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Regeneration dynamics in populations of two hemiparasitic species in wet grasslands

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Abstract. Two semelparous biennial hemiparasites of wet grasslands, *Pedicularis palustris* and *P. sylvatica* (*Scrophulariaceae*), have been declining in the Czech Republic due to land management changes. Regeneration was studied in the field both by observation and experiment. Permanent 1-m^2 plots were set up in populations of both species in order to observe spatial patterns of established seedlings under natural conditions. A manipulative field experiment was conducted to test effects of disturbance regimes on recruitment. Treatments such as mowing, litter and moss removal, and creation of artificial gaps were performed in five replicate 0.25-m^2 plots. Seeds were sown into plots and the number of emerging seedlings was monitored over the growing season.

In the permanent plots, seedlings were clustered around mother plants, particularly in *P. sylvatica*. Seeds successfully germinated early, perhaps getting an early season advantage over neighbouring vegetation. However, high seedling mortality was found in late summer, which might be a result of self-thinning and caused by competition. In both species germination percentage in untreated control plots was low as compared to mown plots and plots with gaps. This supports hypotheses concerning the importance of available safe sites for species regeneration. A regular management regime and local soil surface disturbances seem to be important for the persistence of the two species.

Keywords: Disturbance; *Pedicularis palustris*; *Pedicularis sylvatica*; Management; Regeneration niche; Seedling recruitment.

Nomenclature: Rothmaler (1976) for vascular plants; Váňa (1997) for bryophytes.

Introduction

Pedicularis palustris and *P. sylvatica* (*Scrophulariaceae*), short-lived monocarpic species of wet grasslands, have been declining in their habitats over the last decades throughout Europe (Rosenthal & Fink 1996; Karrenberg 1998; Schmidt 1998; ter Borg 1979, 1985). The reasons of their decline in their community are of particular interest when mechanisms of species coexistence in grassland plant communities are studied (see Grime 1979; van der Maarel 1993; Palmer 1994). In the Czech Republic, these species were previously common on traditionally managed grasslands; but most populations have decreased rapidly in size or became extinct because of the cessation of management (usually mowing) or because of fertilizer application (Hendrych & Hendrychová 1989).

Successful establishment of new plants is a critical step in plant life history (regeneration niche; Grubb 1977, 1988). Differentiation of the regeneration niche is a major determinant of diversity in vegetation. Seedling recruitment of both these species is limited by the availability of safe sites (ter Borg 1979; 1985). Seedling recruitment decreases dramatically after cessation of the regular disturbance regime, such as mowing and grazing, traditionally used in European wet grasslands (Bakker 1989). We assumed that seedlings of these *Pedicularis* species recruit in gaps.

The aim of this study is to compare the regeneration dynamics of the two *Pedicularis* species. Seedling recruitment was monitored in permanent plots and the effect of disturbance regimes, including the creation of artificial gaps, was tested by the use of a manipulative experiment.

Material and Methods

Study species

Pedicularis is one of the largest genera in the family *Scrophulariaceae*, with several hundred hemiparasitic species. *P. palustris* is a hemicryptophyte with a winter bud (Hartl 1974). It occurs in irregularly mown or moderately grazed marshes, wet meadows and dune slacks (Hartl 1974). *P. palustris* prefers wet habitats such as marsh meadows, peatbogs and fens of the *Caricion lasiocarpae*, *Molinion*, *Caricion fuscae* and *Calthenion* communities (Dostál 1989). These habitats are inundated for at least several months of the year. *P. sylvatica* is a biennial, rarely perennial, hemicryptophyte with a winter bud (Hartl 1974). It occurs on moist and sandy or peaty soils within open vegetation. It is a characteristic species of the alliances *Violion caninae* and *Juncion squarrosi* and may occur also in *Caricetea canescenti-fuscae* and *Ericion tetralicis* communities (Westhoff & den Held 1969; Oberdorfer 1979; Dostál 1989). It also grows in woodland edges and paths (pers. obs.; ter Borg 1985). Both *Pedicularis* species usually behave as biennials and have short persistent seed banks (Thompson et al. 1997; ter Borg, Masselink, Jensen pers. comm.). After dispersal seeds of *P. sylvatica* will most likely germinate the following spring. Two separate cohorts of *P. palustris* can be distinguished (Watkinson & Gibson 1987). Seeds of one cohort germinate immediately after dispersal in late summer and overwinter as juveniles (winter annuals). The other cohort overwinters in a 'short persistent seed bank' (Grime et al. 1988) and germinates the following spring (biennials).

