Biologická fakulta Jihočeské univerzity
České Budějovice

Seedling recruitment and establishment of juvenile plants in an oligotrophic wet meadow

(Regenerace rostlin ze semen
a začleňování mladých rostlin do společenstva
vlhké oligotrofní louky)

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Rok vypracování: 1999

Posudek školitele na magisterskou práci Ivany Kotorové

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Práce sestává ze dvou článků, z nichž první je přijat do tisku (Journal of Vegetation Science) a druhý je k odeslání do tisku připraven. Domnívám se, že každý z článků samostatně by bohatě postačil nárokům na magisterskou práci. Obě práce jsou svým charakterem experimentální, s převahou experimentů prováděných v terénu. V každém příspěvku je zpracováno obrovské množství (experimentálních) dat. Data jsou podrobena důkladné statistické analýze, a výsledky analýz jsou rozumně interpretovány. V obou článcích je též odpovídající diskuse s literaturou, která ukazuje autorčin přehled.

Autorka porovnává kompetiční působení společenstva na osm (v některých charakteristikách devět) druhů lučních rostlin, a to v různých stádiích jejich ontogenetického vývoje rostliny. V důsledcích ukazuje, že typ mikrohabitatu, nejvhodnější pro klíčení, nemusí být ještě ideální pro růst a přežívání mladých rostlin. Její porovnání odpovědí různých druhů rostlin na podobný zásah také ukazuje, jak rozdílné mohou být požadavky různých druhů rostlin.

Na práci oceňuji, jak autorka zvládla experimentální část i vyhodnocení dat metodami matematické statistiky, a také, jak zvládla vědeckou diskusi v angličtině. Práce podle mého názoru dokládá vědeckou zralost autorky a plně ji doporučuji k obhajobě.

V Českých Budějovicích 3.2.1999

Jan Lepš

Předkládaná práce se skládá ze dvou samostatných částí psaných ve formě odborného článku. První část „Comparative ecology of seedling recruitment in an oligotrophic wet meadow“ (Srovnávací ekologie regenerace rostlin ze semen ve společenstvu vlhké oligotrofní louky), kterou jsem vypracovala spolu se svým školitelem Janem Lepšem, bude v tomto roce (1999) opublikována v časopise Journal of Vegetation Science. Druhou část „Establishment of young plants in an oligotrophic wet meadow“ (Začleňování mladých rostlin do společenstva vlhké oligotrofní louky) jsem vypracovala samostatně, pouze s použitím uvedené literatury.

V Českých Budějovicích dne 13. ledna 1999 ....

Úvod

Z vlhkých oligotrofních luk ve střední Evropě mizí v současné době celá řada rostlinných druhů. Hlavní příčinou jsou změny v zemědělském využívání těchto luk (především ukončení obhospodařování nebo jeho intenzifikace). Původní druhově bohatá společenstva se postupně mění na porosty s výraznou převahou několika málo dominant. Aby bylo možno zabránit znehodnocení těchto cenných společenstev nežádoucími sukcesními změnami, je třeba lépe poznat mechanizmy, které udržují vysokou druhovou diverzitu.

Comparative ecology of seedling recruitment in an oligotrophic wet meadow

(Srovnávací ekologie regenerace rostlin ze semen ve společenstvu vlhké oligotrofní louky)
(str.4-41)

V souvislosti s udržováním vysoké druhové pestrosti v lučních společenstvech se často hovoří o tzv. regenerační nice, která zahrnuje rozdíly v citlivosti jednotlivých rostlinných druhů k různým faktorům jejich životního prostředí. Tato část práce je zaměřena na studium rozdílů v klíčivosti, v dynamice klíčení, v citlivosti semen k působení nízkých teplot a v úspěšnosti regenerace vybraných rostlinných druhů ze semen v přirozeném lučním společenstvu vystaveném působení různých zásahů, které mění jeho strukturu.

Byly provedeny tři samostatné pokusy, jeden v „laboratorních“ a dva v „polních“ podmínkách. První pokus byl zaměřen na testování klíčivosti a dynamiky klíčení semen 27 vybraných lučních druhů v „laboratorních“ podmínkách. Dále bylo zjišťováno ovlivnění výše zmíněných charakteristik působením nízkých teplot (+4°C a -14°C) na semena po dobu třiceti dní. Ve druhém pokusu byla sledována dynamika klíčení dvanácti druhů v „polních“ podmínkách na ploše s odstraněným drnem, pro šest z těchto druhů (*Achillea ptarmica*, *Betonica officinalis*, *Lychnis flos-cuculi*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Succisa pratensis*) byl navíc hodnocen rozdíl v klíčení semen v plochách, z nichž byly semenáčky průběžně odstraňovány, a v plochách, v nichž byly ponechávány. Třetím pokusem byly zjišťovány rozdíly v úspěšnosti regenerace vybraných šesti druhů (*Angelica sylvestris*, *Betonica officinalis*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*) v lučním společenstvu ovlivněném čtyřmi následujícími zásahy: (1) na počátku stržený drn, v průběhu pokusu dvakrát ročně kosení a na jaře odstraňování stařiny, (2) na počátku pokusu vypletý mech a odstraněna stařina, v průběhu pokusu pak dvakrát ročně kosení a na jaře odstraňování stařiny, (3) na počátku odstraněna pouze stařina, v průběhu pokusu dvakrát ročně kosení a na jaře odstraňování stařiny a (4) neovlivněná „kontrola“ bez jakýchkoli zásahů.

Výsledky ukazují výrazné rozdíly mezi studovanými druhy ve všech zjišťovaných aspektech jejich vegetačních nik. Dále bylo ukázáno, že s určitou omezenou platností je možné z „chování“ druhů v „laboratorních“ podmínkách a z hmotnosti jejich semen předpovídat jejich „chování“ v terénu.

Establishment of young plants in an oligotrophic wet meadow

(Začleňování mladých rostlin do společenstva vlhké oligotrofní louky)

(str.42-88)

Regenerace rostlinných druhů v lučním společenstvu je ovlivněna celým souborem faktorů, zahrnujícím biotické i abiotické vlivy. „Soužití“ velkého množství druhů je zde podmíněno rozdíly v citlivosti jednotlivých druhů k různým faktorům jejich životního prostředí. Se změnami podmínek prostředí se tak může měnit kompetiční úspěšnost jednotlivých druhů. Luční společenstvo si proto lze představit jako dynamickou mozaiku, v níž se v rámci malých prostorových měřítek pro každý jednotlivý druh střídají podmínky příznivé a nepříznivé. Neliší se však pouze jednotlivé rostlinné druhy mezi sebou: jednotlivá vývojová stadia rostlin stejného druhu často vyžadují pro své úspěšné začlenění do společenstva zcela protichůdné podmínky.

Rozdíly v reakci mladých rostlin devíti vybraných lučních druhů (*Angelica sylvestris*, *Betonica officinalis*, *Cirsium palustre*, *Jacea pratensis*, *Myosotis nemorosa*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*) na čtyři různé režimy zásahů byly sledovány v „polním“ pokusu uspořádaném obdobně třetímu pokusu v první části této práce. Stejná ovlivnění porostu kolem vysazených předpěstovaných mladých rostlin byla zvolena za účelem lepšího srovnání podmínek vhodných k regeneraci rostlin ze semen a „ujímání“ mladých rostlin. Hlavním cílem provedeného pokusu bylo zjistit, jak se liší „požadavky“ mladých rostlin jednotlivých sledovaných druhů. Dále bylo zamýšleno provést porovnání získaných výsledků s paralelními studiemi z dané lokality, které by ukázalo shodu nebo rozdílnost v začleňování semenáčků, mladých rostlin a „dospělých“ rostlin do různě ovlivněného porostu. V provedeném pokusu byly v průběhu alespoň dvou vegetačních sezón hodnoceny kromě přežívání vysazených mladých rostlin také změny v jejich morfologii. Pro každou rostlinu bylo zaznamenáváno sedm charakteristik: počet listů na rostlině, největší délka listu, největší šířka listu, výška rostliny, délka stonku, větvení a počet květů na rostlině.

Byly potvrzeny rozdíly mezi jednotlivými druhy i mezi různými vývojovými stadii v rámci těchto druhů. Zároveň však byly pozorovány i určité obecné trendy v hodnotách a změnách zaznamenávaných charakteristik, které byly často společné pro většinu sledovaných druhů.

Comparative ecology of seedling recruitment in an oligotrophic wet meadow

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Abstract

For the regeneration niche to contribute to the maintenance of species diversity assumes interspecific differences in sensitivity of seedling recruitment to environmental conditions. In this paper, we tested differences between several meadow species in response of seed germination to chilling, and in sensitivity of seedling recruitment to microscale heterogeneity. We also compared the dynamics of seedling recruitment in gaps. All responses were studied by manipulative experiments. In the first experiment, seed germination was tested in standard laboratory germination tests, comparing control seeds with seeds chilled at +4°C, and at -14°C for one month. Species showed a variety of responses, from significant increases in germinability after chilling (e.g., *Cirsium palustre*, *Prunella vulgaris*, *Betonica officinalis*, *Angelica sylvestris*) to significant decreases (e.g., *Hieracium umbellatum*, *Succisa pratensis*, *Myosotis nemorosa*, *Selinum carvifolia*). In some species, chilling at +4°C has a similar effect to chilling at -14°C (e.g., *Cirsium palustre*), in others the effect of chilling at +4°C was intermediate (e.g., *Angelica sylvestris*), and in some, there was no effect of chilling at +4°C, but an effect of chilling at -14°C (*Lychnis flos-cuculi*). Different chilling temperatures also affect timing and speed of seed germination under greenhouse conditions. In the second experiment, the dynamics of seed germination under field conditions was studied by sowing seeds into artificially created gaps and following their germination, both where the seedlings were removed after emergence and where they were not removed. Species differ in their germination dynamics: they all begin to germinate at the end of April over a two week interval, but then differentiate into an abrupt maximum and early stopping of germination (in the second half of May), to prolonged germination without a marked maximum. Seedling removal increased the total number of germinated seeds, showing marked density dependence at this stage. In the third experiment, seeds were sown into plots in four treatments ((1) gap treatment, sod stripped, all aboveground vegetation removed, (2) mown and moss layer removed, (3) mown, (4) untouched control) and seedling emergence monitored for three years. Seedling recruitment decreased from treatments (1) to (4), but relative sensitivity differed between species. With increasing seed weight, the difference between gaps and other treatments decreased. All the results show that there are considerable differences in seedling recruitment sensitivity between species.

Keywords: Seed germination, Gap regeneration, Moss competition, Chilling, Dormancy, Germination.

Nomenclature: Rothmaler (1976).

Introduction

Recent explanations of mechanisms that maintain species diversity stress the dynamic nature of processes and species mobility (van der Maarel & Sykes 1993, Herben et al. 1993, Huston 1994). Seedling recruitment is an important part of this mobility (Kalamees & Zobel 1997). Even in communities dominated by clonal plants, some species are dependent on seedling recruitment, and for clonal plants, regeneration by seed is important for the maintenance of genetic diversity (Watkinson & Powell 1993). Seedling recruitment requires specific conditions (Grubb 1977) and is often much more sensitive to environmental conditions and competition than are established plants (Křenová & Lepš 1996, Morgan 1997, Špačková et al. 1998). Such interspecific differences in conditions for seedling recruitment are considered important for the maintenance of species diversity (Grubb 1977, 1988).

Seedling recruitment usually depends on safe sites, microhabitats suitable for emergence and survival of seedlings. Gaps in the vegetation (i.e., places with decreased competition from established plants) are of vital importance for seedling recruitment (Goldberg 1987, Křenová & Lepš 1996). In gap colonization, the initial colonizer has a competitive advantage, and the process has features of founder control (Yodzis 1978). One important factor determining the identity of the initial colonizer could be emergence time. Identity of the initial colonizer may depend on timing of seed release and phenology of seed germination, with gaps originating in different times of the year expected to be colonized by different species (Hobbs & Mooney 1985, 1991). Such variation could thus promote species coexistence. Similarly, differences in seed sensitivity to chilling may alter the identity of the initial colonizer depending upon weather in a particular year, and also might promote species coexistence. However, all these mechanisms depend upon the assumption that seedling recruitment is sensitive to environmental variation, mainly temperature and light, and that species differ considerably in their response (differences in regeneration niche sensu Grubb 1977). The aim of this paper is to test this assumption. We compare the sensitivity of seed germination and seedling recruitment to biotic and abiotic environmental factors in several wet meadow species. First, we compare the sensitivity of seed germination to chilling, look for phenological differences in seed germination between species, and test for possible density-dependent germination suppression. Then, we compare effects of gaps, moss layer, and established vegetation on seedling recruitment in several species.

Study site

This study was conducted in a wet, oligotrophic, species-rich meadow located 10 km south-east of České Budějovice, Czech Republic, 48°57' N, 14°36' E, 510 m a.s.l., near the village Ohrazeni. Mean annual temperature is 7.8 °C, mean annual precipitation is 620 mm (České Budějovice meteorological station, Vesecký 1960). July is the wettest and warmest month with 102 mm of precipitation, and temperatures range from a mean daily minima of 11.6^{o}C to a mean daily maxima of 24.1^{o}C. January (the coldest month) temperatures range from a mean daily minima of -6.2^{o}C to a mean daily maxima of 0.6^{o}C. Soil nutrient levels are low (total nitrogen 6-8g/kg dry soil weight, total phosphorus 400-500mg/kg dry soil weight, C/N ratio 16-20). According to phytosociological classification, the vegetation belongs to *Molinietum caeruleae* (*Molinion*) with some species indicating a transition to *Violion caninae*. Seeds for all the experiments were collected at this locality.

Methods

Experiment 1: SEED-SENSITIVITY TO CHILLING
(Laboratory test of germinability)

Seed germination of 27 species from the study site (Table 1) was tested by germinating 300-3,600 seeds of each species in Petri dishes under greenhouse conditions. Before testing, seeds were stored dry at +20°C for three months after collection. Three different 30 day treatments were used: two chilling treatments (dry seed storage at +4°C and -14°C), and dry seed storage at +20°C. Chilling treatments were intended to reveal whether seeds require a chilling period for germination. In cold winters, several weeks with temperatures below –10°C occur, although temperature regimes in the field are much more complex than those used here. Seeds were then sown into Petri dishes (50-100 seeds per Petri dish) with moist blotting paper in the greenhouse at +20°C. Petri dishes were checked daily and seedlings and rotted seeds counted and removed. Each experiment was terminated when there was no germination for at least one week, but not earlier than 30 days after sowing seeds. (Line drawings of seedlings at different stages of development obtained from this experiment will be available at: http://www.bf.jcu.cz/bio/suspa/seedling.htm.). For statistical analyses, each seed was considered an independent observation. Confidence interval limits for germinability were calculated according to Zar (1984, p.378). Differences in germinability between treatments were tested using 2 by 3 contingency tables. The relative speed of germination was characterized by starting day of germination (number of days after sowing), median day (when half of the seeds that germinated during the entire experiment had germinated), and the day when the last seed germinated. Treatment effects were tested by a version of the median test: for each species a common median day for all three treatments was determined, and then by the use of 2 by 3 contingency tables the number of seeds that germinated before and after the common median in the three treatments were compared.

Experiment 2: DYNAMICS OF SEED GERMINATION IN GAPS

The dynamics of seed germination in artificially created gaps were monitored for 12 species in which seeds were sown in November 1995, and followed over the next growing season. Gaps were made by stripping the sod, and removing all of the aboveground vegetation and most of the roots. Seeds of six of the species (*Achillea ptarmica*, *Betonica officinalis*, *Lychnis flos-cuculi*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Succisa pratensis*) were sown into four artificial gaps of 0.3 x 0.3 m each. Seedlings were removed as they emerged from two of the plots, and were not removed from the other two plots. Seeds of another six species (*Angelica sylvestris*, *Carex hartmanii*, *Carex pallescens*, *Cirsium palustre*, *Hieracium umbellatum*, *Lychnis flos-cuculi*, *Lysimachia vulgaris*) were sown into only two gap plots of 0.3 x 0.3 m, and seedlings were removed from both plots. In the central 0.25 x 0.25 m of each gap plot, 1,000 seeds of each species were sown (only one species per plot), except for *Lychnis flos-cuculi* and *Lysimachia vulgaris* in which 2,000 seeds were sown (also one species per plot). Seedling emergence was monitored at approximately ten day intervals. Differences between species were evaluated by repeated measures ANOVA after log (x+1) transformation in STATISTICA (Anon. 1996).

Experiment 3: THE EFFECT OF LITTER LAYER AND MOSS LAYER ON SEEDLING ESTABLISHMENT

The effect of litter layer and moss layer on seedling establishment was tested in a manipulative field experiment. For six species (*Angelica sylvestris*, *Betonica officinalis*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*) 0.4 x 0.4 m plots were located in four randomized complete blocks, and one additional non-sown randomized complete block for each species was used as a control for natural seed germination and seedling recruitment. In each block, the following treatments were used:

(1) gap (sod stripped, all aboveground vegetation removed),
(2) plot mown and moss layer removed by hand,
(3) plot mown,
(4) untouched control.

In each plot 1,500 seeds of one of the six species were sown (only one species per plot) at the end of March, except for *Serratula tinctoria* where only 750 seeds were sown in treatments (1), (3), and (4) (treatment (2) omitted), due to an insufficient number of seeds available. This experiment was conducted with two of the species (*Selinum carvifolia, Serratula tinctoria*) in 1995, and with five of the species (*Angelica sylvestris, Betonica officinalis, Sanguisorba officinalis, Selinum carvifolia, Succisa pratensis*) in 1996. *Selinum carvifolia* was used in both years to check for differences in results between years. Seedlings were counted for three years in early summer, in midsummer, and in autumn. Gaps (Treatment (1)) were constructed in the second half of March before sowing seeds. Treatments (1), (2), and (3) were mown twice each year after counting seedlings in early summer and in midsummer. Litter was removed from treatments (1), (2), and (3) in March of each year.

Data were evaluated after a logarithmic transformation x'=log (x+1) by a repeated measures ANOVA model in STATISTICA (Anon. 1996). Note that with log-transformed data, the interaction between time and treatment reflects differences in relative changes in time. Let $X_{i,t1}$ and $X_{i,t2}$ be the numbers of seedlings in the i-th treatment at times $t1$ and $t2$ respectively. When the relative changes are constant, i.e., $X_{i.t2}=X_{i.t1}\ .\ k$ for any i (i.e., for all the treatments), then $\log (X_{i.t2}) = \log (X_{i.t1}) + \log (k)$ for any i. Then the lines are parallel and there is no interaction between time and treatment. A significant interaction means that values of k differ according to the treatment. If there is no germination, then k is survival (1-mortality) and the interaction then reflects differences in mortality. As log (x+1) had to be used (because the data contained zeroes), the above hold only approximately. Interspecific differences of the species sown in 1996 were compared using repeated measures ANOVA after log (x+1) transformation. (It would be incorrect to include the two species sown in 1995 because of different census dates for both the species and missing treatment (2) for *Seratula tinctoria.*)

Results

Experiment 1: SEED-SENSITIVITY TO CHILLING
(Laboratory test of germinability)

Species differed in germinability, in speed of germination, in relative sensitivity to chilling treatment, and in response to different chilling temperatures.

Three species did not germinate at all (*Carex hartmannii*, *Carex pallescens*, *Valeriana dioica*), and germinability of *Senecio rivularis* was close to zero (1% for control seeds, no germination after chilling). Germinability of *Luzula campestris* and *Lychnis flos-cuculi* was almost 100%.

In twelve of the studied species, chilling had no significant effect, in five species, chilling decreased germinability and in seven species, germinability was increased (Fig.1). In species where chilling had significant effect, four different response types to chilling were observed. The first response type is a similar effect of both chilling treatments on germinability compared to the unchilled treatment (positive in *Anthoxanthum odoratum, Prunella vulgaris* and *Cirsium palustre*, negative in *Hieracium umbellatum*, *Galium uliginosum* and *Succisa pratensis*). The second response type is a gradual effect (i.e. both +4°C and –14°C has an effect, but effect of –14°C is greater) of storage temperature on germinability (positive in *Angelica sylvestris* and *Betonica officinalis,* negative in *Selinum carvifolia*; *Lysimachia vulgaris* and *Potentilla erecta* showed similar, but non-significant responses). The third type of response is a similar effect of seed storage at +4°C and +20°C compared to seed storage at -14°C (*Lychnis flos-cuculi*, in which germinability was highest after seed storage at -14°C, and *Myosotis nemorosa,* where -14°C decreased the germinability considerably). The fourth response, where seeds stored at +4°C differed from those stored at both the other temperatures was observed in *Jacea pratensis* only, and the differences were not highly significant (P=0.025).

Species also differed in their germination dynamics under greenhouse conditions. Species differed in the starting day of germination (second day after sowing in *Cirsium palustre*, *Jacea pratensis*, and *Lychnis flos-cuculi*, eleventh day in *Potentilla erecta* and *Selinum carvifolia*), in the day when one half of all germinated seeds of a species had germinated (median day), and also in the length of the germination period (Fig.2). Dynamics of seed germination under greenhouse conditions, characterized by the day when half of the seeds had germinated, was also affected by chilling. Although differences were small in the majority of the species, in some species they were highly significant (Fig.2). However, biological and statistical significance need not always correspond to each other: if the germination is fast and with a sharp peak, then a one day difference in median day can be highly statistically significant, but the biological significance may be very small.

Germinability and germination dynamics under greenhouse conditions seem to be two independent characteristics. The median day and germinability at 20°C are not correlated ($r=-0.148$, $n=24$, $P=0.49$, Fig.3). There are species with high germinability and early germination that lasts for only a short time (e.g., *Lychnis flos-cuculi*), high germinability but slow and late germination (e.g., *Galium uliginosum*), low germinability and early germination that lasts for only a short time (e.g., *Achillea ptarmica*), and low germinability and slow and late germination (e.g., *Potentilla erecta*). However, most of the species can be considered transitional between these four extremes. Also, the effect of chilling on germinability and on germination dynamics characterized by the median day seem to be rather independent. We characterized the effect of chilling on germinability by the ratio of germinability after storage at –14°C to germinability after storage at 20°C and similarly the effect on the dynamics by ratio of the median days. Although the correlation coefficient was negative as expected (increase in germinability is connected with a speeding up of germination), the correlation is weak and nonsignificant ($r=-0.372$, $n=23$, $P=0.08$, Fig.4). The effect of dry storage at +4°C tested in a similar way was also non-significant ($r=-0.306$, $n=22$, $P=0.165$).

Experiment 2: DYNAMICS OF SEED GERMINATION IN GAPS

1. Dynamics of seed germination

Repeated measures ANOVA of data from plots with regular seedling removal showed highly significant differences between the 12 studied species ($P<10^{-6}$ both for the effect of species and for interaction between species and time). The effect of species corresponds to the average number of germinated seeds (as the same amount of seeds was sown, this is a test of germinability under field conditions). The interaction between species and time corresponds to differences in germination dynamics.

Seeds of all 12 species started to germinate over a two week interval at the end of April (Fig 5). Species differed in the timing of germination peak (*Achillea ptarmica* and *Lychnis flos-cuculi* had the earliest germination peak). More pronounced are the differences in the sharpness of the germination peak (sharp peak: *Lychnis flos-cuculi, Selinum carvifolia,* no peak: *Carex hartmannii*, *Hieracium umbellatum*), and in the time when germination stopped (*Carex hartmannii*, *Carex pallescens* and *Sanguisorba officinalis* stopped germinating in the second half of May, while *Angelica sylvestris*, *Lysimachia vulgaris* and *Selinum carvifolia* were still germinating at the end of June).

2. Effects of seedling removal

In this part of the experiment, germination in gaps in which seedlings were removed was compared with germination in gaps in which seedlings were not removed. This was done for the six species which were sown into four plots each (*Achillea ptarmica*, *Betonica officinalis*, *Lychnis flos-cuculi*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Succisa pratensis*).

Seedling emergence of five of the six tested species was increased when seedlings were removed (Fig.6), indicating competition between seedlings from the beginning of seedling emergence. The number of seedlings over time decreases in plots with seedlings present (not removed) probably due to a self-thinning effect (i.e., density dependent mortality). For *Succisa pratensis*, early germination was facilitated by the presence of conspecific seedlings. However, after some time, the number of seedlings present decreased by a self-thinning effect.

3. Comparison of germination in field and laboratory tests

Germinability in the field, estimated as a proportion of seeds germinated from the number of seeds sown, was well correlated with germinability in Petri dishes ($r=0.76$, 0.77 and 0.79 for storage temperatures +20°C, +4°C and -14°C respectively, $n=12$, $P<0.01$). Germinability after the lowest temperature chilling provided the best predictor of germinability in the field, although differences between correlation coefficients are small and not significant. Species with low germinability germinated relatively better in the field (*Carex hartmanii*, *Carex pallescens*, *Hieracium umbellatum*, *Achillea ptarmica*, *Sanguisorba officinalis*), whereas species with high germinability germinated relatively better under greenhouse conditions (*Lysimachia vulgaris*, *Lychnis flos cuculi*; Fig.7). The speed of germination in Petri dishes, characterized by the median day of germination, is positively correlated with the speed of germination in the field, which is characterized by percentage of seeds germinated by the second census (Fig.8). Similarly, the percentage of seeds which germinated before end of May in the field can be predicted by the day when the last seed germinated in the greenhouse (Fig.9).However, the correlations were only significant for characteristics of control seed, the correlations for both chilled treatments were weaker and non-significant. Also, the sensitivity to chilling (characterized by the ratios of germinability and median day in chilled and control seeds) is not correlated with any characteristic of the germination speed in the field. Correlation coefficients are non-significant, P>0.20 for all the eight correlation coefficients between germination speed characterized by percentages of germinated seeds at the end of April and at the end of May, and ratios of median day and germinability between control and both chilling treatments).

Experiment 3: THE EFFECT OF LITTER LAYER AND MOSS LAYER ON SEEDLING ESTABLISHMENT

Establishment for all the species was highest in gaps, followed by mown and moss removed, mown, and lastly, control (Figs.10, 11). (Data from the natural seedling recruitment controls were not included, because the number of seedlings of all the tested species was very low: zero or close to zero. This shows that the results are not affected by the natural seed rain.) Effect of treatment was highly significant in all the species, and the interaction between time and treatment was significant in almost all cases (exceptions were *Betonica officinalis*, P=0.051 and *Succisa pratensis*, P=0.138). However, species differ in their relative sensitivity to these factors (Figs.10, 11, Tables 2). In the repeated measures ANOVA of log (x+1) transformed data (Table 2), comparing the dynamics of the five species sown in 1996, all terms are highly significant. The effect of species corresponds to differences in mean species germination over all the treatments (i.e., species differ in the number of germinated seeds). The significant interaction between species and treatment reveals the differences in species sensitivity to particular treatments. Significant interaction between species and time reveals interspecific differences in germination phenology. Significant interaction between treatment and time reveals differences in seedling recruitment dynamics among treatments. Significant interactions between species, treatment, and time reveals interspecific differences in rates of change under various treatments. Differences in sensitivity to various treatments among species can be clearly demonstrated by comparison of the five species (*Angelica sylvestris*, *Betonica officinalis*, *Sanguisorba officinalis* and *Succisa pratensis*, and *Selinum carvifolia* sown in both 1995 and 1996) after the third season (Fig.11). The recruitment of *Betonica officinalis* was successful in all the treatments except control. A similar result was obtained after the third season for *Selinum carvifolia*, whereas recruitment of *Sanguisorba officinalis* was very low in all the treatments, except gap plots (Fig.10).

