

Equivalence of competitor effects and tradeoff between vegetative multiplication and generative reproduction: case study with *Lychnis flos-cuculi* and *Myosotis nemorosa*

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Summary

Effects of graminoid competition and gap size on clonal growth and reproduction of two meadow species, *Lychnis flos-cuculi* and *Myosotis nemorosa*, were studied in an oligotrophic wet meadow and in a pot experiment. In the field experiment, plant height, lateral spread, number of leaves and flowers, and clonal growth characteristics (number of secondary rosettes or shoots produced) were repeatedly measured over three seasons. In the field experiment, young plants of investigated species were transplanted into tussocks of three graminoids: *Molinia caerulea*, *Juncus effusus* and *Nardus stricta*; and into small and large gaps. The effect of all competitive tussock graminoids on the growth of both target species was negative, but not equivalent, and differed between *Lychnis flos-cuculi* and *Myosotis nemorosa*. The species responded to graminoid competition also by changing their geometry and phenology. The positive effect of gaps on both species' clonal growth increased with gap size. Investments into generative and vegetative reproduction were negatively correlated among treatments in *Lychnis flos-cuculi* and positively correlated in *Myosotis nemorosa*. In the greenhouse experiment seedlings of *Lychnis flos-cuculi* and *Myosotis nemorosa* were transplanted into pots with different amounts and spatial patterns of the competitive grass *Holcus lanatus*. Total density but not spatial arrangement of *Holcus lanatus* seedlings had the main competitive effect on the growth of *Lychnis flos-cuculi* and *Myosotis nemorosa*. Vegetative growth of both species was negatively correlated with increasing competitor's density.

Key words: clonal growth, field experiment, gap, *Lychnis flos-cuculi*, *Myosotis nemorosa*, plant competition

Introduction

Temperate zone meadows are among the most species rich plant communities in the world (on the scale of meters) with as many as 50 species per square meter. In Central Europe, they developed in sites where the original forest was cleared and are sustained by the prevention of succession towards forest by traditional

management regimes, i.e., grazing and cutting (Bakker 1989). Species richness declines when a suitable management regime is abandoned. Understanding species interactions in these multi-species communities and conditions that enable species coexistence is important for the conservation of those communities, particularly in the face of present land use changes. This understanding must be based on an intimate knowledge of the

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biology of individual species. Species loss in these communities is mainly because competitively inferior species are outcompeted by their neighbors. This makes the study of competition particularly important. Because all plants use essentially the same resources, all individuals in a community are potential competitors (Goldberg & Werner 1983). Grasses form the matrix of meadow communities and are the most important competitors for both established individuals and seedlings of forbs.

The intensity of competition of neighbors on a target individual is derived from their distance and size (height, leaf area, biomass), and, all else being equal, larger plants have an advantage in asymmetric competition (Connolly & Wayne 1996). The equivalence of growth form hypothesis (Goldberg & Werner 1983) suggests that the growth forms of similar sized species are relevant units of competition. Meadow grasses (and other graminoids) often grow in compact patches with short stolons, and are tall. This competitively strong growth form enables meadow grasses to win in asymmetric competition (Connolly & Wayne 1996). However, even similar species often differ in their density and biomass (Goldberg & Werner 1983; Peltzer et al. 1998), and consequently, in their competitive effect.

Clonal plants can persist in a suitable place, spread vegetatively, and change some morphological parameters in response to neighbor conditions (de Kroon et al. 1994; Oborny & Bartha 1995). The tradeoff between investment of clonal plants into either vegetative spread or sexual reproduction is usually modified by the environment, with vegetative spread being favored in less competitive environment (Caswell 1985; Eriksson 1997).

Gaps in meadow vegetation reduce levels of competition and are ideal microhabitats for growth of individual plants (Mehrhoff & Turkington 1996; Wilson & Tilman 1991; Morgan 1997) as well as seedling recruitment (Křenová & Lepš 1996; Špačková et al. 1998; Touzard et al. 2002), particularly under benign conditions. This is because of open space, light availability, and probably also reduced root competition. In contrast, gaps are more affected by drought, what might be an important disadvantage for drought-sensitive plants and seedlings (Kotorová & Lepš 1999).

The aim of this paper is to evaluate the effects of competition from dominant grasses *Molinia caerulea* and *Nardus stricta*, and *Juncus effusus* (Juncaceae), in contrast to the effects of gaps, on the growth of *Lychnis flos-cuculi* and *Myosotis nemorosa* in an oligotrophic wet meadow. We were particularly interested in competitive effects on clonal spreading and its ratio to generative reproduction.

The second aim of this paper is to evaluate the effect of density and spatial pattern of the competitor *Holcus lanatus* on *Lychnis flos-cuculi* and *Myosotis nemorosa* in a pot experiment under greenhouse conditions. *Holcus lanatus* is a non-tussock grass species common at the locality. It was used because of fast growth, making it suitable for short-term pot experiments.

Materials and methods

Study species

Lychnis flos-cuculi and *Myosotis nemorosa* were selected as target species. Both of them flower regularly, but also exhibit the clonal spread. This combination is very important for comparison of allocation to generative reproduction and vegetative growth under various competitive conditions. Seeds were collected at the experimental field site.

