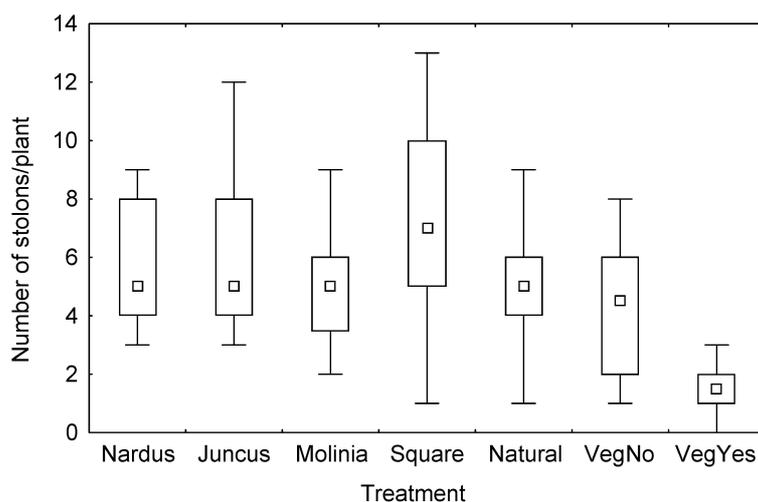


Figure 2. The mean stolon number per plant in the field experiment treatments on 3 July 1999. Treatments: Nardus = *Nardus stricta*, Juncus = *Juncus effusus*, Molinia = *Molinia caerulea*, Square = Square gap, Natural = Natural gap, VegYes = part of Half gap with vegetation, VegNo = part of Half gap without vegetation. The sum of VegYes and VegNo is the mean stolon number per plant in the treatment Half gap.

simulate shading by canopy. The green foil reduced red/far red ratio in the transmitted light to 31% of that in the open, and the photon flux rate to 44%. (Complete spectral characteristics of the light transmitted by the foil are given in Figure 2 of Skálová and Krahulec (1992)). Five treatments, arranged in a completely randomised block design, were: "Control", "A-f 1" and "A-f 1/2" (same as in the first pot experiment), "G-f 1" (the entire pot shaded by green plastic 10 cm × 10 cm square foil), "G-f 1/2" (half of the pot shaded by green plastic 10 cm × 5 cm rectangle foil). In addition to the characteristics from the first pot experiment the angular orientation of each stolon in treatments "A-f 1/2" and "G-f 1/2" was measured twice (22 March, 14 April 2000). Stolons shorter than 0.5 cm were not measured. The experiment was completed 18 April when above ground and below ground biomass were harvested, dried and weighed with precision 0.01 g. The light regime was a 13 h day length.

In both experiments the foils were continually lifted as the plants were growing. The temperature in the growth chamber ranged from 20 °C (night) to 28 °C (day).

Data analysis

Linear scale data measured in the field and laboratory (i.e., stolon number and length, flower number, leaf number and size, biomass, and mean internode length) were analysed using ANOVA, including repeated measures when needed. For post-hoc compar-

isons Tukey's HSD test was used. The Statistica for Windows package (Anon 1996) was used for analyses.

For the "Half gap" treatment in the field experiment and the treatments "A-f 1/2" and "G-f 1/2" in the pot experiment circular statistics were used for analyses of stolon angle and length (Batschelet 1981; Zar 1996). Angles from 1° to 180° signify the side without vegetation in the field and without any foil in the chamber. Angles from 181° to 360° (0°) are directed towards the vegetation or towards the foil side of the treatment. Centroid of each plant was calculated as a centre of gravity of the stolon tips (vectors from the plant centre). The uniformity of distribution of the centroids around a circle was tested by the Rayleigh test (Batschelet 1981). We used parametric one-sample second-order analysis of angles (Zar 1996) for testing the significance of the mean angle of the stolons (the existence of a significant mean angle express that the angles are not circularly uniformly distributed, i.e., there is a preference for some part of the circle). Mean angle and centroid are not synonymous. Mean angles are computed using the frequencies of the stolon directions only (ignoring their lengths) and centroids are computed using the real length of the stolon. Angular linear correlation (Zar 1996) tested the dependency of the stolon lengths on the direction of the plants clonal spreading. All of the statistical methods were programmed in Visual Basic editor. To test the hypothesis of stolon growth preference on the side with or without vegetation, or with green, alu-