Study sites

Study sites for both species are situated in South Bohemia, Czech Republic, close to České Budějovice. Mean annual temperature is 7.8 °C and mean annual precipitation is 620 mm (Syrový 1985).

Pedicularis palustris - Dívčice

Observation and field experiments were carried out at Dívčice, 20 km northwest of České Budějovice, 49°06' N, 14°19' W, 380 m a.s.l. This site contains one of the last remaining populations in the region, which has been declining over the last five years from hundreds of generative *P. palustris* to only a few individuals (Bastl pers. comm.). The *P. palustris* population occurs at the border between a wet mesotrophic *Molinion* meadow and a *Caricion gracilis* stand.

Pedicularis sylvatica - Ohrazení

The *P. sylvatica* population was studied in a wet meadow, situated between an agricultural field and pine-oak woodland. The meadow was regularly mown until the late eighties, when it was abandoned. This meadow is located 10 km southeast of České Budějovice, 48°57' N, 14°36' E, 510 m a.s.l. The vegetation is characterized by the *Molinion* alliance.

Spatial pattern of seedling recruitment

Field observations were carried out in one 1-m^2 permanent plot, divided by a grid into 0.1 m × 0.1 m subplots within each species population. In August 1997 all fertile plants (already dead, releasing seeds, hereafter called mother plants) were marked and their position on the grid recorded. Seedlings in each subplot in the grid were counted in May 1998. Seedling spatial patterns were characterized by the variance:mean ratio, both of the number of individuals per subplot and the dependence of seedling number in a cell on the distance of the cell centre from the nearest mother plant.

Manipulative field experiment – effect of disturbance regimes on recruitment

A manipulative field experiment was started in August 1997 in each site. The experiment was arranged in five randomized complete blocks of 0.5 m × 0.5 m plots. Plots were divided into 25 subplots of 0.1 m × 0.1 m. Capsules of both species containing ripe seeds were collected in the beginning of July 1997 (*P. palustris*) and by the beginning of May 1997 (*P. sylvatica*) at the respective sites and stored at room temperature until August. 90 seeds of each species were sown by hand into the nine central subplots to minimize edge effects. By experimental sowing we can eliminate the effects of dispersal and study effects of treatments on germination and establishment only. In each block, the following treatments were used:

P. palustris: (1) untreated control; (2) mowing, where the aboveground biomass was cut and litter removed; (3) litter and moss removed without mowing; (4) small gaps were created (five gaps per plot, 5 cm in diameter cutting the sod about 3 cm deep and turning it upside down).

P. sylvatica: (1) control; (2) mowing with litter removal; (3) litter and moss removal; (4) small gaps (five gaps per plot, 5 cm in diameter) were created cutting the sod about 3 cm deep and turning it upside down; (5) large gaps (five gaps per plot, 10 cm in diameter) by cutting the sod about 3 cm deep and turning the cut portion upside down; (6) mowing, where the aboveground biomass was cut and both the litter and moss removed. In order to prevent the burying of seeds