***Lychnis flos-cuculi* L.** (Caryophyllaceae) – ragged robin. $2n = 24$. *Lychnis flos-cuculi* (called *L. flos-cuculi* hereafter) occurs from lowlands to mountains (up to 1300 m a.s.l. in Central Europe), mostly in wet meadows, ditches, and light alder woods. Deep, nutrient rich soils are preferred (Hegi 1979; Grime et al. 1987). It is able to successfully colonize disturbed vegetation-free mesotrophic sites (Hopkins et al. 1998). The number of *L. flos-cuculi* populations is decreasing in Central Europe, because meadows are drained and converted into arable or fallow land (Hauser & Loeschke 1996; Šourková 1990); however, the decrease is not as pronounced as in many other grassland species and *L. flos-cuculi* is still common.

L. flos-cuculi is a 20–60 cm high hemicytopyte. It forms a vegetative rosette of leaves from the center of which grows a floral stem. Flowering occurs in May and June (Šourková 1990). *L. flos-cuculi* is sometimes considered biennial or short-lived perennial (Hegi 1979), sometimes long-lived perennial (Grime et al. 1987; Biere 1995). The plant can create secondary daughter rosettes from axillary buds of stem origin (Hegi 1979; Grime et al. 1987; Šourková 1990). Secondary rosettes usually remain attached to the mother rosette longer than one growing season and form an interconnected clone up to 25 cm in diameter. Klimeš & Klimešová (1999 a, b) classify *L. flos-cuculi* as “*Rumex obtusifolius* clone type”, i.e., with underground shoots of stem origin shorter than 10 cm, with a low spreading speed (only a few cm per year) (Kl imeš & Klimešová 1999 a, b; Klimeš et al. 1997). *L. flos-cuculi* plants have a short primary root (5–8 cm) and weak lateral roots. They are strongly influenced by nutrient levels and water conditions (Hegi 1979). Some *L. flos-cuculi* plants (26–74%) contain arbuscular mycorrhizae (Grime et al. 1987). Seeds have rapid and very high germination rates, both in the field (93%) and laboratory (98%) (Kotorová & Lepš 1999).

***Myosotis nemorosa* BESSER** (Boraginaceae) – forget-me-not. $2n = 22$. *Myosotis nemorosa* (called *M. nemorosa* hereafter) is a species from the taxonomically complex group *Myosotis palustris* agg. There are only few taxonomic treatments of this complex that include caryological investigations

(Przywara 1983; Štěpánková 1993). There are no ecological studies of *M. nemorosa*. An ecophysiological study of *M. palustris* is available; however, it is not clear whether the *M. palustris* group or *M. palustris sensu stricto* was investigated (Biemelt et al. 1996; Schlüter et al. 1996). Often the species within the group are not distinguished, and some published data on *Myosotis palustris* may also include *M. nemorosa*.

Myosotis nemorosa is considered to be an annual to long-lived perennial hemicryptophyte species. In Central Europe it occurs from lowlands to mountains up to 1400 m a.s.l. Typical habitats are wet meadows, spring areas and wet woods. It flowers from May to August. Plants of *M. nemorosa* form short below-ground shoots of stem origin (Štěpánková 2000). Seeds have rapid and relatively good germinability (65% in the field and 80% under greenhouse conditions) (Kotorová & Lepš 1999).

Study site

The study site is a wet, oligotrophic, species-rich meadow 10 km south-east of České Budějovice, Czech Republic, 48°57' N, 14°36' E, at 510 m a.s.l. Mean annual temperature at the České Budějovice Meteorological Station (400 m a.s.l.) is 7.8°C; mean annual precipitation is 620 mm. Soil nutrient levels are low (total nitrogen 6–8 g/kg dry soil weight, total phosphorus 400–500 mg/kg dry soil weight, C/N ratio 16–20) (Kotorová & Lepš 1999). Phytosociologically, the vegetation belongs to the Molinion with some elements of the Violion caninae. Graminoids *Molinia caerulea*, *Nardus stricta*, *Holcus lanatus*, and *Juncus effusus* and sedges (*Carex*, 10 spp.) are dominants. The community is species rich (up to 40 species per m²), with many meadow species – for example *Angeľlica sylvestris*, *Betonica officinalis*, *Galium boreale*, *Lychnis flos-cuculi*, *Myosotis nemorosa*, *Sanguisorba officinalis*, *Succisa pratensis*, *Scorzonera humilis*. The aboveground biomass in June (peak) varies between 240 and 330 g·m⁻². In recent years the meadow has been mown annually. Other experiments investigating species coexistence and effect of competition are running concurrently at this locality (Špačková et al. 1998; Lepš 1999; Kotorová & Lepš 1999; Zelený 1999; Titus & Lepš 2000; Petruš & Lepš 2000).

Field experiment design

The field experiment was established in June 1998, in a randomized block design. Laboratory grown seedlings (sized four to six leaves) of both target species, were transplanted using starter (Jiffy) pots into 14 (*M. nemorosa*) and 7 (*L. flos-cuculi*) 1 m² blocks. Each block contained five treatments into which seedlings were transplanted as follows, one seedling per one treatment: *Molinia caerulea* tussock (*Molinia*), *Nardus stricta* tussock (*Nardus*), *Juncus effusus* tussock (*Juncus*), a small, mainly natural gap in the vegetation about 10 cm in diameter (here called Small gap), and artificially cleared space in the vegetation about 20 cm in diameter (here called Big gap). The