minium or no foil a one sample t-test was used: the angles were transformed from a circular scale to a linear scale. Only the X coordinates of tips were used: a negative value means an orientation to the side with vegetation or foil, positive value the orientation to the open space. The one-sample t-test then tested the null hypothesis that the mean value of the X coordinate is zero. The last question investigated the difference between the vegetation and gap sides (or with and without foil sides) in the stolon internode length using ANOVA. The centroids, or mean angles, were used, instead of all angles, to avoid the mutual dependency of the measured angles within an individual (see Cain (1989)).

Results

Effects of different types of competitors and shading

In the field transplant experiment, three different competitors and three different gaps were used. Both clonal spreading and sexual reproduction of *P. vulgaris* transplants were affected by the treatment. The number of newly originated stolons was similar in all the treatments (Figure 2). Individuals transplanted to bunches of graminoid competitor had greater mean stolon length ($F = 7.85$; $p = 3 \times 10^{-6}$) and the mean internode length ($F = 9.13$; $p = 3 \times 10^{-6}$) than in gap treatments (Figure 3, Table 1). The mean internode length in "Square gap" was only 60% of the "Nardus" one. The average number of leaves per plant was almost the same in all the treatments. There were no significant differences among graminoid competitors in their effect on any morphological characteristic of clonal growth of *Prunella*. The treatment "Half gap" resulted in shorter internodes (85%) and higher amount of stolons in the vegetation removed part (Figure 2). The average number of leaves in vegetation free part was three times higher than in the part with vegetation (27.1 versus 8.5). No plants flowered in the first season, and only a minority did during the second season. The frequency of flowering differed among the treatments (contingency table, chi-square = 11.3, $df = 5$, $p < 0.05$). Most flowering plants were found in "Nardus" (25%), then in "Molinia" (15%), in "Square gap" (10%), and "Half gap" (5%). No flowering plants were found in "Juncus" and "Natural gap".

In the first pot experiment, aluminium foil was used to simulate the lower availability of light in vegetation. The important role of light quantity is appar-

ent in all of the ANOVA results (Table 2). All the levels of shading significantly impacted growth of *P. vulgaris* with the most shaded treatment being the most impacted. The size of the two completely developed leaves was the highest in the "Control" and decreased with shading ($F = 16.87$; $p < 10^{-6}$), as well as the number of stolons ($F = 14.35$; $p = 4 \times 10^{-4}$) and the total leaf number ($F = 16.14$; $p = 3 \times 10^{-4}$). In the treatments "Control" and "A-f 1/2" the greatest mean stolon lengths ($F = 4.61$; $p = 0.005$) and also the largest mean internode lengths ($F = 3.21$; $p = 0.028$) were observed. The summary results from the first pot experiment are in Table 2.

In the second pot experiment, we changed not only the quantity but also the quality of light by changing R/FR ratio using the green foil. Pronounced differences in above ground (Figure 4) and below ground biomass were found ($F > 40.88$; $p < 10^{-6}$ in both). All treatments except "A-f 1/2" and "G-f 1/2" were significantly different from each other (Tukey HSD test). The size of the two completely developed leaves decreased in order (C, G-f 1/2, A-f 1/2, G-f 1, A-f 1; means are 15.6, 15.6, 14.9, 12.5, 4.9 cm; $p < 10^{-6}$). The number of leaves decreased in the same order ($F = 12.2$; $p < 10^{-4}$, means are 63, 51, 48, 37, 4). The treatments also differed in the number of stolons decreasing in the same order ($F = 122.89$; $p < 10^{-6}$, means are 9.4, 8.2, 7.7, 6.6, 0.3). Mean stolon length was about 4 cm and did not differ among treatments ($p = 0.8$). The mean internode length was largest in the treatment "G-f 1" (Figure 4, $p = 0.05$), the internodes in the "Control" were 80% of the length of internodes in "G-f 1".