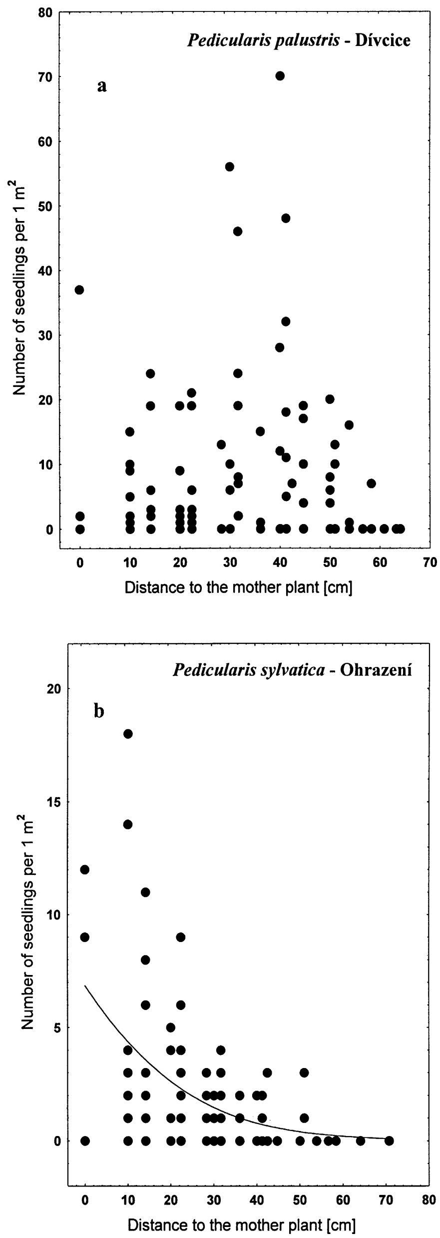

Fig. 1. Dependence of the number of seedlings in a 0.1 m × 0.1 m cell on the distance from the mother plant in **a.** *Pedicularis palustris* and **b.** *P. sylvatica*. The significant relationship ($p <$ 0.05) was fitted by LOWESS regression. Note the different scales on the y-axis.

and standing water, gaps were shallow. Small-sized gaps only were created in *P. palustris* because of the very wet conditions and in the tall vegetation large gaps would be permanently filled with water. Both small and large sized gaps could be created in the short drier grassland occupied by *P. sylvatica* to study the effect of gap size on seedling recruitment. In drier *P. sylvatica* sites the effect of moss removal in mown plots on seedling establishment could also be studied. The following mosses were found in *P. sylvatica* plots: *Aulacomnium palustre*, *Climacium dendroides*, *Hylocomium splendens*, *Polytrichum commune*, *Rhytidiadelphus squarosus*, *Scleropodium purum*.

The number of emerging seedlings was monitored monthly over the growing season from April to August. In total 25 subplots in each 0.5 m × 0.5 m plot were studied with respect to possible seed dispersion from the central nine sown subplots. Periodic sampling provided information about seedling emergence until June. July and August data provided information on seedling survival.

Data analysis

The LOWESS regression in the non-linear estimation module in STATISTICA (Anon. 1996) was used to fit the relationship between seedling density and distance from the mother plant in permanent plots. A univariate repeated measures ANOVA model in STATISTICA (Anon. 1996) reflecting the block structure of the experiment was used to analyse data from the manipulative field experiment. In the repeated measures analysis the between-subject variation corresponds to differences between observed sampling units (block and treatment) and the within-subject variation corresponds to changes in time. Data were evaluated after logarithmic transformation $x' = \log (x + 1)$. Note that with log-transformed data, the interaction of time and treatment reflects differences in relative changes in time.

Results

Spatial pattern of seedling recruitment

Seedling spatial pattern was clustered (variance:mean ratio >> 1) in both species. In *P. palustris*, the highest number of seedlings was found 30 - 40 cm from mother plants. Only a few seedlings were found either within 10 cm of mother plants or further than 60 cm (Fig. 1a). In *P. sylvatica*, the number of seedlings decreased monotonically with distance from mother plants (Fig. 1b); the relationship was significant ($p < 0.05$).

