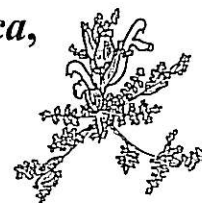


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**Inter- and intraspecific interactions in populations of  
*Pedicularis palustris* and *Pedicularis sylvatica*,  
two rare species of wet grasslands**



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Bakalářská práce

Vedoucí: Jan Šuspa Lepš

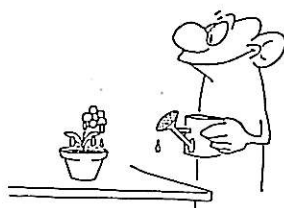
1999

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

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...*Martina Pásková*.....



# Inter- and intraspecific interactions in populations of *Pedicularis palustris* and *Pedicularis sylvatica*, two rare species of wet grasslands

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**Abstract.** Habitat requirements, population structure, dynamics and life history of two rare hemiparasites of wet grasslands, *Pedicularis palustris* and *P. sylvatica* (Scrophulariaceae) were studied. Both species were previously common, but have been declining in the last decades. Several populations in Bohemia, Czech Republic, were surveyed and two populations of *P. palustris* and three populations of *P. sylvatica* were selected for detailed investigation. Demography data were obtained by two years of monitoring permanent plots. Effect of disturbance regime on seedling recruitment and rosette survival was studied in a manipulative experiment. Treatments included mowing, creation of artificial gaps, and litter and bryophyte removal. Declining populations of both species were found in sites where traditional management, i.e. mowing or grazing, have been abandoned. Spatial patterns of seedlings of both species were highly aggregated, and rosettes and mature plants were distributed regularly. The decrease in aggregation can be explained by a density-dependent mortality, particularly in late summer. Winter annual and biennial life cycles were found in *P. palustris*. Only biennial plants of *P. sylvatica* were found. In both species, a winter bud is formed to survive winter. In *P. sylvatica* survival probability, plant size and reproductive effort are positively correlated with winter bud size. Both species require a disturbance regime for their seedling recruitment. On a microscale (0.01 m<sup>2</sup>), seedling abundance of both species was higher in gaps; *P. palustris* seedlings avoided microhabitats with present litter. This supports hypotheses concerning the importance of available safe sites for species regeneration. The populations differ in their net reproductive rate of increase ( $R_0$ ), and also pronounced spatial variability of  $R_0$  within populations was found. A regular management regime seems to be important for persistence of both *Pedicularis* species.

**Keywords:** Antropogenic disturbance; Conservation; Density-dependent mortality; Hemiparasitism; Gap; Management; Regeneration niche; Seedling recruitment

**Nomenclature:** Rothmaler (1976), vascular plants; Váňa (1997), bryophytes

## Introduction

Two hemiparasitic *Pedicularis* species (Scrophulariaceae), *P. palustris* and *P. sylvatica* are declining among many other plant species in Central European wet grasslands (Ter Borg 1979, 1985; Ter Borg et al. 1980; Rosenthal & Fink 1996; Karrenberg, 1998; Rixen 1998; Schmidt 1998). In the Czech Republic, these species were previously common but have decreased rapidly over the last decades due to drainage or abandonment of their habitat (Hendrych & Hendrychová 1989). In Central Europe, meadows at lower elevations are anthropogenic in origin, having been used for hay production, and require traditional management practices, i.e., mowing and no or limited fertilization, to maintain their diverse species assemblage (Bakker 1989; Oostermeijer et al. 1994). Recently, due economic pressures, management practices of these meadows have changed dramatically, either intensified by fertilization or meadows have been abandoned. Both processes produce changes in species composition that are accompanied by extirpation of some species and an overall loss of species diversity (Bakker 1989). When traditionally managed these meadows are quite diverse, often containing  $>50$  species per  $m^2$ , many of which are endangered (Klimeš, Jongepier & Jongepierová 1995; Křenová & Lepš 1996). The importance of disturbance regimes to plant persistence lies in the relationship between the spatial and temporal scale of the disturbance and disturbance intensity, and the plant's population size and timing of life history stages. Many rare plants require habitat disturbance of intermediate level for regeneration (Hobbs & Huenneke 1992; Pavlovic 1994), hemiparasitic plants particularly (Marvier & Smith 1997).

Successful establishment of new plants is a critical step in plant life history; see the 'regeneration niche' of Grubb (1977 and 1988). Differentiation of the regeneration niche is a major determinant of diversity in vegetation (Grubb 1977 and 1988; Rusch 1988; Rush & van der Maarel 1992; van der Maarel 1993; van der Maarel & Sykes 1993). Seedling recruitment of both *Pedicularis* species is limited by the availability of safe sites for seedling establishment (Ter Borg 1979, 1985, comp. Křenová & Lepš 1996 for *Gentiana pneumonanthe*). The availability of suitable safe sites for seedling establishment decreases dramatically after cessation of the regular disturbance regime, such as mowing and grazing, traditionally used in Central European wet grasslands (Bakker 1989).

Two approaches were used in this study in order to study life history stages and dependency on disturbance in the two *Pedicularis* species. For the life history stages permanent plot field observations were conducted. The study of dependency upon disturbance demanded experimental manipulations. These approaches were performed in habitats and in microsites important for seedling emergence (comp. Silvertown 1981; Winn 1985; and Ryser 1993).

The regeneration dynamics of both *Pedicularis* species were studied with a particular regard to disturbance heterogeneity. Following Grubb's (1977) concept of the regeneration niche, safe sites for seedling establishment in gaps were expected in both *Pedicularis* species. I assumed that recruitment of seedlings will vary with gap size and larger gaps might favor seedling recruitment (comp. Fenner 1985;



McLellan et al. 1997).

The aims of this study were as follows: (1) by surveying *Pedicularis* populations found the ecological requirements of both species, (2) to describe important aspects of species population structure, dynamics and life cycles on the basis of monitoring permanent plots, and (3) to test the effect of various disturbance regimes on population dynamics by the use of a manipulative experiment.

## Material and Methods

### *Study species*

*Pedicularis palustris* and *P. sylvatica*, two species of one of the largest genera in the family Scrophulariaceae, with several hundred species, all hemiparasitic, are the subjects of this study.

*P. palustris* is a hemicryptophyte with an annual or biennial life cycle, forming an overwintering bud and thickened root. It occurs throughout Europe in irregularly mown or moderately grazed marshes, wet meadows, and dune slacks (Hegi 1975). In my plots only the subspecies *palustris* occurs. In the Czech Republic, *P. palustris* prefers wet habitats with a year-round high water table and nutrient rich soils, such as marsh meadows, mires, moors, peatbogs and fens of the *Caricion lasiocarpae*, *Caricion fuscae*, *Molinion* and *Calthenion* communities (Dostál 1989; Oberdorfer 1993; Moravec 1995). *P. sylvatica* is an Atlantic and Subatlantic biennial, rarely perennial hemicryptophyte with a winter bud (Hegi 1975). It is found in open vegetation on moist and sandy or peaty, acid and nutrient poor soils, with a high water table. In Central Europe it is a characteristic species in grassland vegetation of the alliances *Violion caninae* and *Juncion squarrosi* and may also be found in *Caricion fuscae* and *Ericion tetralicis* communities (Dostál 1989; Oberdorfer 1992, 1993; Moravec 1995). It also grows in woodland edges and paths (pers. obs.; Ter Borg 1985). Only the subspecies *sylvatica* is known from the Czech Republic.

Both *Pedicularis* species are obligate non-specific hemiparasites and have a wide range of hosts. Several monocot and dicot herbs and occasionally shrubs have been reported as hosts in the field and in growth experiments (e.g., Heinricher 1924; Weber 1976; Ter Borg 1985). Excavated plants from the study sites had haustorial connections with several co-occurring species, e.g., *Nardus stricta*, *Plantago lanceolata* and *Potentilla erecta* for *P. sylvatica* and *Carex gracilis*, *Holcus lanatus* and *Lychnis flos-cuculi* for *P. palustris*.

Both species were previously common in traditionally managed grasslands (Hendrych & Hendrychová 1989), but most populations have recently decreased in size or become extinct because of fertilizer application and/or the cessation of traditional management (usually mowing). These species are successful in early succession stages, but usually cannot persist in the late stages of secondary succession (Jensen & Schrautzer 1998; Rixen 1998).

### *Study sites*

During a field survey of *Pedicularis* populations, carried out between 1997 and 1998 in the

southern and northern part of Bohemia, Czech Republic, seven *P. palustris* and thirteen *P. sylvatica* sites were studied (see Appendix 1). Changes in population sizes (increase, decline, fluctuation, and no changes) were found when compared current populations sizes to former sizes referred to in the literature and by local people. At each site the occurrence of disturbance and type of management regime were recorded. Vegetation was analyzed using phytosociological relevés of 4×4m plots and for calculations van der Maarel's (1979) ordinal transformation of the Braun-Blanquet scale of abundance and dominance was used. Two *P. palustris* and three *P. sylvatica* sites, all located in South Bohemia (Table 1), were selected for detailed vegetation studies, demography observations and field experiments. The sites differ in their vegetation and management regimes (Table 2).

#### *P. palustris*

The Divčice population contains one of the last remaining populations in the region, which has been declining over the last five years from hundreds of reproductive individuals to only a few (Bastl; Štech, pers. comm.). The population occurs at the transition between a wet mesotrophic meadow of *Molinion* and a *Caricion gracilis* stand. The Horusice population is scattered within a *Caricion gracilis* stand in an inundated area adjacent to the Horusický fishpond. The species occurs in only a few open areas and within willow groves.

#### *P. sylvatica*

Populations of *P. sylvatica* were studied in oligotrophic wet meadows in Ohrazení, Javorník and Ruda, all of which are located between agricultural fields and woodland. The meadow at Ruda is close to a large peatbog. The Javorník and Ruda populations are large and have persisted for decades whereas fluctuations in size and spatial pattern have been observed in the population located in Ohrazení (pers. obs.; Lepš pers. comm.). The vegetation of all the meadows is currently characterized by the *Molinion* alliance with remnant fragments of *Violion-caninae* for which *P. sylvatica* is an indicator species (Moravec et al. 1995).

#### *Design of permanent and experimental plots and sampling*

Field demography observations were carried out in 1 m<sup>2</sup> permanent plots, divided by a grid into 0.1×0.1m subplots, within populations of both species. In August 1997 three plots were established in each *P. sylvatica* site and one plot in each *P. palustris* site because of the limited size of *P. palustris* populations. Three age stages were distinguished in the populations of both *Pedicularis* species: fertile plants, rosettes and seedlings. In August 1997, all fertile plants (already dead, releasing seeds, hereafter called mother plants (M97), and all rosettes with winter buds (R97) were marked and their position in the grid recorded. Number of seeds (s97) per each M97 in each plot was estimated. *P. palustris* autumnal seedlings (S97) were counted in each subplot at both sites. In April 1998 the number of surviving individuals of the R97 stage which become fertile, were recorded and hereafter called M98. From April

1998 to May 1998 the number of seedlings S498 (the '4' is in reference to the month) and S598 were counted in each subplot at all sites. In May and July the number of seeds (s98) per each M98 in each plot of *Pedicularis sylvatica* and *P. palustris* respectively was estimated. No seedlings emerged past June in *P. sylvatica*. From June to August the rosettes grew up from the seedlings (the last seedling stage was called S698 afterwards rosettes (R98) were considered). In *P. palustris* new seedlings emerged from seeds released from M98, thus seedlings from June to September (S6-S998) were counted. In October rosettes present before winter were counted and marked in both *Pedicularis* species.

A manipulative field experiment was established at each site in August 1997. The experiment was arranged in five randomized complete blocks of 0.5×0.5m plots. Plots were divided into 25 subplots of 0.1×0.1m. Two sets of blocks, sown and unsown in Divčice site and one unsown set in Horusice were established in the *P. palustris* populations. In two *P. sylvatica* populations in Ohrazení and Javorník both sown and unsown sets were established and only unsown set of blocks in Ruda site was set up. In unsown plots, regeneration in treatments based on natural seed pool was studied. By experimental sowing I can separate the effect of dispersal and study the effect of treatment on regeneration only. For sown plots seeds were collected in the respective localities from capsules at the beginning of July 1997 (*P. palustris*) and in the middle of May 1997 (*P. sylvatica*) and stored in dry at room temperature until August 1997. Seeds were sown in August. Ninety seeds of each species were sown by hand into the 9 central subplots to minimize edge effects. In each block, the following treatments were applied:

*P. palustris*: (1) control, where vegetation remained undisturbed, (2) mowing, where the above-ground biomass was cut and litter removed; (3) litter and bryophytes removed without mowing; (4) gaps (5 gaps per a plot, 5 cm in diameter) were created cutting the sod ~3 cm deep and turning it upside down.

*P. sylvatica*: (1) control; (2) mowing; (3) litter and bryophyte layer removal; (4) small gaps (5 gaps per a plot, 5 cm in diameter) were created cutting the sod ~3 cm deep and turning it upside down; (5) large gaps (5 gaps per a plot, 10 cm in diameter) were created the same way as small gaps; (6) mowing, where the above-ground biomass was cut and both litter and bryophytes were removed. In order to prevent standing water and burying of seeds, gaps were shallow. Small sized gaps only were created in *P. palustris* because of very wet conditions and in tall vegetation large gaps would be permanently filled with water. On the other hand both small and large sized gaps could be created in short stature drier grassland occupied by *P. sylvatica*. In drier *P. sylvatica* sites also the effect of moss removal in mown plots on seedlings establishment could be studied. For lists of bryophyte species found in the study plots see Appendix 2. Within the plots natural minor gaps ~3 cm radius at maximum occurred and despite the effort, vegetation and particularly bryophyte removals led to minor soil disturbances. With the exception of litter removal treatment, remnants of litter layer were present in other plots. In June the occurrence of both created and natural gaps and litter were recorded in each of the 25 subplots within each plot to determine the effect of disturbance (gaps) and litter on seedling recruitment.

The number of emerging seedlings was monitored monthly from April to September over the 1998 growing season. All 25 subplots in each plot were studied although only the 9 central subplots were sown to avoid treatment edge effect. However seeds were probably dispersed before germinating all over plot. Periodic monthly sampling provided information about successive seedling emergence from April until June. Data sampled from July to September provided information about rosette survival.