Angular analysis

Field treatment "Half gap" did not have centroids distributed uniformly around the circle ($p < 0.02$), except for the measurement of 31 May (Table 3). The non-uniform distribution of centroids is shown in Figure 5. Both mean angles and centroids were directed toward the vegetation removed part (Table 4, Figure 5). No significant correlations between stolon growth direction and their real length or mean internode length were found, but the mean internode length in vegetation removed parts was 85% of the part with vegetation. There was no dependency of the length on the angle. However, some preferences in stolon growth orientation were observed. The number of the centroids pointed to the side without the vegetation was significantly greater ($p < 0.05$) in three measure-

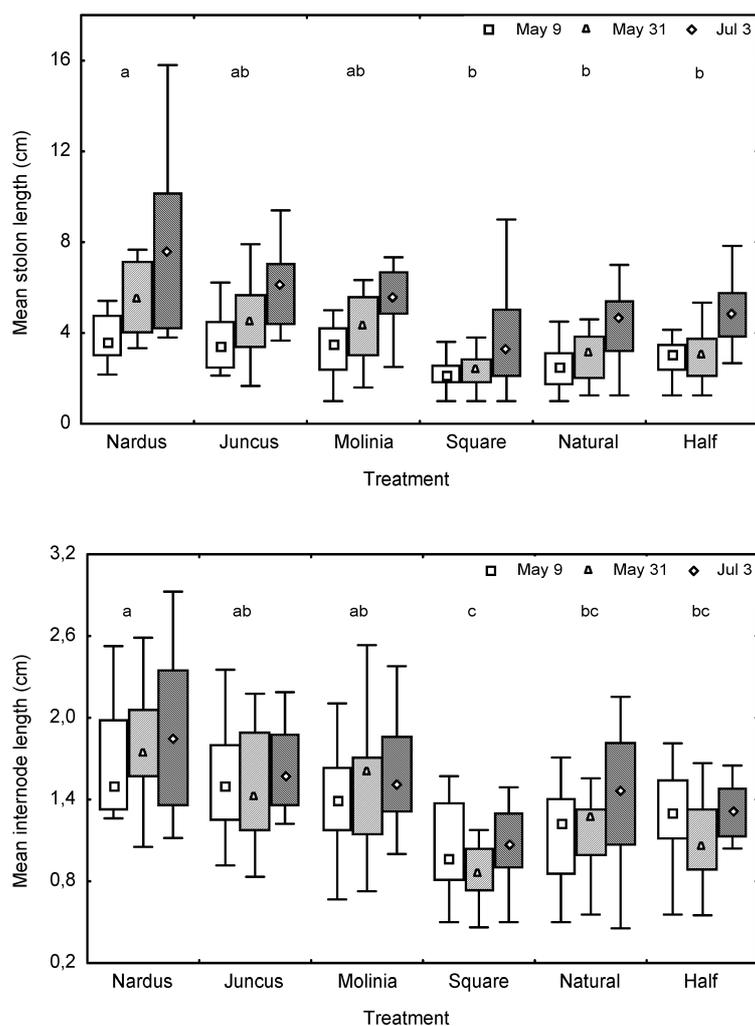


Figure 3. Treatment effect on stolon formation and internode lengths in three measurements in the field experiment. Median; Box: 25%, 75%; Whisker: Non-Outlier Min, Non-Outlier Max. Identical letters on the top of the figure correspond to nonsignificant ranges ($p > 0.05$) for the measurement on 3 July 1999 (Tukey HSD test). Treatments: Nardus, Juncus, Molinia, Square, Natural (see Figure 2) and Half = Half gap.

Table 1. Results summary from the field experiment in Ohrazení 1998–1999. Effects of treatments on morphological and clonal growth characteristics of *Prunella vulgaris*. "p" are significance levels for the main effect and for interaction with time in the repeated measurement ANOVA, or for the chi-square test of contingency tables for the proportion of flowering plants.