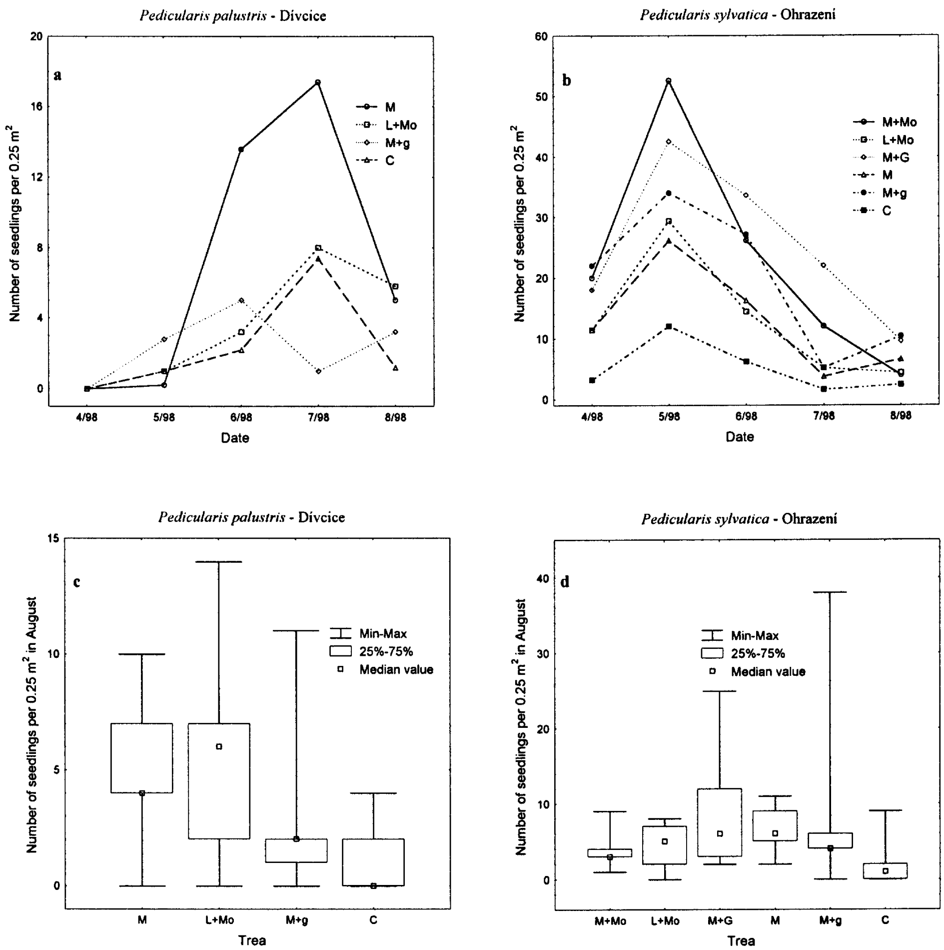

Fig. 2. Germination dynamics of *Pedicularis palustris* seedlings from April (4/98) to August (8/98) in the manipulative field experiment. **a.** *P. palustris*. Treatments were: **M**: mowing with litter removal; **L+Mo**: litter and moss removed without mowing; **M+g**: small gaps created in mown plot; **C**: control. Time × Treatment interaction was statistically significant ($p < 0.05$). For **b.** *P. sylvatica* treatments were: **M+Mo**: mowing with litter removal; **L+Mo**: litter and moss removed without mowing; **M+G**: large gaps created in mown plot; **M**: mowing with litter removal; **M+g**: small gaps created in mown plot; **C**: control. The effect of treatment was statistically significant ($p < 0.05$). Number of seedlings was average number per plot (out of 90 seeds sown). Box and whisker plots of seedling counts in August: **c.** *P. palustris*; **d.** *P. sylvatica*. Differences among treatments were not statistically significant. Note the different scales on the *y*-axis.

Manipulative field experiment – effect of disturbance regimes on recruitment

P. palustris. Seedling density increased from April to July in all treatments except in plots with gaps. The highest number of seedlings was recorded in July in mown plots (18 per 0.5m × 0.5m plot), in plots with litter and moss removed (8), and in control plots (8). From July to August the number of seedlings declined in these treatments. In plots with gaps the highest number of seedlings occurred in June (5) and some new seedlings were recorded in August (Fig. 2a). The Time × Treatment interaction was significant ($p < 0.05$) revealing differences in dynamics between treatments. High variability within treatments was found in August (Fig. 2c) and consequently differences between treatments were not significant. It should be noted that the control yielded the lowest number of seedlings surviving until the end of the season.