Table 3 summarizes all studies conducted.

#### *Data analysis*

Multivariate analyses-with constrained ordinations in the CANOCO package (ter Braak & Šmilauer 1998) were used for evaluation of the composition of vegetation at *Pedicularis* sites. The dependence of species composition on disturbance regime and the dependence of species composition in treated plots on the treatment type were analyzed. Redundancy analysis (RDA), a method based on a linear response was used because explanatory variables were mostly categorical. CANODRAW and CANOPOST (Šmilauer 1992) were used for graphical output.

All the other analyses were performed in the STATISTICA package (Anon 1996). Demography data were subjected to two- or multi-way ANOVA models (analysis of pattern, seedling recruitment in gaps and within litter, and life history data). Spatial patterns were analyzed by evaluation of the Lloyd index ( $Li$ ) of patchiness (Pielou 1977) as follows:

$$Li = \frac{\frac{s^2}{\bar{X}} - 1}{\bar{X}} + 1$$

where  $s^2$  is variance and  $\bar{X}$  mean, both of the number of individuals per subplot. In a randomly distributed population the index value is 1. When the individuals in a population die randomly (density-independent mortality), then the value of  $Li$  does not change over time.  $Li$  was calculated for each plot based on the number individuals in the subplots and consequently reflects small-scale distribution.

The correlation between seedling density in  $0.1 \times 0.1$  m subplots within the  $1 \text{ m}^2$  permanent plots observed in June, July and August and the distance to mother plants, calculated from their position in permanent plots, was evaluated by the non-parametric Spearman rank correlation coefficient.

Analysis of variance (ANOVA, repeated measures with block nested within locality) was used to analyze seedling counts from the field experiment, separately for each *Pedicularis* species. In the model the between-subject variation corresponds to differences between observed sampling units (site, block and treatment) and within-subject variation corresponds to changes in time and interactions with time to differences in dynamics among sites. Data were evaluated after logarithmic transformation  $x' = \log(x)$

+1). With log-transformed data, the interaction of time and treatment reflects differences in relative changes in time.

Logistic regression was used to evaluate the relationship between rosette survival and winter bud diameter and the relationship between winter bud diameter and plant height and the number of flowers were analyzed by a univariate regression model.

The fertility of mother plants was estimated as a product of average number of capsules per individual and average number of seeds per a capsule. Following survival probabilities were estimated: (1) Probability that a seed will germinate and form a seedling, was estimated as a ratio of seedlings at the first census to estimate of the number of seeds produced previous year by all the mother plants in the quadrat. (2) Survival probabilities between life stages were estimated as ratio of individuals in corresponding censuses. In biennial *P. sylvatica* probabilities from two cohorts observed in single year were combined to obtain the complete two-year cycle. The rate of population increase over a generation,  $R_0$  was estimated.  $R_0 = \sum l_x * m_x$ , where  $l_x$  is the proportion of individuals in a cohort surviving from seed to age  $x$  and  $m_x$  is fecundity of an individual of age  $x$  (Silvertown 1993) For all stages, except mature plants,  $m_x$  was 0, thus  $R_0$  was a product of the proportion of seeds surviving to maturity and the fecundity of mature plants.

## Results

### *Vegetation and habitat*

*Pedicularis* species were found inhabiting semi-natural sites that were abandoned, managed (mown and grazed) or trampled. Several stages of succession and levels of disturbance were observed in the study sites. Trends in population sizes with respect to disturbance regime were observed. In mown sites of *P. palustris* two increasing populations and one population without a change in size were found. The two populations of *P. palustris* in abandoned sites were declining. In one trampled and one grazed site, changes in the *P. palustris* populations were not found. In mown sites of *P. sylvatica* two increasing and three populations of fluctuating size were found. In the one *P. sylvatica* grazed site a fluctuating size of population occurred. I analyzed three *P. sylvatica* populations in abandoned sites; one was fluctuating in size and two were declining. In three of the four trampled sites the population was increasing and in the fourth population changes were not found. Species composition of the vegetation in relationship to the disturbance regime (i.e. mowing, grazing or trampling) is displayed in Fig. 1; Appendix 3 contains the species codes used.

A total of 190 plant species were recorded. At the seven *P. palustris* sites 110 species were identified and 137 species were recorded at the thirteen *P. sylvatica* sites. Seventy species (37 % of the total) were found in at least one site of each of the species. Two other hemiparasites from the same family were found growing with *P. sylvatica*: *Euphrasia stricta* on a wood path and *Rhinanthus minor* in a meadow.



Characteristics of vegetation analyzed in plots at study sites are summarized in Table 2 and Appendix 4 which shows also the list of frequent species and floristic similarity among study sites. In the manipulative experiment overall species composition in relation to treatment was analyzed. Non-significant differences in overall species composition among treatments were found in the plots of both *Pedicularis* species.

#### *Spatial pattern of age stages in permanent plots*

Mother plants and rosettes were distributed evenly within all of the studied populations of both *Pedicularis* species ( $Li \ll 1$ ) in 1997 and in 1998, except of the slightly clustered *P. sylvatica* population ( $Li$  was 2.1) at Ohrazení in 1998. Between-year and between-site differences in the distributions of life history stages in *P. palustris* populations were observed (Table 4). Seedlings that germinated in spring were distributed in clusters (often  $Li > 10$ ). A portion of seedlings recruited in April and then new seedlings emerged over time until June. In June seedlings of winter annual plants of *P. palustris* recruited from fresh seeds and spring seedlings of biennials were mixed in plots. Mortality caused a decline in seedling numbers in autumn. In both species there is a pronounced difference between highly aggregated seedlings and evenly dispersed rosettes and mature plants (Table 4 a; b)

#### *Spatial pattern of recruited seedlings under manipulated conditions*

Seedlings and rosettes in all *Pedicularis*' treated plots were clustered (often  $Li > 10$ ) (Tables 5 and 6). In all treatments the clustering intensity decreased from July to August. In June control plots had the highest seedling density in both species. The maximal clustering of July rosettes of *P. palustris* was in plots with gaps. For *P. sylvatica* the highest clustering occurred in control plots. In all plots, there is a pronounced decline in  $Li$  between July and August. Figs 2-5 compare changes in Lloyd index in treatments throughout time and among sites. Lloyd index did not significantly differed both among treatments and sites in both species.

#### *Effect of the mother plant on seedling shadow*

In most of the examined plots, seedling were found with the highest density at 5-20 cm from the mother plant. Correlations (Spearman coefficient) between the April, May and June seedling number in subplots within  $1\text{m}^2$  and the distance to the mother plant are shown in Table 7. Seedling of *P. palustris* in Dívčice were distributed to 70 cm from mother plants and the relationship between number of seedlings and the distance to the mother plant was not significant (Fig. 6). Correlations were found between the distance to the mother plant and April and May seedlings in Horusice. For *P. sylvatica* these correlations were found in most of sites. The relationships for the highly significant correlations in Ruda are shown in Fig. 7. However, correlations for June were in most sites non-significant (Table 7).

### *Dynamics of seedling recruitment*

Table 8 summarizes the highest seedling numbers recorded in all treatments and all sites for both species.

*P. palustris* - Seedling density increased from April to June in all treatments. From June to September the number of rosettes (grown up from seedlings) declined in mown plots. In plots with gaps the seedling number declined from June to July, and increased in August, then again decline until September (Fig. 8). Plots without litter and bryophytes and control plots yielded the lowest number of seedlings across the season. Seedling numbers in the litter and bryophyte removal treatment peaked in May and then declined until September. Control plots contained the most seedlings in July. Treatments did not differ significantly according to the dynamics of seedling recruitment and almost no seedlings survived until the end of the season in treated plots (Fig. 9). Only the Time and Time\*Site interactions were significant ( $P < 0.05$ ).

*P. sylvatica* - Germination was high from April to May in all treatments. The highest seedling densities were recorded in all treatments in May. From July to August the number of seedlings declined in all treatments (Fig. 10). The lowest number of seedlings occurred in control plots. Seedling number differed in treatments, sites and time (significant effect of these variables,  $P < 0.05$ ). The relative proportions were constant over time (non-significant Time\*Treatment interaction). Sites differed significantly and Site\*Time (Fig. 11) and Site\*Treatment\*Time interactions were significant ( $P < 0.05$ ).

### *Seedling recruitment in gaps and within litter layer*

The response of seedling and rosette density to the occurrence of micro-scale gaps showed highly significant difference ( $P < 0.01$ ) in both species. Seedlings and rosettes of both *Pedicularis* species were more abundant in gaps (Fig. 12 and Fig.13). An absence of litter did not cause an increase in seedling recruitment (test non-significant) for *P. sylvatica*, however, for *P. palustris* significant differences were obtained ( $P < 0.05$ ; Fig. 14 and Fig. 15).

### *Regeneration effort and reproductive rate*

Success in regeneration of each *Pedicularis* species was analyzed in a life table. Demography data of winter annual plants of *P. palustris* and biennials of *P. sylvatica* were obtained. Probabilities of survival from one stage of life history to another and the reproductive rate  $R_0$  were evaluated (see Figs 16 and 17). Within population variation in survival probabilities and  $R_0$  was extremely high. The number of mother plants and rosettes fluctuated between years in both species. Seedling density showed a declining tendency in dependence on the initial density in April. In *P. palustris* the highest number of seedlings recruited in spring was recorded in May; however these seedlings did not survive until June. Seeds

released from mature plants in June germinated immediately and seedlings recruited reached their maximum in July; then their numbers declined. The dynamics of seedling recruitment of winter annual plants in Horusice site was not as dynamic as in the Dívčice population. Few seedlings survived to rosettes in both *Pedicularis* species (Fig. 18 and Fig. 19).

#### *Survival of P. sylvatica rosettes*

The diameter of the bud which is build at the end of the first year varied in *P. sylvatica* from a minimum of 2.28 mm to a maximum of 20.18 mm (mean 8.9 mm and standard deviation 4.3 mm). Bud diameter was found to be a good predictor for rosette winter survival. Rosette survival depended significantly on winter bud diameter (logistic regression,  $\chi^2 = 16.8$ ,  $P < 0.01$ ; Fig. 20). Both plant height and number of flowers per plant were highly dependent on winter bud diameter ( $r = 0.57$  and  $r = 0.67$  respectively, Figs. 21 and 22).

#### **Discussion**

The occurrence of the two *Pedicularis* species and their population viability are recently confined to anthropogenic disturbance regime (mowing, grazing and trampling). Species habitat requirements overlap i.e., species grew together at the Kvilda site (in Appendix 1). The *Pedicularis* species did not show any strict affinity to any particular vegetation types. I found species across a wide range of grassy and marshy communities similarly to other authors (see Ter Borg 1985; Rosenthal & Fink 1996; Karrenberg 1998 and Schmidt 1998). A large *P. palustris* population inhabited an early successional restored meadow on arable land where corn, weedy species (e.g. *Avena sativa*, *Triticum aestivum*, *Falopia convolvulus*, and *Tripleurospermum maritimum*) and meadow species were mixed (Jestřebí II site, see Appendix 1). However the ecological range of plant communities is limited by habitat requirements, particularly groundwater requirements. This has been shown for many rare plants (Grootjans & Klooster 1980; Grootjans et al. 1988, 1996; Grootjans & Diggelen, 1995; Grootjans & Duren, 1995). Both *Pedicularis* species can grow only under conditions of high water table (see Blažková 1973; Ter Borg 1985; Hendrych & Hendrychová 1989; Lammerts et al. 1995; Roelofs et al. 1996; Rosenthal & Fink 1996; Rooy & Verhoeven, unpubl.). The studied *Pedicularis* species require a disturbance regime for their persistence. Although plants were found in both disturbed and undisturbed habitats, populations with a tendency to increase or fluctuate in size were found only in places with a certain disturbance regime (e.g., mowing and trampling). The importance of intermediate disturbance intensity for the viability of populations has been shown for many rare plant species (Menges 1990; Pavlovic 1994), for example, *Gentiana pneumonanthe* (Křenová & Lepš 1996; Oostermeijer et al. 1992, 1994 and 1996). I observed some rare plant species in regularly disturbed *Pedicularis* sites, e.g., the fern *Ophioglossum vulgatum*, carnivorous plants *Drosera rotundifolia* and *Pinguicula vulgaris*, and orchids



*Dactylorhiza majalis*, *Epipactis palustris* and *Leucorchis albida*. This illustrates the probable disturbance dependence of many rare species.

Regarding *Pedicularis* hemiparasitic life strategy, neighboring individuals are both competitors, and also potential host plants. It is often extremely difficult to determine the host of particular plant in the field because of the dense involved root system in grassland underground and extremely fragile *Pedicularis* roots and haustoria. Similarly to Marvier & Schmidt (1996), I assessed four broad host groups only: grasses, other graminoids, forbs and legumes. Several studies show that perennials, i.e. grasses and legumes are particularly good hosts (Macior 1980; Watkinson & Gibson 1989; Marvier 1996; Seel et al. 1993). In both *Pedicularis* species, the number of seedlings and rosettes increased in plots with litter and bryophytes removed. Similar to Špačková et al. (1998) the effect of removal treatments on total plant species composition was not significant in experimental plots of both *Pedicularis* species after the first year of the experiment. Non-significant differences in species composition with respect to treatments might be expected even after long-term observations (comp. Špačková 1998).