Small gaps mimic naturally empty space between tussocks in the vegetation, the Big gaps result from major disturbances (e.g. rooting by wild pigs). Accordingly, both, the above- and the below-ground, vegetation were removed from the Big gaps. The gap types differed accordingly by both, size of above-ground opening, and intensity of belowground competition. The plot was mown with a sickle at the beginning of the experiment. Gaps were renewed each year at the beginning of the season. Litter was removed at the time of plot establishment and again in springs 1999 and 2000. Vegetative and reproductive characteristics of each *L. flos-cuculi* and *M. nemorosa* were measured four times over the 1998 growing season (July 7 and 29, August 26, October 23), seven times over the 1999 growing season (April 27, May 11 and 31, June 14 and 29, July 21, September 11), and some characteristics were recorded in June 2000 (June 9). The following characteristics were recorded: height of the standing above-ground stem (mm), length of the longest leaf (mm), width of the clone (= clone projection) originating from a transplant (horizontal distance of the two more distant shoots) (mm), number of leaves, number of secondary rosettes (for *L. flos-cuculi*), number of shoots (for *M. nemorosa*), number of flowers, and number of flower stems per flowering plant (for *L. flos-cuculi*).

Pot experiment design

A pot experiment was established on January 29, 2000. Laboratory grown seedlings of the target species were transplanted into the center of 8×8cm pots, one seedling per pot. Four treatments were applied, differing in *Holcus lanatus* density and spatial pattern: control without *Holcus lanatus* (Control), five *Holcus lanatus* seedlings on half of the soil surface in the pot (here called Half-5), ten *Holcus* seedlings on half of the soil surface in the pot (here called Half-10), ten *Holcus lanatus* seedlings on the entire soil surface in the pot (here called Whole-10). Plants were grown for two months in a light regime of 14 hours light and 10 hours dark with temperature fluctuating between 26°C (day) and 20°C (night). *Holcus*, which grew much faster, was cut four times during the experiment. Pot positions were randomized and vegetative characteristics on each plant were measured and counted eleven times in regular intervals during the experiment. Measured characteristics were: height of the above-ground stem (mm), length of the longest leaf (mm), width of the longest leaf (mm), width of plant (mm), number of leaves, number of secondary rosettes (for *L. flos-cuculi*). At the end of the experiment, target plant dry weight was determined. Height and density of competitor increased gradually with growth of *L. flos-cuculi* and *M. nemorosa* plants during the experiment, and in the end pots were filled with roots of *Holcus* in all treatments.

Statistical analyses

Differences between treatments were evaluated by repeated-measures ANOVA (Anonymus 1998), for each year separately. The ANOVA was conducted with all the individuals that

Table 1. Significance of effects in repeated measures ANOVA for *Lychnis flos-cuculi* characteristics (where only one measurement was analyzed, simple one-way ANOVA was conducted). "Main" corresponds to the main effect of treatment, "interaction" means the interaction between treatment and time. Where the main effect was significant, it is followed by significant pairs in multiple comparisons (Newman-Keuls test). For example, (BG > J, M) means that the plants in Big Gap were significantly greater than plants in both *Juncus* and *Molinia* treatments for the particular characteristic. In 1998, number of secondary rosettes was analyzed for one measurement only (23.10.), other vegetative characteristics were analyzed for three measurements (5.7., 29.7. and 26.8.). In 1999, five measurements of all vegetative characteristics (27.4., 11.5., 31.5., 14.6. and 29.6.), two measurements of number of flowers (31.5. and 14.6.) and one measurement of number of flower stems per flowering plant only (14.6.) were analyzed. In 2000, only one measurement is available. Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

		1998			1999			2000	
		F	p	Post-hoc comparison	F	p	Post-hoc comparison	F	p
Secondary rosettes	main	2.66	0.052	* BG > J	3.08	0.03	* BG > J	0.37	0.83
	interaction	–	–	–	0.96	0.51	–	–	–
Number of leaves	main	0.90	0.47	–	1.41	0.26	–	–	–
	interaction	1.44	0.35	–	0.92	0.55	–	–	–
Number of flowers	main	–	–	–	0.76	0.56	–	–	–
	interaction	–	–	–	1.40	0.26	–	–	–
Number of flower stems per flowering plant	main	–	–	–	2.68	0.067	* BG > J, N, SG, M	–	–
	interaction	–	–	–	–	–	–	–	–
Clone projection (mm)	main	–	–	–	1.18	0.34	–	2.63	0.07
	interaction	–	–	–	1.94	0.02	–	–	–
Plant height (mm)	main	5.01	0.003	** J > BG * J > SG, M, N	1.47	0.24	–	–	–
	interaction	2.80	0.01	–	1.24	0.25	–	–	–
Longest leaf (mm)	main	1.12	0.37	–	1.52	0.23	–	–	–
	interaction	2.48	0.02	–	1.03	0.43	–	–	–

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, – = not enough data for statistical analysis

survived the analyzed season. Based on their distribution characteristics, data were $\log(x + 1)$ transformed to improve normality and homoscedasticity. If the main effect was significant, the Neuman-Keuls test was used for post-hoc comparisons, as a reasonable compromise between control of Type I error inflation and power of the test (Underwood 1997). In the repeated-measures ANOVA, the main (i.e., treatment) effect corresponds to average differences between treatments over the entire analyzed period; treatment interactions with time signify differences in the seasonal dynamics of the analyzed variable. (Each year was analyzed separately to prevent the confounding of seasonal and between year dynamics.) As temporal changes are rather trivial, significance of the Repeated measures factor (time) is not reported in the tables. Some of the vegetative characteristics (e.g. number of shoots of *M. nemorosa*) did not change during the first season – in this case, the simple one-way ANOVA was used for one of the measurements. Similarly, for the only measurement in 2000, the simple one-way ANOVA was conducted.