The observed number of seedlings changed considerably over time (Fig.10). The number of *Serratula tinctoria* seedlings increased steadily from the first season, because the density of seedlings was very low, as was intraspecific competition, and new seedlings appeared each growing season (no seedlings of *Serratula tinctoria* were found in plots with only natural recruitment). Increases in seedling numbers at the beginning of each new season were also observed for *Angelica sylvestris*, *Sanguisorba officinalis* and *Selinum carvifolia*, but the final number of seedlings was lower than in the first season. Decreases in number of seedlings of *Betonica officinalis* and *Succisa pratensis* were quite gradual. This was caused by seedlings from the first growing season being big enough to inhibit new seed germination at the beginning of the next growing seasons. An explanation for this effect may be the fact that seedlings of *Betonica officinalis* and *Succisa pratensis* have perennial leaves, whereas the leaves of seedlings of *Angelica sylvestris*, *Sanguisorba officinalis*, *Selinum carvifolia* and *Serratula tinctoria* die in the autumn.

Differences in seedling numbers between *Selinum carvifolia* sown in 1995 and in 1996 in the nine corresponding dates are not significant (F=6.733, df=1,3, P=0.081), even though the census dates were not exactly the same. This indicate reproducibility of obtained results. However, differences suggest caution in interpretations and importance of not only spatial, but also temporal replications in field experiments.

The number of seedlings in various treatments expressed as a percentage of seedlings present in gaps can be taken as a measure of a competitive effects on seedling recruitment. The effect of competition decreases with seed weight: when the seed weight is higher, then the relative differences between gaps and other treatments are smaller. The correlation between seed weight and relative recruitment success is positive for all the treatments in all three years (Table 3), but often not significant. However, the power of the test is low, because only six species (five in moss removal plots) are used and the range of seed weight is small.

Discussion

The investigated species differ in response to all of the studied characteristics. However, the results should be interpreted with caution. For example, the two *Carex* species (*C. hartmanii*, *C. pallescens*) that did not germinate in laboratory tests germinated under field conditions (albeit with low germination). They probably require chilling in a wet environment. Our simple germination tests cannot cover all the possible demands for breaking dormancy in various species (Nikolaeva et al. 1985). Nevertheless, field and laboratory germinations are highly correlated: about 60% (=r^2) of between species variability in germinability under field conditions can be explained by germinability under greenhouse conditions. Species with low germinability (in both tests) usually germinate relatively better in the field, whereas the opposite is true for species with high germinability. Low germinability is probably connected with dormancy. Our simple tests were not able to mimic complex field conditions, which could be necessary for breaking dormancy. The negative effect of pathogens, predators, etc., in the field is evident as a decrease in germinability. However, this effect is more than compensated in species where field conditions increase germination by breaking dormancy, usually species with low greenhouse germinability. Consequently, we are only able to detect this in the species where germinability is not considerably increased under field conditions, usually those with high germinability in the greenhouse.

We have found also large interspecific differences in germination dynamics, both under greenhouse and field conditions. The speed of germination under greenhouse conditions provides a rough estimate for the germination dynamics in the field. Species with fast germination in Petri dishes started to germinate in the field early and germinated fast (at the end of April), whereas species where some seeds germinated more than one moth after the sowing seeds into Petri dishes germinated in the field in June yet. However, the relationship is weak.

In Experiment 2 the difference between the total number of seedlings that germinated in plots with seedlings removed, and the number of seedlings present in plots with seedlings not-removed can be explained by seedling mortality and by suppression of seed germination caused by the presence of seedlings. Although these effects cannot be separated in our data, field observations indicate that both are important: although the newly emerged seedlings can not be unequivocally distinguished and counted in the non-removal plots, a rough estimate based on seedling size suggested that more new seedling appeared during the late intervals in removal plots. We expect that this is not only a result of direct resource competition, but that other effects related to dense seedling cover (e.g., changes in red/far-red ratio) may play a part as well. This shows that population size can be strongly density regulated. Mortality of seeds in the soil is usually not considered to be a density dependent factor (e.g., Begon et al. 1986, p. 558), but when the number of germinating seeds decreases with increasing seedling density, total seed mortality probably increases (any time period seeds remain in the soil increases their chance of being eaten, rotting, etc.).

Regardless of the mode of dispersal, the distribution of seeds within a plot is not uniform (Wilson 1992) and is often very clumped. This means that if there is high seedling density in a gap, then the seedlings often belong to one species. This phenomenon increases the effect of intraspecific competition (Pacala 1986). Germination suppression and seedling mortality during self-thinning is then affected mainly by the density of the species.

Environmental and biotically-generated heterogeneity and its effect on seedling recruitment are often considered to be important for the maintenance of species diversity (Grubb 1977, 1988). Interspecific differences in sensitivity to environmental conditions are necessary for these mechanisms to operate. For example, when gaps in the community are colonized with subsequent founder control (Yodzis 1978), the time of gap creation is important if germination time differs between species (Hobbs & Mooney 1985). Also, weather can influence the colonization of gaps (Hobbs & Mooney 1991). Particular species (and their ecotypes) germinate in waves variously situated in time (Gulmon 1992, Masuda & Washitani 1992). Differences between species in timing of germination in our study are probably too small to cause large differences in gap colonization due to variation in timing of gap creation. However, differences can be important when we consider weather conditions: the last late frosts appear in the study area in the first half of May, which is the time when species differ considerably in percentage of germinated seeds. Those differences can greatly influence seedling recruitment. Earlier germination can give an advantage to a species, if frost does not come, but is fatal for seedlings if there is a frost. This might be the cause of large variability in both number and composition of seedlings over the years in the same locality (Špačková 1998). Similar phenomenon was also observed in other habitats (Titus & del Moral 1998)

Genetically fixed differences in response to chilling exist between species, between populations, and also within populations (Meyer & Kitchen 1994). However, the relationship is probably complex. We have not found any relationship between species response to chilling and timing of seed germination in the field. Similarly, Schütz & Milberg (1997) concluded that their data from laboratory experiments on the germination of various populations of *Carex canescens* could not be used to predict differences in timing of seedling emergence in the field.

Generally, few meadow species form long-term persistent seed banks (Bekker et al. 1998). This corresponds to our results: the majority of seeds sown in our experiments germinated during the season following seed production. However, some of the remaining seeds germinated in subsequent seasons.

Seedling recruitment is probably the most sensitive part of the life cycle, sensitive to both the effect of living vegetation and litter. Whereas the effect of living biomass is often found on both established plants and seedlings, the effect of litter is usually more important for seedling recruitment and growth (Foster & Gross 1997). Litter was removed at the beginning of each season from all plots except the untreated control, and control has the lowest number of seedlings for all the species.

Seed size was found to be positively correlated with relative success of seedling recruitment in competition influenced plots in comparison with gaps. Smaller seeds are usually associated with lower recruitment under more competitive situations (Gross 1984, Westoby *et al.* 1996). This is not surprising, because the energy stored in large seeds enables these seeds to overcome difficult conditions under litter and dense vegetation (reserve effect, Westoby *et al.* 1996). The correlations were not always significant, probably because of the low number of species tested and small range of seed weights. In a similar study (Křenová & Lepš 1996), *Gentiana pneumonanthe*, the species with much smaller seeds was found to be completely dependent on gap regeneration. On the contrary, in old fields in Michigan, larger-seeded species were not significantly more likely to emerge in undisturbed vegetation than were smaller-seeded species (Goldberg 1987). However, the emergence studies in Michigan included both the effect of seed density and probability of germination, whereas in our experiment, the seed density was constant. The recruitment of the species with the largest seeds (*Angelica sylvestris*) was the least suppressed in comparison with gap plots. This is in good agreement, with a parallel study at the locality where *Angelica sylvestris* was found to perform best in unmown plots (Lepš 1999). However, in that study the number of seedlings of *Sanguisorba officinalis* and *Betonica officinalis* were found to be lower in mown plots than in unmown plots, whereas here these species were found to be considerably suppressed in the unmown control. Mowing influences not only conditions for seed germination and seedling establishment, but also seed production: *Sanguisorba officinalis* and *Betonica officinalis* are late flowering species, and this effect over-compensates for the positive effect of mowing on seedling recruitment.

Mosses usually have small or no effect on established plants, however, they influence seedling recruitment. Mechanisms influencing germination include changes in quantity and quality (red/far-red ratio) of light under the bryophyte layer, mechanical prevention of seeds from reaching the soil surface, and allelopathic effects (van Tooren 1990, During & van Tooren 1990). The role of moss layer in seed germination in grassland communities can be both protective (e.g., Ryser 1990), and inhibitive (Keizer et al. 1985, van Tooren 1990, Špačková et al. 1998). For example, the moss layer can protect seeds from predation (van Tooren 1988). The protective role is more important in dry grasslands (Ryser 1990), or in communities with temporal desiccation (During & van Tooren 1990). The effect of the moss layer on vascular plants may change from the seed to the seedling stage. Our results also show a significant negative effect of the moss layer on germination, but the intensity of the effect varies between species, and changes over time. In nature, moss layer cover is positively influenced by similar factors as seedling recruitment (e.g., by mowing, Lepš 1999). This is the reason why moss layer and seedlings might be positively correlated (i.e., found in similar microhabitats) even when moss suppresses the seedling recruitment.

All of the species tested for the effect of treatments on seedling recruitment are polycarpic perennials, except *Angelica sylvestris*, which is often monocarpic (Grime et al. 1988). Seedling recruitment suppression in polycarpic perennials will first change population demographic structure, and only after that will the population decline, depending on species longevity (none of the tested species exhibit pronounced clonal lateral spread). *Angelica sylvestris* is very well equipped for seed regeneration: the seeds are relatively large, enabling germination in shade. The flowering plant produces large quantities of winged seeds that are released through the winter, so that the seeds can disperse on the surface of the snow.

Seedling recruitment is usually positively affected by disturbance, and the positive effect increases with disturbance intensity and differs among species. However, the same disturbance might have negative effects on growth and seed production, and the magnitude of these effects is also species specific. These differences between species together with disturbance heterogeneity are important factors in promoting species coexistence.

Acknowledgments

The research was supported by Mattoni Awards for Studies of Biodiversity and Conservation Biology to I.K. and by the Grant Agency of the Czech Republic (grant GAČR 204/96/0522). We are indebted to Jonathan Titus for critical reading of the manuscript and correcting our English, and to Deborah Goldberg and Tomáš Herben for helpful critical comments on the manuscript.

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Figure captions

Fig.1. (Experiment 1) Germinability under greenhouse conditions with 95% confidence intervals after dry seed storage at +20°C, after dry chilling at +4°C, and after dry chilling at -14°C. Statistical significance of the effect of seed storage temperature is indicated as follows: * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

Fig.2. (Experiment 1) Germination dynamics characterized by the median day (when half of the seeds that germinated during the entire experiment had germinated, displayed by a marker) and germination period (between days when the first and the last seed germinated, whiskers). The statistical significance of the effect of seed storage temperature is indicated as follows: * - $P<0.05$, ** - $P<0.01$, *** - $P<0.001$.

Fig.3. (Experiment 1): Relationship between germination dynamics characterized by median day and total germinability. The two characteristics appear to be independent ($r=-0.148$, $n=24$, $P=0.49$).

Fig.4. (Experiment 1): Relationship between the effect of dry seed storage at –14°C on total germinability and on germination dynamics. The effect on germination dynamics is expressed by the median day ratio (i.e., ratio of the median day of germination of seeds stored at –14°C to median day of seeds stored at +20°C), the effect on germinability is expressed by germinability ratio at the two temperatures. The relationship is not significant ($r=-0.372$, $n=23$, $P=0.08$). The dotted lines correspond to a ratio equal to one, i.e., no effect of chilling.

Fig.5 (Experiment 2): Dynamics of seed germination in artificially-created gaps with removed seedlings. Dates are given in the form day.month.

Fig.6 (Experiment 2): Dynamics of seed germination in artificially-created gaps with seedlings removed and not removed (present). Dates are given in the form day.month.

Fig.7. Comparison of germinability in field and greenhouse conditions. Correlations are high (r=0.76, 0.77 and 0.79 for storage temperatures +20°C, +4°C and −14°C, P<0.01 for all). Differences between correlation coefficients are not significant. The line corresponds to the same germinability in greenhouse and in the field.

Fig.8. Relationship between germiantion speed in laboratory (expressed as the median day for control seeds) and germiantion speed in the field expressed as percentage of the seeds having germinated before April. 26 of all the seeds germinated during the whole experiment (r=-670, P=0.048). Regression line (percentage=44.6-2.14 median day) with 95% confidence band is shown.

Fig.9. Relationship between germination speed in laboratory (expressed as the day when the last seed germinated) and germination speed in the field expressed as percentage of the seeds having germinated before May 30 of all the seeds germinated during the whole experiment (r=-0.744, P=0.022). Regression line (percentage = 103.96-0.216 end) with 95% confidence band is shown.

Fig.10 (Experiment 3): The effect of treatments on seedling establishment. (1) GAP, (2) plot mown and MOSS layer removed, (3) plot MOWN, (4) untouched CONTrol. Dates are given in the form day.month.year.

Fig.11 (Experiment 3): Box and whisker plot displaying median, interquartil range (box), and range (whiskers) of numbers of seedlings of four species sown in 1996 in four treatments ((1) GAP, (2) plot mown and MOSS layer removed, (3) plot MOWN, (4) untreated CONTrol) at the end of the first season.

Table 1. (Experiment 1): List of tested species (full names and used abbreviations).

Full name	Abbre-viation	**Full name**	Abbre-viation	**Full name**	Abbre-viation
Achillea ptarmica	**AchPta**	*Galium uliginosum*	**GalUli**	*Ranunculus auricomus*	**RanAur**
Angelica sylvestris	**AngSyl**	*Hieracium umbellatum*	**HieUmb**	*Ranunculus flammula*	**RanFla**
Anthoxanthum odoratum	**AntOdo**	*Jacea pratensis*	**JacPra**	*Sanguisorba officinalis*	**SanOff**
Betonica officinalis	**BetOff**	*Luzula campestris*	**LuzCam**	*Scorzonera humilis*	**ScoHum**
Carex hartmanii	**CarHar**	*Lychnis flos-cuculi*	**LycFlo**	*Selinum carvifolia*	**SelCar**
Carex pallescens	**CarPal**	*Lysimachia vulgaris*	**LysVul**	*Senecio rivularis*	**SenRiv**
Cirsium palustre	**CirPal**	*Myosotis nemorosa*	**MyoNem**	*Serratula tinctoria*	**SerTin**
Cynosurus cristatus	**CynCri**	*Potentilla erecta*	**PotEre**	*Succisa pratensis*	**SucPra**
Galium boreale	**GalBor**	*Prunella vulgaris*	**PruVul**	*Valeriana dioica*	**ValDio**

Table 2. (Experiment 3): Results of repeated measures ANOVA model comparing seedling recruitment of five species sown in 1996 (*Angelica sylvestris, Betonica officinalis, Sanguisorba officinalis, Selinum carvifolia, Succisa pratensis*) in (1) gaps, (2) mown and moss removal plots, (3) mown plots, and (4) untreated control. Species and treatment are the fixed factors, block is the random factor and its effect is not tested. Time is the repeated measures factor. Interaction terms with block are used as error terms.

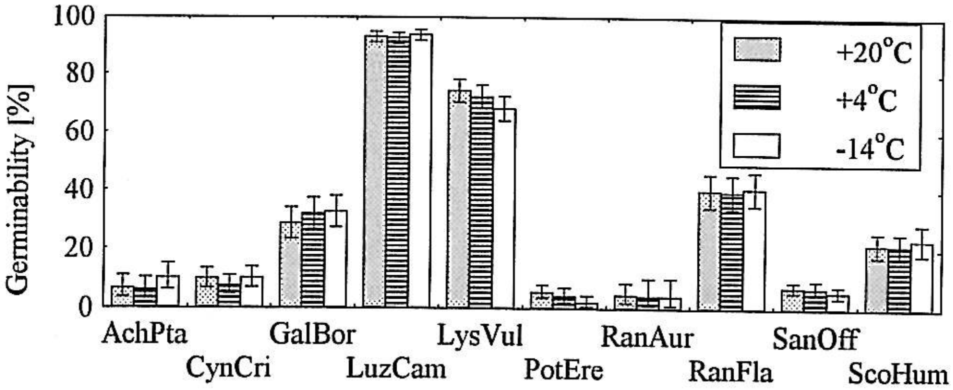
FACTOR	EFFECT		ERROR		F	P
	df	**MS**	**df**	**MS**		
Species	4	30.24	12	0.78	38.80	**0.0000**
Block	3	0.31				
Treat.	3	48.24	9	0.18	269.00	**0.0000**
Time	9	3.28	27	0.08	43.42	**0.0000**
Species*Block	12	0.78				
Species*Treat.	12	1.22	36	0.35	3.48	**0.0018**
Block *Treat.	9	0.18				
Species*Time	36	0.77	108	0.04	21.10	**0.0000**
Block *Time	27	0.08				
Treat. *Time	27	0.06	81	0.04	1.73	**0.0312**
Species*Block*Treat.	36	0.35				
Species*Block*Time	108	0.04				
Species*Treat.*Time	108	0.06	324	0.03	2.00	**0.0000**
Block *Treat.*Time	81	0.04				
Species*Block*Treat.*Time	324	0.03				

Table 3. (Experiment 3): The effect of treatments on seedling: seedling recruitment in differently treated plots expressed as percentage of seedlings in the treatment as compared to number of seedlings in gaps (more than 100% means that the recruitment was more successful than in gaps). Four treatments were used: (1) GAP, (2) plot mown and MOSS layer removed, (3) plot MOWN, (4) untreated CONTrol. Two of the species were observed since 1995 (*Selinum cavifolia*: SelCar-95, *Serratula tinctoria*: SerTin - treatment (2) is missing for this species), five of the species (*Angelica sylvestris*: AngSyl, *Betonica officinalis*: BetOff, *Sanguisorba officinalis*: SanOff, *Selinum carvifolia*: SelCar-96, *Succisa pratensis*: SucPra). The last two rows present the correlation coefficient (r) of the relative success versus seed weight and the corresponding significance value. For the calculation, the average of the two values for *Selinum carvifolia* is used.

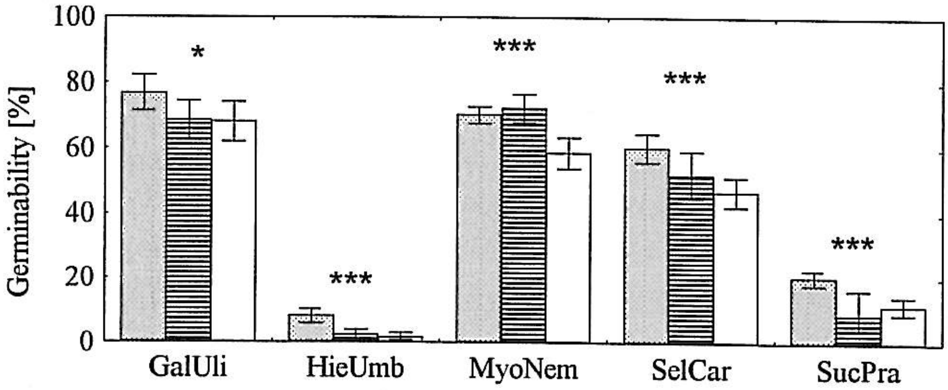
SPECIES	**Seed weight** [mg per seed]	NUMBER OF SEEDLINGS AS A PERCENTAGE OF SEEDLINGS PRESENT IN GAPS at the end of:								
		first season			**second season**			**third season**		
		MOSS	MOWN	CONT.	MOSS	MOWN	CONT.	MOSS	MOWN	CONT.
SelCar-95	0.929	59.06	11.61	2.10	69.33	60.00	25.33	37.45	31.87	3.19
SerTin	0.516	---	7.14	0.00	---	30.77	0.00	---	16.67	0.00
AngSyl	1.215	59.12	14.71	7.06	54.32	45.68	13.58	108.78	86.34	40.98
BetOff	0.979	97.51	78.44	6.88	68.18	52.48	3.72	75.21	70.25	3.86
SanOff	0.887	16.67	11.11	1.11	27.40	24.66	1.37	24.07	20.37	3.70
SelCar-96	0.929	60.42	32.64	6.25	92.41	72.78	12.66	72.41	68.97	6.90
SucPra	1.026	65.01	58.56	17.00	53.44	41.87	5.51	61.41	40.51	3.22
r	---	0.279	0.328	0.582	0.077	0.402	0.545	**0.918**	**0.803**	0.686
P	---	0.650	0.522	0.225	0.902	0.429	0.264	**0.027**	**0.054**	0.133

Fig.1

No effect of storage temperature



Negative effect of low storage temperatures



Positive effect of low storage temperatures

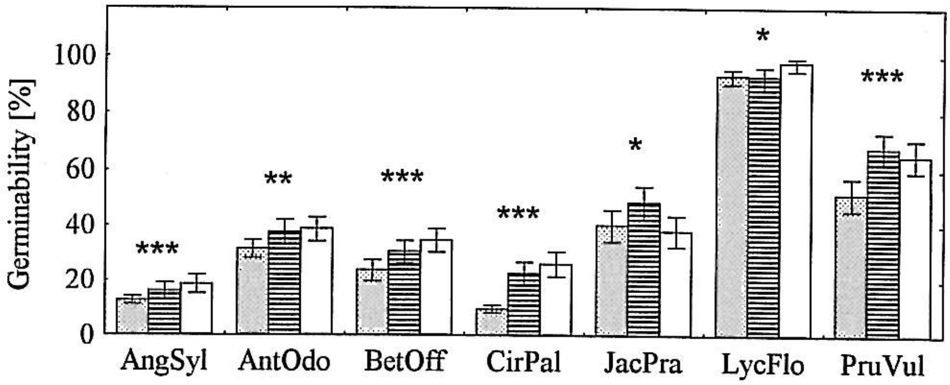
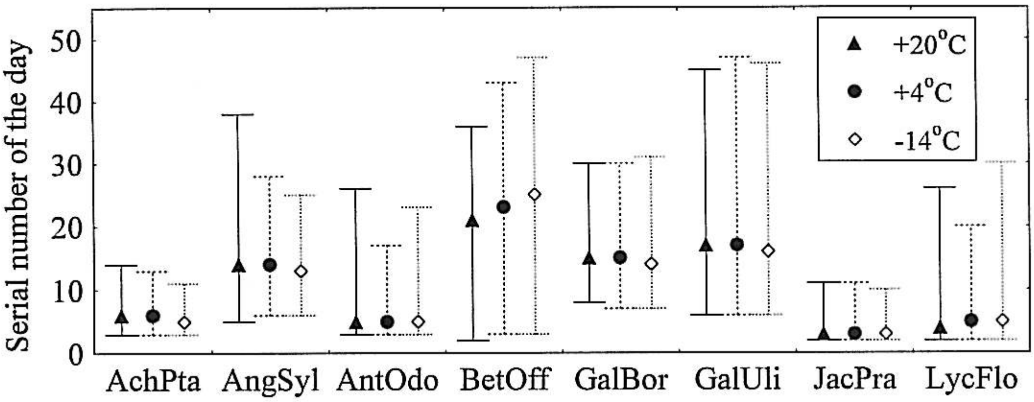
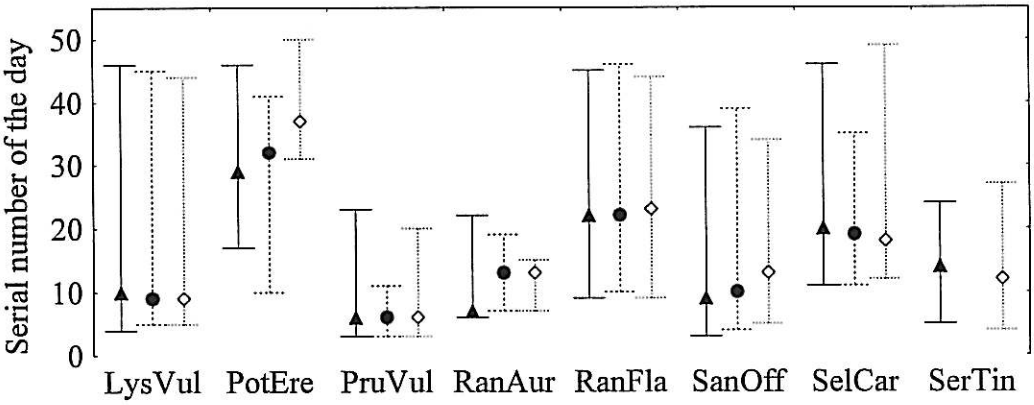