Population structure and processes in *Pedicularis* species were studied considering their life history. Both species are reported as semelparous biennials, the only two biennial species within the European hemiparasitic Scrophulariaceae (Hegi 1975). Biennial life history requires higher seed production to achieve the same efficiency as annuals. Generally the biennial strategy is successful only under special conditions (see e.g. Hartl 1977; De Jong et al. 1987; Klinkhamer et al. 1987; Kelly 1985;). Most biennials exhibit plasticity in their life history traits (Klimeš 1989). Winter annual life cycle was studied e.g. in *Erigeron canadensis* (Regehr & Bazzaz 1979)

Biennial and rarely perennial *P. sylvatica* are known (Hegi 1975). *Pedicularis palustris* ssp. *palustris* is a biennial or winter annual and subspecies *opsiantha* is an annual (Ter Borg et al. 1980, 1985). In populations of *P. palustris* just winter annual or biennial cohort may occur or both may overlap (Karrenberg 1998, Rosehtal & Fink 1996, Schmidt 1998). In July winter annual fruiting plants release seeds, which germinate immediately after dispersal in late summer and overwinter as juveniles and flower the next July. In populations at my study sites both cohorts were present. However, the demography data collected in the permanent plots shows that the biennials were strongly reduced. Seedlings recruited in spring often did not survive until June when new seedlings start to emerge from fresh seeds. In June no seedlings were observed while spring seedling died and new seedling have not emerged yet.

Under manipulated conditions only biennials were found and the winter annuals were eliminated due to an absence of fruiting adults. Ter Borg (1985) and Watkinson & Gibson (1987) show demography data for biennials from a dune system in the Netherlands with different water table levels and a  $R_0$  value ranging from 0.05 to 4.59. I monitored winter annuals and the  $R_0$  range from 0.04 to 0.4 with differences between sites. Similar to Ter Borg (1985) I found the highest mortality in seedlings. Demography data for *P. sylvatica* (Ter Borg 1985) were collected for one year only, thus are not really comparable to mine. My

data shows large within- and among-population variability which may be caused by fluctuating environmental conditions, such as a variable water table level (reported by Ter Borg 1985; Rosettehal & Fink 1996). At the Javorník site *P. sylvatica* prospers, where higher precipitation make the climate closer to that of Atlantic populations.

Both *Pedicularis* species have short term persistent seed bank (Grime et al. 1988, Thompson et al. 1997; Ter Borg, Ab Masselink, Jensen pers. com.) Experimental test of seed germination after burying in the soil showed three-year germinability of *P. palustris* (Jensen, pers. com.) and two-year germinability of *P. sylvatica* (Petrů, unpubl.) However the major part of seeds of both species germinate in the first year after dispersal, thus the persistence of populations is due to time limited seed source seriously endangered.

The survival of rosettes is connected with the growth of a winter bud, which differs in structure and morphology between the two species. The survival of winter buds depends upon their diameters, however, this relationship was studied in *P. sylvatica* only. Survival probability monotonously increased with bud width. To the contrary, Ter Borg (1979) shows an optimum curve where species survival of the largest winter buds was less than that of medium-sized buds, for both *P. sylvatica* and *P. palustris*. In *P. sylvatica* plant size and reproductive effort are positively correlated with winter bud size (comp. Gross 1981). Number of flowers was considered as reproductive effort, although the number of seeds would be more precise. Nevertheless in nearly all cases flowers were fertilized and seeds were set. Ter Borg (1985) suggests that plant size and survival of first year individuals appeared to be positively correlated with openness of the plant cover.

Some demographic studies have been made on other rare *Pedicularis* species (e.g., Menges et al. 1986; Gawler et al. 1987; Menges 1990). Populations of *Pedicularis furbishiae*, a perennial plant growing on river banks, were also positively affected by natural disturbance (fluctuation water level in river). Some other similarities to my study species can be found. The growth rate of populations varied presumably due to environmental fluctuations. Menges (1990) studied both within-population and metapopulation processes. Metapopulation processes may be responsible for the distribution and occurrence of populations on large or regional scale as Menges (1990) modeled for *P. furbishiae*. This might be argued by the two *Pedicularis* species.

Changes in the spatial pattern of life history stages, from clusters of seedlings to a regular distribution of rosettes and mothers over time, shows strong density-dependent regulation within populations of both *Pedicularis* species. Despite new seedlings recruiting into plots until July under both natural and manipulated conditions, seedling density declined over time as a consequence of intraspecific interactions. Beginning in July density-dependent mortality affected rosette survival. However, seedling density differed locally and often fluctuated under the particular microclimatic conditions, such as temperature, air humidity or soil water availability (comp. Ter Borg 1985). These conditions as they

fluctuated in time were either favourable to seedling recruitment or caused their mortality in uneven proportions. In *P. palustris* a spring seedling pattern of biennials was repeated in the autumn by winter-annuals. The effect of intraspecific competition in annuals has been shown by Symonides (1983, 1984); Symonides & Boryslawski (1986); Pacala (1986) and Westoby & Howell (1986), and Kotorová & Lepš (1999) show it for several meadow species.

A clustered pattern of seedlings found in all sites of both species corresponds with the distribution of dispersed seeds around mother plants (called a 'seed/seedling shadow', Janzen 1971). Under natural conditions, the strongest correlation was found between the distance to the mother and number of seedlings recruited until May. In May the germination of seedlings was the highest. With increasing seedling mortality, the pattern weakens. *P. palustris* often did not follow the typical shape of the relationship (comp. Fenner 1992), probably because of plant height. The height of fruiting *P. palustris* is usually 30-60 cm, however, plants usually broke below the middle. Broken stems usually fall a distance of 20-40 cm and seeds drop out of capsules at this distance from the mother plant. In contrast, fruiting *P. sylvatica* are low and drop seeds in their close vicinity. However, in Horusice, plants of *P. palustris* were a similar height as *P. sylvatica* and the relationship show the same shape. The role of postdispersal seed transport by water in *P. palustris* (Ter Borg 1985; Rosenthal & Fink 1996) and myrmecochory in *P. sylvatica* (Berg 1954) still requires further investigation. Fenner (1985) shows more clumping in rare species than in common species and suggests that clumping of rare species reflects narrow regeneration requirements that are only met in isolated patches.

Manipulation of the natural conditions tested the effect of management regimes (mowing and grazing simulated by the creation of gaps) at a small scale and the effect of different microsites (in gaps, litter and moss) on seedling recruitment. The number of established seedlings depended upon seed dispersal and germination, seedling establishment and mortality. Sown plots were situated outside the center of populations, thus treatment effect on seedling recruitment and survival was separated from the effect of dispersal. However, natural seed sources are present in sown plots and add to the number of recruited seedlings from sown seeds. Comparing the germination success of both species in the field experimental plots, *P. palustris* had lower germination than *P. sylvatica* and the same results were obtained by laboratory germination tests (Petrů unpubl.). Different germination between species can be caused by limited population size and seed pool, or external factors such as weather and differences among habitats. Low seed germination of *P. palustris* may be caused, for example, by an unfavorable regime of water level fluctuation. Seeds of *Pedicularis* do not germinate under water (Ter Borg 1985). Rooy and Verhoeven (unpubl.) observed successful establishment in a dry spring that supported germination followed by a wet summer that prevented the plants from drying out. In my experiment a dry summer contributed to seedling mortality regardless of treatment type. This was in addition to the effects of self-thinning and competition from established neighboring vegetation. The dynamics of seedling

recruitment showed the same trend over different treatments. However different course of seedling recruitment and roset survival in particular treatments was observed when site by site was analyzed (see Petrů & Lepš 1999). Nevertheless plots where gaps were created and mown plots with litter removed provided favorable conditions for seedling recruitment. Litter/bryophyte removal treatments clearly affect the seedling stage of a number of meadow species (Rabotnov 1969; Werner 1974; Goldberg 1983; Keizer et al. 1985; Monk et al. 1985; van Tooren 1988 and 1990; Carson & Peterson 1990; During et al. 1990; Facelli & Pickett 1991; Facelli & Facelli 1993; Ryser 1993; Špačková et al. 1998; Kotorová & Lepš 1999). Seedling emergence of *Pedicularis* species were slightly favored by this treatment at a micro-scale. *Pedicularis palustris* preferred microhabitats with only the litter removed. This can be supported by results of Karrenberg' (1998) experiment in which a negative effect of litter on *P. palustris* germination was found. Concerning the bryophyte layer, Lepš (1999) found a positive correlation between bryophyte presence and seedlings, i.e., they were found in similar microhabitats. In nature, bryophyte cover is positively influenced by similar factor as is seedling recruitment, e.g., by mowing (Lepš 1999). Gap size was important for seedling recruitment of both *Pedicularis* species over time. With increasing gap size the number of surviving seedlings in a gap increases (Fenner 1985). McConnaughay & Bazzaz (1987) found in several annual plants that while survivorship was greater in larger gaps, the probability of reaching preproductive maturity increased with increasing gap size for all the species. In *P. sylvatica* more seedlings were found in larger gaps, nevertheless survival of rosettes did not differ according to gap size. I created small gaps of size 5 cm radius and larger gaps of 10 cm to test the response of seedling establishment under different intensity of disturbance. However gaps of larger size than 5 cm radius are rare in grasslands (Silvertown & Smith 1988; Hook et al. 1994; McLlellan et al. 1997).

Seedling recruitment is sensitive to the effect of living vegetation due to light competition (see Van Tooren 1990; Špačková et al. 1998, Kotorová & Lepš 1999). *Pedicularis* species begin their life cycle earlier than does the neighboring vegetation which enables the seedlings to recruit without being outcompeted. This early germination may also be an advantage in their hemiparasitic life history.

To conclude, several studies were conducted here in order to understand ecology of the two rare species: *Pedicularis palustris* and *P. sylvatica* in their habitats on community and population level. The broad-scaled survey of populations revealed that both species grow in wide range of vegetation types, however both of them are dependent on a disturbance regime and /or early succession stages. *Pedicularis palustris* particularly show dependence on high water table. Species require openness in vegetation, thus a sort of habitat disturbance. For parasitic plants Marvier & Smith (1997) have shown how these plants depend upon particular disturbance regimes for their continual existence and that they require proper frequency of disturbance while they dependent upon prior colonization by their hosts.

Population studies were carried out on spatial and temporal scales and all stages of life cycle were considered. Decrease in clumping intensity indicated strong density dependent mortality in stage of

rosettes (between July and August). In the within-population processes sexual reproduction is important for persistence of both *Pedicularis* species. Regeneration of species is vulnerable in many steps in their life history. Experiments show positive response of regeneration effort to disturbance regime and spatial heterogeneity even on individual level. The lack of a persistent seed bank in both *Pedicularis* species, with high spring germination and high late summer mortality can cause pronounced inter-year fluctuations, making the species prone to local extinctions. Mowing or extensive grazing seems to be proper management regimes for species existence and populations viability.

Both community and population approach used here contribute to understanding the demography of particular species and together with promoting disturbance heterogeneity are of significant importance for the maintenance of species diversity.

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Table 1. Characteristics of study sites of both *Pedicularis palustris* and *Pedicularis sylvatica*: geography, meteorology (© Meteorological Institut in České Budějovice (ČB); nearest station: a-České Budějovice, b-Borkovice, c-Kašperské Hory, d-Hluboká nad Vltavou, e-Lomnice nad Lužnicí, f-České Budějovice, g-Vacov, h-Ruda. + 1998 average precipitation not available; \*pedology data not sampled nor measured due to soil inundations.

Study species	Study site	Geographical location		Altitude [m] a.s.l.	Meteorology			Pedology			
		Distance referred to ČB [km]	Geog. coordinates		Annual mean temperature [°C]	Annual precipitation [mm]	pH	Relative water capacity	C [%]	N [%]	C/N
	Dívčice	20 NW	49°06' N 14°19' W	380	7.9 <sup>a</sup> (9.1)	593 <sup>d</sup>	5.43	47.6	16.7	1.05	15.8
	Horusice	25 NE	49°09' N 14°41' E	415	7.7 <sup>b</sup> (8.6)	600 <sup>e</sup>	*	*	*	*	*
	Ohrazení	10 SE	48°57' N 14°36' E	510	7.9 <sup>a</sup> (9.1)	596 <sup>f</sup>	4.96	37.9	6.74	0.5	13.5
	Javorník	70 SW	49°07' N 13° 39' W	850	6.0 <sup>c</sup> (7.2)	847 <sup>g</sup>	5.54	36.9	5.44	0.35	15.5
	Ruda	30 NE	49°08' N 14°43' E	420	7.7 <sup>b</sup> (8.6)	610 <sup>h</sup>	4.81	29.7	9.33	0.67	13.8

**Table 2.** Characteristics of vegetation and management regimes in both *Pedicularis palustris* and *Pedicularis sylvatica* study sites. \* biomass and litter not sampled, due to inundations and grazing by deer or rodents in July 1998.

Study species	Study site	Vegetation				Management Type	
		No. of species per 1 m <sup>2</sup>	Biomass (without <i>Pedicularis</i> ) [g/m <sup>2</sup> ]	Litter [g/m <sup>2</sup> ]	Biomass/litter		
							
<i>P. palustris</i>	Dívčice	16	255.3	153.5	1.66	abandoned	
<i>P. palustris</i>	Horusice	8	.*	.*	.*	abandoned	
<i>P. sylvatica</i>	Ohrazení	33	275.6 - 335.6	36.3 - 166.6	1.7 - 9.4	mown biyearly mown once a year + overgrazed	
<i>P. sylvatica</i>	Javorník	31	159.9 - 208.1	4.4 - 4.7	36.3 - 44.3		
	<i>P. sylvatica</i>	Ruda	31	214.2 - 295.1	12.9 - 31.7	9.3 - 16.6	mown twice a year

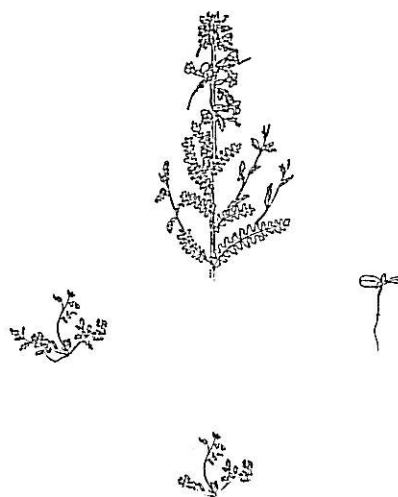
**Table 3.** Overview of studies at *Pedicularis* study sites. \* project conducted in only *P. sylvatica* plots because not enough *P. palustris* winter buds were found.