Dependence of flowering on plant size at the end of the previous growing season was analyzed by logistic regression.

Results

Field experiment

Lychnis flos-cuculi (Table 1)

Mortality of *L. flos-cuculi* clones was very low during whole experiment (only 3 plant died during the experiment). During the first season rosettes differed in height (both main effects and interaction with time significant) (Table 1). The tallest rosettes were found in *Juncus*, and differed from all other treatments; the plant responded to the competitive effect of this species by vertical position of its leaves in *Juncus*. Vertical orientation and size increase resulting in higher plants were observed in the two other competitive grasses also, but the effect was much less pronounced. The length of the leaves did not differ among treatments, therefore the plant height was determined mainly by leaf orientation, vertical

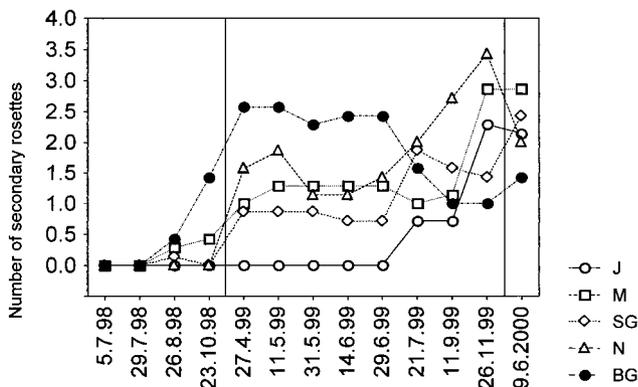


Fig. 1. The average number of secondary rosettes of *Lychnis flos-cuculi* plants in each of five treatments during 1998 and 1999 seasons and at the beginning of the 2000 season. Dates are in the form day.month.year. (Repeated measurements ANOVA for the whole study period, treatment: $F = 2.07$; $p = 0.11$, interaction with time: $F = 2.06$; $p < 0.001$). Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

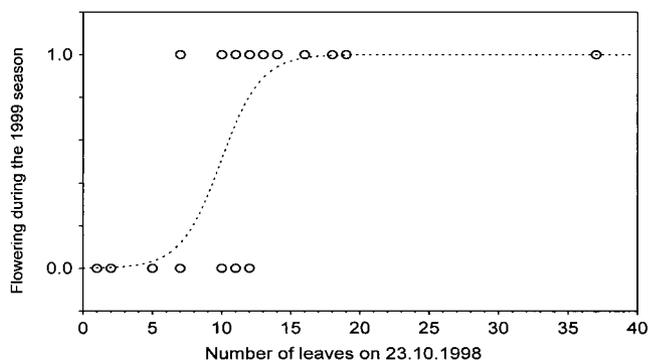


Fig. 3. Dependence of flowering of *Lychnis flos-cuculi* plants in 1999 on the number of leaves in autumn 1998 (0 – flowerless, 1 – flowering). Dependence is described by the logistical function: $Y = \exp(-6.821 + (0.687) \times x) / (1 + \exp(-6.821 + (0.687) \times x))$, $p < 0.01$.

orientation causing the plants being higher. Rosettes in *Nardus*, unlike in the other treatments, maintained the vertical orientation of their leaves (and consequently, their higher height) until October; in the other competitive grasses and both gaps rosettes vertical orientation was maintained only till August, and then decreased. In Big gap, the leaves were in a horizontal position over the entire season, and plants were the shortest of all the treatments. During the second season *L. flos-cuculi* formed the largest clones with the highest number of secondary rosettes in the Big gap (Figs 1, 2). Plants in Big gap had larger clone diameters and more secondary rosettes than in all other treatments, especially in

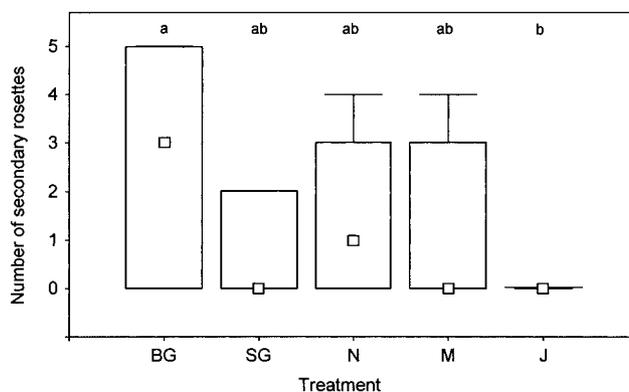


Fig. 2. The average number of secondary rosettes of *Lychnis flos-cuculi* plants in each of five treatments at the top of the second season (June 29, 1999). ANOVA: $F = 2.70$; $p < 0.05$. Median, interquartil range (box) and extremes (whiskers) are displayed. Lowercase letters signify non-significant ranges in the Newman-Keuls test. Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

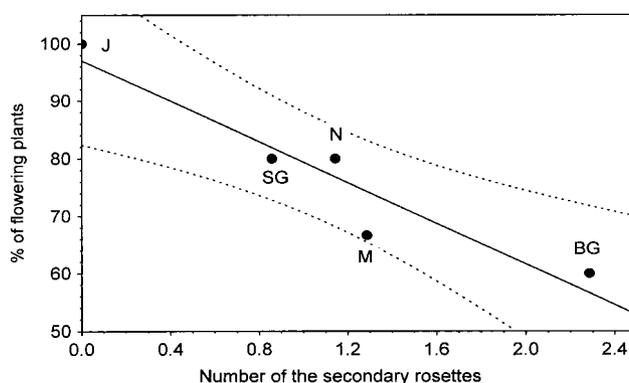


Fig. 4. Linear regression of % of flowering plants of *Lychnis flos-cuculi* and average numbers of secondary rosettes in each of five treatments on May 31, 1999. $F = 27.7$; $p = 0.01$; correlation coefficient $r = -0.95$. Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