P. sylvatica. Germination mainly occurred in April and May in all treatments varying from 10 in control plots to 54 with moss removal. From May to August the number of seedlings in all treatments declined. However, from July to August the number of seedlings slightly increased in mown plots and in plots with small gaps (Fig. 2b). The number of seedlings differed according to treatment (significant effect of Treatment, $p < 0.05$), but the relative proportions were roughly constant over time (non-significant Time × Treatment interaction). Differences at the end of the season were not significant, probably because of the high variability within treatments (Fig. 2d). Again, the control yielded the lowest number of seedlings.

Discussion

Distribution of dispersed seeds around mother plants (called a 'seed shadow', Fenner 1992) corresponds with a clustered spatial pattern of seedlings found in both species sites. The distance of maximum seedling density can be influenced by the nature of the seed source (Fenner 1992). Differences between species are probably attributable to different plant heights. The height of fruiting *P. palustris* is 30-60 cm, however, plants usually break below the middle. Broken stems fall a distance of 20-40 cm and seeds drop out of capsules at this distance from the base of the stem. Fruiting *P. sylvatica* plants are low and drop seeds in their close vicinity. Consequences of postdispersal seed transport (hydrochory in *P. palustris* and myrmecochory in *P. sylvatica*) need further investigation.

Both species begin their life cycle much earlier than the neighbouring vegetation. We assume that optimal light conditions at this time enable the seedlings to recruit without being outcompeted (see van Tooren 1990; Špačková et al. 1998). This early germination may also be an advantage in their hemiparasitic life history.

The number of established seedlings depends on seed dispersal, germination, seedling establishment and mortality. *P. palustris* had lower germination than *P. sylvatica*. This might be caused by weather and different habitat condition. Rooy & Verhoeven (1985 unpubl.) show that seed germination of *P. palustris* is strongly influenced by water level fluctuation. They found that the best seedling establishment occurred in dry springs followed by wet summers preventing the plants from drying out. In our experimental plots high water levels in March and April 1998 caused poor germination at the beginning of the season. During a later dry period, from May to July 1998, germination percentage increased. A dry summer probably contributed to seedling mortality; in addition to the effects of self-thinning and competition from the established neighbouring vegetation. For example, gaps were exposed to direct sun and became dry during the summer. In mown plots and mown plots with litter removed, seedling establishment was successful (cf. Karrenberg 1998). The unmown control provided the worst conditions for species regeneration. Large variability within treatments probably reflects differences in microclimate, including air humidity (ter Borg 1985). *Pedicularis sylvatica* reached maximum germination in May with the lowest number of seedlings in control plots, and the highest in mown plots with moss removed and plots with large and small gaps. Seedlings of *P. sylvatica* recruited better in large-sized gaps compared to small ones. Extreme values in box and whisker for plots with gaps can be caused, in the case of *P. sylvatica*, by various microclimate and habitat differences causing variability in seedling counts. Litter removal studies (Carson & Peterson 1990; Špačková et al. 1998) have shown that created microhabitats may favour some plant species. However, our results do not show any seedling sensitivity to litter removal, even when in combination with moss removal.

For the *Pedicularis* species studied the lack of a persistent seed bank, with high spring germination and high late summer mortality can cause pronounced between-year fluctuations, making the species prone to local extinction. The seedling establishment phase is critical for population persistence (cf. Křenová and Lepš 1996) and in turn establishment is most influenced by management practices. Our experiments show a positive response of regeneration effort to most disturbance regimes, similar to other parasitic plants (Marvier & Smith 1997). Cessation of traditional management usually results in a decline of safe sites. This in turn causes suppression of seedling recruitment and can eventually lead to species extinction and a decline in species diversity.

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