Objective	Project	Conditions		
		natural surveyed sites	natural permanent plots	manipulated experimental plots
Community and environmental relations	<i>Vegetation and habitat</i>	✓	✓	✓
Population structure	<i>Spatial pattern of age stages</i>		✓	
	<i>Spatial pattern of recruited seedlings</i>		✓	✓
	<i>Effect of mother plant on seedling shadow</i>		✓	
Regeneration dynamics	<i>Dynamics of seedling recruitment</i>			✓
	<i>Seedling recruitment in gaps</i>			✓
Life history consequences	<i>Regeneration success and relative reproductive rate</i>		✓	
	<i>Survival of rosettes</i>		✓ *	

**Table 4.** Spatial pattern of age stages under natural conditions. Mean Lloyd index values among age *Pedicularis* life stages (M = mothers, R = rosettes, S = seedlings, 97, 98 = years, 4, 5, 6, 8, 10 = month) all sites pooled; a) *P. palustris*, b) *P. sylvatica*; † missing values; in bold clustering (both values and stages,  $Li > 1$ ); levels of clustering: <sup>+</sup>  $1 < Li < 10$ , <sup>++</sup>  $10 < Li < 100$ , <sup>+++</sup>  $Li > 100$

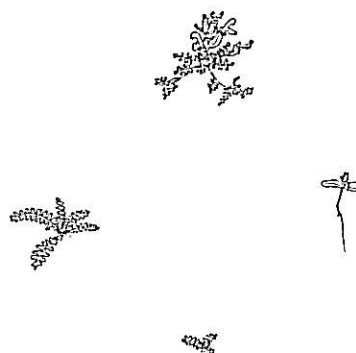
a)

Age stage	Lloyd index			
<i>P. palustris</i>				
	mean	st.dev.	min	max
M97	0.10	0.09	0.03	0.16
R97	0.06	0.02	0.04	0.07
S4	<b>9.40<sup>+</sup></b>	<b>4.10<sup>+</sup></b>	<b>6.50<sup>+</sup></b>	<b>12.30<sup>++</sup></b>
S5	<b>4.70<sup>+</sup></b>	<b>2.97<sup>+</sup></b>	<b>2.60<sup>+</sup></b>	<b>6.80<sup>+</sup></b>
M98	0.10	0.08	0.04	0.16
S6	<b>10.70<sup>++</sup></b>	<b>7.21<sup>+</sup></b>	<b>5.60<sup>+</sup></b>	<b>15.80<sup>++</sup></b>
S8	<b>6.85<sup>+</sup></b>	<b>2.76<sup>+</sup></b>	<b>4.90<sup>+</sup></b>	<b>8.80<sup>+</sup></b>
S10	<b>9.40<sup>+</sup></b>	†	<b>9.40<sup>+</sup></b>	<b>9.40<sup>+</sup></b>
R98	0.13	†	0.13	0.13




b)


Age stage	Lloyd index			
<i>P. sylvatica</i>				
	mean	st.dev.	min	max
M97	0.37	0.35	0.06	1.00
R97	0.19	0.27	0.01	1.00
S4	<b>34.25<sup>++</sup></b>	<b>25.51<sup>++</sup></b>	<b>10.80<sup>++</sup></b>	<b>104.50<sup>+++</sup></b>
S5	<b>13.31<sup>++</sup></b>	<b>10.57<sup>++</sup></b>	<b>2.90<sup>++</sup></b>	<b>41.50<sup>++</sup></b>
S6	<b>33.79<sup>++</sup></b>	<b>30.18<sup>++</sup></b>	0.87	<b>99.20<sup>++</sup></b>
R98	0.16	0.21	0.00	0.50
M98	<b>1.18<sup>+</sup></b>	<b>1.97<sup>+</sup></b>	0.03	6.05



**Table 5.** Spatial pattern of seedlings and rosettes of *Pedicularis palustris* under experimental conditions over time. Differences in Lloyd index values for age stages among treatments in *P. palustris* experimental plots. Treatments: M = mown, L&B rem = litter and bryophytes removed, g = gaps, Ctrl = control, S6 = June seedlings, R7 = July rosettes, R8 = August rosettes. All sites were pooled; in **bold** clustering (both values and treatments,  $Li > 1$ ); levels of clustering: <sup>+</sup>  $1 < Li < 10$ , <sup>++</sup>  $10 < Li < 100$ , <sup>+++</sup>  $Li > 100$

Treatment	Age stage	Lloyd	index		
	<i>P. palustris</i>				
		Mean	st.dev.	min	max
M	S6	<b>9.40<sup>+</sup></b>	<b>2.83<sup>+</sup></b>	<b>7.40<sup>+</sup></b>	<b>11.40<sup>++</sup></b>
	R7	<b>7.97<sup>+</sup></b>	<b>2.74<sup>+</sup></b>	<b>6.03<sup>+</sup></b>	<b>9.90<sup>+</sup></b>
	R8	<b>6.43<sup>+</sup></b>	<b>2.97<sup>+</sup></b>	<b>3.10<sup>+</sup></b>	<b>8.80<sup>+</sup></b>
L & B rem	S6	<b>5.81<sup>+</sup></b>	<b>7.76<sup>+</sup></b>	0.32	<b>11.30<sup>++</sup></b>
	R7	<b>3.90<sup>+</sup></b>	<b>4.81<sup>+</sup></b>	0.50	<b>7.30<sup>+</sup></b>
	R8	0.97	0.06	0.90	<b>1.00<sup>+</sup></b>
G	S6	<b>11.26<sup>++</sup></b>	<b>4.82<sup>+</sup></b>	<b>8.10<sup>+</sup></b>	<b>16.8<sup>+</sup></b>
	R7	<b>56.63<sup>++</sup></b>	<b>40.18<sup>++</sup></b>	<b>22.70<sup>++</sup></b>	<b>101.00<sup>+++</sup></b>
	R8	<b>5.73<sup>+</sup></b>	<b>2.42<sup>+</sup></b>	<b>3.00<sup>+</sup></b>	<b>7.60<sup>+</sup></b>
Ctrl	S6	<b>30.30<sup>++</sup></b>	<b>23.19<sup>++</sup></b>	<b>13.90<sup>++</sup></b>	<b>46.70<sup>++</sup></b>
	R7	<b>11.60<sup>++</sup></b>	<b>3.54<sup>+</sup></b>	<b>9.10<sup>+</sup></b>	<b>14.10<sup>++</sup></b>
	R8	<b>6.43<sup>+</sup></b>	0.71	<b>5.80<sup>+</sup></b>	<b>7.20<sup>+</sup></b>

**Table 6.** Spatial pattern of seedlings and rosettes of *Pedicularis sylvatica* under experimental conditions over time. Differences in Lloyd index values for life stages among treatments in *P. sylvatica* experimental plots. Treatments: M = mown, M + B rem = mown and bryophytes removed, L&B rem = litter and bryophytes removed, G = large gaps, g = small gaps, Ctrl = control, S6 = June seedlings, R7 = July rosettes, R8 = August rosettes. All sites were pooled; ; in **bold** clustering (both values and treatments,  $Li > 1$ ); levels of clustering: <sup>+</sup>  $1 < Li < 10$ , <sup>++</sup>  $10 < Li < 100$ , <sup>+++</sup>  $Li > 100$

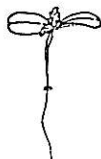

Treatment	Age stage	Lloyd index			
	<i>P. sylvatica</i>				
		mean	st.dev.	min	max
M	S6	4.88 <sup>+</sup>	1.43 <sup>+</sup>	2.60 <sup>+</sup>	6.30 <sup>+</sup>
	R7	8.62 <sup>+</sup>	6.36 <sup>+</sup>	2.60 <sup>+</sup>	15.60 <sup>++</sup>
	R8	2.62 <sup>+</sup>	0.98	1.50 <sup>+</sup>	3.60 <sup>+</sup>
M + B rem	S6	4.74 <sup>+</sup>	2.00 <sup>+</sup>	2.40 <sup>+</sup>	7.20 <sup>+</sup>
	R7	4.08 <sup>+</sup>	1.40 <sup>+</sup>	2.40 <sup>+</sup>	5.60 <sup>+</sup>
	R8	2.03 <sup>+</sup>	1.19 <sup>+</sup>	1.30 <sup>+</sup>	3.80 <sup>+</sup>
L & B rem	S6	9.48 <sup>+</sup>	4.88 <sup>+</sup>	2.90 <sup>+</sup>	14.90 <sup>++</sup>
	R7	8.72 <sup>+</sup>	4.31 <sup>+</sup>	3.10 <sup>+</sup>	14.20 <sup>++</sup>
	R8	3.24 <sup>+</sup>	2.03 <sup>+</sup>	1.00 <sup>+</sup>	5.40 <sup>+</sup>
G	S6	4.48 <sup>+</sup>	2.09 <sup>+</sup>	2.20 <sup>+</sup>	6.90 <sup>+</sup>
	R7	3.94 <sup>+</sup>	1.27 <sup>+</sup>	2.30 <sup>+</sup>	5.50 <sup>+</sup>
	R8	2.66 <sup>+</sup>	1.24 <sup>+</sup>	1.20 <sup>+</sup>	4.60 <sup>+</sup>
g	S6	5.04 <sup>+</sup>	4.68 <sup>+</sup>	1.90 <sup>+</sup>	13.30 <sup>++</sup>
	R7	5.06 <sup>+</sup>	3.28 <sup>+</sup>	2.40 <sup>+</sup>	10.50 <sup>++</sup>
	R8	2.68 <sup>+</sup>	2.30 <sup>+</sup>	0.90	6.60 <sup>+</sup>
Ctrl	S6	7.34 <sup>+</sup>	6.48 <sup>+</sup>	1.50 <sup>+</sup>	15.60 <sup>++</sup>
	R7	10.97 <sup>++</sup>	6.81 <sup>+</sup>	3.20 <sup>+</sup>	15.90 <sup>++</sup>
	R8	4.30 <sup>+</sup>	2.75 <sup>+</sup>	1.60 <sup>+</sup>	7.10 <sup>+</sup>



**Table 7.** Spatial pattern of seedlings under natural conditions in dependence on the distance to the mother plant. Spearman rank correlation coefficients between April, May and June 1997 seedling numbers and distance to mother plant for both species, *Pedicularis palustris* and *Pedicularis sylvatica*. \*\*\* $P < 0.001$ , \*\*  $0.001 < P < 0.01$ , \*  $0.01 < P < 0.05$ ; Dis = distance of  $0.1 \times 0.1 \text{ m}$  subplots within  $1 \text{ m}^2$  to the mother plants; Apr, May, Jun = number of seedlings counted in respective months in subplots.

<i>P. palustris</i>				<i>P. sylvatica</i>			
Spearman				Spearman			
Site	Dis & Apr	Dis & May	Dis & Jun	Site	Dis & Apr	Dis & May	Dis & Jun
<i>Dívčice</i>	-0,05	0,17	-0,06	Ohrazení	-0.20***	-0.30***	-0.11
Horusice	-0,30***	-0,40***	-0,16	Javorník	-0.26***	-0.044	0.12*
<i>palustris</i> (all sites pooled)	-0,12	-0,12	-0,34***	<i>Ruda</i>	-0.29***	-0.39***	-0.01
				<i>sylvatica</i> (all sites pooled)	-0.38***	-0.25***	0.06

**Table 8.** Summary of seedling counts in the manipulative experiment. Highest seedling numbers per 0.25 m<sup>2</sup> in respective months counted in treated plots of both species and highest seedling numbers in respective months in experimental plots in study sites. Treatments: G = large gaps, g = gaps, M = mown, M + B rem = mown and bryophytes removed, L & B rem = litter and bryophytes removed, Ctrl = control plots; s = sown plots, u = unsown plots). **Bold** treatment and site with the maximal seedling number for each species.

<i>P. palustris</i>			<i>P. sylvatica</i>		
Treatment	Month	No. of seedlings	Treatment	Month	No. of seedlings
g 	Jun	3	<b>G</b> 	<b>May</b>	<b>32</b>
<b>M</b>	<b>Jun</b>	<b>6</b>	<b>g</b>	<b>May</b>	<b>32</b>
L & B rem	May	2	M	May	16
Ctrl	Jul	2	M+B rem	May	25
			L & B rem	May	20
			Ctrl	May	10
<i>Site</i>			<i>Site</i>		
<b>Dívčice - s</b>	<b>Jul</b>	<b>5</b>	Ohrazení - s	May	16
Dívčice - u	Jun	3	Ohrazení - u	May	16
Horusice	May	2	<b>Javorník - s</b>	<b>Jul</b>	<b>63</b>
			Javorník - u	Jul	10
			Ruda	May	16