Question: Are there any differences between the treatments in:	Answer	p main effect	p interaction with time
-the number of all stolons	no	0.403	0.088
-the number of the leaves of each stolon	no	0.293	0.773
-the mean stolon length	yes	3×10^{-6}	7×10^{-5}
-the mean internode length	yes	1×10^{-6}	0.006
-the proportion of fertile plants	yes	0.043	–

ments in the field experiment (Table 5, Figure 5). The internode lengths of stolons pointed into the vegeta-

tion did not significantly differ from the ones of stolons pointed out of the vegetation.

Table 2. The average values of morphological characters from the first pot experiment. All the ANOVA results were highly significant ($p < 0.001$).

Treatment	Leaf size (cm)	Number of stolons	Number of leaves	Stolon length (cm)	Internode length (cm)
Control	12.8	5.2	29.3	38.0	1.3
A-f 1	6.0	2.0	12.9	18.3	0.8
A-f 1/2	12.0	4.7	26.9	34.8	1.3
A-f 3/4	9.3	4.0	20.4	23.6	0.9

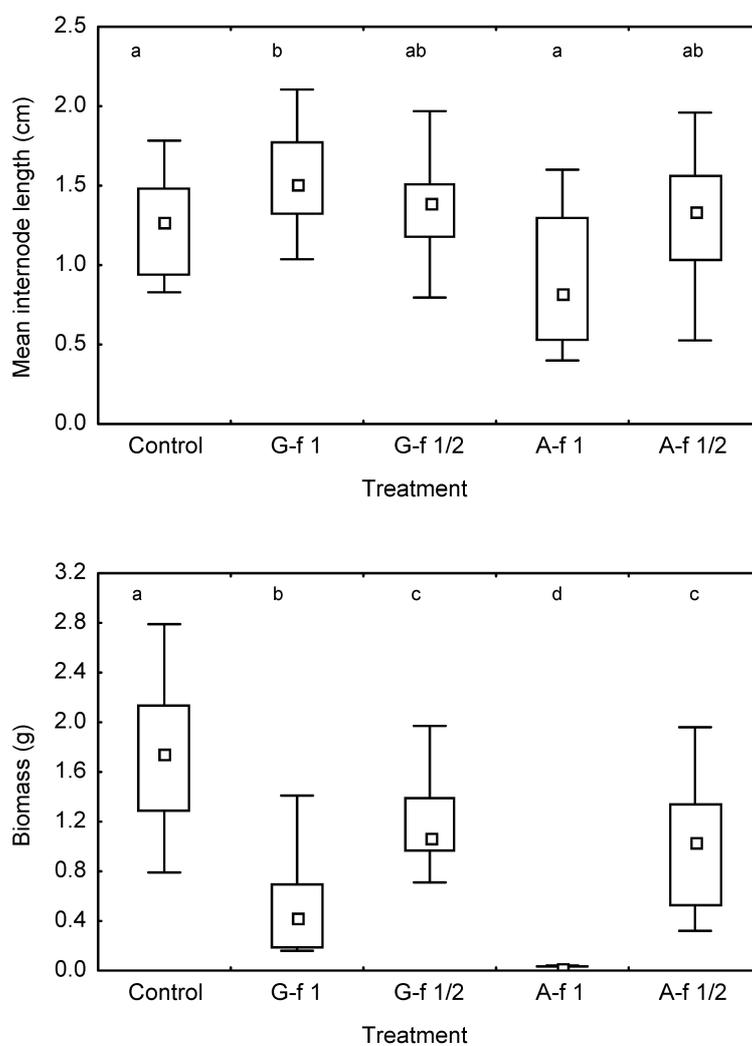


Figure 4. Mean internode length and aboveground biomass of target plants in the second pot experiment. Identical letters on the top of the figure correspond to nonsignificant ranges ($p > 0.05$) for the harvesting date measurement (Tukey HSD). Treatments: Control, G-f 1 = Green square foil shading all the pot, G-f 1/2 = Green foil shading half of the pot, A-f 1 = Aluminium square foil shading all the pot, A-f 1/2 = Aluminium foil shading half of the pot.