Juncus. There were differences between treatments in the dynamics of secondary rosettes. Especially in the second half of the growing season the number of secondary rosettes rapidly decreased in Big gap in contrast to the other treatments, where it increased (Fig. 1). Treatments also differed, although not significantly, in the number of flowering plants – in *Juncus* tussocks every plant flowered, but in Big gap, only 60% flowered (Fig. 4). However, only in Big gap there were plants of *L. flos-cuculi* able to produce more than one flowering stem per plant (average of 2.5 stems per flowering plant). Plant width dynamics differed, with a decrease in the *Juncus* treatment, and an increase in the

second half of the season in *Molinia* and *Nardus*. The size of sterile rosettes in all treatments at the end of the first growing season was a good predictor of the probability of flowering in the next year (Fig. 3). Mean flower number and mean secondary rosette number over the five treatments were negatively correlated, although not statistically significant ($r = -0.68$; $F = 2.58$; $p = 0.206$ on July 1999). Percent plants flowering and mean secondary rosette numbers were significantly negatively correlated across treatments (Fig. 4).

In the beginning of the 2000 season differences among treatments disappeared. Flowering of *L. flos-cuculi* plants was very poor during the 2000 season; only 20 percent of all plants were able to produce flowering stem(s), and most of these were subsequently grazed by slugs. The extremely poor performance in this year was probably caused by drought in April and May 2000 (Precipitation during April and May 2000 was 56.7 mm, whereas average from 1994 to 2002 is 113.2 mm, all from the Ledenice meteorological station, ca 4 km from the experimental site).

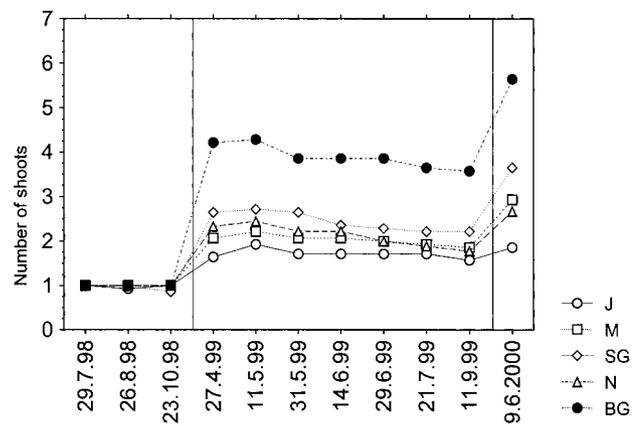


Fig. 5. The average number of shoots of *Myosotis nemorosa* in each of five treatments in the three growing seasons. Dates are in the form day.month.year. (Repeated measurements ANOVA for the whole study period, treatment: $F = 5.92$; $p < 0.001$, interaction with time: $F = 3.10$; $p < 0.001$; Newman-Keuls test: *** $BG > J$; ** $BG > M$; * $BG > N, SG$). Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

Table 2. Significance of effects in repeated measures ANOVA for *Myosotis nemorosa* characteristics (where only one measurement was analyzed, simple one-way ANOVA was conducted). “Main” corresponds to the main effect of treatment, “interaction” means the interaction between treatment and time. Where the main effect was significant, it is followed by significant pairs in multiple comparisons (Newman-Keuls test). In 1998, number of shoots was analyzed for one measurement only (26. 8.), other vegetative characteristics were analyzed for three measurements (5. 7., 29. 7. and 26. 8.). In 1999, six measurements of all vegetative characteristics (27. 4., 11. 5., 31. 5., 14. 6., 29. 6. and 21. 7.), five measurements of number of flowers (11. 5., 31. 5., 14. 6., 29. 6. and 21. 7.) and seven measurements of number of shoots (27. 4., 11. 5., 31. 5., 14. 6., 29. 6., 21. 7. and 11. 9.) were analyzed. In 2000, only one measurement is available. Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

		1998			1999			2000		
		F	p	Post-hoc comparison	F	p	Post-hoc comparison	F	p	Post-hoc comparison
Number of shoots	main	1.63	0.18	–	5.71	0.001	*** $BG > J$ ** $BG > M$ * $BG > N, SG$	3.71	0.009	** $BG > J$ * $BG > N$
	interaction	–	–	–	0.49	0.98	–	–	–	–
Number of leaves	main	3.5	0.013	* $J < BG, M$	5.96	<0.001	*** $BG > J$ ** $BG > SG, N$ * $BG > M$	–	–	–
	interaction	2.1	0.040	–	0.98	0.49	–	–	–	–
Number of flowers	main	–	–	–	3.2	0.02	* $BG > J$ (0.056967 $M > J$)	1.78	0.15	–
	interaction	–	–	–	2.7	0.001	–	–	–	–
Clone projection (mm)	main	–	–	–	3.1	0.02	* $BG > J$	2.57	0.049	* $BG > J$
	interaction	–	–	–	1.4	0.14	–	–	–	–
Plant height (mm)	main	0.20	0.94	–	1.1	0.34	–	–	–	–
	interaction	0.53	0.83	–	0.9	0.55	–	–	–	–
Longest leaf (mm)	main	0.58	0.68	–	0.77	0.55	–	–	–	–
	interaction	0.96	0.47	–	0.98	0.49	–	–	–	–

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, – = not enough data for statistical analysis.