Fig.2

No effect of storage temperature



No effect of storage temperature



Significant effect of storage temperature

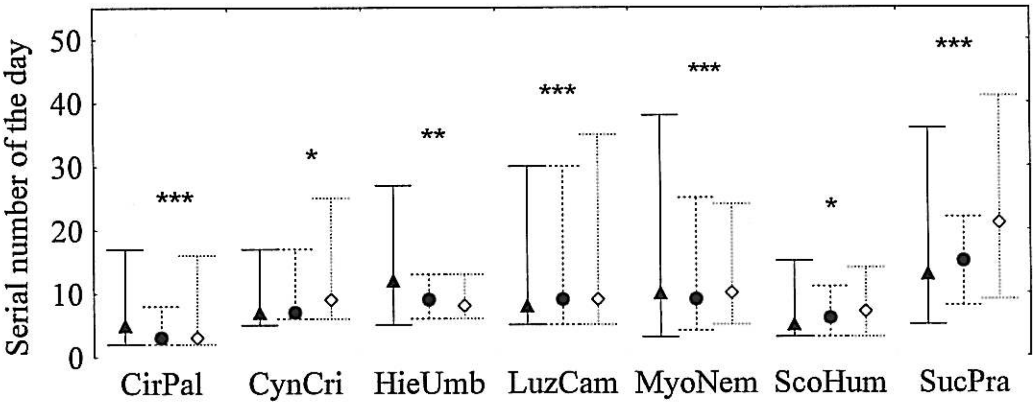


Fig.3

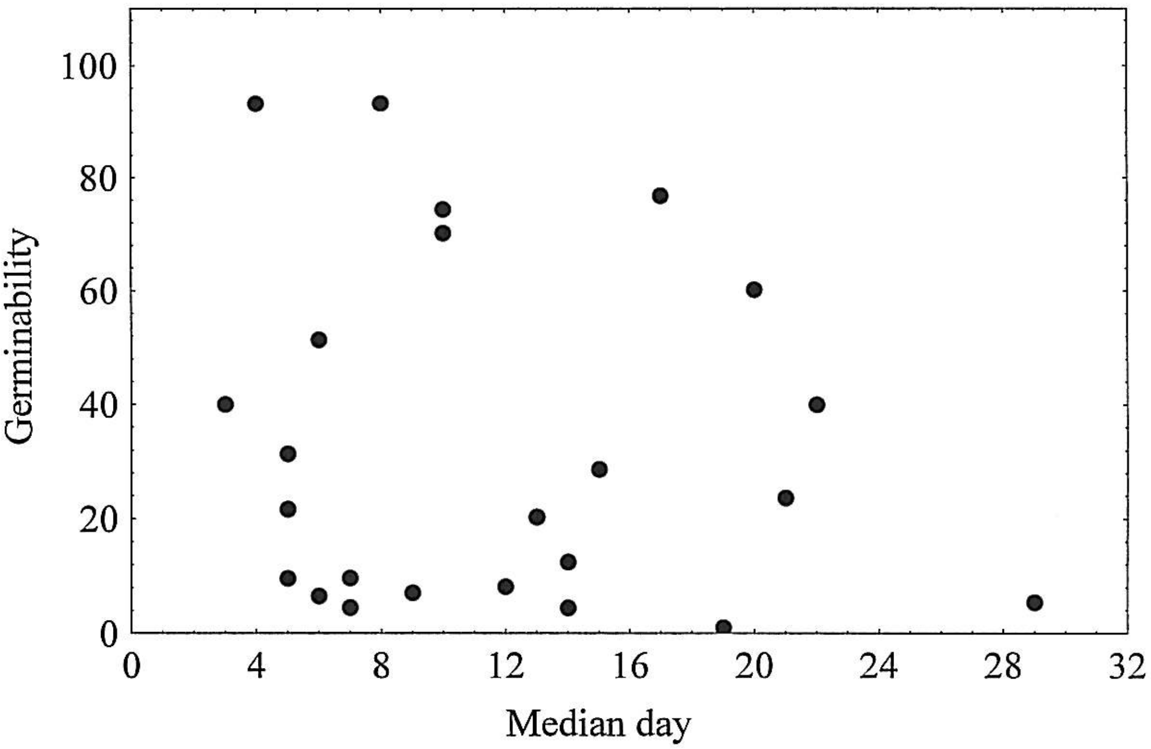


Fig.4

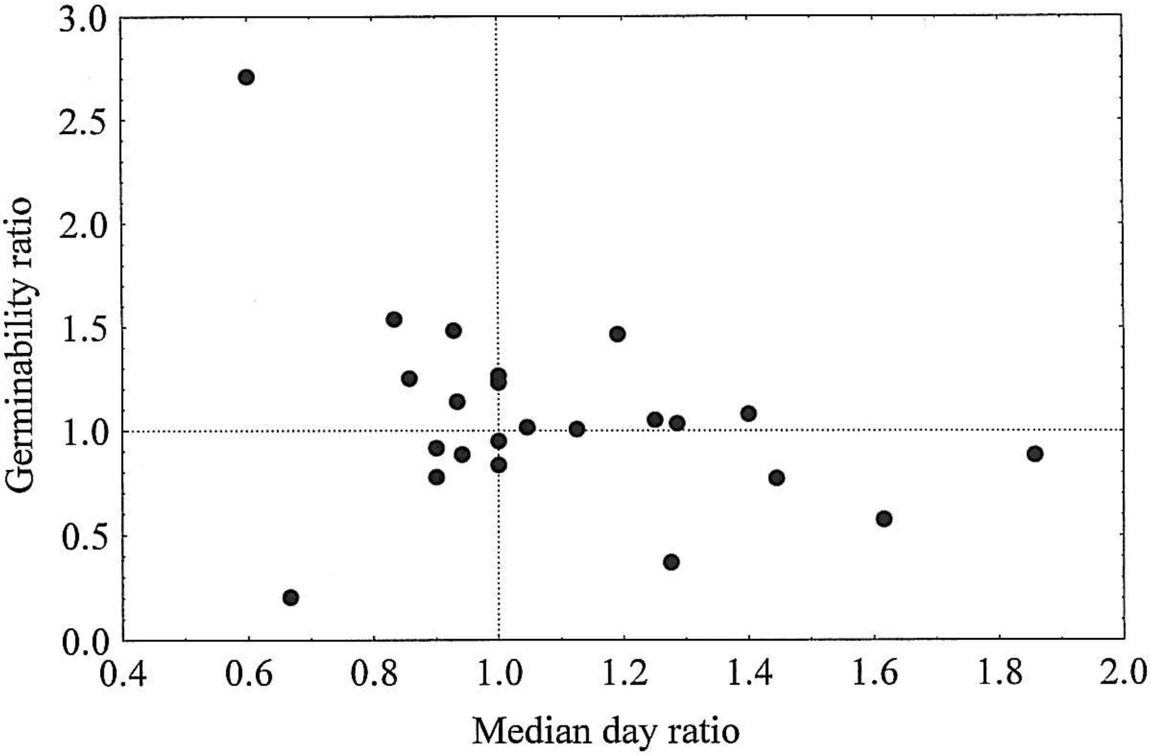

3.0
2.5
2.0
1.5
1.0
0.5
0.0
Germinability ratio
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Median day ratio

Fig.5

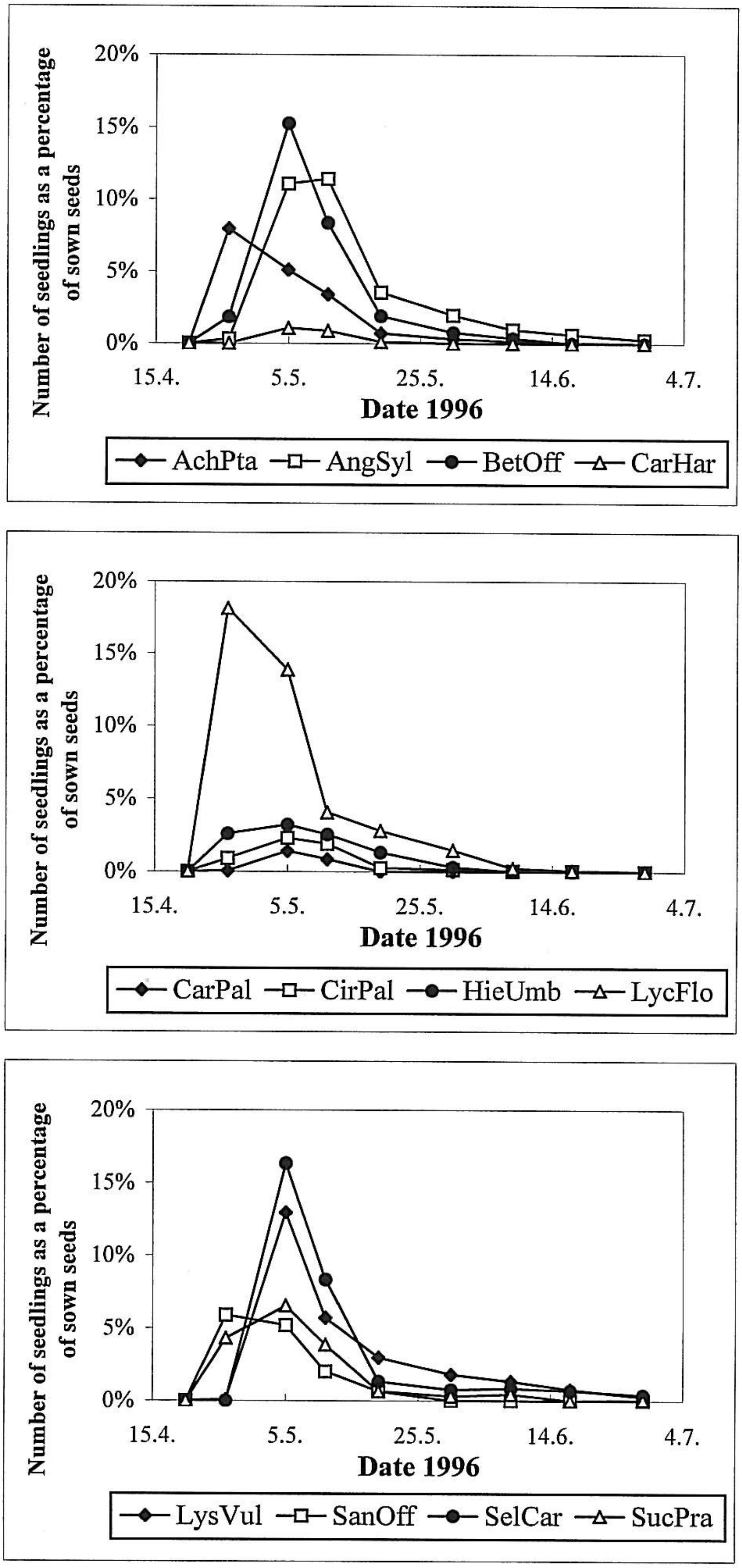
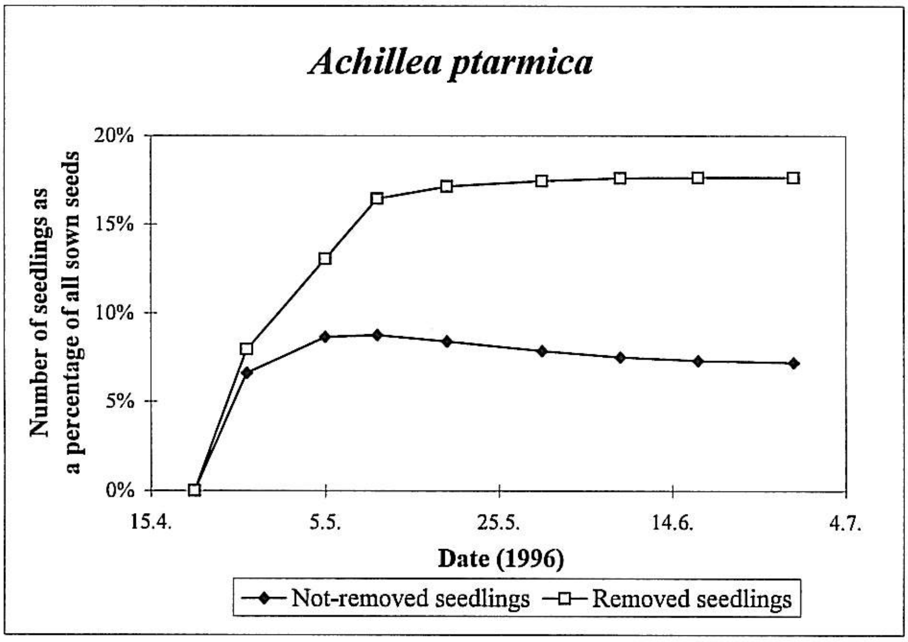
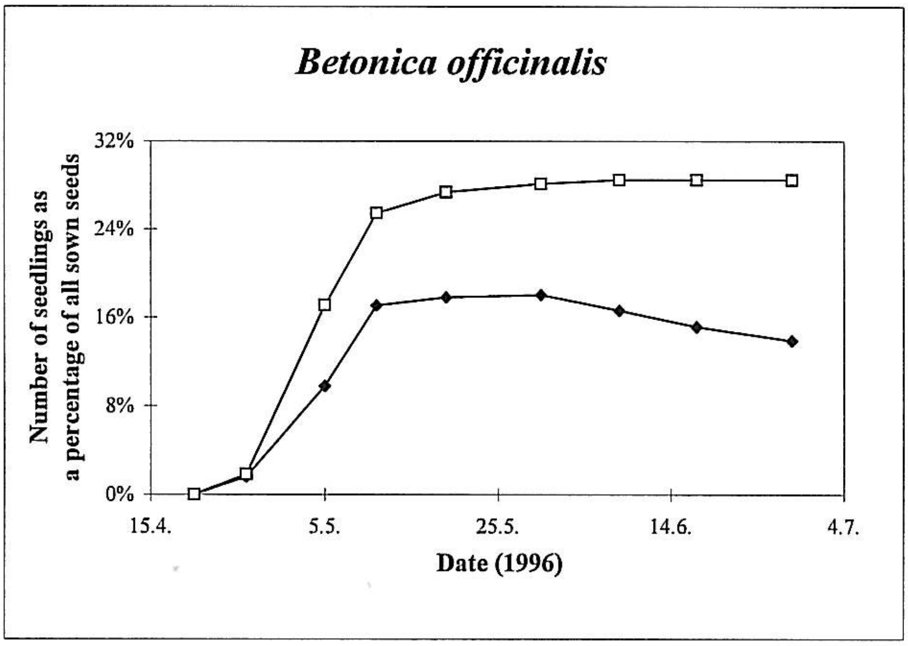

Number of seedlings as a percentage of sown seeds
20%
15%
10%
5%
0%
15.4.
5.5.
25.5.
14.6.
4.7.
Date 1996
AchPta
AngSyl
BetOff
CarHar
Number of seedlings as a percentage of sown seeds
20%
15%
10%
5%
0%
15.4.
5.5.
25.5.
14.6.
4.7.
Date 1996
CarPal
CirPal
HieUmb
LycFlo
Number of seedlings as a percentage of sown seeds
20%
15%
10%
5%
0%
15.4.
5.5.
25.5.
14.6.
4.7.
Date 1996
LysVul
SanOff
SelCar
SucPra

Fig.6 - 1


Achillea ptarmica


Betonica officinalis

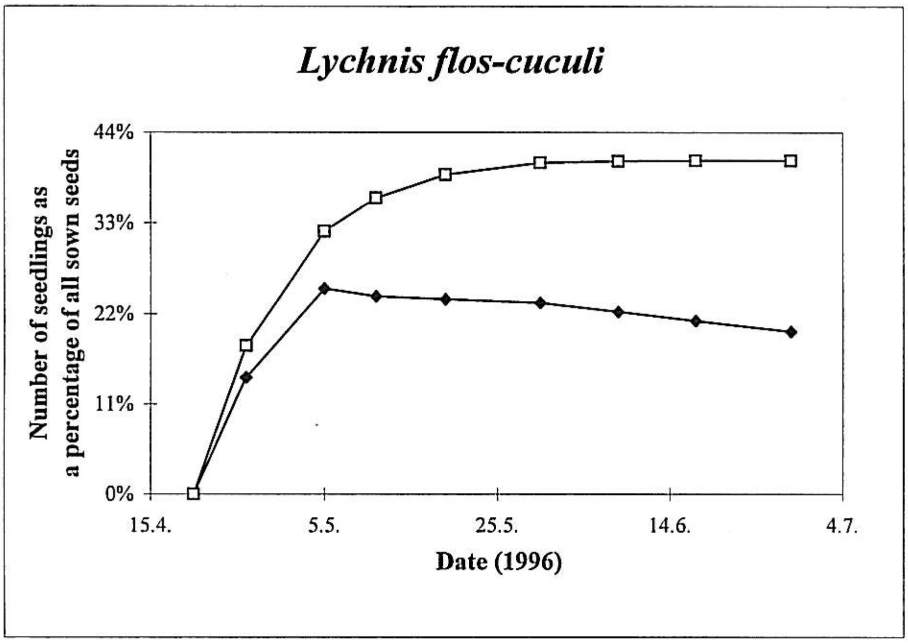
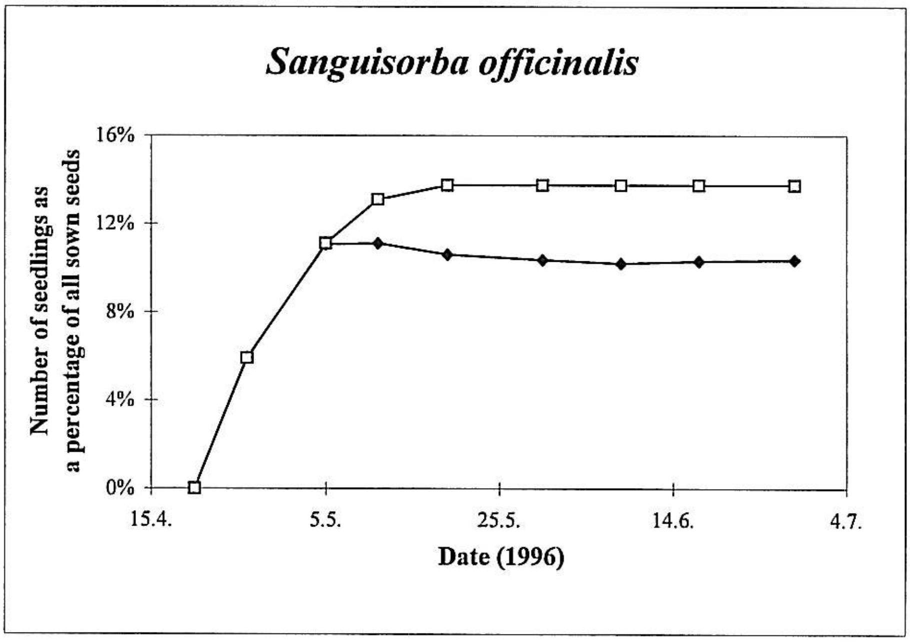
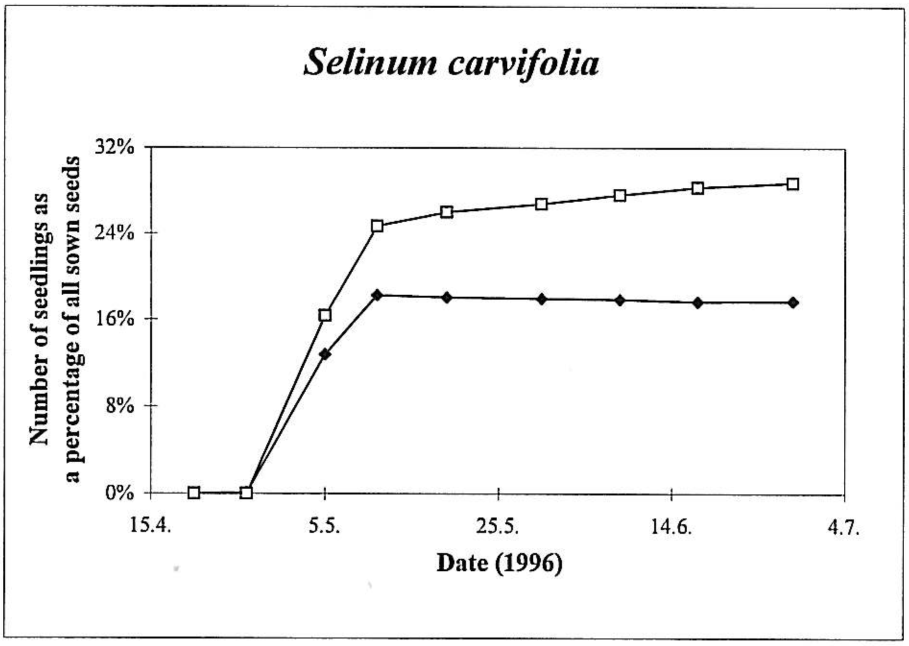

Lychnis flos-cuculi

Fig.6 - 2


Sanguisorba officinalis


Selinum carvifolia

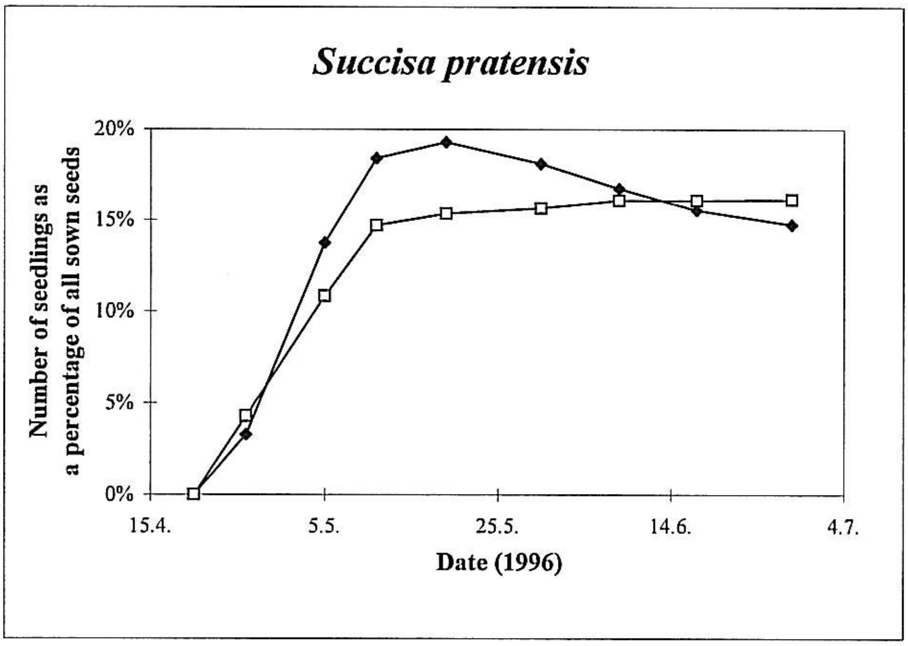

Succisa pratensis

Fig.7

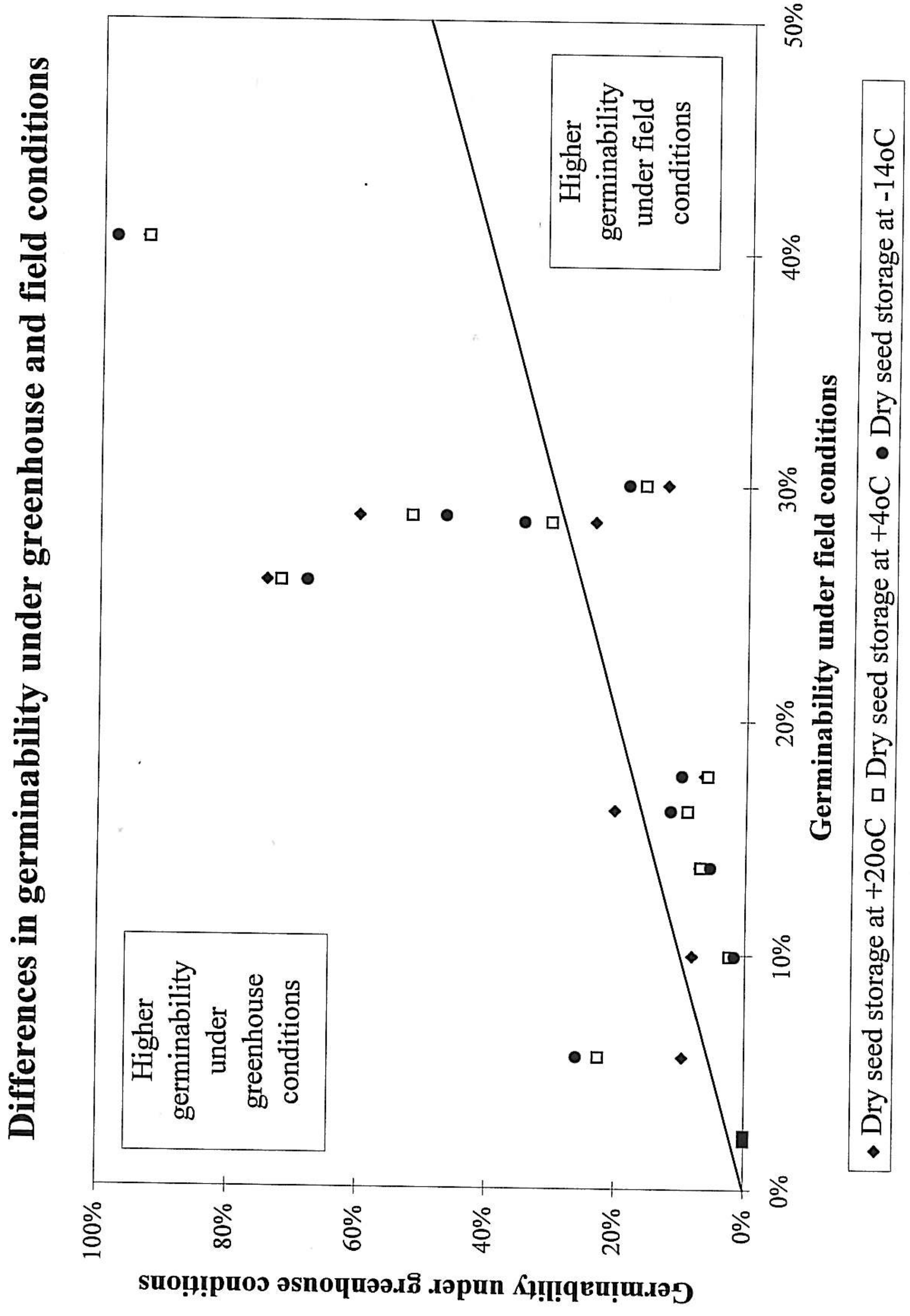

Differences in germinability under greenhouse and field conditions
Germinability under greenhouse conditions
0%
20%
40%
60%
80%
100%
Germinability under field conditions
0%
10%
20%
30%
40%
50%
Higher germinability under greenhouse conditions
Higher germinability under field conditions
◆ Dry seed storage at +20oC
□ Dry seed storage at +4oC
● Dry seed storage at -14oC

Fig.8

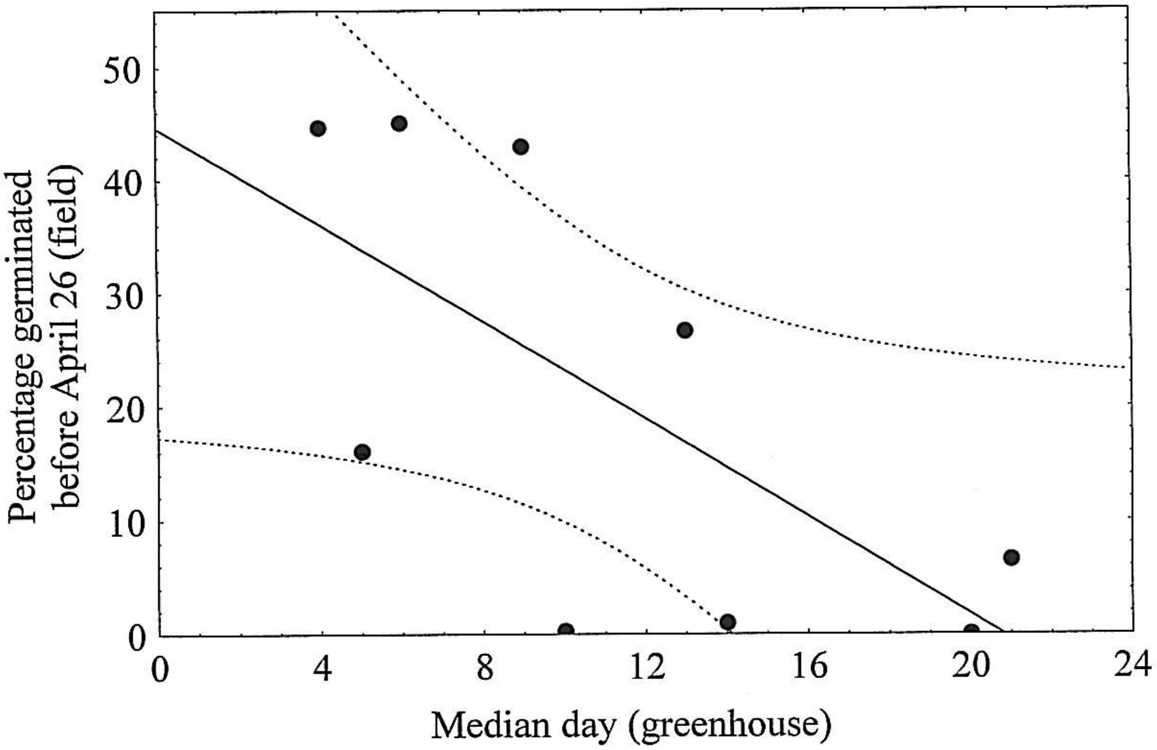

Percentage germinated before April 26 (field)
50
40
30
20
10
0
0
4
8
12
16
20
24
Median day (greenhouse)