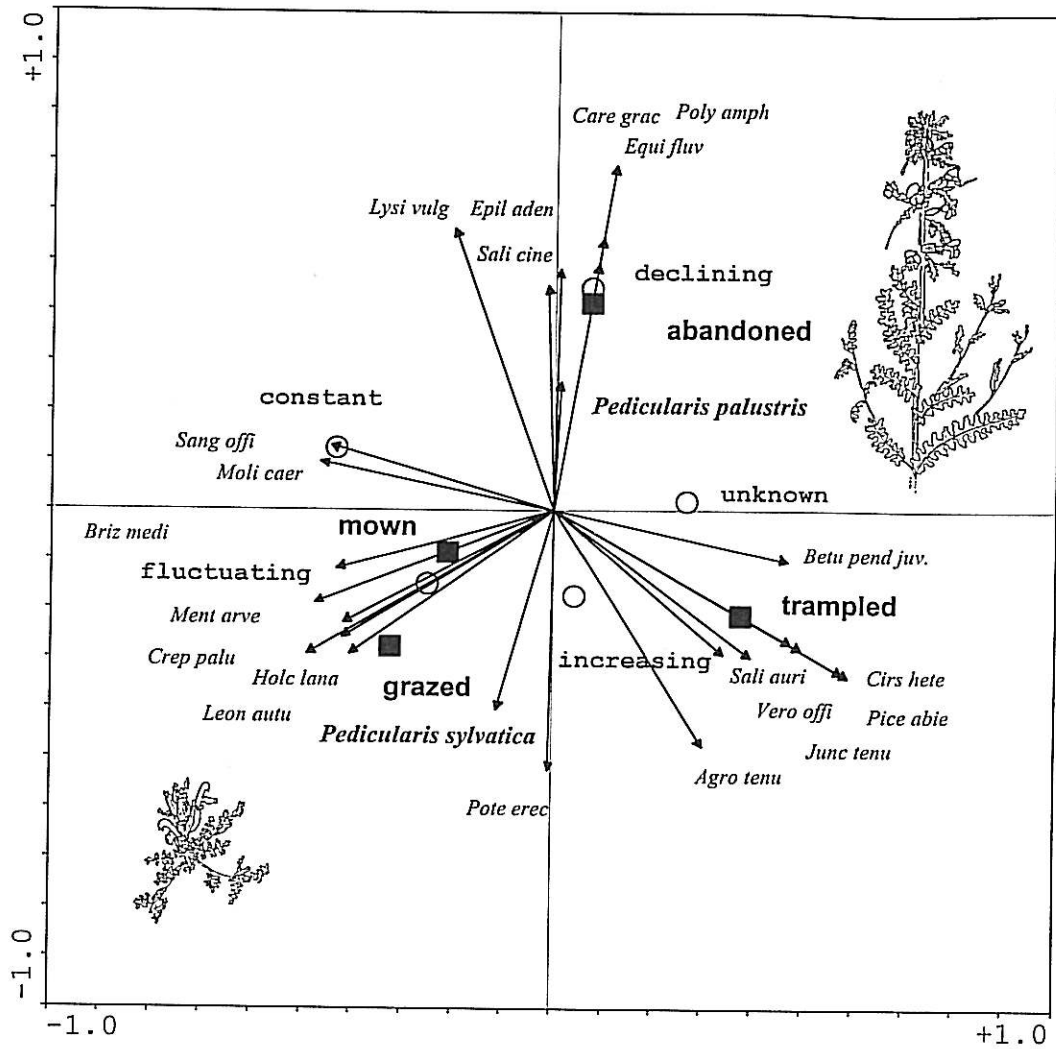


Fig. 1. RDA analysis. Distribution of species composition of vegetation at all *Pedicularis palustris* and *Pedicularis sylvatica* surveyed sites in relation to disturbance regime (squares). Trends in sizes of populations (circles) at sites of both *Pedicularis* species were reflected ex-post into ordination diagram. Abbreviations of species name are defined in Appendix 3. Test of all canonical axes non-significant.

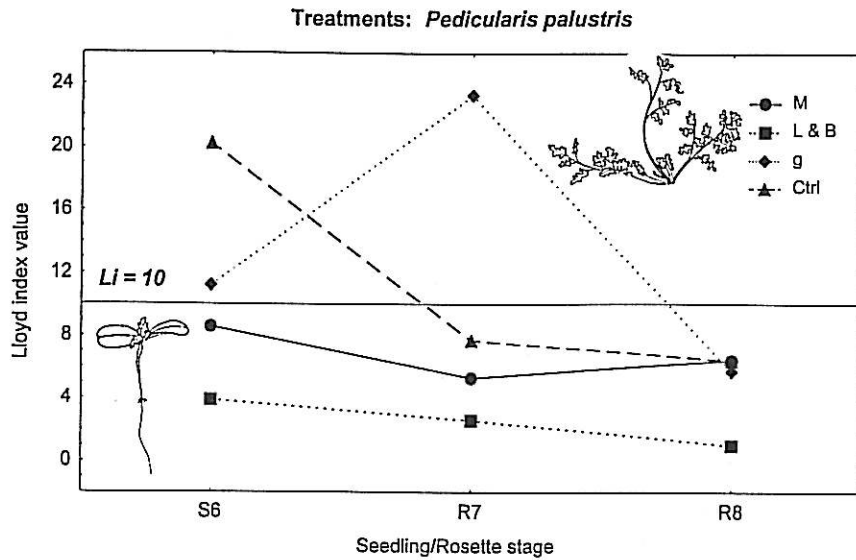


Fig. 2. Age structured spatial pattern of *Pedicularis palustris* under experimental conditions. Comparison of Lloyd index values between different treatments of 0.5×0.5m in three life cycle stages of *P. palustris* with all sites pooled. Treatments: M = mowing, L & B = litter and bryophyte layer removed, g = gaps were created, Ctrl = control; stages: S6 = seedlings in June, R7 and R8 = rosettes in July and August.

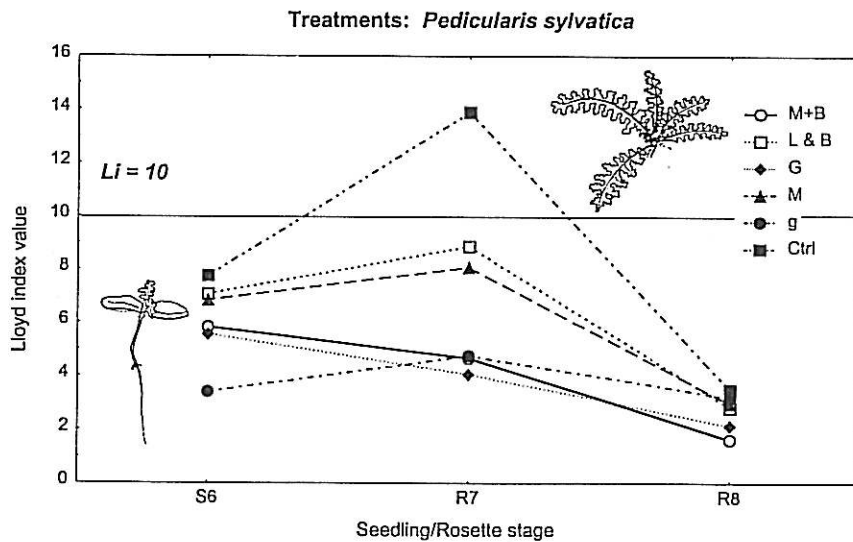


Fig. 3. Age structured spatial pattern of *Pedicularis sylvatica* under experimental conditions. Comparison of Lloyd index values between different treatments of 0.5×0.5m in three life cycle stages of *P. sylvatica* with all sites pooled. Treatments: M + B = mowing and bryophyte layer removed, L & B = litter and bryophyte layers removal, g = small gaps created, G = large gaps created, M = mowing, Ctrl = control; stages: S6 = seedlings in June, R7 and 8 = rosettes in July and August.

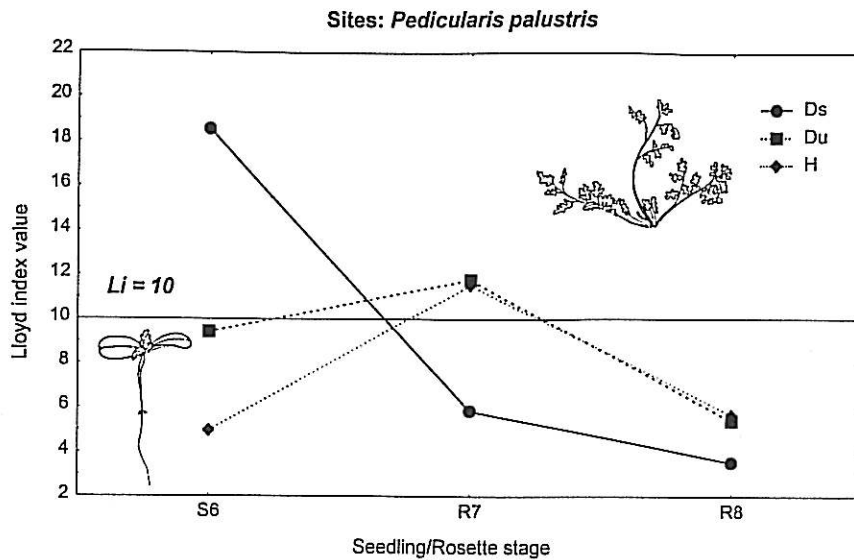


Fig. 4. Age structured spatial pattern of *Pedicularis palustris* under experimental conditions. Comparison of Lloyd index values between experimental plot sites with three life cycle stages of *P. palustris* with all treatments pooled. Sites: Ds = Dívčice sown plots, Du = Dívčice unsown plots, H = Horusice unsown plots; stages: S6 = June seedlings, R7, 8 = rosettes in July and August.

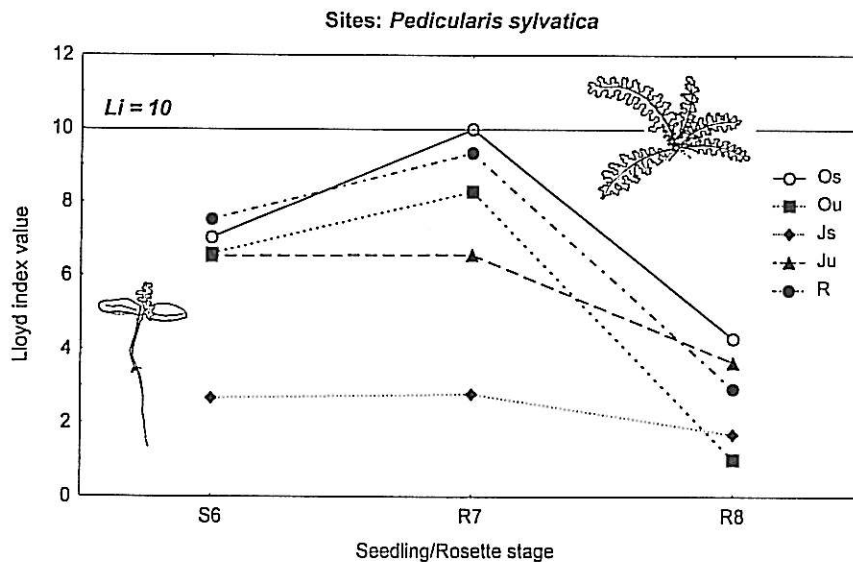


Fig. 5. Age structured spatial pattern of *Pedicularis sylvatica* under experimental conditions. Comparison of Lloyd index values between experimental plot sites with three life cycle stages of *P. sylvatica* with all treatments pooled. Os = Ohrazení sown plots, Ou = Ohrazení unsown plots, Js = Javorník sown plots, Ou = Javorník unsown plots and R = Ruda site; stages: S6 = June seedlings, R7, 8 = rosettes in July and August.

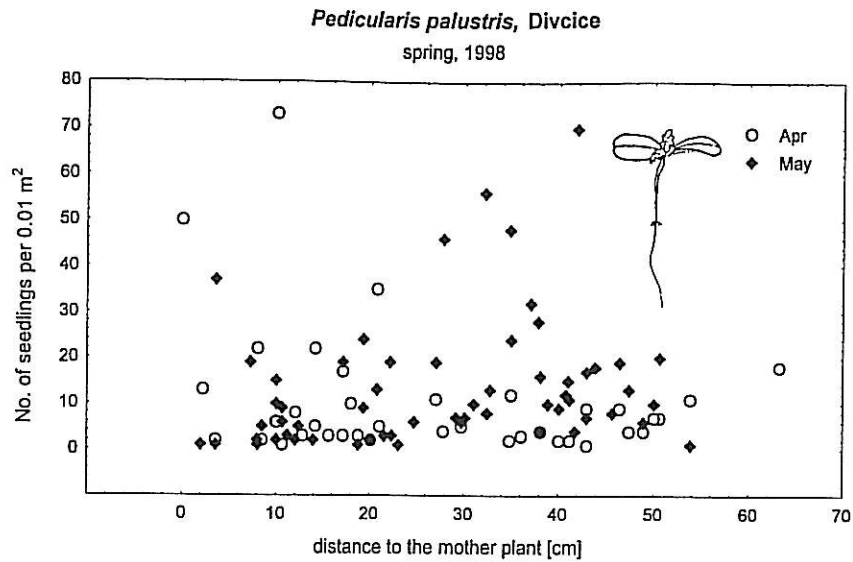


Fig. 6. Distribution of *Pedicularis palustris* seedlings around mother plants over time in a permanent plot of 1m<sup>2</sup> at the Divčice site. Dependence of the number of *P. palustris* seedlings in April and May in 0.1×0.1m subplots on the distance to the mother plant. Correlations (Spearman's coefficient) were non-significant.