Myosotis nemorosa (Table 2)

The mortality of *M. nemorosa* clones was very low during whole experiment. During the first (1998) season, treatments differed in the number of leaves only, with highest numbers of leaves in Big gap, and smallest numbers in *Juncus*. Plants in Big gap also differed in their dynamics from the other treatments, retaining a high number of leaves until October, whereas in the other treatments the number of leaves decreased earlier.

During the second season *M. nemorosa* produced secondary shoots (Fig. 5), and nearly all the secondary shoots flowered. The highest number of shoots, and consequently the highest number of leaves and flowers and the widest clone were found in Big gap in comparison with all other treatments. Shoot number, as did the other characteristics, decreased in tussocks, in the order Small gap, *Nardus*, *Molinia*, and the lowest numbers were in *Juncus*. Shoot number remained almost constant in all the treatments during the season 1999. The number of leaves were the highest in Big gap too, in comparison with other treatments. Number of flowers and clone projection was the lowest in *Juncus*, in comparison with Big gap, and *Molinia*. There were differences in flowering dynamics across treatments – in *Juncus* the peak of flowering was at the end of July, whereas in Big gap and other treatments, flowering finished at the end of June. All the plants produced flowering stems. Investments into generative (represented by flower number) and vegetative (number of shoots) reproduction of *M. nemorosa* across treatments were positively correlated (Fig. 6).

The differences among treatments persisted (although decreasingly obviously) until the third season, with the biggest clones with the highest number of shoots and largest clone projection in Big gap, and the lowest clones were in *Juncus* again, and then in *Nardus*. The positive correlation between number of shoots and number of flowers was the same, as in 1999.

Pot experiment

In the end of experiment, competitive treatment pots were filled with *Holcus lanatus* tillers, both the half-treatments only on the half of the pot surface. The lower parts of all competitive pots were strongly filled by roots. After two months, the biggest plants of *L. flos-cuculi* and *M. nemorosa* species were in the Control. The biomass of *L. flos-cuculi* and *M. nemorosa* was lower in all competitive treatments – Whole-10, Half-5 and Half-10 – in comparison with Control, but in the Half-5 treatment the biomass was intermediate between Control and other competitive treatments, and significantly

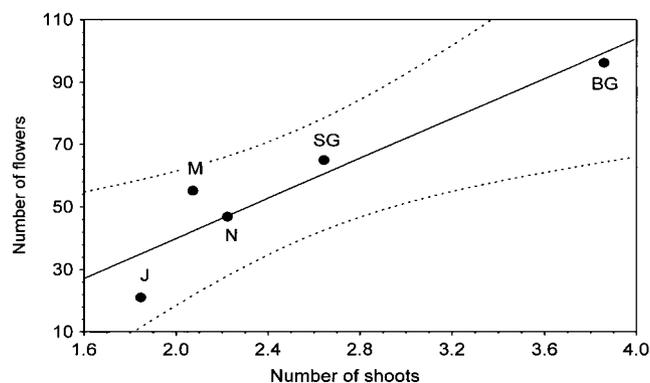


Fig. 6. Linear regression of average number of flowers and average number of vegetative shoots of *Myosotis nemorosa* in each of five treatments on May 31, 1999. $F = 20.01$; $p = 0.02$; correlation coefficient $r = +0.93$. Treatment abbreviations: J – *Juncus*, M – *Molinia*, SG – Small gap, N – *Nardus*, BG – Big gap.

higher than in both other competitive treatments (Fig. 7). Differences were highly significant for all the measured characteristics. *L. flos-cuculi* produced the most secondary rosettes in Control, and least in Whole-10 and Half-10. Plants of *L. flos-cuculi* produced many more secondary rosettes under all treatments in the pot experiment (average 7.24 per plant, maximum 17 rosettes per plant) in just two months, than under field conditions during two seasons (average 1.43 per plant, maximum 5 rosettes per plant). The differences in the number of rosettes among treatments were significant ($F = 4.95$; $p = 0.006$) and total biomass even more so ($F = 23.61$; $p < 0.001$). Plants of *M. nemorosa* did not produce shoots under greenhouse conditions during the two month experiment.

Discussion

Our study confirms that both the species are capable of clonal persistence on suitable sites over the three seasons of the experiment (and very probably much more), although *Myosotis nemorosa* is sometimes considered to be a species with no or only low clonal potential and limited life span (e.g. database of Klimeš & Klimešová 1999b). *Myosotis nemorosa* is able to form shoots of stem origin and *Lychnis flos-cuculi* multiplies with daughter rosettes from auxillary buds. This clonal growth facilitates species persistence.