Fig.9

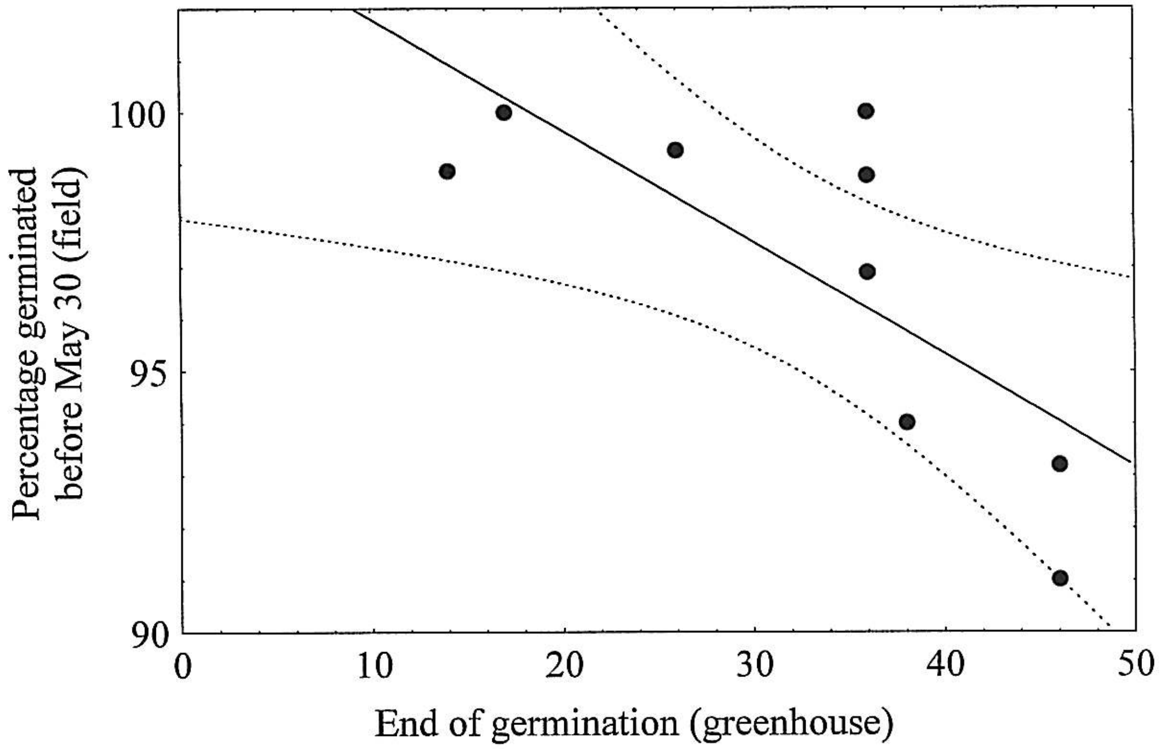
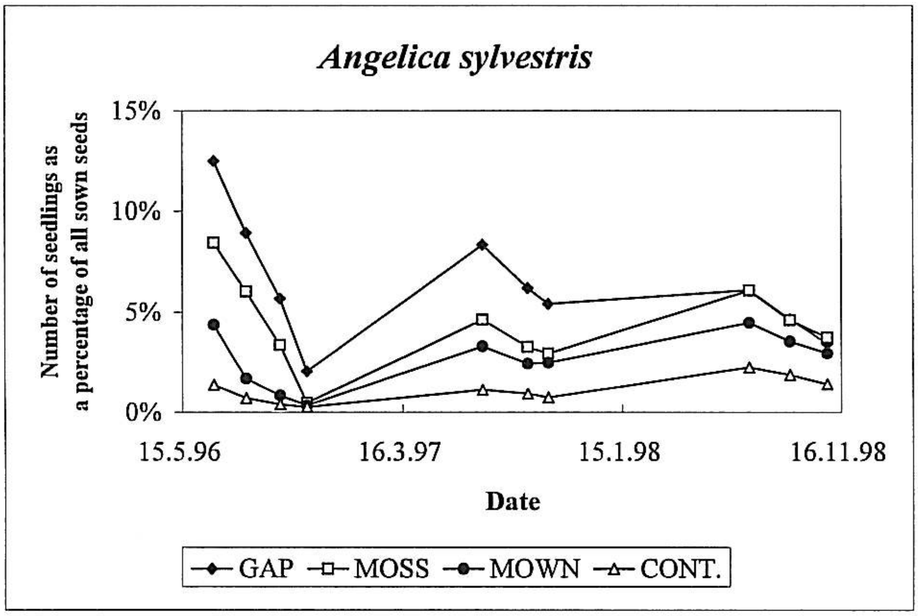
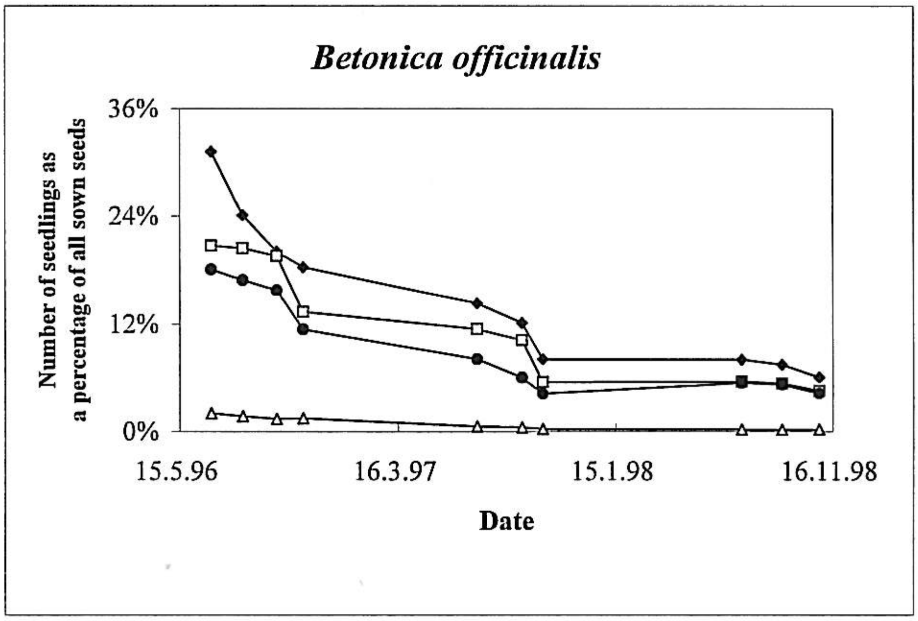

Percentage germinated before May 30 (field)
100
95
90
0
10
20
30
40
50
End of germination (greenhouse)

Fig.10 - 1


Angelica sylvestris
Number of seedlings as a percentage of all sown seeds
15%
10%
5%
0%
15.5.96
16.3.97
15.1.98
16.11.98
Date
GAP
MOSS
MOWN
CONT.


Betonica officinalis
Number of seedlings as a percentage of all sown seeds
36%
24%
12%
0%
15.5.96
16.3.97
15.1.98
16.11.98
Date

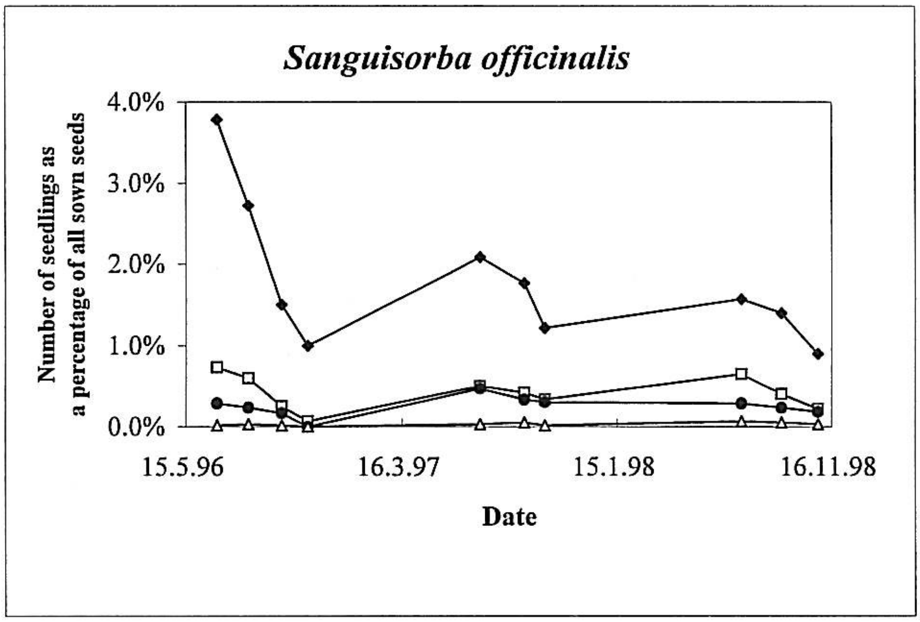
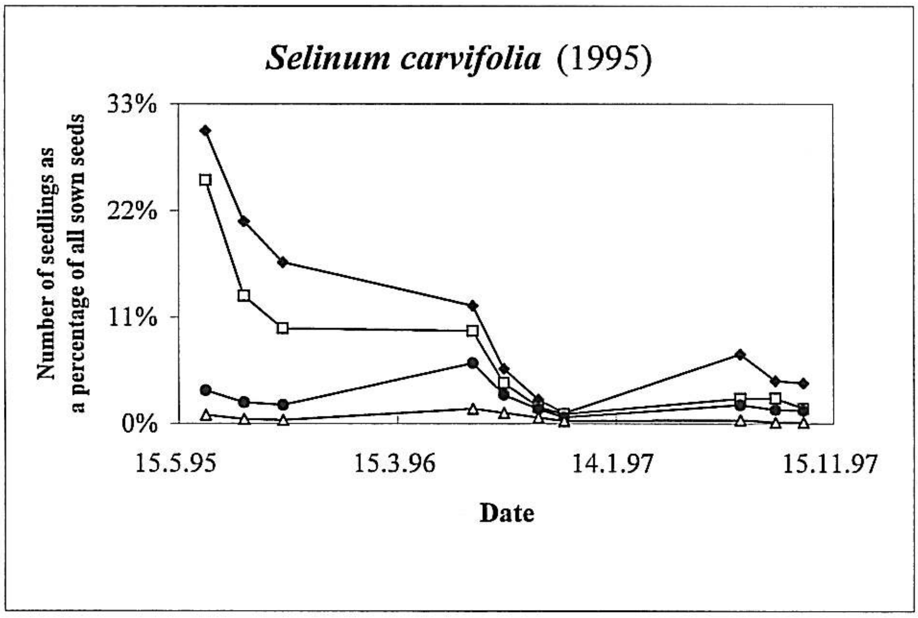
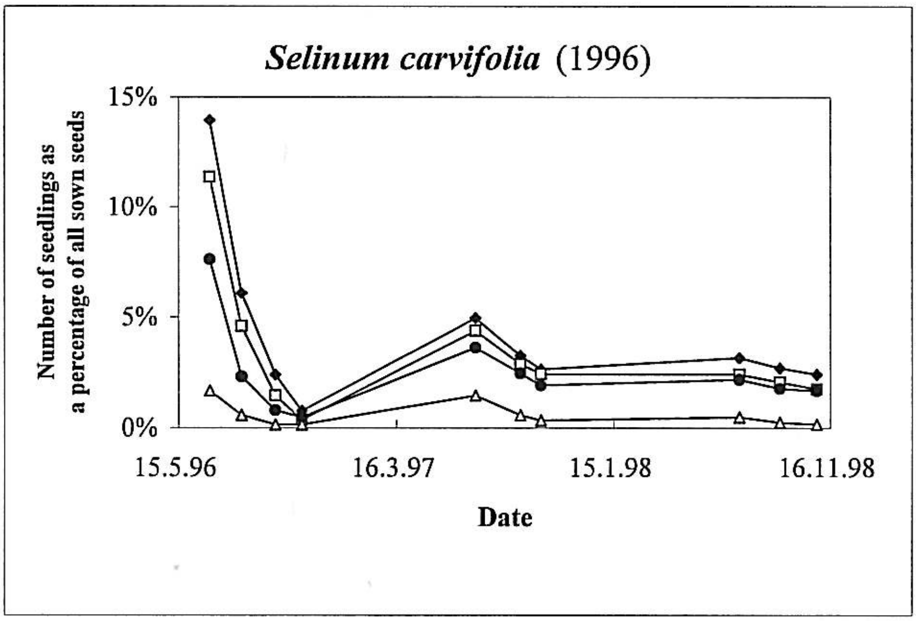

Sanguisorba officinalis
Number of seedlings as a percentage of all sown seeds
4.0%
3.0%
2.0%
1.0%
0.0%
15.5.96
16.3.97
15.1.98
16.11.98
Date

Fig.10 - 2


Selinum carvifolia (1995)
Number of seedlings as a percentage of all sown seeds
33%
22%
11%
0%
15.5.95
15.3.96
14.1.97
15.11.97
Date


Selinum carvifolia (1996)
Number of seedlings as a percentage of all sown seeds
15%
10%
5%
0%
15.5.96
16.3.97
15.1.98
16.11.98
Date

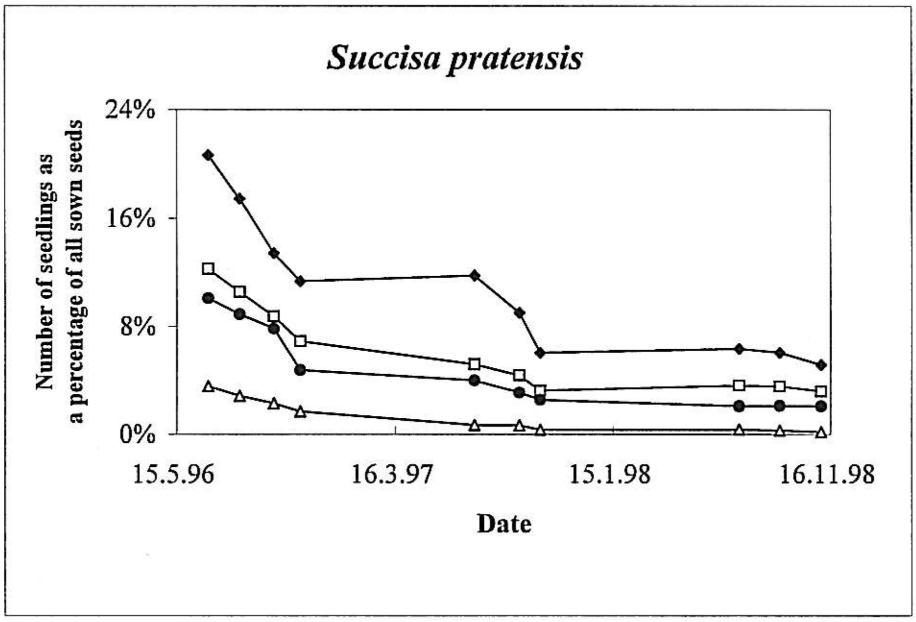

Succisa pratensis
Number of seedlings as a percentage of all sown seeds
24%
16%
8%
0%
15.5.96
16.3.97
15.1.98
16.11.98
Date

Fig.10 - 3

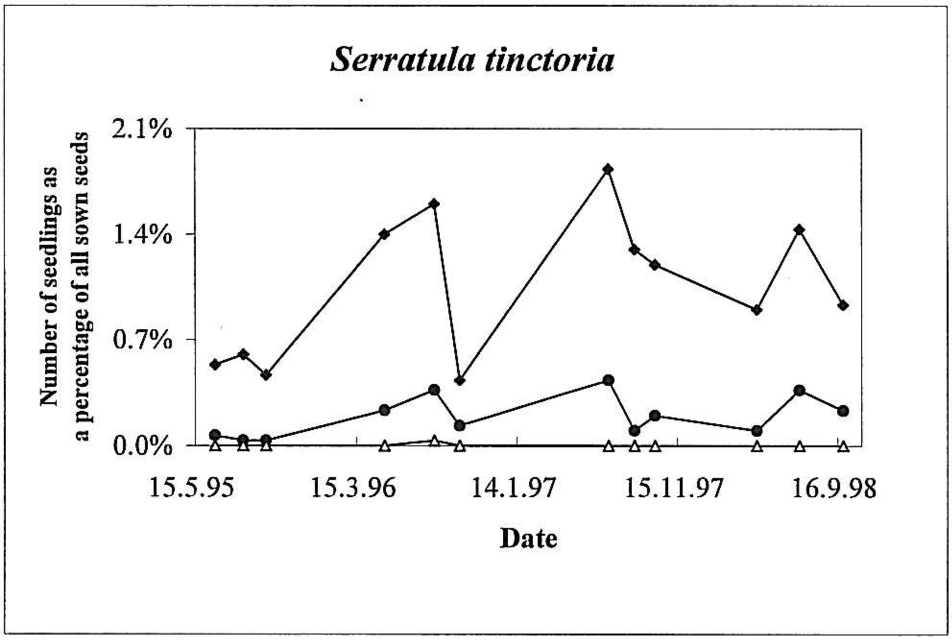
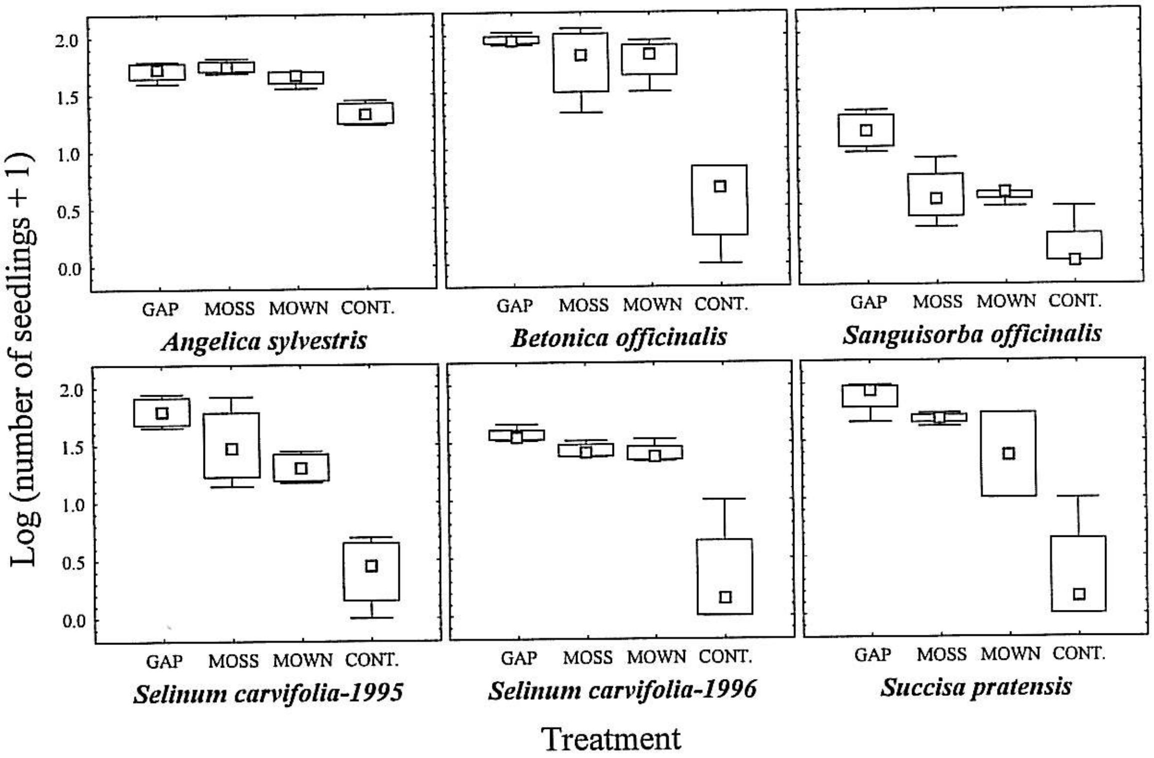

Serratula tinctoria
Number of seedlings as a percentage of all sown seeds
2.1%
1.4%
0.7%
0.0%
15.5.95
15.3.96
14.1.97
15.11.97
16.9.98
Date

Fig.11


Log (number of seedlings + 1)
2.0
1.5
1.0
0.5
0.0
GAP
MOSS
MOWN
CONT.
Angelica sylvestris
Betonica officinalis
Sanguisorba officinalis
Selinum carvifolia-1995
Selinum carvifolia-1996
Succisa pratensis
Treatment

Establishment of juvenile plants in an oligotrophic wet meadow

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Abstract

Interspecific differences in regeneration enable species coexistence in oligotrophic species-rich wet meadow communities in Central Europe. Moreover, conspecific plants in different stages of their life cycles differ in sensitivity to various abiotic and biotic factors of the environment, and often require different specific conditions for the establishment. Differences between nine wet meadow species (*Angelica sylvestris*, *Betonica officinalis*, *Cirsium palustre*, *Jacea pratensis*, *Myosotis nemorosa*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*) in establishment of juvenile plants in variously treated plots were tested in manipulative field experiments. Juvenile plants in jiffy-pots were trans-planted into plots with four treatments: (1) gap, e.i., sod stripped, all the above-ground vegetation removed, (2) mown and moss layer removed, (3) mown, (4) untouched control, and monitored within at least two vegetation seasons. Plots with treatments (1), (2), and (3) were regularly mown and the litter layer was removed from them. Seven morphological characteristics were recorded: the number of leaves, maximal leaf length, maximal leaf width, plant height, stalk length, sprigging (e.i., the number of lateral leaf rosettes and/or shoots), and the number of flowers. Data showed that particular treatments affected tested plants differently, species differed in their responses to particular treatments, and particular species differed in changes in measured characteristics conditioned by the conducted treatment. However, some general trends in changes of the characteristics were observed, e.g., the number of leaves, leaf width, stalk length, sprigging and flowering were highest in gaps, followed by plots with moss-removed at the beginning of the experiment, and the differences between tested plants increased in time; mortality was highest in untreated plots and often also in gaps.

Keywords: Meadow, Plant establishment, Manipulative experiment, Competition, Morphological changes, Gap regeneration, Moss, Litter layer, Mowing.

Nomenclature: Vascular plants: Rothmaler (1976), bryophytes: Corley et al. (1981).

Introduction

Oligotrophic species-rich meadows are man-made communities maintained by traditional management (e.g., mowing) for centuries (Bakker 1989). Meadows belong at a scale of one to several square meters to the world's most diverse communities (Kull & Zobel 1991). Recently, in a consequence of political and social changes in West and Central Europe during last decades, oligotrophic meadows are often abandoned or their management has been intensified (e.g., using fertilizer). Both of these processes result in a species diversity decrease, the valuable species-rich communities are replaced by stands dominated by only a few competitively strong species. These changes stress the importance of understanding mechanisms of the maintenance of species diversity.

Suggested mechanisms include both suppression of seedling recruitment and changes in competitive relationship among established plants (Tilman 1993, Křenová & Lepš 1996, Špačková et al. 1998). Also species mobility (van der Maarel & Sykes 1993, Herben et al. 1993, Huston 1994) can be used to explain mechanisms that maintain species diversity. Seedling recruitment is an important part of this mobility (Kalamees & Zobel 1997), even in communities dominated by clonal plants (e.g., its role in maintaining genetic diversity; Watkinson & Powell 1993). It usually depends on suitable microhabitats (e.g., gaps: Křenová & Lepš 1996) and is often much more sensitive to environmental conditions and competition than established plants (Křenová & Lepš 1996, Morgan 1997, Špačková et al. 1998). Interspecific differences in seedling recruitment requirements to specific conditions are considered to be important to the maintenance of species diversity (Grubb 1977), but also differences in sensitivity of different stages of a plant life cycle to various environmental factors play a role. For example, seedling recruitment and small juvenile plants may be strongly affected by moss layer (van Tooren 1990, During & van Tooren 1990) which effect can be both protective (e.g., Ryser 1990), and inhibitive (Keizer et al. 1985, van Tooren 1990, Špačková et al. 1998), whereas established plants are usually not affected by bryophytes. Litter layer which can be considered to be one of the features of the competitive strategy (Grime 1979, Facelli & Facelli 1993) can influence plants in a similar way as bryophytes. Established plants are generally much less sensitive to these factors. Suppression of seedling recruitment in perennials that do not exhibit pronounced clonal spread will change population demographic structure first, and only after that the population will decline. However, it depends on species longevity and also on possible changes in competitive relationship between established plants. Thank to complicated structure of meadow communities based on lots of various interactions between established plants and their environment including both biotic and abiotic factors, there is a delay in response of the established vegetation to applied treatments (Špačková et al. 1998, Lepš 1999) whereas the seedling recruitment response was affected immediately (e.g., Špačková et al. 1998). Conspecific seedlings and established plants may also considerably differ in their sensitivity to the same treatment. For example, mature plants of late flowering species *Betonica officinalis* and *Sanguisorba officinalis* were cosiderably suppressed in their seed production in mown plots whereas their seed germination and seedling establishment were positively influenced by mowing (Lepš 1999, Kotorová & Lepš 1999).

Various aspects of competition have been studied in many field and greenhouse experiments (Goldberg & Barton 1992). Two contrasting hypotheses about the relationship between vascular plant competition and habitat productivity are currently discussed: (1) increasing habitat productivity results in high growth rates and large amount of biomass which is followed by increasing intensity of both shoot and root competition (Grime 1979, Keddy 1989), and (2) with increasing standing crop, competition for light becomes more important, whereas competition for below-ground resources decreases (Tilman 1982). According to Grime (1979), the intensity of competition increases with soil fertility and decreases with stress. Wilson & Tilman (1991, 1993) have shown that root competition is relatively more important at lower levels of soil nutrients. With increasing soil productivity, competition for nutrients become less important and the importance of competition for light increases. Competition for light is probably more asymetric then competition for nutrients. It is much easier to succeed in competition for light than in competition for nutrients which are distributed patchily in three dimensions whereas light can be simply captured by the tallest plants (Huston & DeAngelis 1994, Weiner & Thomas 1986).

The aim of this paper is to test effects of gaps, moss layer, and established vegetation on establishment of juvenile plants that are the phase of the life cycle between seedling and established plant stage. Competitive relationships between juvenile plants and both bryophytes and vascular plants, competing both as a living biomass and persisting litter, were studied. Gap plots with all the above-ground vegetation removed (including moss layer and, of course, litter) were used as an environment without or with lowest intensity of competition. Moss-removal plots were used to test the effect of vascular plants under the mowing regime on the juvenile plants. In mown plots, the effect of the moss layer cover was added to the effect of vascular plants under the mowing regime. Control plots stayed untreated, mimic the meadow community after the cessation of mowing: all the moss layer, litter layer and living biomass competition were affecting juvenile trans-plants in controls. Other studies show that cessation of the disturbance regime leads to decrease in species richness (e.g., Bakker 1989, Lepš 1999): the positive effect of disturbance is usually explained by promoting non-equilibrium coexistence avoiding exclusion of competitively weak species (e.g., Huston 1979, Křenová & Lepš 1996). For example, mowing, the regular disturbance regime applied in meadows for centuries, stabilized species composition of meadow communities, so any changes in it lead to exclusion of some species (e.g., Lepš 1999). By mowing the tall plants are removed disproportionately more (Grime et al. 1987) and asymmetry in competition for light is highly reduced at least for some time, so survival of weak competitors for hight is enabled.

The presumption of this study was that there are differences among species in establishment of juvenile plant individuals in differently treated plots and that juvenile plants of particular species respond to the same treatment differently from conspecific seedlings and established plants.

Study site

The experiment was conducted in a wet, oligotrophic, species-rich meadow located near the village Ohrazeni which is situated 10 km south-east of České Budějovice, Czech Republic, 48°57' N, 14°36' E, 510 m a.s.l. Mean annual temperature is 7.8°C, mean annual precipitation is 620 mm (České Budějovice meteorological station, Vesecký 1960). July is the wettest and warmest month with 102 mm of precipitation, and temperatures range from a mean daily minima of 11.6°C to a mean daily maxima of 24.1°C. January (the coldest month) temperatures range from a mean daily minima of -6.2°C to a mean daily maxima of 0.6°C. Soil nutrient levels are low (total nitrogen 6-8g/kg dry soil weight, total phosphorus 400-500mg/kg dry soil weight, C/N ratio 16-20). According to phytosociological classification (Moravec et al. 1995), the vegetation belongs to ad *Selino-Molinietum caeruleae* K. KUHN 1937 from alliance *Molinion* (diagnostical species: e.g., *Molinia caerulea, Selinum carvifolia, Betonica officinalis, Potentilla erecta, Scorzonera humilis, Succisa pratensis*). The stand includes also some species indicating a transition to *Violion caninae* (e.g., *Briza media, Carex pipulifera, Carex pulicaris, Dantonia decumbens, Nardus stricta, Pedicularis sylvatica*). Two phytosociological relevés are presented in Table 1. Seeds for the cultivation of trans-plants were also collected at this locality.