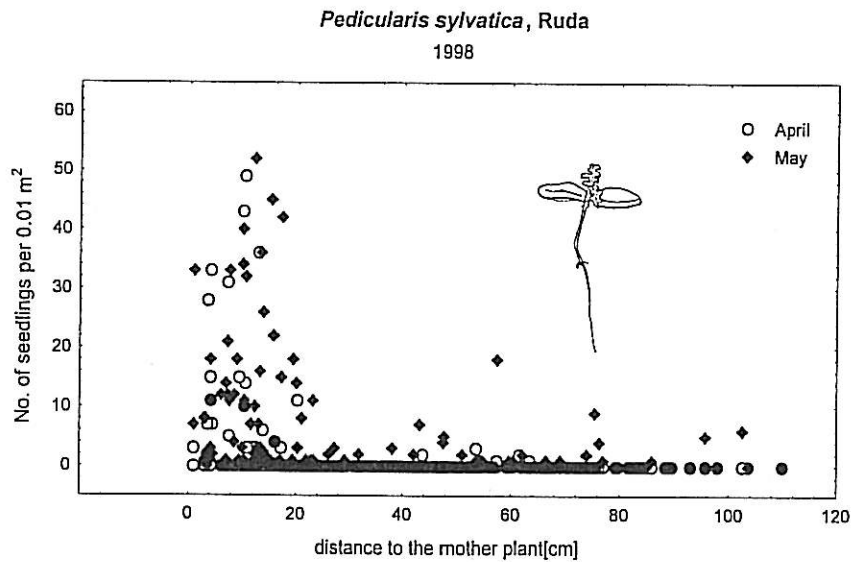
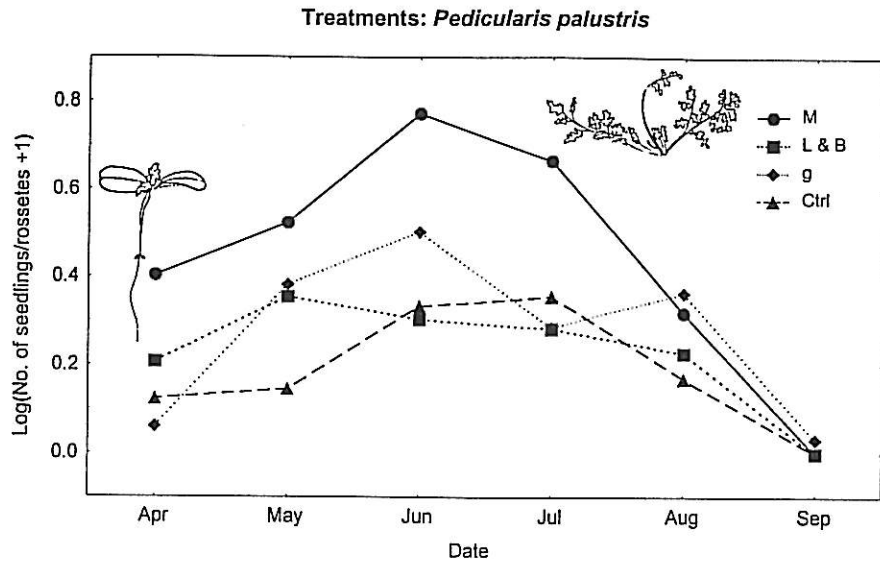
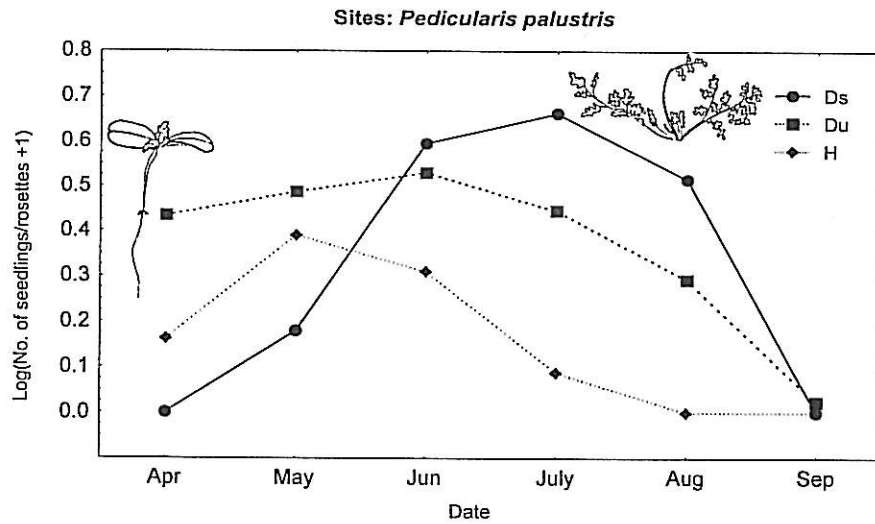


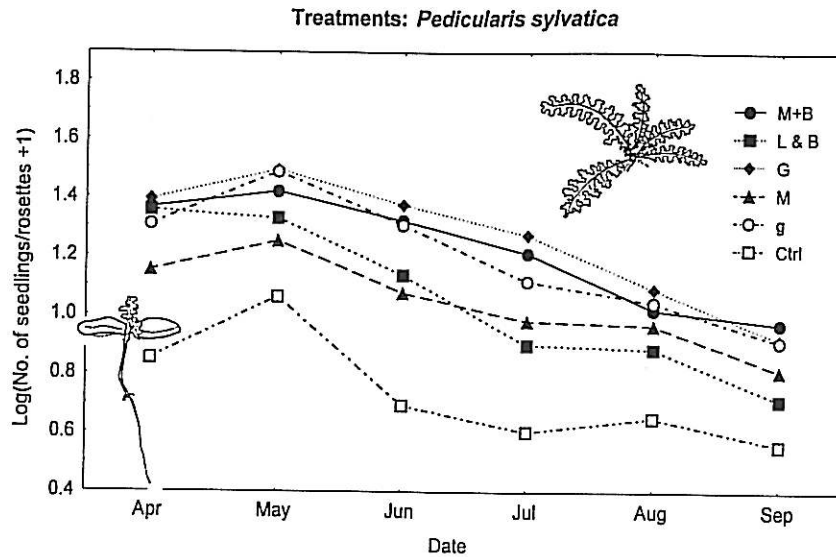
Fig. 7. Distribution of *Pedicularis sylvatica* seedlings around mother plants over time in a permanent plot of 1m<sup>2</sup> at the Ruda site. Dependence of the number of *P. sylvatica* seedlings in April and May in 0.1×0.1m subplots on the distance to the mother plant. Correlations (Spearman's coefficient) is -0.29 for distance versus April seedlings;  $P < 0.001$ , and -0.39 for distance versus May seedlings;  $P < 0.001$ .



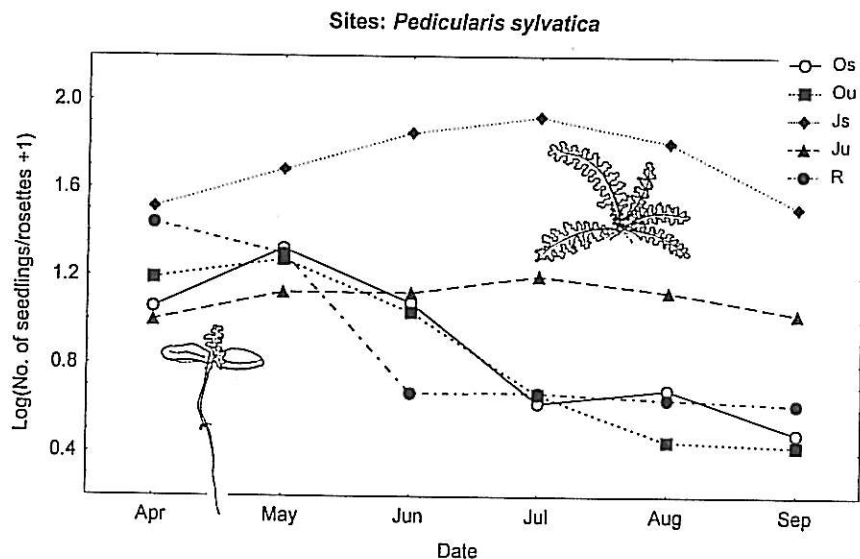
**Fig. 8.** Seedling establishment and mortality of *Pedicularis palustris* under experimental conditions; treatment comparison. Dynamics of recruitment and mortality of *P. palustris* seedlings and rosettes over time. From April to September 1998 in different treatments with all sites pooled. Treatments: M = mowing, L&B = litter and bryophyte removal, G = gaps were created, Ctrl = control.



**Fig. 9.** Seedling establishment and mortality of *Pedicularis sylvatica* under experimental conditions; site comparison. Dynamics of recruitment and mortality of *Pedicularis palustris* seedlings and rosettes over time. From April to September 1998 in study sites with all treatments pooled. Sites: Ds = Dívčice sown plots, Du = Dívčice unsown plots, H = Horusice. Time\*Site Interaction,  $P < 0.05$ .

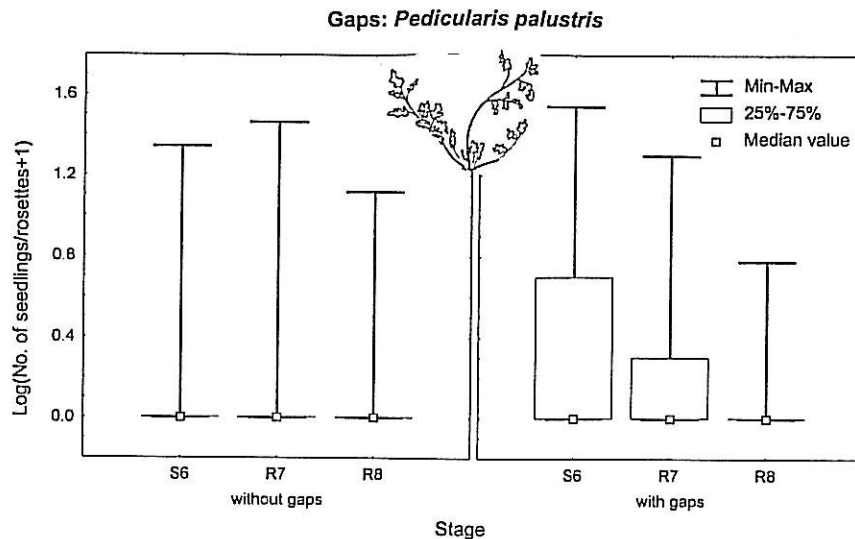


**Fig. 10.** Seedling establishment and mortality of *Pedicularis sylvatica* under experimental conditions; treatment comparison. Dynamics of recruitment and mortality of *P. sylvatica* seedlings and rosettes over time. From April to September 1998 in different treatments with all sites pooled. Treatments: M + B = mowing and bryophyte removal, L & B = litter and bryophyte removal, G = large gaps created, M = mowing, g = small gaps created, Ctrl = control.

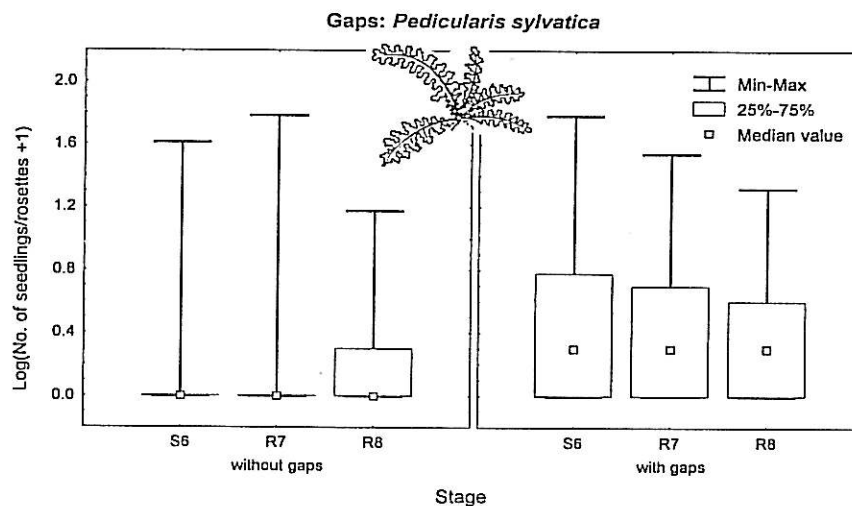


**Fig 11.** Seedling establishment and mortality of *Pedicularis sylvatica* under experimental conditions; site comparison. Dynamics of recruitment and mortality of *P. sylvatica* seedlings and rosettes over time. From April to September 1998 in study sites with all treatments pooled. Sites: Os = Ohrazení sown plots, Ou = Ohrazení unsown plots, Js = Javorník sown plots, Ou = Javorník unsown plots and R = Ruda site. Time\*Site Interaction,  $P < 0.05$ .

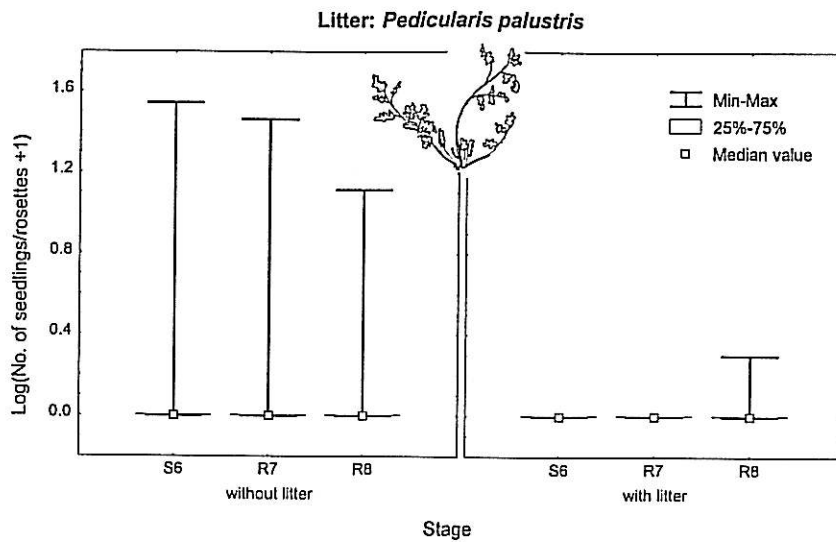




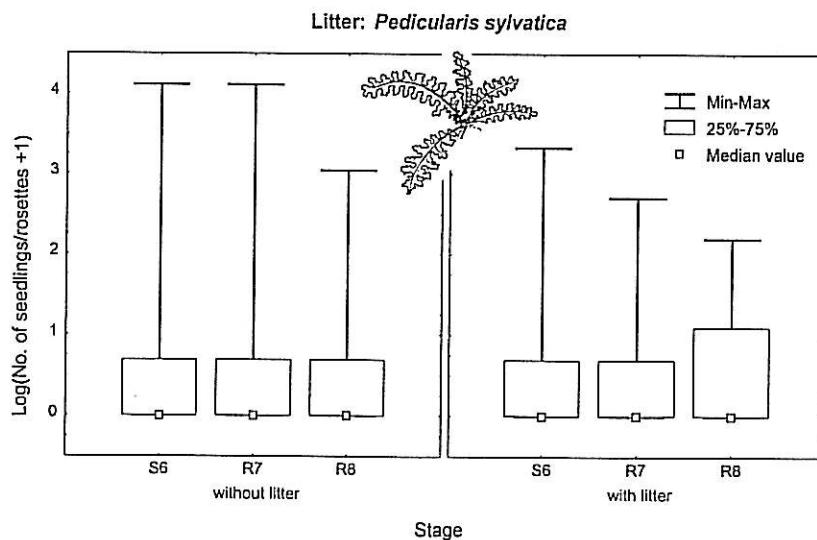
**Fig. 12.** Seedling establishment and mortality of *Pedicularis palustris* in gaps (both natural and created) on a microscale. Differences in seedling and rosette number found in 0.1×0.1m subplots in treated plots in the experiment with and without gaps over time. All treatments and all sites were pooled. Stages: S6 = June seedlings, R7 and R8 = rosettes in July and August. Box-whisker plots; differences in seedling number in plots with and without gaps,  $P < 0.01$ .