The experimental results show that the growth of both investigated species, *L. flos-cuculi* and *M. nemorosa*, was affected by neighbor competition. As expected, both species grew better in gaps without competition, particularly in the Big gap treatments; however, we

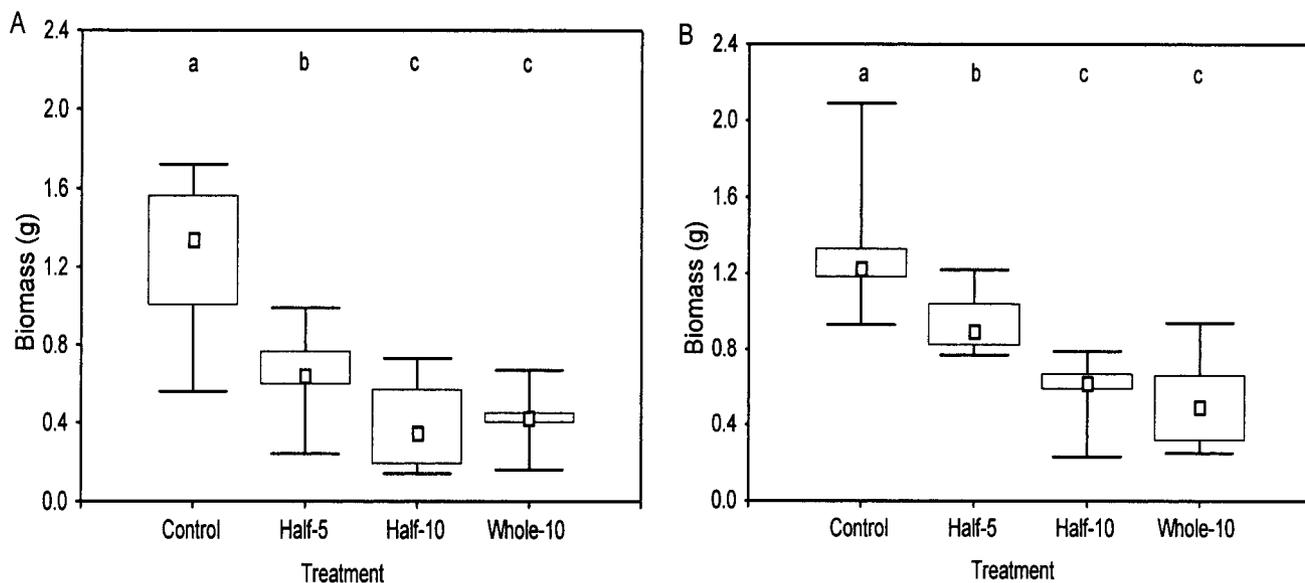


Fig. 7. The weight of dry biomass of (A) *Lychnis flos-cuculi* (ANOVA: $F = 23.61$; $p < 0.001$) and (B) *Myosotis nemorosa* (ANOVA: $F = 22.13$; $p < 0.001$) in each of four treatments at the end of pot experiment. Median, interquartile range (box) and extremes (whiskers) are displayed. Overlap letters above each bar signify non-significant ranges in the Newman-Keuls test. Treatment abbreviations: Control, Half-5, Half-10 and Whole-10.

recognized some differences between *L. flos-cuculi* and *M. nemorosa*. In *M. nemorosa*, each of the shoots flowered, regardless of the treatment, and most performance characteristics were highest in Big gap. In *L. flos-cuculi* most characteristics did not differ between treatments. But in *L. flos-cuculi* under high competitive stress in *Juncus* tussocks, all the rosettes created flowering stems, but no secondary rosettes. In Big gaps, by contrast, the plants invested in secondary rosettes, but the percentage of flowering plants was the lowest of all the treatments. Nevertheless, unlike in the other treatments, the individuals that flowered in the Big gap, have had formed multiple stems – one flower stem per rosette. Also, it appeared that the gap environment is not only a competition free space, but is also more prone to environmental extremes – the drought in the third season was particularly harmful to *L. flos-cuculi*. Our non-quantitative observations also suggest that seedlings and young plants in gaps are more prone to slug grazing.

The effect of all competitive tussock graminoids on the growth of both target species was negative, but not completely equivalent (Tables 1 and 2). Competitive graminoids *Molinia caerulea*, *Juncus effusus* and *Nardus stricta* are of similar growth forms and therefore their competitive abilities could be expected to be similar (Goldberg & Werner 1983; Peltzer et al. 1998). They all are polycarpic perennial hemicryptophytes growing in similar sites in tussock patches (Grime 1987). The results show that *Juncus* has a stronger com-

petitive effect in comparison with *Molinia* and *Nardus*, concordantly for both focal species. *M. nemorosa* plants in *Molinia* treatment had even significantly more leaves and flowered more than in *Juncus* (Table 2). Differences in competitive effects could be explained by differences in the detailed morphology of the competitors. *Juncus* tussocks are very compact without spaces, with daughter offshoots clamped to mother ramets. They grow very fast in spring, and in June they have about fifty percent more aboveground green biomass than *Molinia*, which exhibits maximal growth late in the season. *Nardus* tussocks are also very compact, but they are the lowest and with narrow leaves. The bulk of *Nardus* tussocks is formed by dead leaf biomass and only the green middle of tussock is formed by living biomass. The middle of a tussock is a suitable microhabitat for seedling recruitment, according to a study of Zel ený (1999) conducted at the same locality. In contrast, *Molinia* forms relatively open tussocks with larger spaces between tillers. It creates the highest amount of biomass with the end of summer (when it is flowering) and in autumn, and its litter persists until the following spring because decomposition is very slow. During this period of time *Molinia* suppresses the other species.

We investigated only microhabitats in the middle of tussocks. It may be the case that *Juncus* exhibits the highest competitive effects in the middle of tussocks, whereas the other two species have the highest competition at the circumference of the tussocks, through litter accumulated there. Our results suggest that species

dynamics are modified by not only the growth form of the competitors, but also by the competitor's phenology.