General characteristics of tested species

Angelica sylvestris (*Apiaceae*)

A.s. is a monocarpic or polycarpic perennial, semi-rosette hemicryptophyte with a stout root stock. Flowering stems may reach 150 cm. Leaves are divided, 2-3-pinnate, the number of leaves is low, length of basal leaves is up to 60 cm, their area may be higher than 100 cm^2. *A.s.* flowers from July to September and it sets seeds from September onwards. *A.s.* benefits in localities where management allows the development of a larger summer peak in shoot biomass. Regeneration is entirely by seeds. Population often consists of a few matute flowering individuals associated with many juvenile plants, each with one or two small leaves and existing in an apparently suppressed condition beneath the vegetation canopy (Dostál 1989, Grime et al. 1988).

Betonica officinalis (*Lamiaceae*)

B.o. is a polycarpic perennial, semi-rosette hemicryptophyte with a short woody rhizome. Stems are erect, up to 80 cm high. Leaves are mostly basal and stay green in winter. *B.o.* grows continuously at low temperatures. It flowers in June and August. Seeds mature late during autumn months and they are released slowly. Seeds germinate in the spring. *B.o.* is a slow-growing, rosette-forming herb which is mainly restricted to short turf on unfertile soils. It showes a pronounced summer peak in both biomass and leaf canopy (Dostál 1989, Grime et al. 1988).

Cirsium palustre (*Asteraceae*)

C.p. is a monocarpic perennial, semi-rosette hemicryptophyte. Immature plants consist of a leaf rosette of hairy, ovate, spiny leaves, each of which is sometimes more than 40 cm^2. Leaves of *C.p.* are relatively long-lived. Adult flowering plants have high erect stems (120 cm) with spiny, pinnatifid decurrent leaves. *C.p.* flowers in August. Seed production is often high (700 seeds per plant). After flowering and fruiting, plants die in late autumn. The low-growing rosettes are very dependent upon short turf or open vegetation for establishment, and may develop for several years before flowering. In shade, *C.p.* may persist without flowering. *C.p.* regenerates by means of wind-dispersed seeds, many of which germinate in spring (Dostál 1989, Grime et al. 1988).

Jacea pratensis (*Asteraceae*)

J.p. is a polycarpic perennial, semi-rosette forming hemicryptophyte. Shoots are often branched, up to 120 cm high. Leaves are hairy, lanceolate. Flowers are produced from July to August (Dostál 1989). Fruits are shed from August onwards, some may be retained in the inflorescence after the death of the shoot in autumn. *J.p.* regenerates mainly by means of seeds but with some slight capacity for vegetative spread. New shoots emerge in spring.

Myosotis nemorosa (from *M. palustris* group, *Boraginaceae*)

M.n. is a rhizomatous, biennial or perennial helofyte or semirosette hemicryptophyte with creeping runners. Stems are erect, flowering stems up to 50 cm high. Shoot leaves are shorter than 5 cm. *M.n.* flowers from June to September and sets seeds from August to October. *M.n.* regenerates vegetatively to form clonal patches, and by seeds germinating in gaps during spring. Older stems break down to leave as isolated daughter-plants (Dostál 1989, Grime et al. 1988).

Sanguisorba officinalis (*Rosaceae*)

S.o. is a polycarpic perennial, semi-rosette hemicryptophyte with woody stock. Stems are erect and high up to 100 cm. Leaves are mainly basal, pinnate. It flowers in August and September (Dostál 1989). The canopy of *S.o.* is low. All leaves are dying in the autumn. *S.o.* regenerates by seeds.

Selinum carvifolia (*Apiaceae*)

S.c. is a perennial. Stems are erect, up to 100 cm high. Leaves are 3-4-pinnate with deeply lobed segments. *S.c.* flowers from July to September (Dostál 1989). All leaves are dying in the autumn. *S.c.* regenerates entirely by seeds.

Serratula tinctoria (*Asteraceae*)

S.t. is a polycarpic perennial, semi-rosette hemicryptophyte. Stems are erect, up to 100 cm high, usually branched above. Leaves are subglabrous with bristle-tipped teeth. *S.t.* flowers from July to September (Dostál 1989). All leaves are dying in the autumn. *S.t.* regenerates by means of seeds.

Succisa pratensis (*Dipsacaceae*)

S.p. is a polycarpic perennial, semi-rosette hemicryptophyte with short vertical rhizome. Stems are erect, flowering shoots are up to 100 cm high. Ovate-lanceolate, slightly hairy leaves, (leaf length 10-30 cm, leaf area smaller than 40 cm^2) stay green in winter and survive for up to one year. Foliage is typically appressed to ground. *S.p.* flowers from July to September. Some fruits are shed green, some retain until winter. *S.p.* regenerates almost entirely by seed in spring. Vegetative spread through the production of lateral shoots is possible but rare. *S.p.* is a slow-growing long lived plant which often does not flower until its four year. It reaches maximum abundance in short turf (Dostál 1989, Grime et al. 1988).

Methods

The effect of litter layer, moss layer, and the living biomass on the establishment of juvenile plants of nine meadow species (*Angelica sylvestris*, *Betonica officinalis*, *Cirsium palustre*, *Jacea pratensis*, *Myosotis nemorosa*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*) was tested in a manipulative field experiment where differently treated plots were located in randomized complete blocks. In each block, following treatments were used when the experiment started (end of June): (1) gap (sod stripped, all the above-ground vegetation and most of the roots removed by hands), (2) plot mown, litter and moss layer removed by hands, (3) plot mown, litter layer removed by hands, (4) untouched control. During the experiment, litter was removed from treatments (1), (2), and

(3) in March of each year, treatments (1), (2), and (3) were mown around the tested trans-plants twice an year in early summer and in midsummer (after measurement).

Seven morphological characteristics were studied: the number of leaves, maximal leaf length, maximal leaf width, plant height, stalk length, sprigging (e.i., the number of lateral leaf rosettes and/or shoots), and the number of flowers. Plants were measured firstly at the end of the vegetation season when they were transplanted to the field, since the next (the second) vegetation season they were measured three times a year (in early summer, in midsummer and in the autumn).

The experiment started in 1995 with *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*, in 1996 with *Cirsium palustre*, and in 1997 with *Angelica sylvestris*, *Betonica officinalis*, *Jacea pratensis*, *Myosotis nemorosa*, *Sanguisorba officinalis*. Seeds from the locality were germinated in Petri dishes with most blotting paper in the greenhouse. Seedlings were removed just after their germination and were cultivated in jiffy-pots also in the greenhouse. Obtained juvenile plants were in jiffy-pots trans-planted to the field at the end of June. The number of tested trans-plants was as high as it was possible to obtain (32-100 plants per one species).

Summary information about the experiment is in Table 2.

Data were evaluated by ANOVA models in SYSTAT and STATISTICA for Windows (Anon. 1996) and in Redundancy Analysis (RDA) in CANOCO (ter Braak 1990, ter Braak & Šmilauer 1998; CANODRAW and CANOPOST (Šmilauer 1992) were used for graphical output). RDA, a method based on a linear species response, was used because the explanatory variables were mostly categorical. The standardization and centring of morphological characteristics was used to get their values on comparable scales. Logarithmic transformation x'=log(x+1) was used for the seven morphological variables, because all of them have not normal, but positively skewed distribution including zeroes.

Results

For the general evaluation of the experiment, comparisson of state at the beginning of the experiment and in the half of the second vegetation season was selected. Logarithmic transformation x'=log(x+1) was used for the seven observed morphological variables (the number of leaves, maximal leaf length, maximal leaf width, plant height, stalk length, sprigging and the number of flowers) due to their distribution and also non-homogenous variance of the data of particular species (*Angelica sylvestris*, *Betonica officinalis*, *Cirsium palustre*, *Jacea pratensis*, *Myosotis nemorosa*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*) that naturaly differ in their morphology. After the logarithmic transformation, the interaction species*treatment reflects in a meaningful way the interspecific differences in the effects of particular treatments.

The number of leaves per one plant (Fig.1) was strongly affected by the treatment (P<0.0001) and it changed from the beginning of the experiment to the half of the second vegetation season considerably differently for particular species (interaction species*treatment: P<0.0001). For all the species, the highest average number of leaves per one plant was found in gaps.

The effect of the treatment to the maximal **leaf length** (Fig.2) was highly significant (P=0.0020), and its effect to particular species considerably differed (interaction species*treatment: P=0.0044). For *Myosotis nemorosa* and *Succisa pratensis*, the leaves were longest in gaps, followed by moss-removal treatment, mowing and lastly untreated controls (similar result would be probably obtained for *Angelica sylvestris* if herbivores were not present). The longest leaves in gaps were also observed in *Cirsium palustre* and *Serratula tinctoria*, but the order of treatments by the leaf length was: gap > control > moss-removed > mown. On the contrary, the shortest leaves in gaps and the longest in controls were observed in *Betonica officinalis* and *Jacea pratensis*. That indicate two interacting antagonistic trends: (1) plants in gaps are generally bigger than in other treatments, so all their morphological characteristics are in gaps the highest, (2) due to higher plant cover in controls, plants have to produce longer leaves to be successful in the competition for light. However, other environmental factors may be important too (e.g., suppressing plants by herbivores, mainly in *Angelica sylvestris*).

The maximal **leaf width** (Fig.3) was considerably affected by the treatment (P<0.0001). The common trend for the species was recorded: leaf width decreased from gaps, followed by moss-removal plots, mown plots and lastly, controls. The exception was *Angelica sylvestris* that was often attacted by herbivores which reduced the plant vitality and growth. However, the specifity of particular species in reaction in leaf width to the treatment was also almost significant (interaction species*treatment: P=0,0581) which reflected differences in relative proportions of the species reaction to the particular treatments (e.g., most pronounced differences in *Succisa pratensis*).

Plant height (Fig.4) was given at the beginning of the experiment by the leaf slope and leaf length for all the species except *Myosotis nemorosa*, where the stalk was present in several plants already. In the field, rosette leaves of plants in untreated control plots were situated vertically, so plant height was almost equal to the leaf length for the plants that have not stalk yet. Rosette leaves of plants in plots with lower competition were situated much more horizontally which conditioned lower plant height in these trans-plants when they did not product a stalk yet. It can be demonstrated well by *Betonica officinalis* and *Sanguisorba officinalis*. Good examples of this phenomenon shown markably in presented data were also *Cirsium palustre* and *Jacea pratensis* in control, mown and moss-removal plots (respectively control and mown plots) only, because trans-plants of these species formed flowering shoots in environments with low intensity of competition during the second vegetation season already. Nevertheless, the main factor determinating plant height was the presence of a stalk (best examples of this: *Myosotis nemorosa*, *Succisa pratensis*). Both the effects of treatment and species*treatment interaction were highly significant (P<0.0001).

The number of leaves, **stalk length** (Fig.5), sprigging and flowering seemed to be characteristics affected by the treatment and species*treatment interaction the most (P<0.0001 in all these cases). Stalk was formed during the second vegetation season only in *Cirsium palustre*, *Jacea pratensis*, *Myosotis nemorosa* and *Succisa pratensis*. In *Sanguisorba officinalis* and *Selinum carvifolia*, the stalk was produced only by one plant (one plant in a gap plot in *S.o.* and one plant in a control plot in *S.c.*) in all the treatments together, so the value of this information for generalization is very low. *Myosotis nemorosa* formed flowering stems of almost the same height in all the treatments: in the half of the second vegetation season, in gaps the stems were found in all the trans-plants, the stem production in following treatments decreased in order moss-removal, mown and lastly, control where the presence of stalks was quite rare. *Succisa pratensis* produced high shoots frequently in gap and moss-removal plots. In mown plots, the stalk production started later (and was less frequent), so in the half of the second vegetation season, stalks still had not finished their growth to the full size. In *Jacea pratensis*, the stalk production was restricted to trans-plants in gaps and moss-removal plots, stalks of plants in moss-removal plots were generally less frequent, shorter and less branched. *Cirsium palustre* formed flowering shoots in several trans-plants in gap plots only and due to the fact, that *C.p.* is a monocarpic plant, all these plants died at the end of the vegetation season.

Sprigging (e.i., forming lateral buds, leaf rosettes and shoots; (Fig.6)) was restricted to *Jacea pratensis*, *Myosotis nemorosa* and *Succisa pratensis.* Active lateral buds were in the half of the second vegetation season also found in several plants of *Betonica officinalis* and *Cirsium palustre* in gaps, but probably only as a regeneration mechanism after mechanical damage: they usually did not persist and no lateral shoots were produced from them. For all the three species with lateral branching (*Jacea pratensis*, *Myosotis nemorosa*, *Succisa pratensis*), the considerably highest the number of lateral shoots was found in gaps and none (respectively almost none in *Jacea pratensis*) was found in untreated controls. In *Myosotis nemorosa*, sprigging seemed to have a clonal character: particular shoots seemed to become independent plants after some time. This is probably the mechanism that enable surviving of this biennial plant to the next vegetation season after its flowering and fruiting. Higher intensity of branching in *Jacea pratensis* and *Succisa pratensis* in plots with low competition may indicate possibility of vegetative spreading of these species, but no evident lateral spread was observed.

In the half of the second vegetation season, four of the nine species (*Cirsium palustre*, *Jacea pratensis*, *Myosotis nemorosa* and *Succisa pratensis*) flowered and also one flowering plant of *Selinum carvifolia* was found (in control). *Myosotis nemorosa* flowered in all of the treatments (all trans-plants in gaps were flowering), flowering of *Jacea pratensis* and *Succisa pratensis* was restricted to gaps and moss removal plots, trans-plants of *Cirsium palustre* flowered only in gaps. The number **of flowers** (Fig.7) was the highest in *Myosotis nemorosa* where almost one thousand flowers per one plant (clone originating in one trans-plant) in a gap was recorded several times, lower, but still very high the number was found in moss removal plots and then in mown plots. In controls, none or less than fifty flowers per one plant of *Myosotis nemorosa* were found. These huge differences in the number of flowers were given mainly by the number of flowering shoots. *Succisa pratensis* had only one or two flowers per one plant and recorded data were similar for trans-plants in gaps and moss-removal plots. Flowering shoots of trans-plants of *Jacea pratensis* in moss-removal plots were less branched than in gaps, so the number of flowers was lower (not more than three flowers per one plant in moss-removal plots, whereas in gaps also ten flowers per plant were recorded). The average the number of flowers per flowering trans-plant of *Cirsium palustre* in gaps was sixteen which is much lower than is usual for *C.p.* plants naturaly growing at the study site.

Specific effects of particular treatments to the species were tested by repeated measures ANOVA and by Redundancy Analysis (RDA) after logarithmic transformation $x'=\log(x+1)$.

Angelica sylvestris (Fig.8)

Angelica sylvestris was observed within two vegetation seasons which was too short time to observe most of the life cycle of tested trans-plants. From the seven recorded characteristics only four (the number of leaves, maximal leaf length, maximal leaf width and plant height) could be used for the evaluation of the effects of particular treatments: no stalk production, sprigging and flowering was observed. The number of leaves and plant height significantly depended on the time of the measurement ($P=0.0009$ and $P=0.0419$, respectively), the effect of treatment was significant for the number of leaves ($P<0.0001$) and maximal leaf width ($P=0.0047$) and almost significant for maximal leaf length ($P=0.0594$).

Mortality of plants started during the first vegetation season in controls, during the second season some plants from other treatments died too. Mortality was highest in untreated control plots as a result of the most intensive competition. The second treatment due the order by mortality was gap where the trans-plants were exposed the most to the herbivore predation. This was the reason why the trans-plants from moss-removal plots have the highest vitality: (1) for small trans-plants, the moss competition was an important negative factor and (2) the established vegetation protected small plants from herbivores. In the second vegetation season these plants were big enough to stay damaging by herbivores. The protective role of established vegetation is probably more important than moss competition: the effect of moss-removal plots is similar to the effect of plots only mown, but not to gaps.

For the establishment of the juvenile trans-plants of *Angelica sylvestris*, the moss-removal plots were the best: the mortality of plants was very low and their vitality was high in these plots which was well shown in all the recorded characteristics. Plants in controls were exposed to the strong competition of moss and litter layer and established vegetation. Weaker plants were gradually driven to the extinction, but vital plants produced long vertically situated leaves that enhances the observed plant height. This was the reason for the highest variability of the recorded characteristics in trans-plants in controls.

Betonica officinalis (Fig.9)

For trans-plants of *Betonica officinalis*, two vegetation seasons were also insufficient time to form flowering shoots, so only five of the seven studied characteristics were recorded (the number of leaves, maximal leaf length, maximal leaf width, plant height and sprigging). Sprigging was very rare: only three of all the 100 trans-plants (two in gaps and one in moss-removal plot) producted one lateral bud per plant which was only temporary. It seemed to be only a mechanism of regeneration after mechanical damage of a plant which was in gaps and moss-removal plots much more common than in untreated plots and plots only mown. Other four recorded characteristics were considerably affected by the time of the measurement ($P<0.0001$ in all cases). For the number of leaves, maximal leaf length and plant height, also effests of treatment ($P=0.0120$, $P=0.0013$ and $P=0.0005$, respectively) and time*treatment interaction ($P=0.0130$, $P=0.0427$ and $P=0.0066$, respectively) were significant. Leaf width seemed to be similar in all the treatments (the effect of treatment: $P=0.4591$) and changed in all the treatments in the similar way in time (the time*treatment interaction: $P=0.4530$).

First plant died during the first vegetation season in a control plot, but since the beginning of the second vegetation season, the mortality of plants in gaps, moss-removal and control plots seemed to be almost the same (15-25% at the end of the second vegetation season). No mortality in mown plot was observed. As in *Angelica sylvestris*, mortality in controls was a result of intensive competition which starts since trans-planting the juvenile plants to the community, mortality in gaps (and for *Betonica officinalis* also in moss-removal plots) was conditioned especially by herbivore predation which was most intensive at the beginning of the new growing season thanks to perenniallity of leaves of this species. Obtained results showed that for the establishment of the juvenile transplants the mown plots are the most convenient: the moss competition had much weaker negative effect than damaging plants by herbivores.

The highest the numbers of leaves per one plant were observed in gaps whereas the maximal leaf length and plant heiht and the highest variability in these two characteristics were found in plants in controls (plant height depended on leaf length and the leaf slope only, because no stalk was form yet) which can be considered to be a clear result of the competition for light.

Cirsium palustre (Fig.10)

A monocarpic plant species *Cirsium palustre* was observed for three vegetation seasons. As it was a plant species growing fast especially in the environment with very low intensity of competition (e.i., in gaps), all the life cycle was terminated (plant death after fructification) in 36% of the juvenile plants trans-planted to gaps during the time of observation. However, flowering was restricted to trans-plants in gaps. Surviving trans-plants in all the other treatments stayed in a vegetative stage as a leaf rosettes: the stalk growth was associated with flowering, so it was restricted to trans-plants in gaps that become mature. Sprigging was also restricted to trans-plants in gaps in the first season, in the second season it appeared also in several plants in moss-removal plots. It seemed to be also just a regeneration mechanism after plant damage, but some of the lateral buds persisted for a long time and formed leaf rosettes that in several cases probably became independent daughter-individuals. For the number of leaves, maximal leaf length, maximal leaf width and plant height, the effect of the measure time was determining (P<0.0001 in all these cases) and also the time*treatment interaction was highly significant (P<0.0001, P=0.0011, P=0.0020 and P=0.0002, respectively).

During the first season, mortality was much higher in mown plots (24%) than in controls (8%). However, at the end of the third vegetation season it was the same in both these treatments (44%). In gaps, almost the same amount of trans-plants died during the three vegetation seasons of observation (36%: the percentage does not include plants dead after terminating their life cycle) whereas in moss-removed plots it was only 16%. That indicates that gaps promote fast maturation of plants which leads to early seed production, but there is also a bigger chance for the plants to be damaged. Plants in vegetative stage with the highest vitality were characteristic for the moss-removal plots: juvenile transplants were not suppressed by moss competition in moss-removal plots as it was in plots only mown and in controls, so the juvenile trans-plants earlier grew to the stage relatively independent on the moss layer. The positive protective effect of established vegetation resulted together with the absence of moss competition the highest percentage of surviving trans-plants in moss-removal plots in comparisson with all the other treatments. However, flowering seemed to be suppressed by the living biomass of other vascular plants.

The number of leaves per one plant was highest in gaps and after the first season also in moss-removal plots. Plant height conditioned just by the leaf slope and leaf length was highest in untreated controls as a result of presence of the dense cover of living plant biomass and dead biomass in these plots.

Jacea pratensis (Fig.11)

Trans-plants of *Jacea pratensis* were observed within two vegetation seasons. The effects of time, treatment and treatment*time interaction were highly significant for all the studied characteristics except maximal leaf length (the number of leaves, maximal leaf width, plant height, stalk length, the number of lateral shoots and the number of flowers: $P<0.01$ in all the cases except the effect of treatment on plant height and the number of flower per one plant where it was $P=0.0404$ and $P=0.0237$, respectively). Leaf length seemed to be affected only be the time of the measurement ($P<0.0001$). Trans-plants started to flower in the second vegetation season, but stalk growth and flowering were restricted to plants in gaps and moss-removal plots.

Mortality was recorded firstly at the beginning of the second vegetation season in controls and gaps in almost the same intensity (two (8%) and one (4%) trans-plants in all the plots with the same treatment). Till the end of the second vegetation season, the highest amount of plants died in controls (36%) whereas the mortality in gaps stayed low: at the end of the second vegetation season it was as high as the mortality in moss-removal and mown plots was (4-8%).

The number of leaves was considerably highest in plants in gaps, followed by plants in moss-removal plots. Similar result was obtained for maximal leaf width, whereas leaf length seemed to be independent on the treatment. Plant height was considerably affected by the presence of stalk, for sterile plants the leaf slope seemed to be the most important. *Jacea pratesis* produced stalk only in adult plants that were ready to flower. Stalks of plants in gaps were much more branched and higher than in plants in moss-removal plots: therefore the number of flowers per one plant was also considerably higher in gaps. Sprigging (e.i., forming lateral leaf rosettes and basal lateral shoots) was most intensive in gaps, but also appeared in all the other treatments which can indicate the real possibility of vegetative spread by forming lateral shoots that may become independent on the mother-plant.

Myosotis nemorosa (Fig.12)

Myosotis nemorosa, the fast growing biennial with common clonal growth, was observed within two vegetation seasons. Some of the juvenile trans-plants in gaps became adult during the first vegetation season already. In the second vegetation season, flowering plants were found in all the treatments. Although *Myosotis nemorosa* is usually characterised as a biennial, no mortality caused by flowering was observed because of the clonal features of its growth. From the field observations, it was evident that fertile shoots died after they set seeds, but living daughter-plants stayed at the same place and most of them flowered in the next growing season. Effect of the treatment on all the seven studied characteristics was highly significant ($P<0.001$ in all the cases) as well as the effect of time, the time*treatment interaction was significant for the number of leaves and flowers per one plant ($P=0.0344$, $P=0.0007$, respectively).

Mortality starting in the first vegetation season in controls was restricted to untreated controls and mown plots during the whole second vegetation season. That indicates that juvenile plants of *Myosotis nemorosa* are sensitive to moss competition and mainly to the litter layer, but thanks to their clonality are quite resistant to mechanical damage.

Almost all the trans-plants in gaps formed during the second vegetation season large clones consisting of many flowering shoots with a large the number of leaves and flowers. Intensive growth of trans-plants in other treatments was supressed by the competition with other vascular plants and mainly at the beginning also by the moss and litter layer. At the end of the second vegetation season, clones in gaps were usually big enough to compete one to each other, so the differences between „plants“ in gaps and moss-removal plots became less striking. Clonal growth of trans-plants in untreated controls was suppressed, only a few daughter-plant rosettes were found round flowering shoots, sterile plants usually did not sprig. The maximal stalk length was similar in plants in all the treatments, however, it increased from gaps to controls, similarly to plant height.

Sanguisorba officinalis (Fig.13)

Trans-plants of *Sanguisorba officinalis* were observed within two growing seasons. At the end of the second vegetation season, one trans-plant in gap was found flowering, all the other surviving trans-plants were present as leaf rosettes: therefore only four morphological characteristics (the number of leaves per one plant, maximal leaf length, maximal leaf width and plant height) could be used for the evaluation. All these four characteristics depended considerably on time ($P=0.0058$, $P<0.0001$, $P=0.0006$ and $P<0.0001$, respectively), the effects of treatment and the time*treatment interaction was significant only in the number of leaves per one plant ($P=0.0237$ and $P<0.0001$, respectively).

Evaluation of mortality could be distorted by the fact that all the above-ground parts of plants of *Sanguisorba officinalis* are relatively short-lived. The leaves appear late in the spring and die in early autumn (during September), so, only the data from the half of the second vegetation season may be used to evaluate the real number of surviving plants. The highest mortality was found in controls (48%). Mortality of juvenile plants trans-planted to three other treatments was much less and decreased from gaps (20%) to mown plots (8%). That indicate that the effect of litter layer and/or living biomass present in controls is much more important than moss competition and damage of plants in plots with sparse vegetation cover.

Plants growing in gaps had more leaves which were shorter and wider than leaves of plants in other treatments, especially controls. From gaps to controls, the number of leaves per one plant and leaf width decreased and leaf length and plant height which was given by leaf length and leaf slope increased.

Selinum carvifolia (Fig.14)

Selinum carvifolia was studied within two vegetation seasons. During that time, only one flowering plant was found in an untreated plot, all the other surviving plants in all the treatments stayed sterile. No sprigging was observed. The effect of time on the number of leaves, maximal leaf length, maximal leaf width and plant height was highly significant ($P<0.0001$), but no significant effects of treatment and time*treatment interaction were detected.

For the mortality, the first vegetation season seemed to be decisive: most of the trans-plants died during the first growing season. At the end of the experiment, mortality was highest in untreated controls (46%), followed by mown and moss-removal plots (33% in both), the smallest number of trans-plants died in gaps (17%). Nevertheless, this experiment was conducted in 1995 and in years 1995, 1996, the damaging of plants by animals was much lower than in 1998.

Although one flowering plant was found in a control, trans-plants in gaps seemed to have the highest vitality. The number of leaves and the leaf length decreased from gaps to untreated controls.

Serratula tinctoria (Fig.15)

Trans-plants of *Serratula tinctoria* were observed within four vegetation seasons. Two plants in gaps became adult and started to be fertile in the third growing season, in all the other treatments, surviving trans-plants stayed as sterile leaf rosettes for the whole experiment. So, the stalk production and flowering was found to be restricted to gaps as well as sprigging. The production of lateral leaf rosettes started in two biggest plants in gaps in the fourth growing season and it seemed to may be an origin of independent daughter-plants. The number of leaves per one plant, maximal leaf length, maximal leaf width and plant height changed significantly with the date of the measurement ($P<0.0001$ in all these cases), the effects of the treatment ($P=0.0008$, $P=0.0195$, $P=0.0060$ and $P=0.0259$, respectively) and time*treatment interaction ($P<0.0001$, $P<0.0001$, $P=0.0001$ and $P<0.0001$, respectively) were also found significant for these four morphological characteristics.

As in *Sanguisorba officinalis*, the leaves and shoots of *Serratula tinctoria* are also short-lived, especially controls. They often start to grow not earlier than in the first half of May, and in the mid-October, all the above-ground parts of a plant may be already found dead. First plants died in the first vegetation season which seemed to be decisive for the total mortality of juvenile plants trans-planted to gaps and moss-removal plots. The highest mortality was recorded in untreated controls, mortality in gaps seemed to be the lowest, but the differences between gaps, moss-removal and mown plots in mortality were not striking.

Trans-plants in gaps had evidently the highest vitality: two of them became fertile during the experiment and maximal values of all the recorded morphological characteristics were observed in plants in gaps including the maximal leaf length and plant height. Vitality of trans-plants in moss-removal plots became higher than in plants in mown plots during the first vegetation season which indicate the importance of moss competition to the juvenile plants. The negative effect of litter layer and/or the high living biomass was shown by the highest mortality in controls and the lowest values of recorded morphological characteristics except plant height given by the leaf slope.