In growth chamber treatments ("A-f 1/2" and "G-f 1/2") the hypothesis of uniform centroid distribution was not rejected (Table 3). In addition we did not find

a significant mean angle in the treatment with altered light quality "G-f 1/2", but in the treatment "A-f 1/2" we found a significant mean angle which indicates

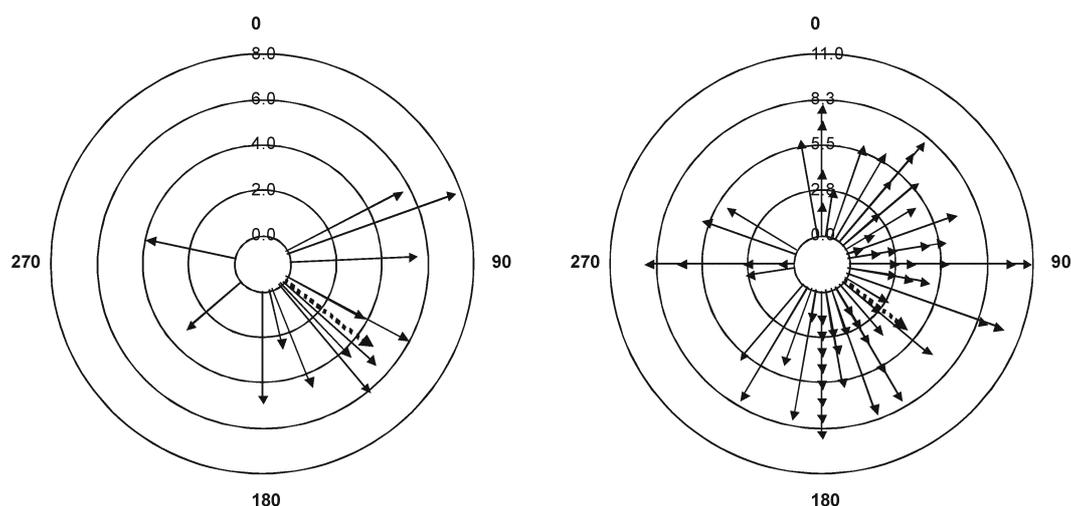


Figure 5. Distribution of the centroids (left) and stolon tips (right) in the treatment "Half gap". The thick discontinuous arrows represent the mean angles. The section from 0° to 180° is the stripped part of the treatment. The numbers in each circle means the distance from the plant centre in cm. Ohrazení, 3 July 1999.

Table 3. The Rayleigh test (Batschelet 1981) of the uniform distribution of centroids around the circle. The significant treatments have a non-uniform distribution of centroids. Significance based on critical values tables (Zar 1996).

Date	Treatment	z	p
9 May 1999	"Half gap"	4.31	< 0.02
31 May 1999	"Half gap"	2.86	0.05 < p < 0.1
3 July 1999	"Half gap"	5.54	< 0.005
12 August 1999	"Half gap"	5.51	< 0.005
22 March 2000	"G-f 1/2"	1.75	0.1 < p < 0.2
22 March 2000	"A-f 1/2"	2.25	0.1 < p < 0.2
14 April 2000	"G-f 1/2"	0.89	0.2 < p < 0.5
14 April 2000	"A-f 1/2"	2.47	0.05 < p < 0.1

non-uniform centroid distribution (Zar 1996) (Table 4). Mean angles, if significant, and centroids were mostly directed toward the unshaded parts (Table 4, Figure 6). There was no dependency of the stolon length on the angle of growth, but in all measurements, except the treatment "G-f 1/2" on 14 April 2000, centroids had preference ($p < 0.05$) for the positive values, i.e., for the side without shading (see Table 5, Figure 6). There was no significant difference in internode length between the side with and without foil. The interesting result, albeit not significant, was in the treatment "G-f 1/2" at 14 April 2000 where stolons with longer internodes showed tendency to be oriented to the side with the green foil ($p = 0.07$).