**Fig. 13.** Seedling establishment and mortality of *Pedicularis sylvatica* in gaps (both natural and created) on a microscale. Differences in seedling and rosette number found in 0.1×0.1m subplots in treated plots in the experiment with and without gaps over time. All treatments and all sites were pooled. Stages: S6 = June seedlings, R7, R8 = rosettes in July and August. Box-whisker plots; differences in seedling number in plots with and without gaps,  $P < 0.01$ .



**Fig. 14.** Effect of litter on regeneration of *Pedicularis palustris* on a microscale. Differences in seedling and rosette number found in 0.1×0.1m subplots in treated plots in the experiment with and without litter layer over time. All treatments and all sites were pooled. Stages: S6 = June seedlings, R7, 8 = rosettes in July and August. Box-whisker plots; differences in seedling number in plots with and without litter,  $P < 0.05$ .



**Fig. 15.** Effect of litter on regeneration of *Pedicularis sylvatica* on a microscale. Differences in seedling and rosette number found in 0.1×0.1m subplots in treated plots in the experiment with and without litter layer over time. All treatments and all sites were pooled. Stages: S6 = June seedlings, R7, 8 = rosettes in July and August. Box-whisker plots; non-significant differences in seedling number in plots with and without litter.

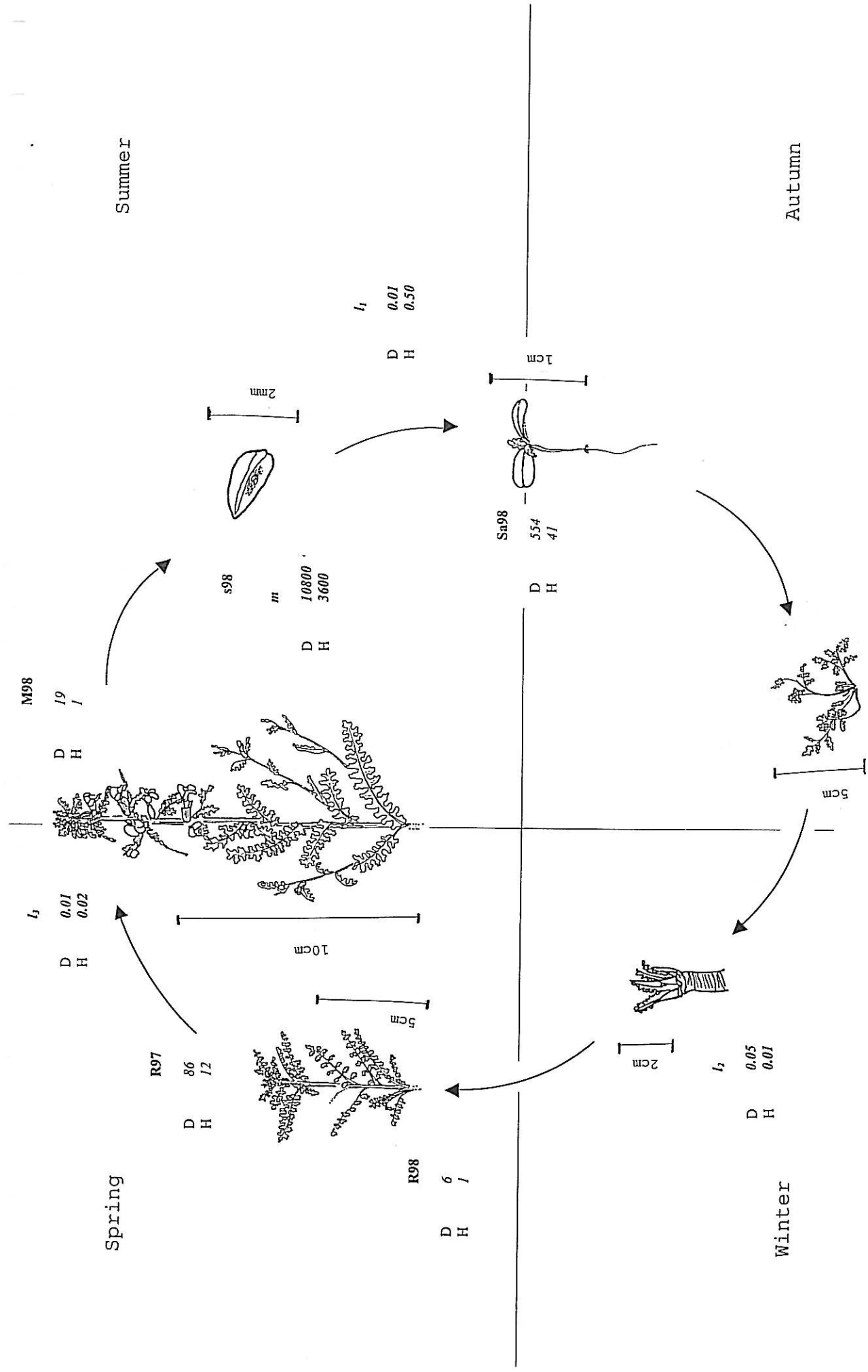


Fig. 16. Winter-annual life cycle of *Pedicularis palustris*; life table data from plot sites: D=Divorce, H=Horuice; stage - M = mothers, s = seeds; seed production is based on counts of fruits; the number of seeds per fruit was counted in five samples, with ca. 18 seeds per fruit; S = seedlings, R = rosettes, a = autumn, 97, 98 = year; m = estimated No. of seeds of all plants;  $I_1 - I_3$  = probabilities of survival of respective stages to following stage,  $R_0$  = net reproductive rate. Numbers.m<sup>2</sup>

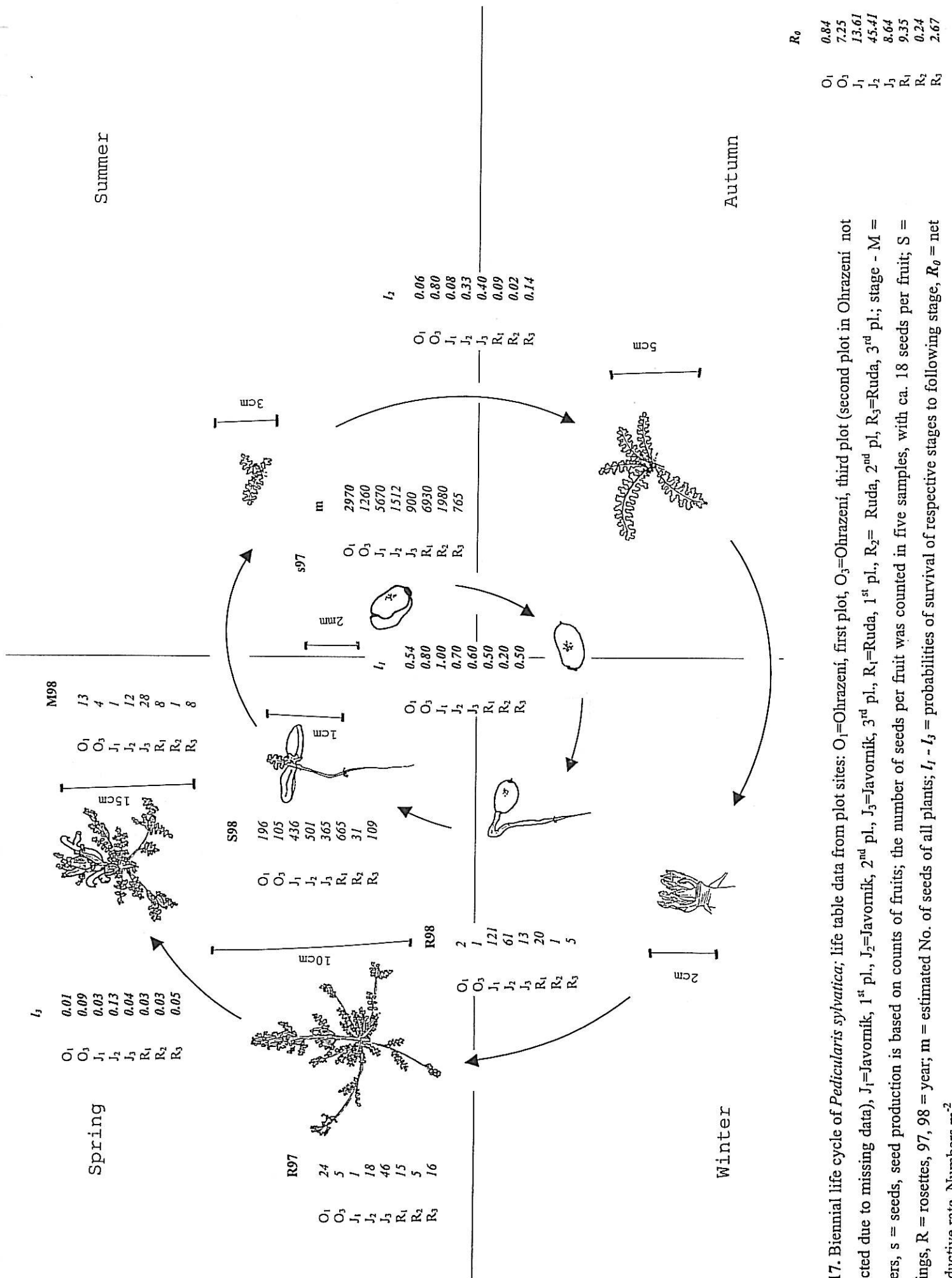


Fig. 17. Biennial life cycle of *Pedicularis sylvatica*; life table data from plot sites:  $O_1$ =Ohrazení, first plot,  $O_3$ =Ohrazení, third plot (second plot in Ohrazení not subjected due to missing data),  $J_1$ =Javorník, 1<sup>st</sup> pl.,  $J_2$ =Javorník, 2<sup>nd</sup> pl.,  $J_3$ =Javorník, 3<sup>rd</sup> pl.,  $R_1$ =Ruda, 1<sup>st</sup> pl.,  $R_2$ = Ruda, 2<sup>nd</sup> pl,  $R_3$ =Ruda, 3<sup>rd</sup> pl.; stage - M = mothers, s = seeds, seed production is based on counts of fruits; the number of seeds per fruit was counted in five samples, with ca. 18 seeds per fruit; S = seedlings, R = rosettes, 97, 98 = year; m = estimated No. of seeds of all plants;  $l_1 - l_3$  = probabilities of survival of respective stages to following stage,  $R_0$  = net reproductive rate. Numbers.m<sup>-2</sup>

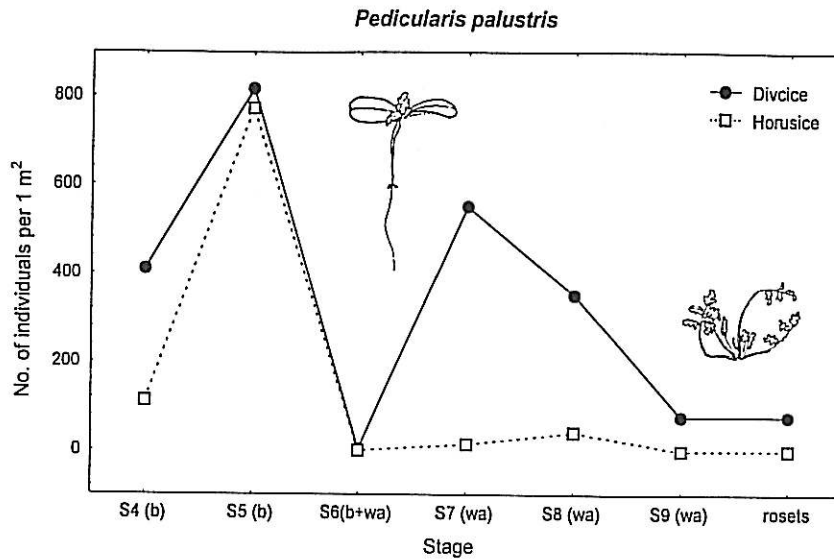


Fig. 18. Dynamics in *Pedicularis palustris* life cycles stages under natural conditions. Changes in number of individuals in 1m<sup>2</sup> of particular age stage over time at Divčice and Horusice study sites. Stages: S4 - 9 = April - September seedlings, b = biennial cohort, wa = winter annual cohort, b + wa = in June biennial and winter-annual cohorts have met in plots; most of spring seedlings of biennials died and new seedlings of winter annual plants did not emerged yet.

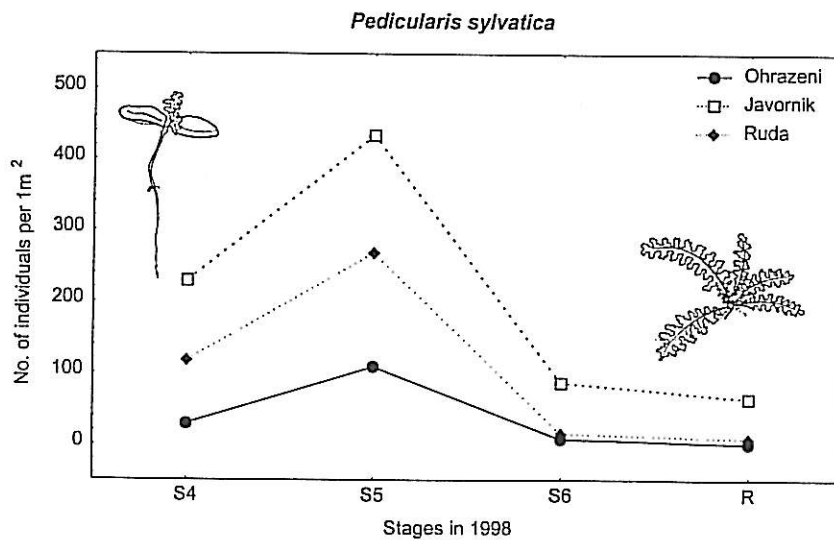
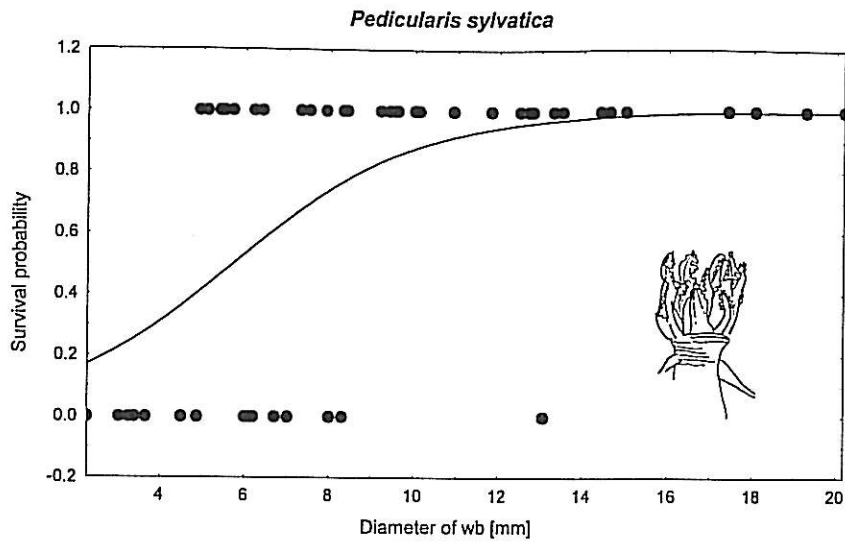


Fig. 19. Dynamics in *Pedicularis sylvatica* life cycles stages under natural conditions. Changes in number of individuals in 1m<sup>2</sup> of particular age stage over time at Ohrazení, Javorník and Ruda study sites. Stages: S4 - 6 = April - June seedlings of biennial plants.