The gaps in meadow vegetation represent space with reduced competition, suitable for plant growth. Mehrhoff & Turkington (1996) planted *Trifolium repens* among three neighboring grass species and into cleared spaces and concluded that the major contrast was between competitive and noncompetitive situations, with effects of the three competitors being similar. Morgan (1997) demonstrated positive effects of gaps, increasing with gap size, on the growth, seed production and seedling recruitment of *Rutidopsis leptorrhynchoides* (Asteraceae). Gaps are important for the seedling regeneration of many species (Křenová & Lepš 1996; Špačková et al. 1998; Touzard et al. 2002), because there is space without competition and with a significantly greater amount of light at ground level available (Morgan 1997). In contrast, gaps are more prone to drought (Kotorová & Lepš 1999). It seems that there is some "ideal" gap size, below which competition is too strong, and above which negative effects (drought proneness) start to prevail (Morgan 1997). However, the ideal size would differ among species according to their ecological requirements and most likely differs according to the process studied. In our study, the clonal growth of both focal species was much greater in big gaps. This effect was particularly pronounced in *M. nemorosa*. Small gaps were much less favorable treatments in comparison with Big gaps, which was probably caused mainly by below-ground competition and not only smaller size.

The character of competition also depends on site productivity. Under nutrient rich conditions, above-ground competition prevails, because above-ground biomass increases more with increasing nutrients than below-ground biomass (Šrůtek 1995; Dong et al. 2002), whereas below-ground competition is more important in oligotrophic sites (Gerry & Wilson 1995; Wilson & Tilman 1991). We may reasonably expect that (as in this experiment), root competition is stronger in Small natural gaps than in Big gaps, where below-ground vegetation was removed too. This was probably part of the effect of gap size in our oligotrophic environment too.

Plants responded to competition not only by decreasing growth but also by some morphological features that appear to be adaptive. The primary rosettes of *L. flos-cuculi* were tallest in the *Juncus* competitive treatment; where the plant responded to the competitive effect of this (and also the other two) species by vertical positioning of its leaves. The timing of the change of plants' leaf orientation differed according to the competitor phenology. In Big gaps, the leaves of plants were in a horizontal position and the plants were the lowest of all the treatments across the whole season.

The size of sterile rosettes in all treatments at the end of the first growing season was a good predictor of the probability of flowering and successful growth in the next year. The same results were achieved by Biere (1995) and Hauser & Loeschcke (1996) in their studies. The flowering of *L. flos-cuculi* was very poor in the third season because of extreme drought in the spring 2000 and grazing by slugs. Hauser & Loeschcke (1996), in their study of interaction of drought stress and inbreeding in *L. flos-cuculi*, also suggest a negative effect of drought on flowering. It seems that there might be a pronounced interaction between the effects of microhabitat and climatic events: microhabitats favorable under normal climatic condition might be very unfavorable in periods of extreme drought. If proved this interaction would support species coexistence.

With constant limited resources to invest, a tradeoff between vegetative spread and generative reproduction would be expected (Caswell 1985; Begon et al. 1990). In this case, the competition free space is ideal for fast vegetative spread (clonal plants are at an advantage), whereas the optimal strategy in a highly competitive environment is production of numerous seeds (which could "migrate" either in space or in time). This seems to be the case of *L. flos-cuculi*. A similar trade-off was observed by Biere (1995) in *L. flos-cuculi* populations in less productive sites only, whereas in more productive sites, correlations between vegetative and generative reproduction were generally insignificant or positive.

However, competitiveness of the environment also affects plant assimilative ability. Plants in the competition free environment could be expected to have more photosynthetic energy to invest either into vegetative spread or into flowering, as for *M. nemorosa*. The difference is undoubtedly connected with the morphology of clonal growth. Whereas *L. flos-cuculi* forms secondary rosettes (clonal growth) that never formed flowering stems in the same season (generative reproduction), *M. nemorosa* forms shoots of stem origin that usually bear flowers in the same year. Consequently, any investment into clonal growth is also used for generative reproduction. The numbers of *M. nemorosa* shoots per clone (representing vegetative reproduction) and flowers per clone (representing generative reproduction) were positively correlated among treatments.

In the pot experiment, both species grew most successfully in the control treatment in comparison with pots with *Holcus lanatus* in all three competitive treatments, and the treatment with only five *Holcus lanatus* plants had a less negative effect than both ten *Holcus lanatus* plant treatments. This reinforces the major contrast between competitive and noncompetitive situations (e.g. Mehrhoff & Turkington 1996). *L. flos-cuculi*

plants in controls produced the highest number of leaves, greatest amount of biomass and highest number of secondary rosettes. However, as the differences between the treatments (as measured by the explained sum of squares in ANOVA) were less pronounced for the rosettes than for the biomass, we do not have direct support for the hypothesis that *L. flos-cuculi* responds to competition by restricting its clonal growth. As the conditions in the pot experiments were more favorable than in the field (as reflected by a much higher growth rate), the fast formation of secondary rosettes in the pot experiment supports the conclusion that under favorable condition *L. flos-cuculi* invests more in clonal growth. *M. nemorosa* plants produced the highest number of leaves and biomass in controls and did not produce any shoots in any of the treatments in the short time of the experiment, although the plants flowered at the end of the two months period. Both treatments with ten plants of *Holcus lanatus* had the same negative effect on the focal species regardless of the spatial arrangement of the competitor, whereas the treatment with only five *Holcus lanatus* plants had a less negative effect. This experiment has shown that the speed of development under favorable conditions in the greenhouse was much higher than in the field. Clearly, the physiological potential of plants is strictly limited under the field conditions by both the environment and competition. The comparison of the pot and field experiments also shows how realistic is the pot experiment in comparison with the field experiments (Diamond 1986).

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