Discussion

The common expression of foraging in clonal plants is that plants exploit favourable and avoid unfavourable portions of the habitat by changing their growth response, for example by decreasing stolon length or increasing branching in favourable microsites (Oborny and Cain 1997; Klimešová and Klimeš 1997; Skálová and Krahulec 1992). Under less favourable conditions, plants have fewer but longer spacers (de Kroon and Schieving 1990; Huber-Sannwald et al. 1998; Cain 1994; Dong and de Kroon 1994; Alpert 1999). Foraging has been demonstrated for many plant species, for example, *Hydrocotyle bonariensis* (Evans and Cain 1995), and *Trientalis europea* (Piqueras et al. 1999). As shown by de Kroon and Hutchings (1995), increased branching in favourable microsites can be also interpreted as positive growth response, whereas shortening of spacers can not. Consequently, shortening of spacers under favourable conditions is clearly adaptive response and it could be interpreted as foraging.

Prunella vulgaris, in a manner similar to many other clonal species, has short-living stolons that enable it to place its ramets away from the mother plant. In the graminoid treatments, *P. vulgaris* exhibited a growth form with long stolons that penetrated deep through vegetation. The graminoids represent strong competitors for many herb species (Lepš 1999). For the vegetative growth of *Prunella vulgaris*, the identity of its graminoid competitor is probably not im-

Table 4. The existence of mean angles, their corresponding values and the results of Parametric one-sample second-order analysis of angles using F criterion (Zar (1996), significant values ($p < 0.05$) are shown in bold). Comparison of values of mean angles, centroid angles and length (i.e., distances from the plant centre) in the divided treatments ("Half gap", "A-f 1/2" and "G-f 1/2") in the field and pot experiments. The vegetation free/unshaded part is 0–180°.

Date	Treatment	F Criterion	Mean angle (if it exists)	Centroid Angle	Centroid length (cm)
9 May 1999	"Half gap"	6.95	113°47'	110°24'	3.24
31 May 1999	"Half gap"	5.93	121°50'	102°52'	3.06
3 July 1999	"Half gap"	19.96	122°45'	127°36'	4.85
12 August 1999	"Half gap"	7.05	119°40'	115°07'	4.39
22 March 2000	"G-f 1/2"	0.96		96°44'	1.67
22 March 2000	"A-f 1/2"	4.17	118°04'	98°41'	1.70
14 April 2000	"G-f 1/2"	0.58		39°34'	4.30
14 April 2000	"A-f 1/2"	4.08	105°34'	73°11'	4.24

Table 5. Side preference of centroids. Significant results mean a preference for the vegetation removed/unshaded part. One sample t-test was used to test results. "p" are significance levels.

Date	Treatment	p
9 May 1999	"Half gap"	0.007
31 May 1999	"Half gap"	0.000
3 July 1999	"Half gap"	0.000
12 August 1999	"Half gap"	0.001
22 March 2000	"G-f 1/2"	0.024
22 March 2000	"A-f 1/2"	0.035
14 April 2000	"G-f 1/2"	0.286
14 April 2000	"A-f 1/2"	0.016

portant. The competitors appeared to be equivalent, similarly as in Goldberg and Werner (1983). Visually, it seemed that the long stolon growth form was particularly well developed within *Nardus stricta* which has very dense root and shoot systems with hardly any gaps which would enable *P. vulgaris* to root there. In patches of graminoids, the plants invest energy in stolon growth rather than in root production. Not only would establishment in a turf be difficult, but also the nutrients would probably be depleted by the graminoids (Evans and Cain 1995). Similar behaviour was reported for *Elymus lanceolatus*, which, in response to the dense root system of *Agropyron desertorum*, formed long stolons crossing over the barrier (Huber-Sannwald et al. 1998). Evans and Cain (1995) documented the faster spreading of *Hydrocotyle bonariensis* by stolons veering away from a grassy environment.