Succisa pratensis (Fig.16)

Succisa pratensis was studied within four vegetation seasons. During that time, some plants in all the treatments except controls became mature: only one plant in all the gap plots stayed sterile. Sprigging (e.i., production of lateral shoots and rosettes) was observed also in all the treatments except untreated control plots. It was most intensive in gaps, folloved by moss-removal and lastly mown plots. According to Grime et al. (1988), it could be a mechanism enabling vegetative spreading of this species. However, all the plants (even the most branched ones) looked to be compact individuals. All the seven studied characteristics considerably depended on the measure time ($P<0.0001$ in all the cases), effects of the treatment ($P<0.001$ in all the characteristics except the number of flowers per one plant where P=0.0022) and time*treatment interaction (P<0.0001 in all the cases) were also highly significant.

Mortality of trans-plants of *Succisa pratensis* was very low in all the treatments except controls where it started in the first vegetation season. In gaps, no mortality was observed, mortality in moss-removal and mown plots was low (6% and 11%, respectively). For survival in controls, the first season seemed to be decisive (33% of plants were found dead after the first season, and at the end of the fourth vegetation season, total mortality was 56%). It is in a good agreement with the life form of *Succisa pratensis* which is a rosette-forming plant with perennial leaves: it can succesfully compete with other plants especially at the beginning of a new growing season. This was probably also one of the mechanisms conditioning the high survival of trans-plants in moss-removal and mown plots. The leaves are mostly situated horizontally (sometimes also in control plots) which prevents them from herbivore predation, so the mechanical damage of above-ground parts of plants does not seem to be a very important negative factor. Moreover, *Succisa pratensis* is quite fast growing plant species which could be considered to be another way of avoiding the competition, especially with mosses and narrow and/or slow-growing vascular plants.

For all the studied characteristics, the largest values in trans-plants in gaps were recorded. The vitality of trans-plants in moss-removal plots was the second highest which indicates the importance of moss competition to the juvenile plants. Trans-plants in untreated controls were evidently suppressed: their mortality was the highest, none of them became adult during the four vegetation seasons of the experiment, no sprigging was observed, the number of leaves almost did not change from the state at the beginning of the experiment.

Discussion

Despite many attempts to deduce competition from community patterns (Klimeš 1995, Wilson 1995, Rejmánek & Lepš 1996), manipulative experiments seem to be more reliable tool for demonstrating competition in natural communities (Goldberg 1995). However, in the field experiments, the results may be distorted with side-effects of conducted treatments. For example, neighbouring plant populations could be disturbed and/or remnant roots of removed plants could remain in the soil and become a potential source of nutrients. In this experiment, the moss and litter layer were removed carefully to minimize disturbance of plant populations in treated plots. From gaps, majority of roots was removed. Moreover, the nutrient addition caused by releasing nutrients from decomposing roots was found to be unimportant (Wilson & Tilman 1993). In any competition experiment, tested individuals interact with their neighbours: both the ability to affect the competitor and the ability to withstand the effect of competitor are important (Lepš 1999). Treatments disturbing community structure cause changes not only in stand characteristics and species composition, but also in many abiotic factors of the environment on the microscale (e.g., mowing results in an increase of the soil surface temperature in sunny spring dates: Lepš 1999).

Whereas the effect of living biomass is often found on both established plants and seedlings, the effect of litter is usually more important for seedling recruitment and growth (Foster & Gross 1997). Similarly, mosses usually have small or no effect on established plants, but they influence seedling recruitment (e.g., Špačková et al. 1998). The protective role of moss layer was reported from dry grasslands (Ryser 1990) and communities with temporal desiccation (During & van Tooren 1990), whereas results from our locality revealed a significant negative effect of bryophytes on seedling recruitment (Špačková et al. 1998, Kotorová & Lepš 1999). However, mosses and seedlings might be found in similar microhabitats which indicates that seedling recruitment could be positively influenced by similar factors as moss layer (Lepš 1999)

Striking differences in specific requirements (species niches) both between different species and different stages of their life cycles were observed. In a parallel study from the locality testing seed germination and seedling establishment where the same treatments were used (Kotorová & Lepš 1999), gaps seemed to be the most convenient environment for seed germination and seedling establishement of all tested species (*Angelica sylvestris, Betonica officinalis*, *Sanguisorba officinalis*, *Selinum carvifolia*, *Serratula tinctoria*, *Succisa pratensis*). Seedling recruitment decreased from gaps to controls for all the species, however, these species differed in their sensitivity to particular treatments. According to the study, untreated controls seemed to be worst environment for establishment of juvenile trans-plants of all the nine species: the highest mortality in control plots was recorded. On the contrary, gaps were not found to be suitable the most for *Angelica sylvestris, Betonica officinalis, Cirsium palustre* and *Sanguisorba officinalis* at all, moreover, the mortality in gaps was comparable to mortality in controls in *Angelica sylvestris* and *Betonica officinalis*. Nevertheless, mortality found in these two treatments was based on completely different principles: in untreated plots, plant death was a result of high level of competition, whereas

Fig.10: ***Cirsium palustre*****: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data.** For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=4.145, P=0.005.

Fig.11: ***Jacea pratensis*****: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data.** For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=3.330, P=0.005.

Fig.12: ***Myosotis nemorosa*****: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data.** For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=1.628, P=0.020.

Fig.13: ***Sanguisorba officinalis*****: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data.** For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=1.433, P=0.150.

Fig.14: ***Selinum carvifolia*****: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data.** For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=4.905, P=0.005.

Fig.15: ***Serratula tinctoria*: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data**. For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=3.171, P=0.005.

Fig.16: ***Succisa pratensis*: standardized and centered by morphological variables RDA of log(x+1) transformed morphological data**. For clarity, the morphological characteristics with no or very weak relationships to axes are omitted. Arrows for time*treatment interaction show the direction of relative increase in plots under particular treatment (as compared to other treatments) with time. Test of significance of all canonical axes: F=4.897, P=0.005.

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Table 1: **Species composition of the community**: 5x5 m phytosociological relevés (r = less than 1%, - = absent species):

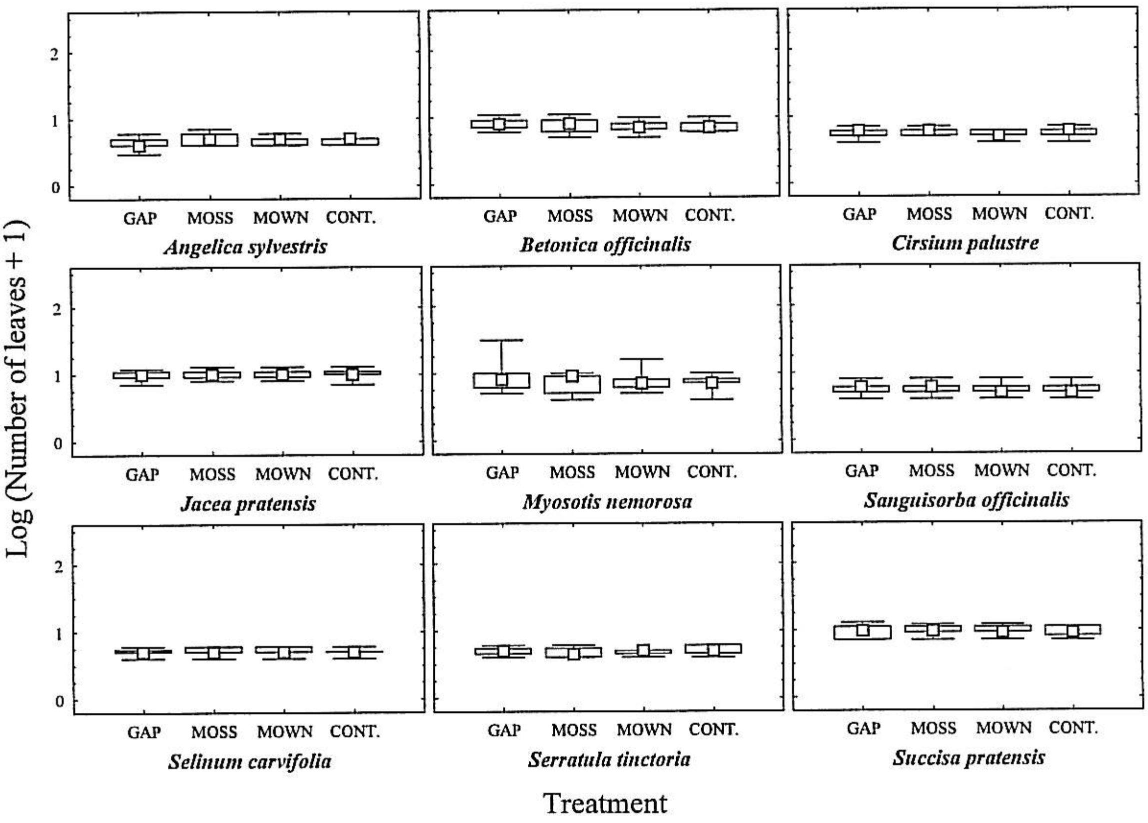
DATE	**June 15, 1995**	**June 19, 1995**		**June 15, 1995**	**June 19, 1995**
SPECIES	COVER [%]	COVER [%]	SPECIES	COVER [%]	COVER [%]
MOSS LAYER	**50**	**60**			
Recorded species: *Aulacomnium palustre, Brachythecium* sp., *Climacium dendroides, Hylocomium splendens, Mnium* sp., *Pseudoscleropodium purum, Rhytidiadelphus squarrosus, Sphagnum* sp.					
HERB LAYER	**95**	**85**			
Graminoids			**Forbs**		
Agrostis canina	1	2	*Rumex acetosa*	r	r
Anthoxanthum odoratum	2	1	*Achillea ptarmica*	r	-
Briza media	2	3	*Ajuga reptans*	2	9
Carex echinata	1	1	*Angelica sylvestris*	3	-
Carex hartmanii	1	1	*Betonica officinalis*	15	2
Carex leporina	r	r	*Calycocorsus stipitatus*	r	-
Carex pallescens	3	4	*Cardamine pratensis*	1	r
Carex panicea	4	8	*Cirsium palustre*	6	10
Carex pilulifera	1	3	*Dactylorhiza majalis*	-	r
Carex pulicaris	1	-	*Galium boreale*	1	1
Carex umbrosa	2	-	*Galium uliginosum*	1	1
Dantonia decumbens	-	2	*Hieracium umbellatum*	r	-
Deschampsia cespitosa	2	3	*Jacea pratensis*	r	-
Festuca ovina	1	7	*Lathyrus pratensis*	1	3
Festuca pratensis	2	r	*Leontodon hispidus*	r	-
Festuca rubra	7	5	*Lotus corniculatus*	-	r
Holcus lanatus	10	2	*Lychnis flos-cuculi*	2	3
Juncus effusus	r	3	*Lysimachia vulgaris*	3	2
Luzula multiflora	2	2	*Myosotis nemorosa*	5	6
Molinia caerulea	20	30	*Pedicularis sylvatica*	-	1
Nardus stricta	7	15	*Pinus sylvestris*	-	r
Poa pratensis	1	-	*Plantago lanceolata*	r	2
Scirpus sylvaticus	1	-	*Plantago major*	r	-
			Potentilla erecta	12	5
			Prunella vulgaris	-	4
			Ranunculus acris	-	1
			Ranunculus auricomus	r	1
			Ranunculus nemorosus	r	1
			Scorzonera humilis	r	1
			Selinum carvifolia	3	5
			Senecio rivularis	3	r
			Serratula tinctoria	-	r
			Succisa pratensis	1	-
			Trifolium sp.	-	r
			Valeriana dioica	-	2
			Veronica chamaedrys	2	r
			Vicia cracca	-	r
			Viola palustris	-	2

Table.2: **Descriprion of the experiment** (data about the experiment).

SPECIES	**Year when the experiment started**	**The number of observed vegetation seasons**	**The number of completelly randomised blocks**	**Plot area [m x m]**	**The number of plants in one plot**	**Total the number of tested plants**
Angelica sylvestris	1997	2	3	0.4 x 0.4	4	48
Betonica officinalis	1997	2	4	0.4 x 0.4	5	80
Cirsium palustre	1996	3	5	0.4 x 0.4	5	100
Jacea pratensis	1997	2	5	0.4 x 0.4	5	100
Myosotis nemorosa	1997	2	3	0.4 x 0.4	5	60
Sanguisorba officinalis	1997	2	5	0.4 x 0.4	5	100
Selinum carvifolia	1995	2	8	0.3 x 0.3	3	96
Serratula tinctoria	1995	4	4	0.3 x 0.3	2	32
Succisa pratensis	1995	4	6	0.3 x 0.3	3	72

Fig.1

Beginning of the experiment



Half of the second season

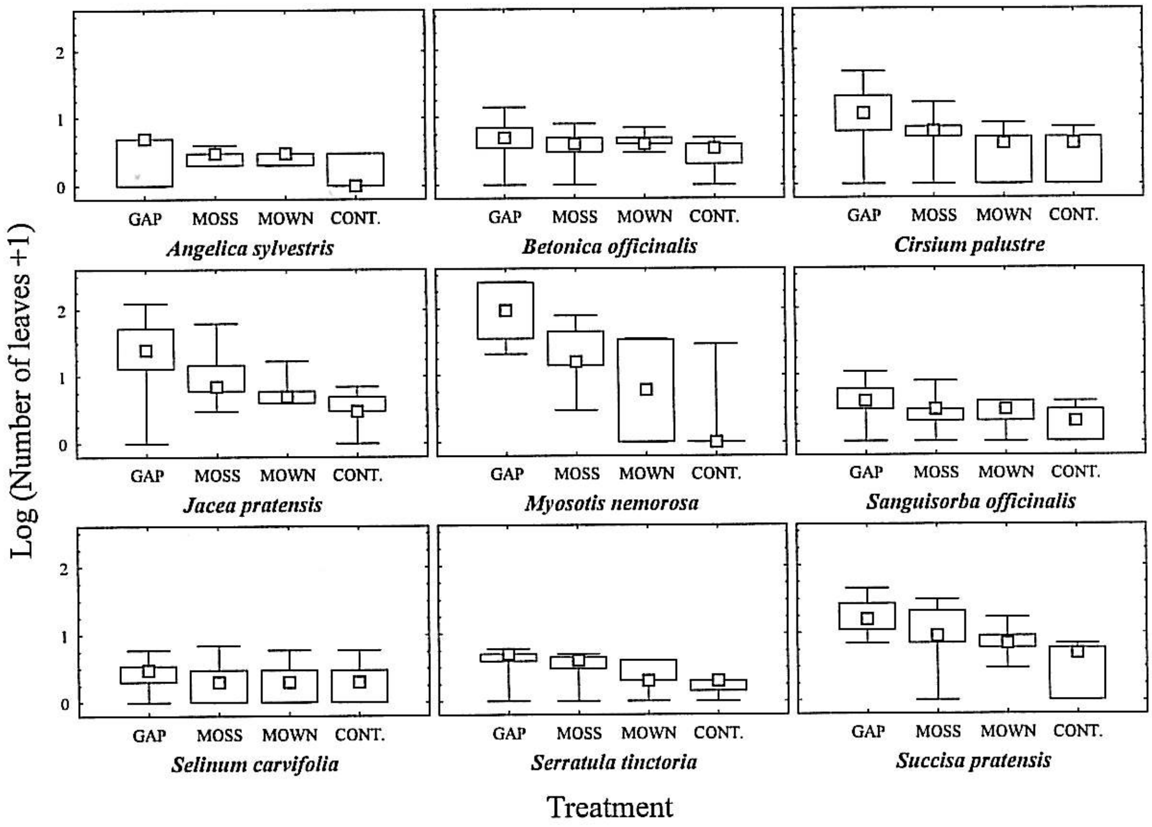
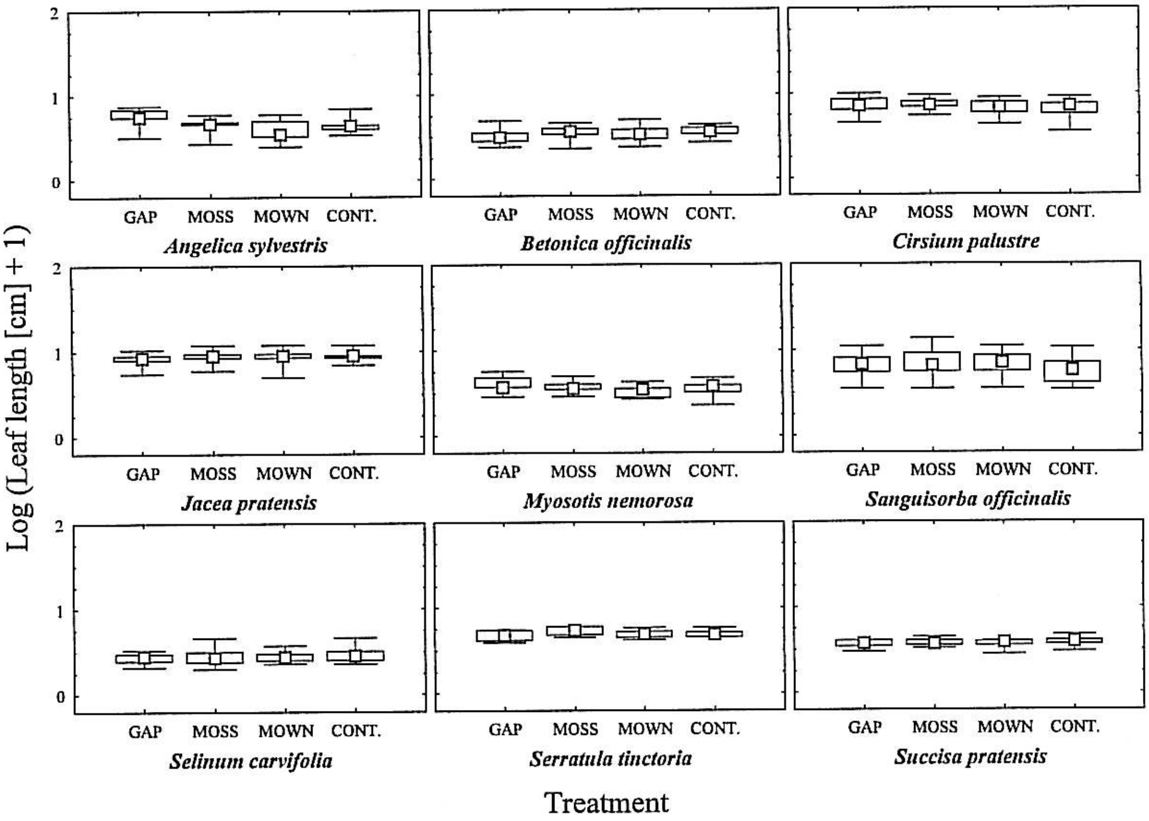


Fig.2

Beginning of the experiment



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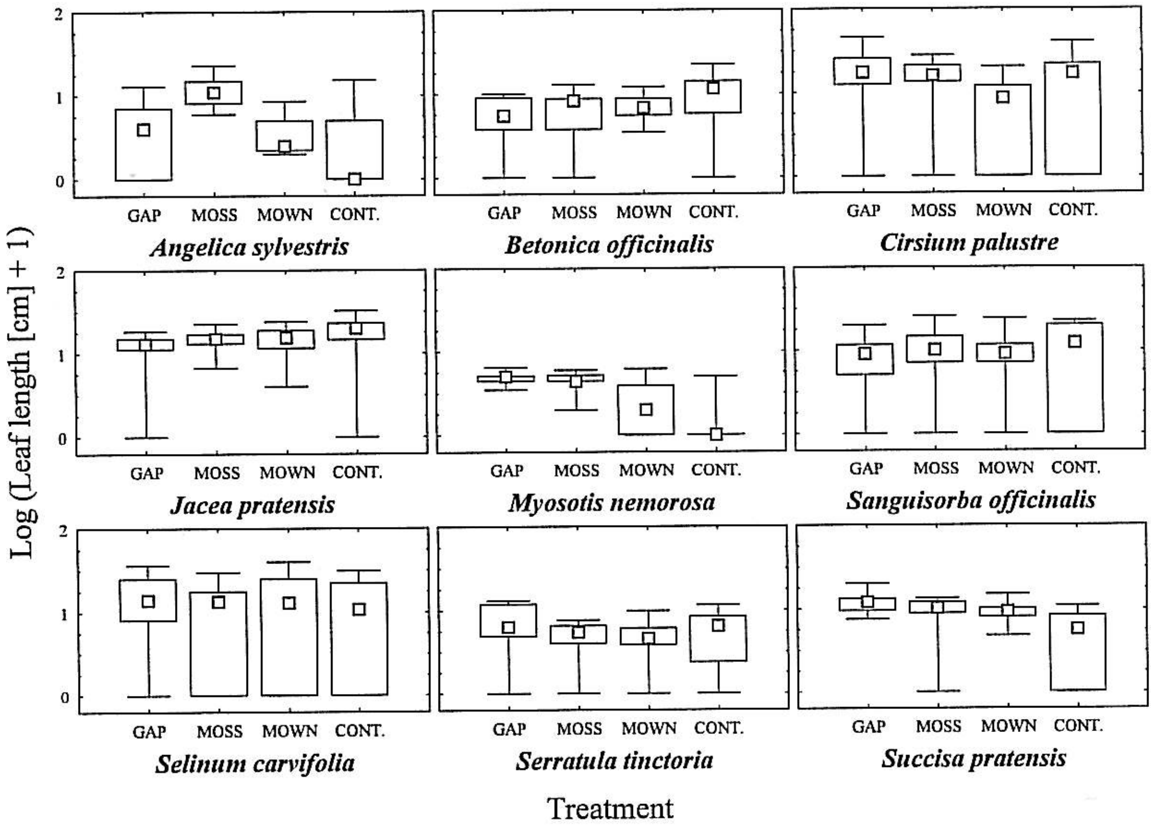
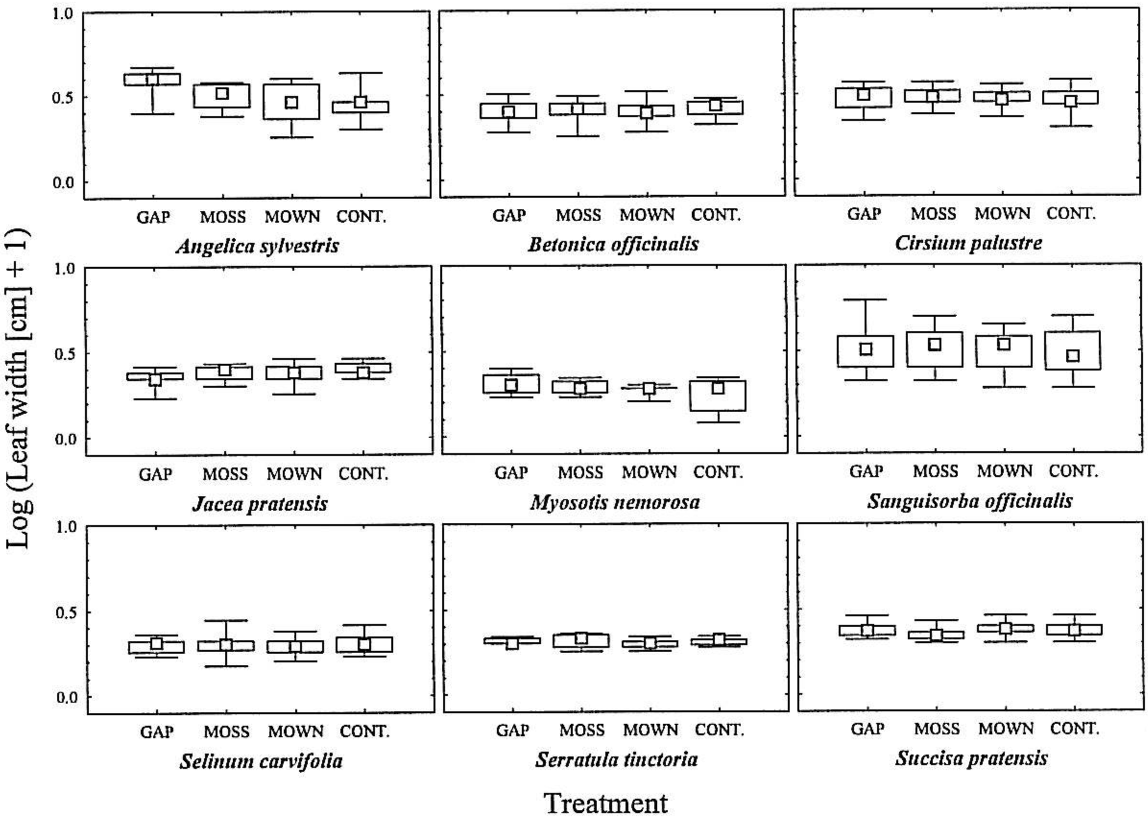


Fig.3

Beginning of the experiment



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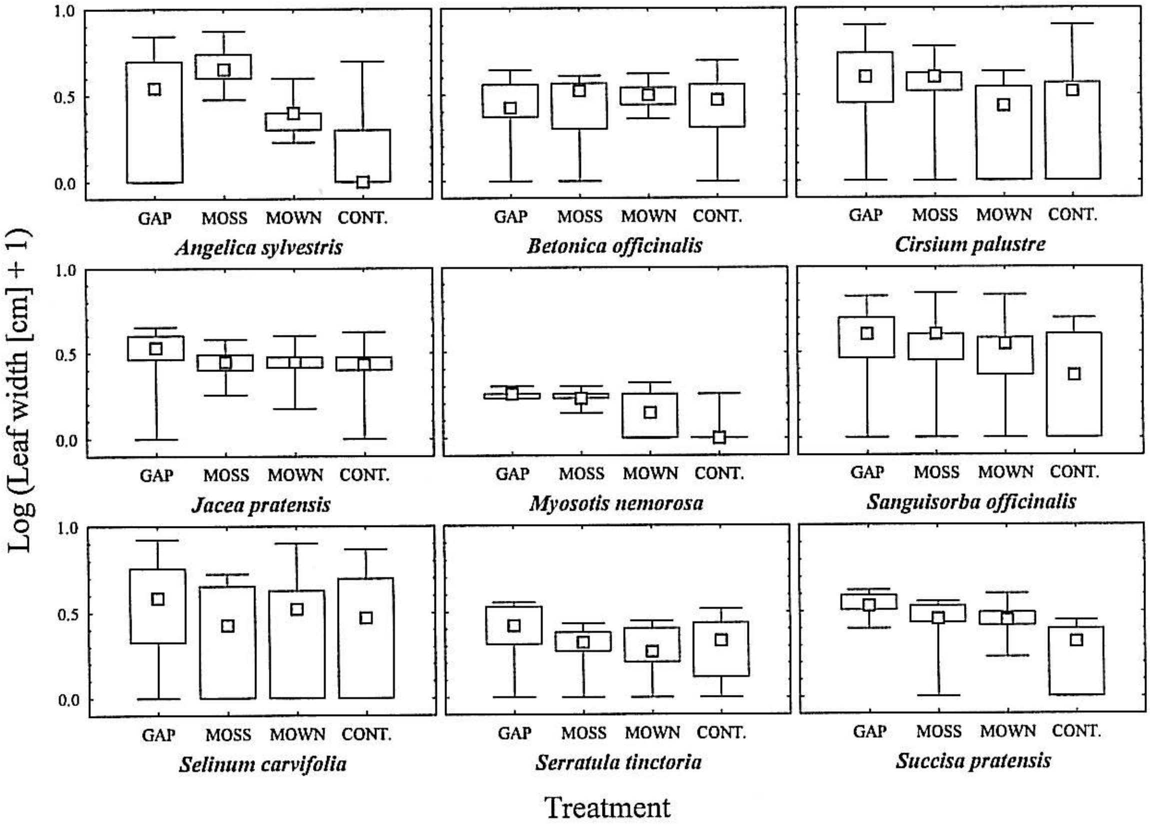