**Fig. 20.** Survival of *Pedicularis sylvatica* rosettes. The dependence of survival probability of rosettes on the diameter of winter bud (wb);  $\chi^2 = 16.8$ ,  $P < 0.01$ ; the relationship fits a logistic curve:  $\text{survival} = \exp(-2.6 + (0.5) \cdot \text{diameter of wb}) / (1 + \exp(-2.6 + (0.5) \cdot \text{diameter of wb}))$

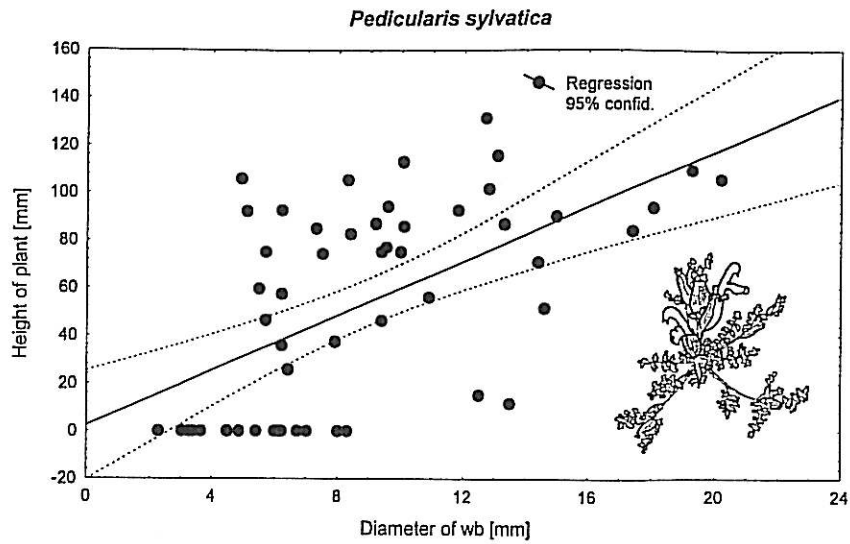


Fig. 21. Height of mature *Pedicularis sylvatica* plants in dependence on the diameter of winter bud (wb);  $r = 0.57$ , the relationship fits a regression curve: height of plant =  $2.39 + 5.76 \cdot \text{diameter wb}$ .

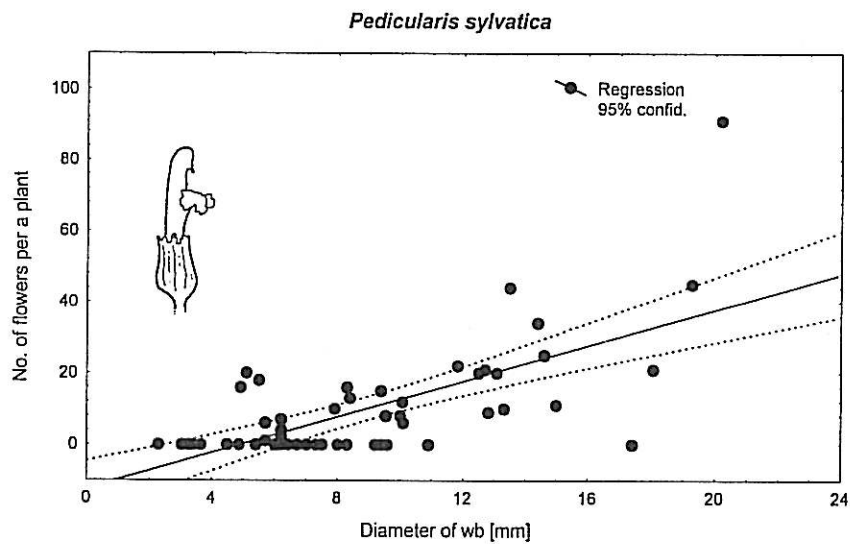


Fig. 22. Reproductive effort of *Pedicularis sylvatica* (in number of flower per a plant; all observed flowers were fertilized and seeds were set) in dependence on on the diameter of winter bud (wb);  $r = 0.67$ ; the relationship fits a regression curve: number of flowers per a plant =  $-12.29 + 2.5 \cdot \text{wb}$ .

**Appendix 1.** List of surveyed *Pedicularis* sites and their characteristics. In **bold** sites selected for detailed demography studies.

***Pedicularis palustris***

South Bohemia:

**Dívčice** - see Table 1.

**Horusice** - see Table 1.

Kvilda - path/ woodland edge near Kvilda village; 20 km SW of Vimperk in the Šumava Mts.; 1000m.

Nová Hůrka - marshland near Nová Hůrka village; 20 km W of Kašperské Hory in the Šumava Mts.; 913m. a.s.l.

North Bohemia:

Jestřebí - wet meadow near Jestřebí village; 10 km SE of Česká Lípa; 320m a. s. l.

Jestřebí II - recovered meadow on arable land in early stage of succession near Jestřebí village; 10 km SE of Česká Lípa ; 320m a. s. l.

Ploučnice - marshland in aluvium of Ploučnice river near Žizníkov village; 5 km E of Česká Lípa; 260m a.s.l.

***Pedicularis sylvatica***

South Bohemia:

**Ohrazení** - see Table 1.

Ohrazení II - wet meadow near Ohrazení village, 10 km SE of České Budějovice; 510m a. s. l.

Kaliště - wet meadow near Kaliště village, 8 km SE of České Budějovice; 500m a. s. l.

**Javorník** - see Table 1.

Javorník II - abandoned meadow near Javorník village, 11 km NW of Vimperk; 840m a. s. l.

Králova - wet meadow near Račov village, 7 km NW of Vimperk; 810m a. s. l.

Králova II - wet meadow near Račov village, 7 km NW of Vimperk; 805m a. s. l.

Vacov - wet meadow near Vacov village, 12 km NW of Vimperk; 760m a. s. l.

**Ruda** - see Table 1.

Šejby - wood path near Šejby village, 8 km S of Nové Hrady; 600m a. s. l

Šejby II - wood path near Šejby village, 9 km S of Nové Hrady; 610m a. s. l

Kvilda - path/ woodland edge near Kvilda village; 20 km SW of Vimperk in the Šumava Mts.; 1000m. a.s.l.

Jílovice - wet meadow in aluvium of the Stropnice river, 10 km W of Suchod n. Lužnicí; 460m a.s.l.



**Appendix 2.** List of bryophyte species recorded by removal in manipulative experiment:

***Pedicularis palustris***

Dívčice sown and unsown plots - *Amblystegium varium*, *Brachythecium rutabulum*, *Ceratodon purpureus*,  
*Climacium dendroides*, *Drepanocladus revolvens*.

Horusice - *Calliergonella cuspidata*, *Drepanocladus revolvens*, *Rhytidiadelphus squarrosus*, *Scleropodium purum*.

***Pedicularis sylvatica***

Ohrazení sown plots - *Aulacomnium palustre*, *Chiloscyphus coadunatus*, *Climacium dendroides*, *Hylocomium splendens*, *Polytrichum commune*, *Rhytidiadelphus squarrosus*, *Scleropodium purum*.

Ohrazení unsown - *Aulacomnium palustre*, *Climacium dendroides*, *Hylocomium splendens*, *Polytrichum commune*,  
*Rhytidiadelphus squarrosus*, *Scleropodium purum*.

Javorník sown and unsown - *Aulacomnium palustre*, *Brachythecium rivulare*, *Bryum pseudotriquetrum*, *Calliergon sramineum*, *Calliergonella cuspidata*, *Hypnum cupressiforme*, *Philonotis fontana*.

Ruda - *Aulacomnium palustre*, *Climacium dendroides*, *Polytrichum formosum*, *Rhizomnium punctatum*,  
*Rhytidiadelphus triquetrus*, *Scleropodium purum*.

**Appendix 3.** List of species shown in Fig. 1; species codes and full names.

Sp. code	Species name	Sp. code	Species name
<i>Agro tenu</i>	<i>Agrostis tenuis</i>	<i>Lysi vulg</i>	<i>Lysimachia vulgaris</i>
<i>Betu pend juv.</i>	<i>Betula pendula juvenils</i>	<i>Ment arve</i>	<i>Mentha arvensis</i>
<i>Briz medi</i>	<i>Briza media</i>	<i>Moli caer</i>	<i>Molinia caerulea</i>
<i>Care grac</i>	<i>Carex gracilis</i>	<i>Pice abie</i>	<i>Picea abies</i>
<i>Cirs hete</i>	<i>Cirsium heterophyllum</i>	<i>Poly amph</i>	<i>Polygonum amphibium</i>
<i>Crep palu</i>	<i>Crepis paludosa</i>	<i>Pote errec</i>	<i>Potentilla erecta</i>
<i>Epil aden</i>	<i>Epilobium adenocaulon</i>	<i>Sali auri</i>	<i>Salix aurita</i>
<i>Equi fluv</i>	<i>Equisetum fluviatile</i>	<i>Sali cine</i>	<i>Salix cinerea</i>
<i>Holc lana</i>	<i>Holcus lanatus</i>	<i>Sang offi</i>	<i>Sanguisorba officinalis</i>
<i>Junc tenu</i>	<i>Juncus tenuis</i>	<i>Vero offi</i>	<i>Veronica officinalis</i>
<i>Leon autu</i>	<i>Leontodon autumnalis</i>		

Appendix 4. List of frequent species recorded at study sites both *Pedicularis* species; frequent species occurred least in two of three study plots of 1 m<sup>2</sup>; in () is the total number of species found in study plots in each category; frequent species followed; \*marked species occurred in all sites

#### *Pedicularis palustris*

##### Divčice

- grasses (4): *Deschampsia cespitosa*, *Festuca rubra*, *Molinia caerulea*.
- other graminoids (2): *Carex gracilis*\*, *C. panicea*, *Eriophorum angustifolium*.
- forbs (9): *Cirsium palustre*, *Equisetum fluviatile*\*, *Galium uliginosum*, *Lychnis flos-cuculi*, *Lysimachia vulgaris*\*, *Peucedanum palustre*, *Sanguisorba officinalis*, *Taraxacum sp.*, *Veronica scutellata*.
- legums (1): *Lathyrus pratensis*.

##### Horusice

- grasses (2): *Holcus lanatus*, *Poa palustris*.
- other graminoids (2): *Carex gracilis*\*, *Juncus effusus*.
- forbs (4): *Equisetum fluviatile*\*, *Galium palustre*, *Lysimachia vulgaris*\*, *Ranunculus repens*.

#### *Pedicularis sylvatica*

##### Ohrazení

- grasses (8): *Anthoxanthum odoratum*, *Briza media*\*, *Cynosurus cristatus*, *Danthonia decumbens*, *Festuca ovina*, *Festuca rubra*\*, *Holcus lanatus*, *Molinia caerulea*.
- other graminoids (9): *Carex hartmanii*, *C. nigra*, *C. pallescens*, *C. panicea*, *C. pilulifera*, *C. pulicaris*, *Luzula campestris*.
- forbs (23): *Betonica officinalis*, *Calluna vulgaris*, *Calycocorsus stipitatus*, *Cerastium holosteoides*, *Galium boreale*, *Plantago lanceolata*, *Potentilla erecta*, *Ranunculus auricomus*\*, *Sanguisorba officinalis*, *Scorzonera humilis*, *Selinum carvifolia*, *Succisa pratensis*.
- legums (2): *Vicia cracca*.

##### Javorník

- grasses (8): *Agrostis tenuis*, *Briza media*\*, *Holcus lanatus*\*.
- other graminoids (7): *Carex flava*, *C. leporina*, *C. nigra*, *Eriophorum angustifolium*.
- forbs (21): *Angelica sylvestris*, *Betonica officinalis*, *Caltha palustris*, *Filipendula ulmaria*, *Galium boreale*, *C. uliginosum*, *Myosotis nemorosa*, *Potentilla erecta*, *Ranunculus auricomus*\*, *Rumex acetosa*, *Succisa pratensis*.
- legums (1): *Trifolium dubium*, *T. pratense*, *T. repens*.

## **Ruda**

- **grasses (9):** *Agrostis tenuis*, *Anthoxanthum odoratum*, *Arrhenantherum elatius*, *Briza media*\*, *Holcus lanatus*\*, *Nardus stricta*, *Poa palustris*.
- **other graminoids (5):** *Carex echinata*, *C. nigra*, *Juncus articulatus*.
- **forbs (17):** *Angelica sylvestris*, *Calluna vulgaris*, *Cirsium palustre*, *Filipendula ulmaria*, *Leucanthemum irtutianum*, *Polygala vulgaris*, *Ranunculus auricomus*\*
- **legums (1):** *Lotus corniculatus*.