In contrast to the bunch grass environment, *P. vulgaris* in gaps had a more condensed growth with short stolons and dense foliage. This growth pattern appar-

ently reflects the lack of aboveground competition and mechanical root and shoot obstructions in the gaps. Inconsistent results in the "Natural gap" can be explained by higher retention of water there or by the influence of neighbouring grass patches. Although the total number of stolons in the field experiment was roughly constant over the treatments, in the split treatment, where the seedling was transplanted on the border between favourable and unfavourable part, three times more stolons ended up in the favourable part. Consequently, the vast majority of leaves was placed into the vegetation free part of the habitat. This could be again considered as a foraging behaviour, also reported for *P. vulgaris* by Schmid (1985b).

In our field experiment, the internode length under favourable light condition was only 60% of that under competitive environment. Based on the model of Sutherland and Stillman (1988), de Kroon and Hutchings (1995) argue that the shortening itself in this range is not sufficient to place a significant amount of ramets or resource acquiring structures in the good patches. In our opinion, this conclusion is dependent on parameters of the model, particularly on the patch size and on the proportion of favourable and unfavourable area. If the area is perceived as a relatively favourable matrix with small unfavourable spots (bunches of competitive grasses), then the elongation of spacers under unfavourable conditions could be a very efficient tool of escape from the unfavourable patches.

The ability to forage is an important part of species' strategies. The creeping *Prunella vulgaris* is an inferior competitor for light. However, its ability to escape from unfavourable conditions by horizontal growth is probably one of the means that enable it to

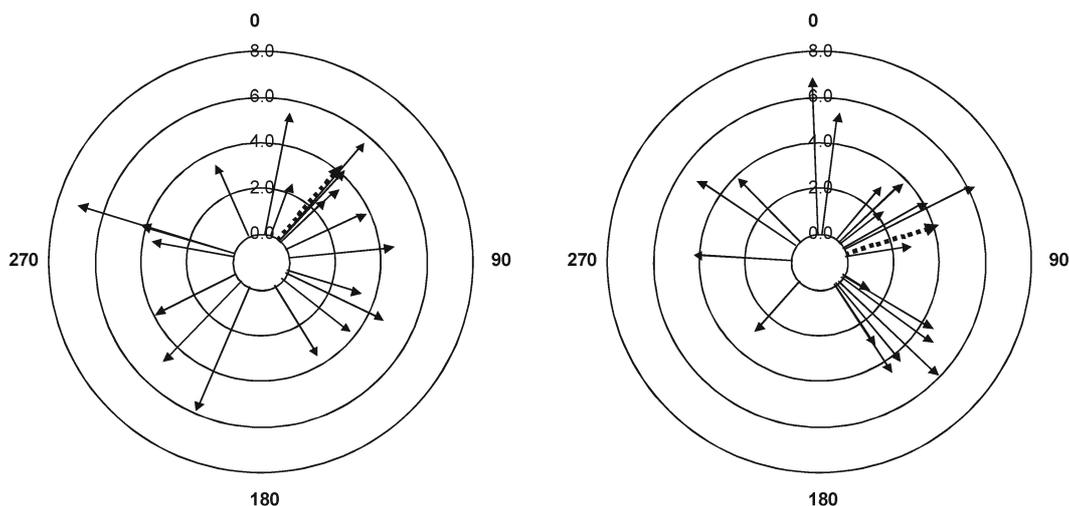


Figure 6. Distribution of the centroids in the treatments "G-f 1/2" (left) and "A-f 1/2" (right) in the second pot experiment (14 April 2000). The thick discontinuous arrows represent the mean angles. The sections from 0° to 180° are the parts without foil. The numbers in each circle means the distance from the plant centre in cm.

survive in competition with much taller plants. The means of clonal growth are important for permanent coexistence in species rich meadow communities, especially in combination with small scale disturbance forming gaps in the vegetation.

The differences in rate of flowering are difficult to interpret. Interestingly, whereas the effect of competitors on vegetative growth was roughly equivalent, marked differences were found in flowering, particularly between plants in *Nardus*, where the flowering was highest of all the treatments, and *Juncus* with no plants flowering. In *Nardus* tussocks, *Prunella* was able to use two escape strategies – forming stolons for short distance escape, and seed production for long distance escape.