Fig.4

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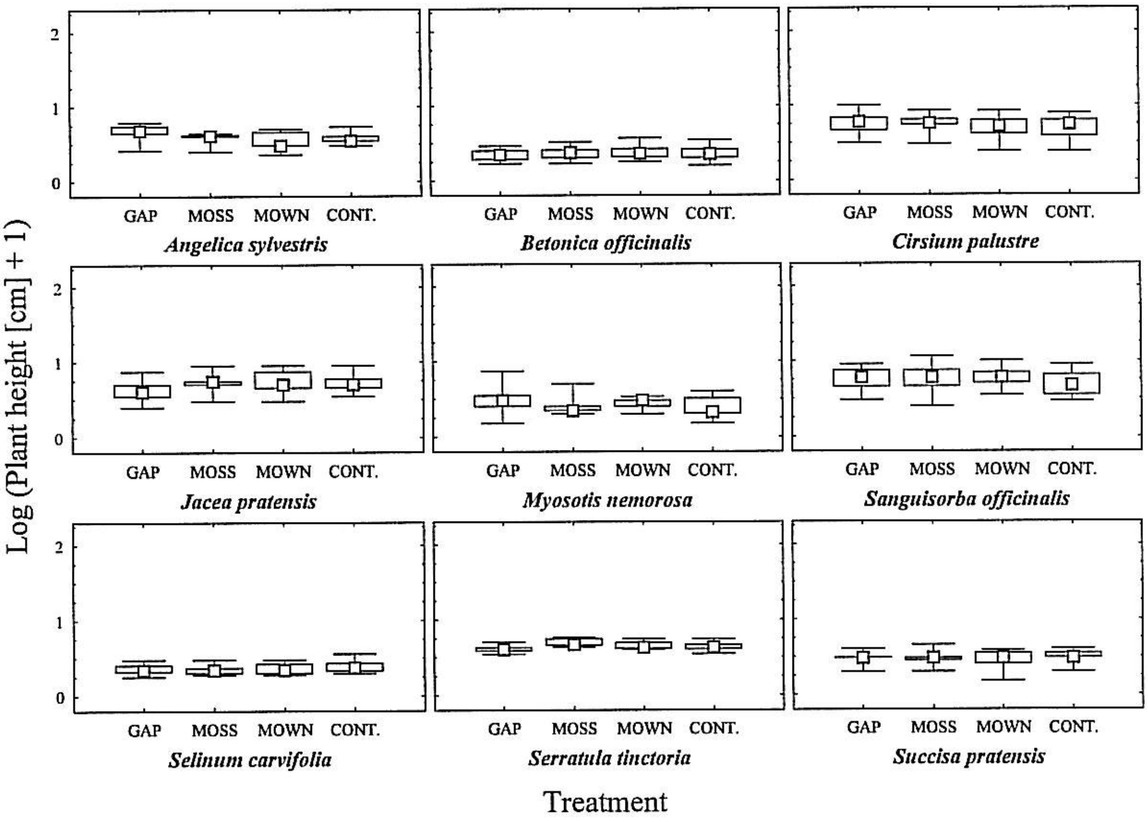

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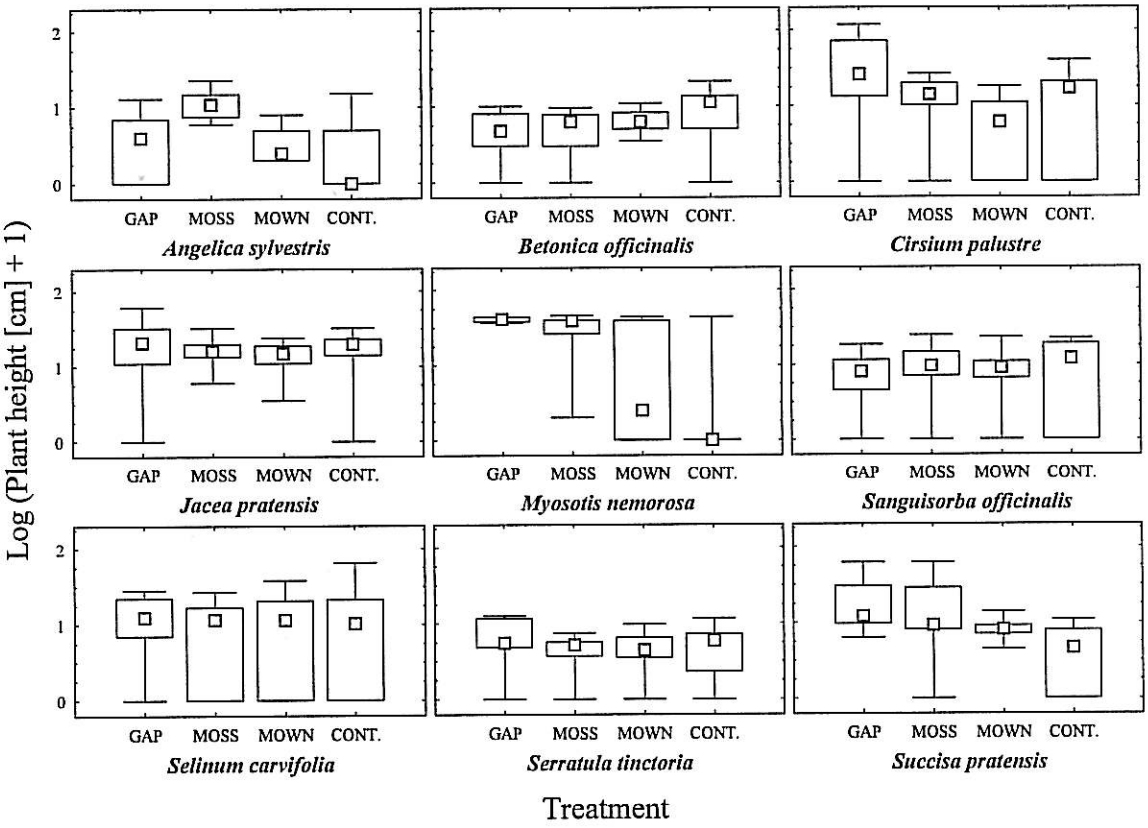

Fig.5

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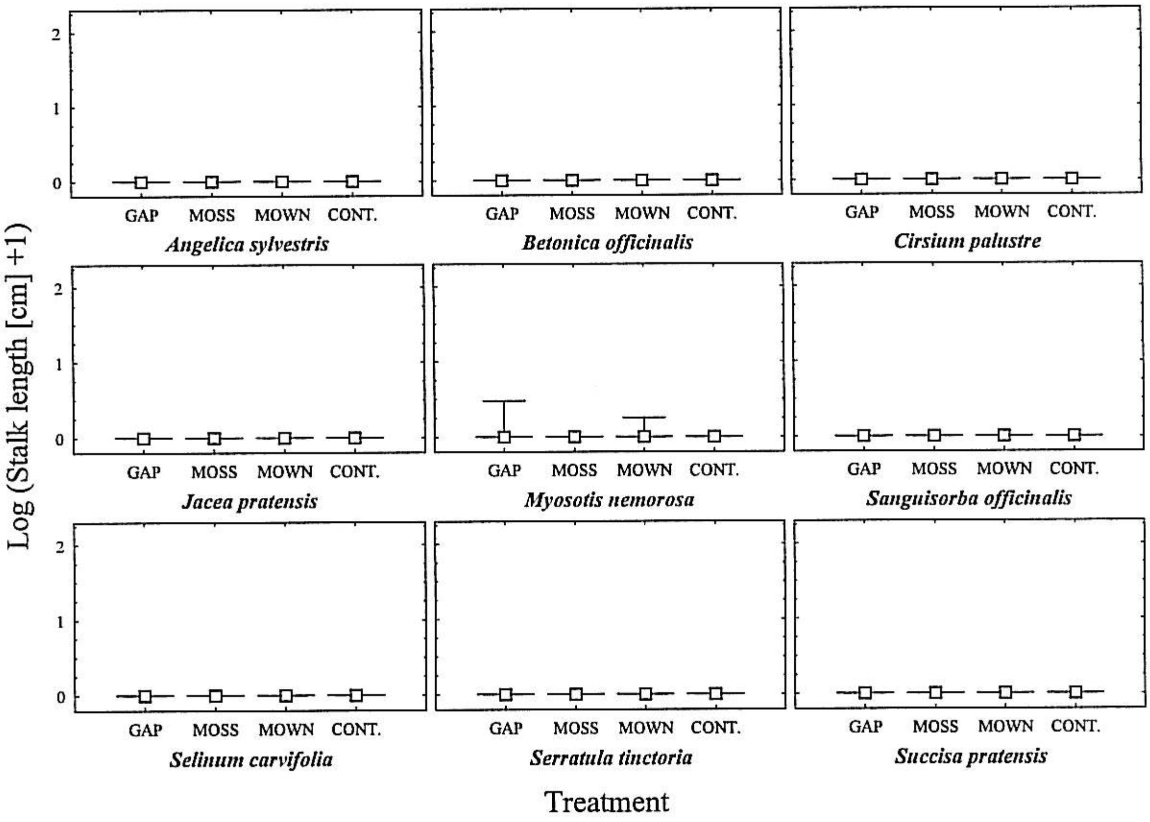

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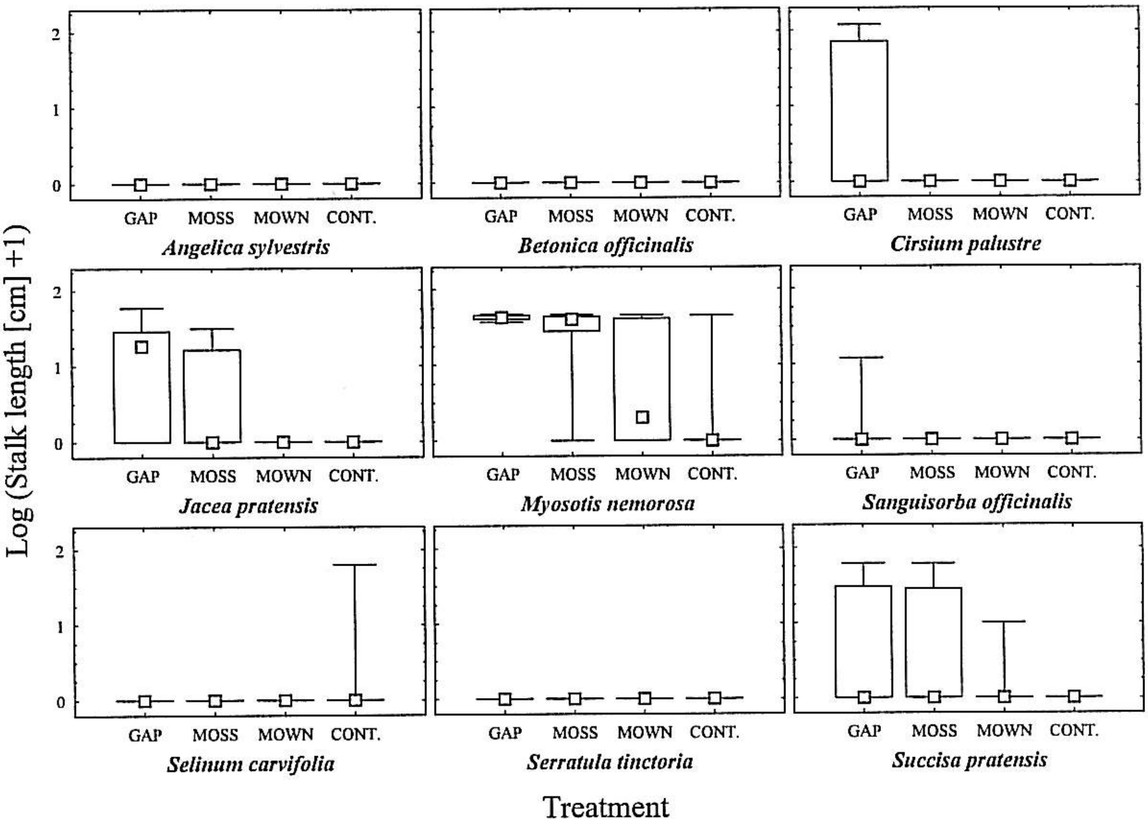
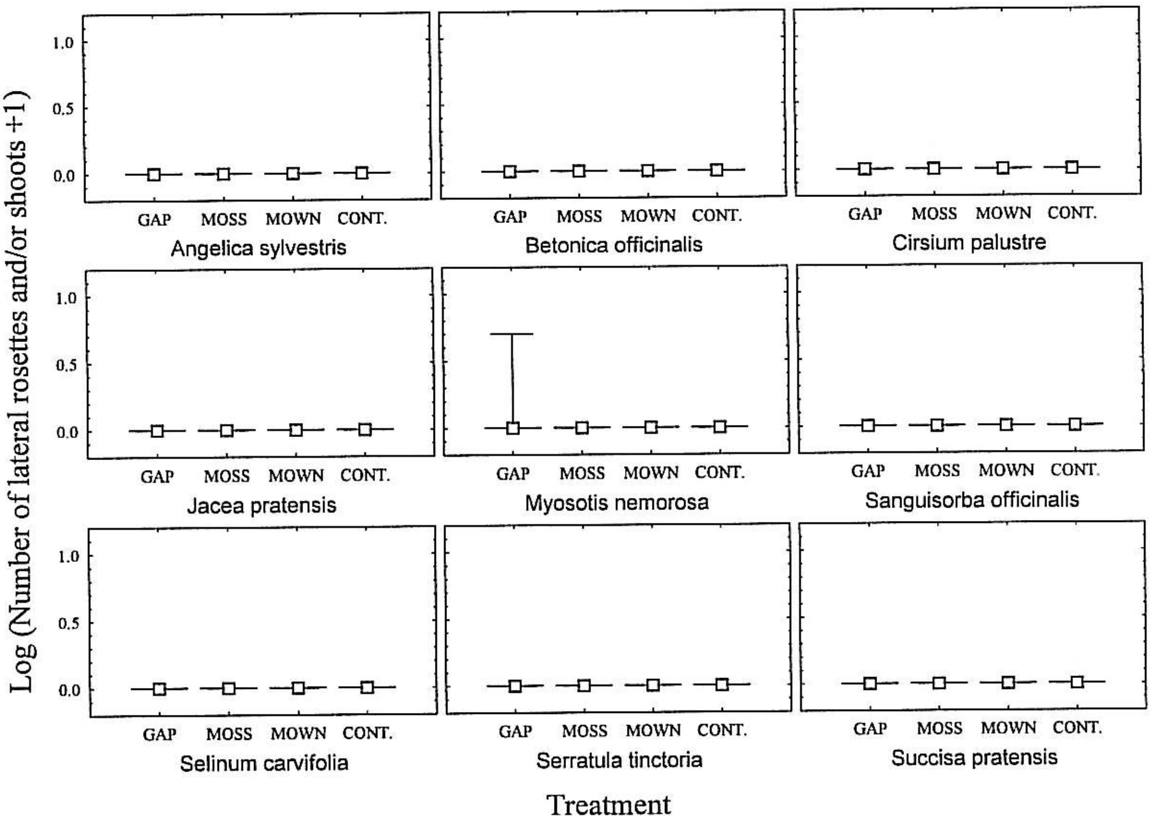


Fig.6

Beginning of the experiment



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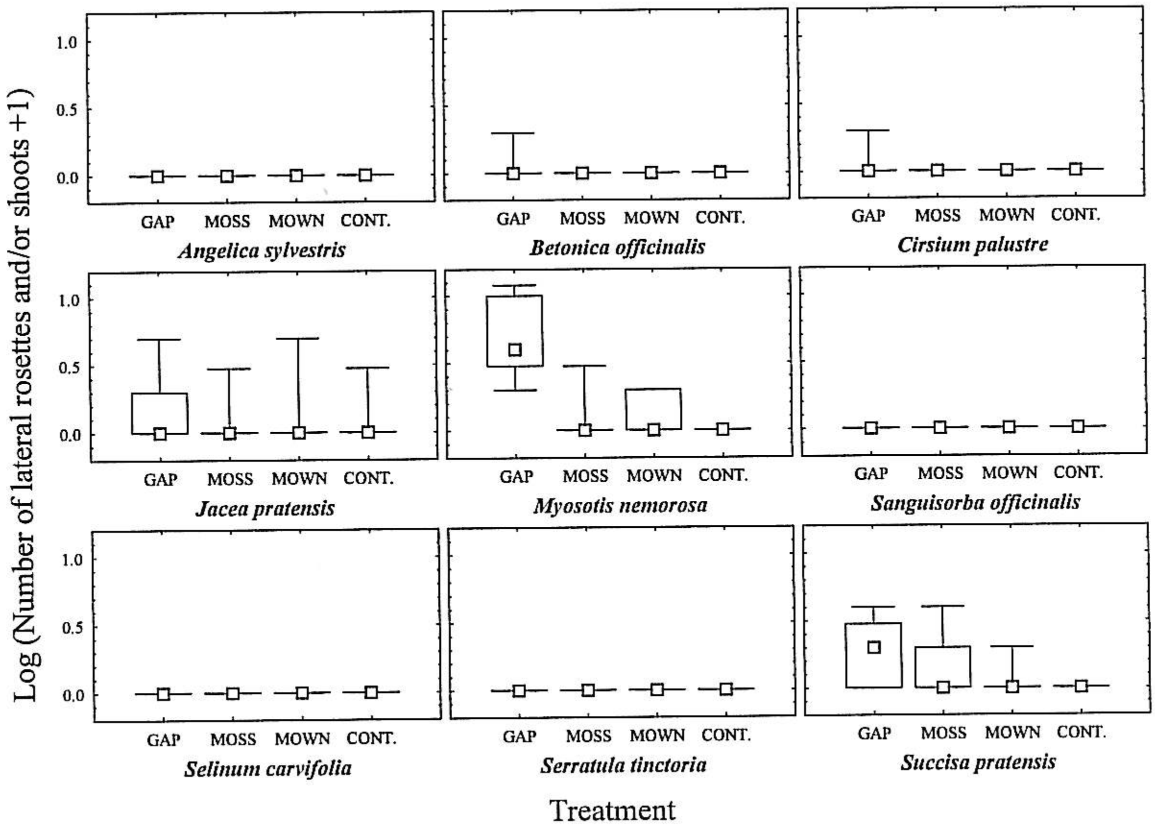
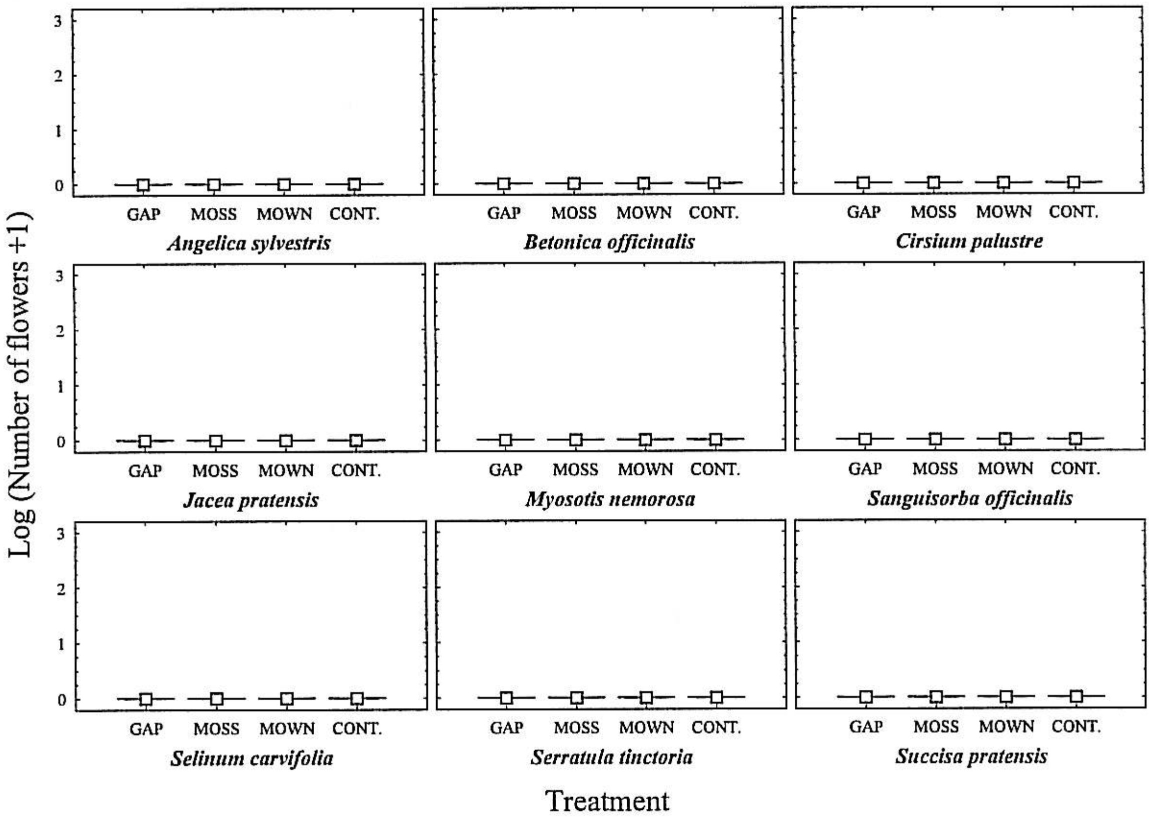