The competitive effect of neighbouring vegetation on stolon growth can be exerted through three factors: changing light quality and quantity, change in nutrient availability, or mechanical obstructions. We expected the light to be the most important for stolon production, and consequently manipulated the light in laboratory experiment. Several studies investigated the effect of changing R/FR ratio on shoot growth parameters. In studies by Skálová and Vosátka (1998) and Skálová and Krahulec (1992), *Festuca rubra* biomass and number of tillers decreased in a low R/FR ratio environment. A similar response in stolon number was found by Dong and de Kroon (1994) in *Cynodon dactylon*. Leeftang (1999) analysed the plant response to R/FR in six species, but did not find any significant differences in spacer length. In our experi-

ments light quantity was decreased by aluminium foil, and both light quality and quantity were decreased by green foil. Contrary to Leeftang (1999), we found an increase in internode length and decrease in number of stolons under low R/FR ratio. Longer stolons (26% longer than in the control) were produced despite the lower plant biomass. Plants growing under low R/FR invested a large part of their remaining energy into escape from unfavourable conditions (see also Huber et al. (1999) and Kembell et al. (1992)). With drastic light shortage, reduced photosynthesis results in a lack of energy (Winn and Evans 1991), constraining stolon growth. In summary, biomass of our plants decreased monotonically with decreased light availability and quality, whereas the stolon length had its maximum in treatment with low R/FR and decreased in both extremes of light availability.

In addition to light, nutrient availability may be higher in gaps because it is not depleted by vegetation (Huber-Sannwald et al. 1998). Nutrients are not only important for biomass production, but also affect plant architecture. High nitrogen level induces a decrease in cytokinin synthesis and consecutive decrease in apical dominance. This causes an increased branching and shortening of spacers (Hutchings and Bradbury 1986).

Few studies have used analyses of angular data, although biological data on circular scale are quite common (Cain 1989). In the field experiment the treatment "Half gap" had non-uniform centroid distribution. It could have two possible causes: 1. most of

Table 6. Influence of competitor and decreased light quality and/or quantity on the growth characteristics of *Prunella vulgaris*.

Level	Factor investigated	Light quality or quantity decrease	Graminoid competitor
Organ	size of leaves	little decrease	Not measured
	total number of leaves	decrease	None
	internode length	little increase (except "A-f 1")	Increase
Stolon	number of stolons	decrease	None or decrease
	mean stolon length	none (except "A-f 1")	Increase
Plant	Biomass	decrease	Not measured

the stolons accumulated in certain sectors of the circle, or 2. a few very long stolons occur in certain sectors. As can be seen in Figure 5, the majority of stolons preferred the stripped part of the treatment and consequently the mean angle was found there. This preference was not necessarily due to high nutrient availability in the areas where vegetation was removed or due to the low R/FR ratio on the other side. It could be simply caused by mechanical obstruction to the stolon penetration into the vegetation, and/or by root interactions between *P. vulgaris* and neighbouring species (see also Huber-Sannwald et al. (1998)). The combination of all the three factors was most probable.

The situation in the pot experiment was slightly different. We were not able to reject the hypothesis of uniformity of centroid distribution, but in the treatment "A-f 1/2", the mean angle was significant, revealing that plants responded to the low light by greater accumulation of stolons on the side without shading. However, no side preference was revealed in a similar treatment with green foil; low R/FR ratio did not prevent the stolons from growing to the shaded part.

Conclusions

The effects of treatment type on the clonal growth characteristics of different plant organisation levels are summarised in Table 6. It seems that *P. vulgaris* can distinguish between favourable and unfavourable patches in heterogeneous environments and is able to respond by changing its morphology – stolon and internode length, stolon production and orientation. *Prunella vulgaris* assumed a penetrating guerrilla type of growth in the presence of any graminoid competitor, while in their absence, plant growth was more condensed with shorter internodes. In the pot experiment, the number of stolons decreased under shading.

In heterogeneous treatments, *P. vulgaris* was able to place the majority of its stolons in the favourable parts of its surrounding environment. Two strategies are used to reach out of unfavourable spots – prolongation of vegetative spacers, and increased generative reproduction.

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