Fig.7

Beginning of the experiment



Half of the second season

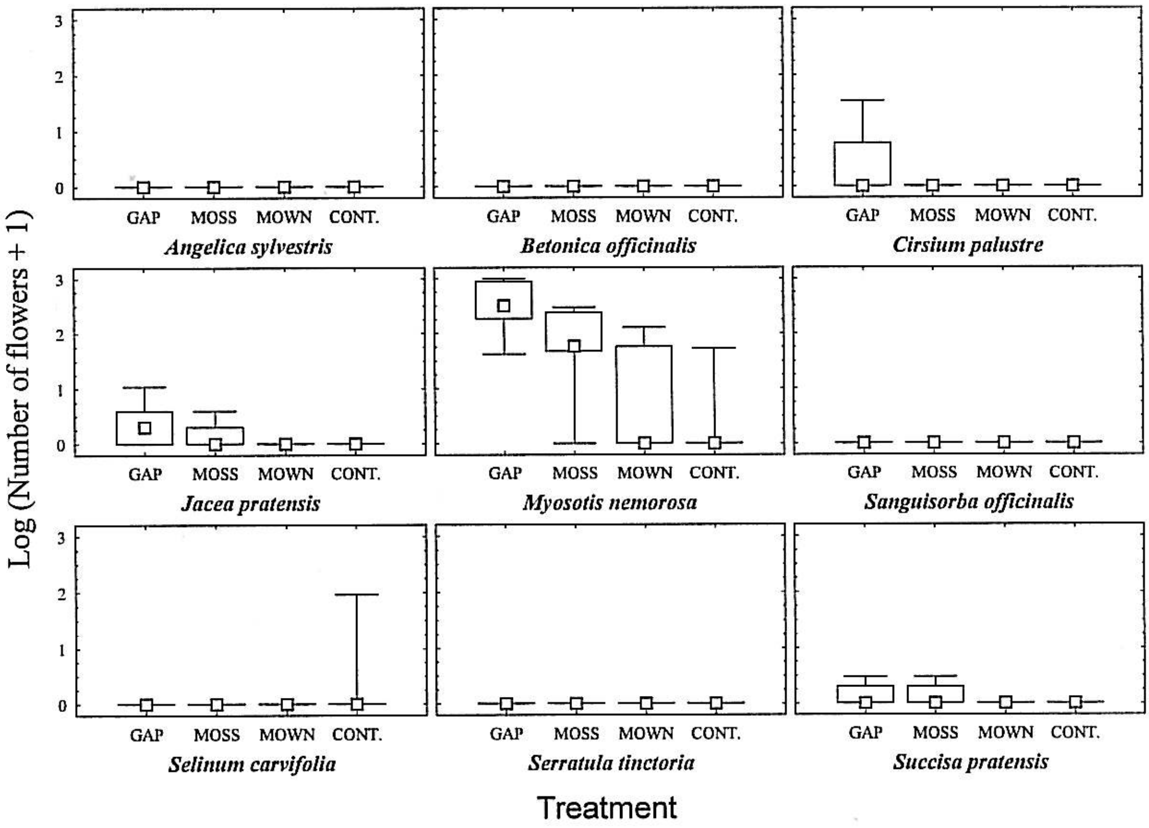


Fig.8: *Angelica sylvestris*

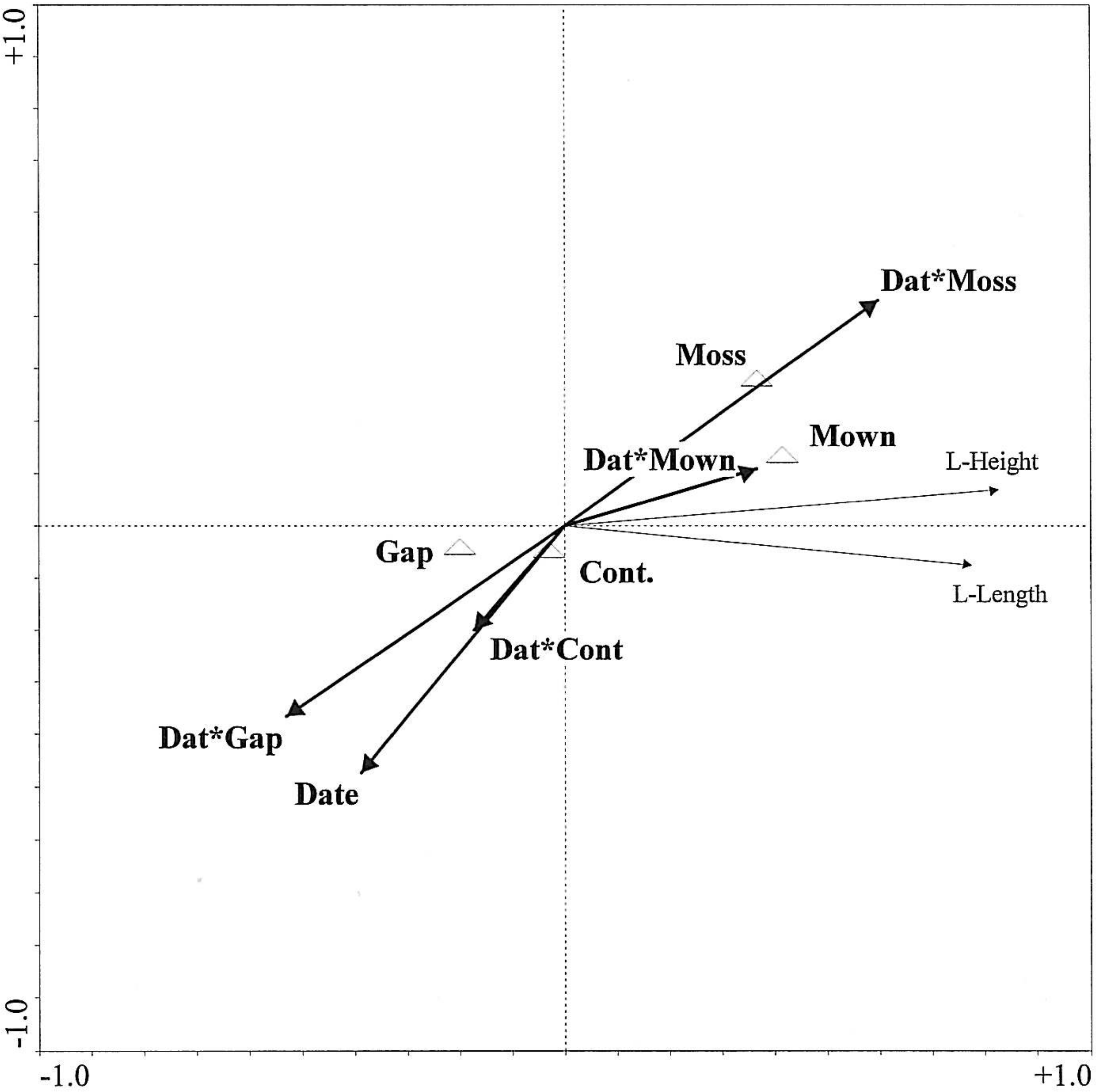


Fig.9: *Betonica officinalis*

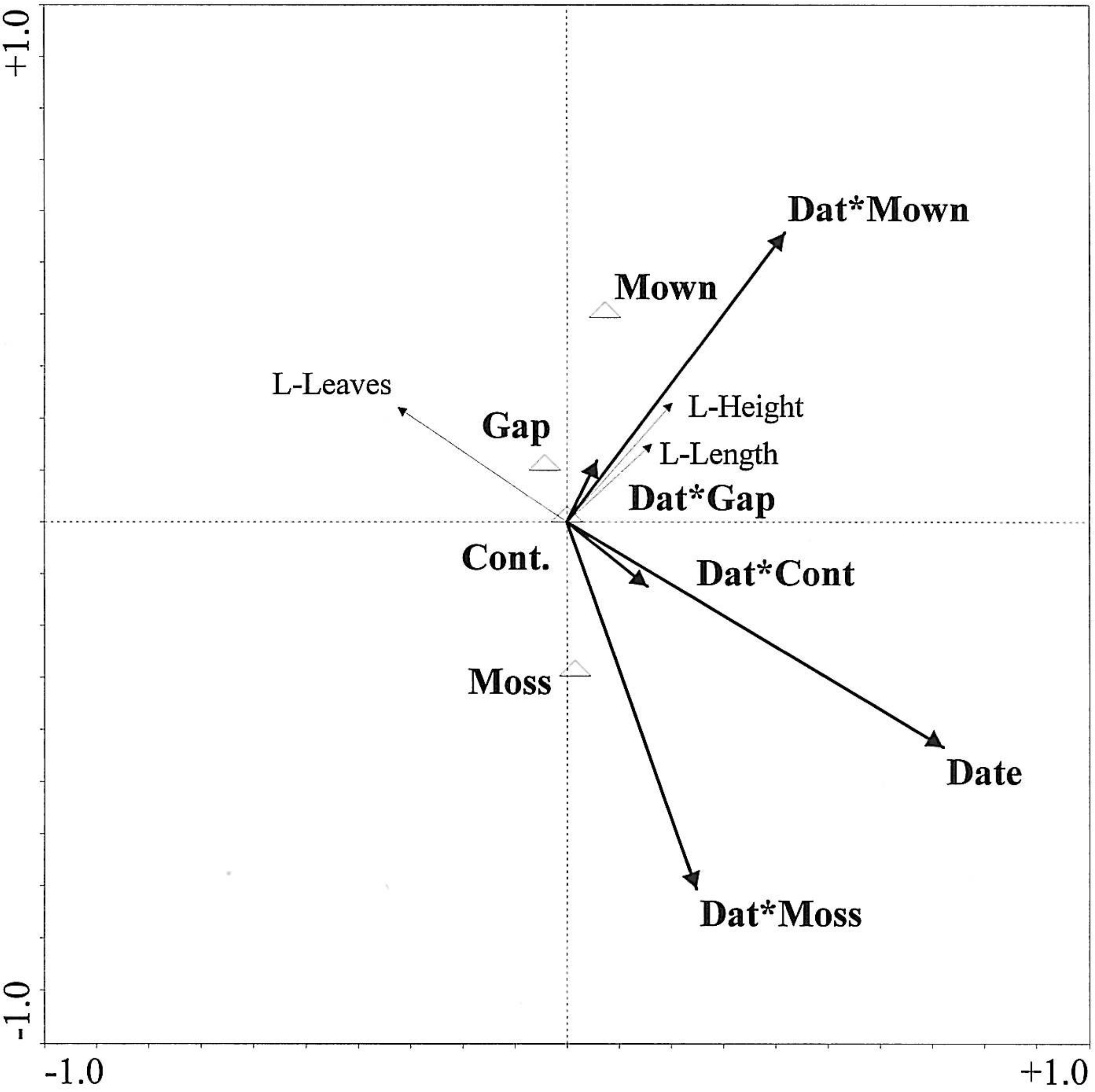


Fig.10: *Cirsium palustre*

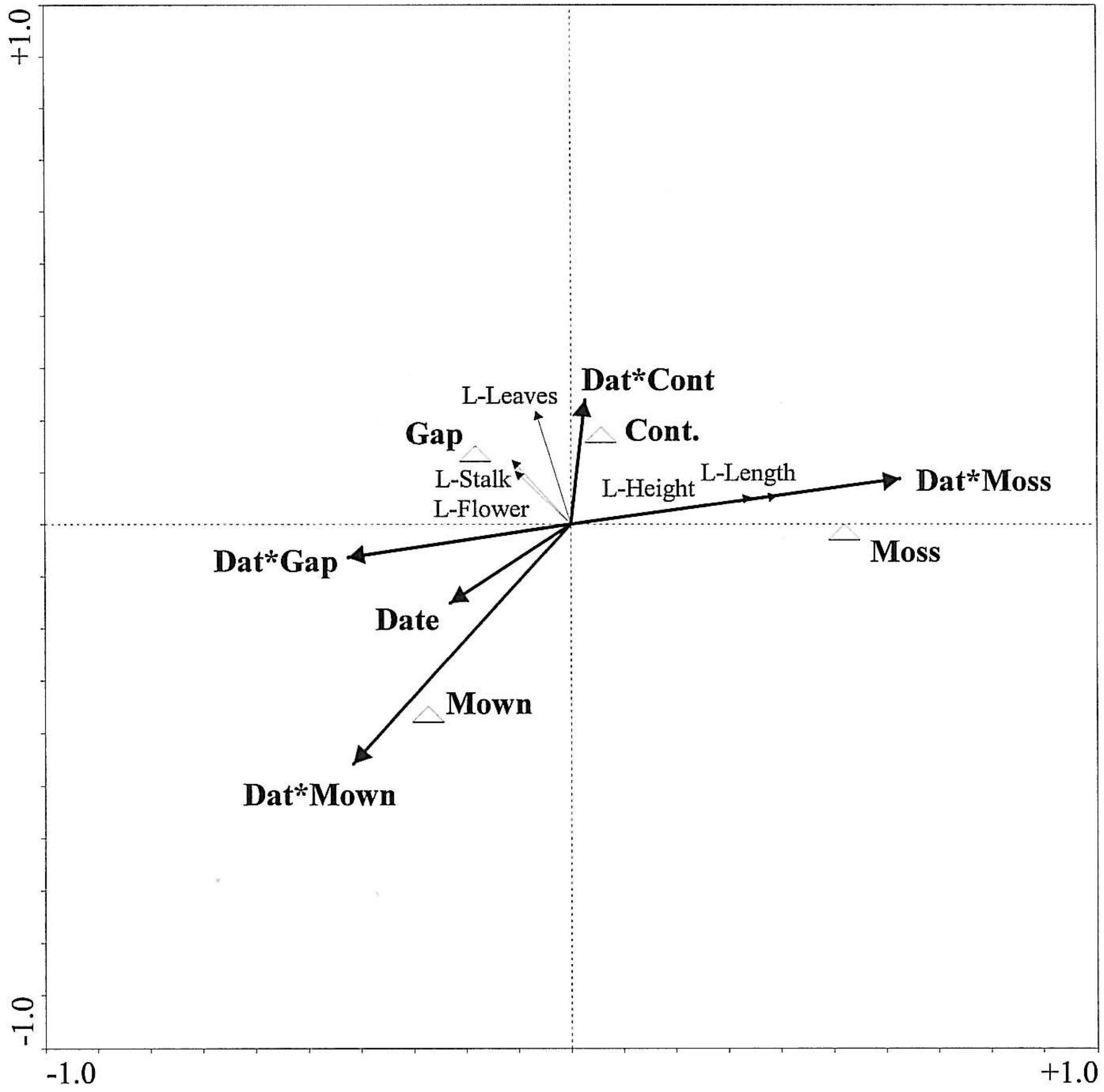


Fig.11: *Jacea pratensis*

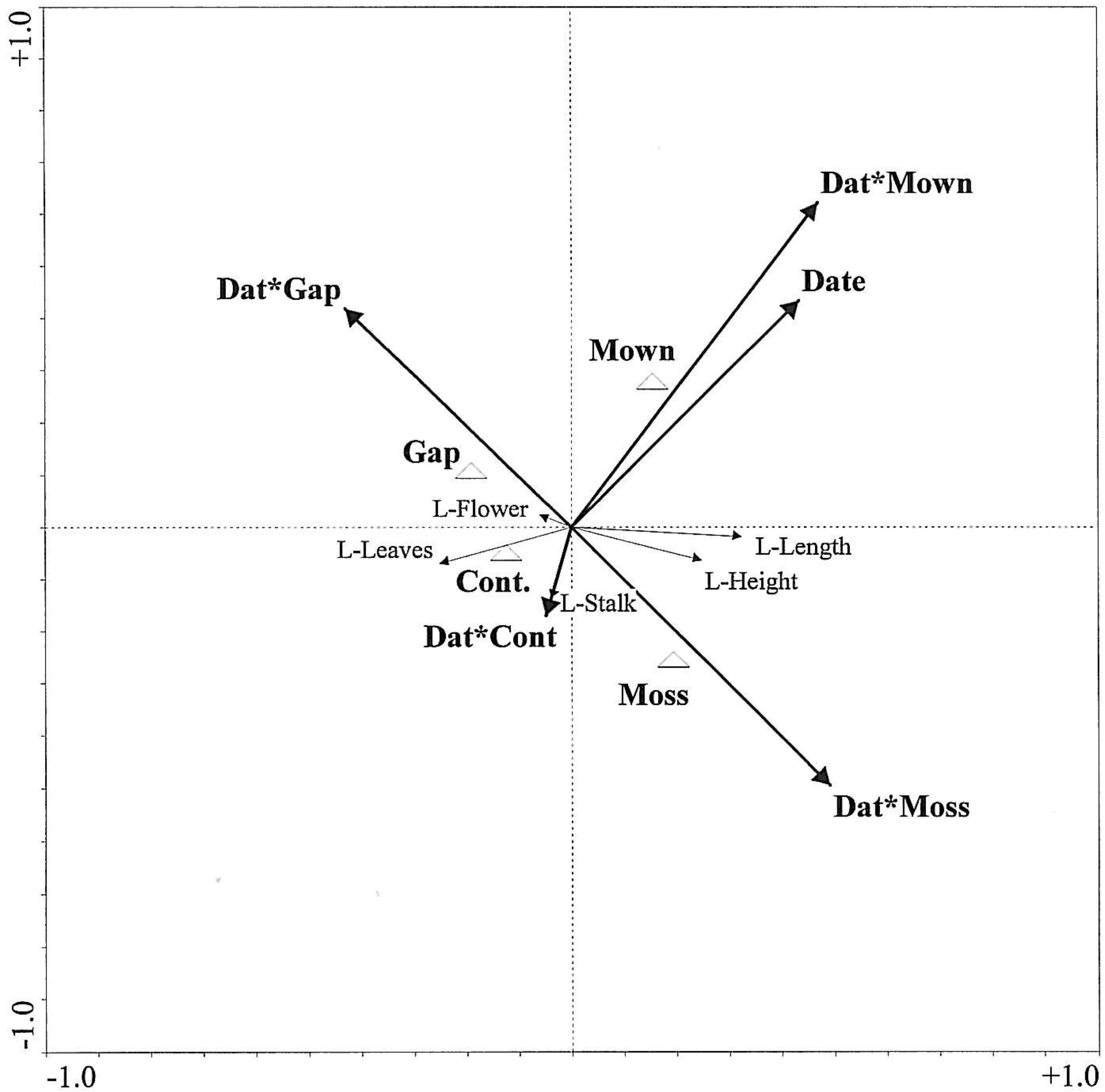


Fig.12: *Myosotis nemorosa*

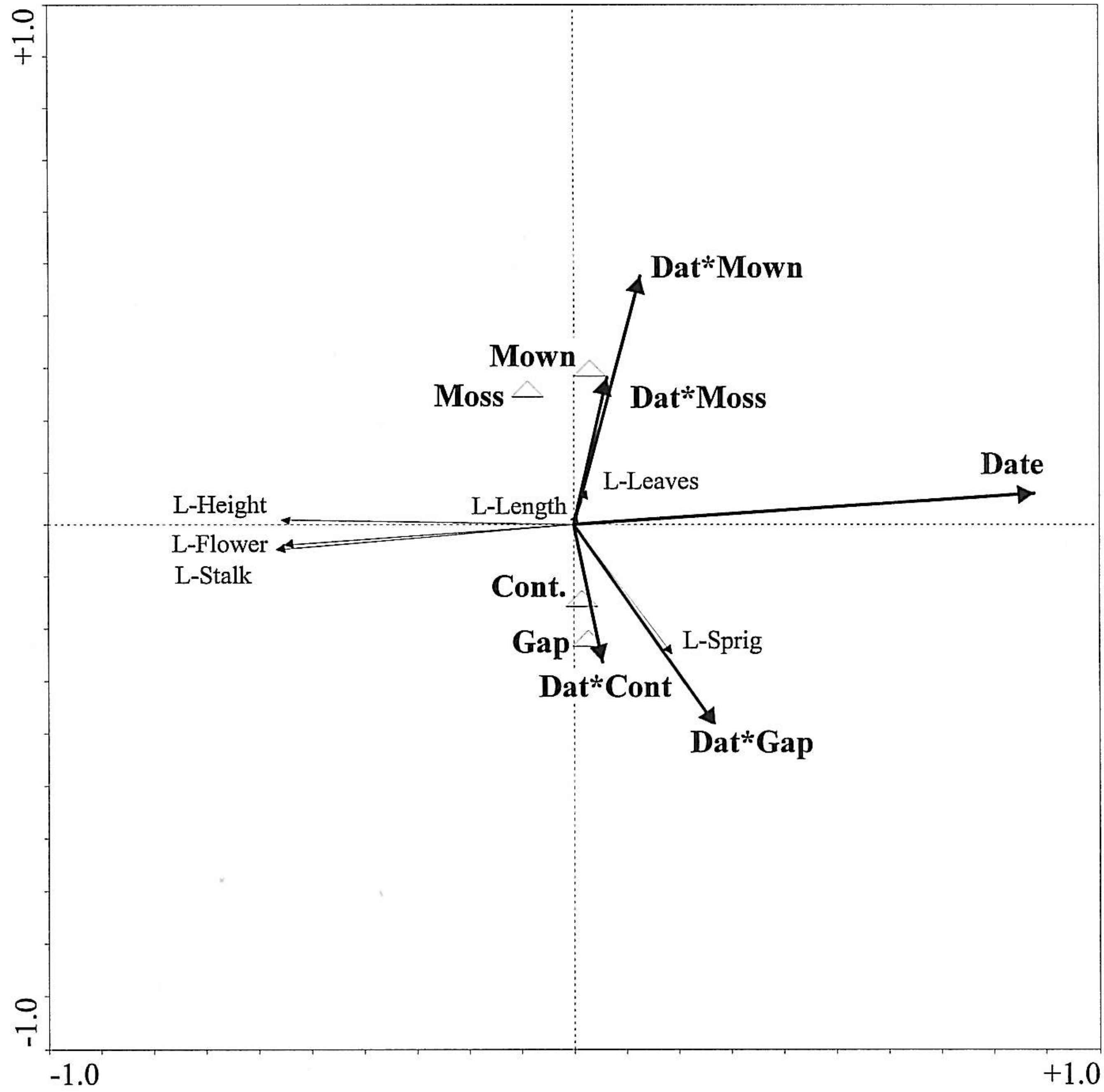


Fig.13: *Sanguisorba officinalis*

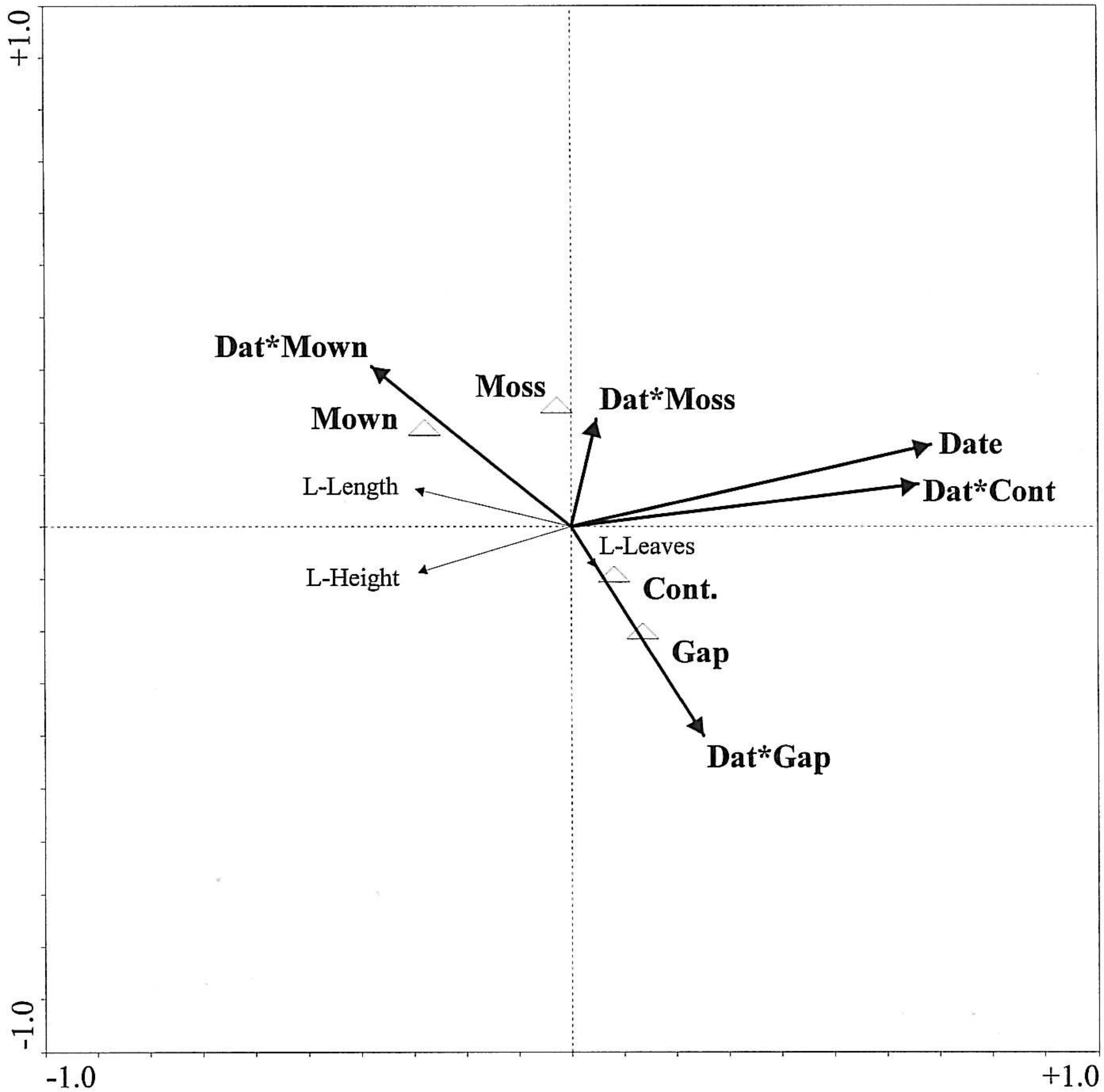


Fig.14: *Selinum carvifolia*

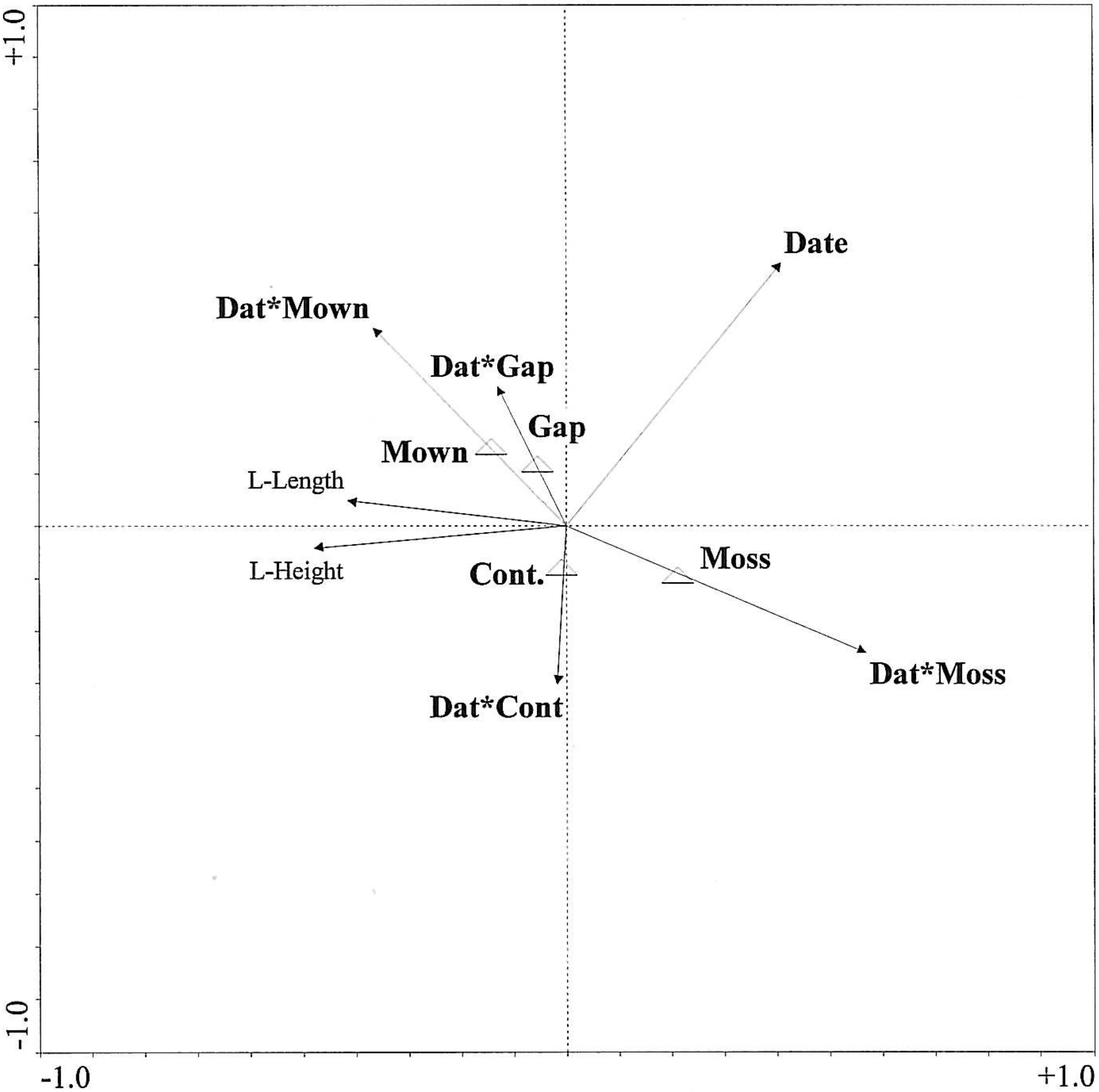


Fig.15: *Serratula tinctoria*

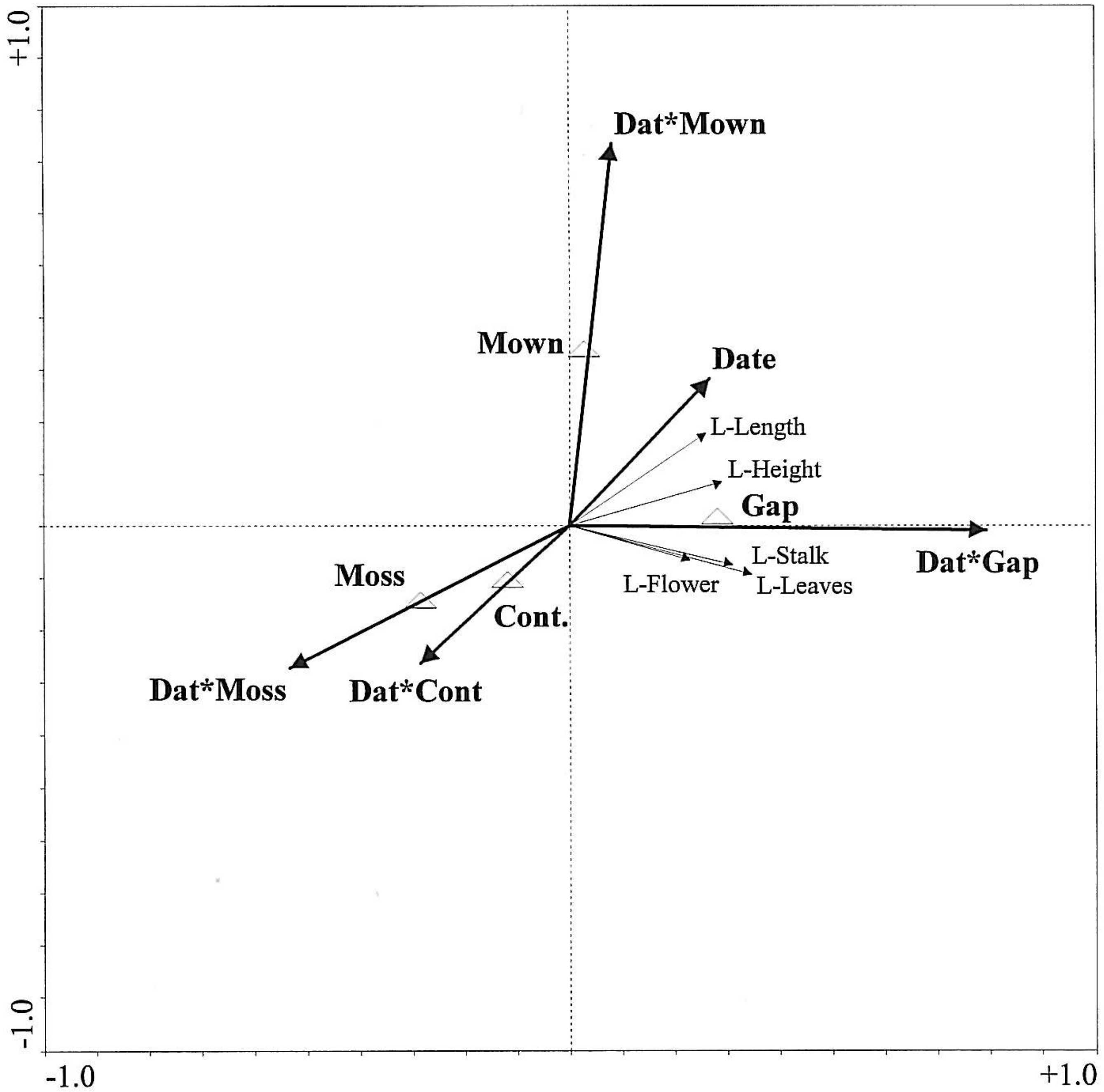


Fig.16: *Succisa pratensis*