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Growth, survival and generative reproduction in a population of a widespread annual hemiparasite *Melampyrum pratense*

Monika Průšová[1]*, Jan Lepš[1,2], Milan Štech[1] & Jakub Těšitel[1]**

[1] *Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-37005 České Budějovice, Czech Republic; jakub.tesitel@centrum.cz*
[2] *Institute of Entomology, Academy of Sciences of the Czech Republic*

Abstract: *Melampyrum pratense* is one of the most successful root-hemiparasitic species of temperate Europe occurring in various habitats including both forest and open communities. The species shares its life history traits (large seeds, annuality, lack of clonality) with most of other hemiparasitic Orobanchaceae. Due to lack of vegetative propagation, the reproductive success of a *M. pratense* individual largely depends on the seed production. We used an individual-based observation of ontogenetic development of plants and analysed the development of spatial distribution of individuals to reveal links between fecundity of individuals and their vegetative growth in the context of population dynamics within one growing season. We demonstrated a tight dependency of seed production on vegetative growth and survival till the end of the growing season. Plants that were still alive and big (due to a high number of lateral branches) in the end of August produced the highest numbers of seeds. These were several times higher than the population average due to positively skewed distribution of seed production across individuals. The rate of premature mortality was rather low (below 50%) once seedlings successfully emerged and was most likely caused by intraspecific competition. By contrast, moderate level of herbivory (stem clipping by grazers) had a limited effect on the survival and the inflicted biomass losses seemed compensated. Therefore, despite being an annual, *M. pratense* appears well-adapted to its life in perennial-dominated forest communities, which is also underpinned by its hemiparasitic strategy providing essential resources and allowing to avoid below-ground competition.

Key words: demography; hemiparasitism; *Melampyrum*; population; reproduction; seed

Introduction

Most of the temperate hemiparasitic Orobanchaceae occur in rather stable communities where competition or stress present the limiting factors. Species of the genus *Melampyrum* growing often in forest communities represent a typical example. Surprisingly, the vast majority of these species (all in the case of *Melampyrum*; Soó & Webb 1972) are also annuals (Těšitel et al. 2010), often the only annual species in communities dominated by perennials (Karlsson 1974; Strykstra et al. 2002). This paradox seems to be allowed by the hemiparasitic lifestyle enabling the annual hemiparasites to compete with co-occurring perennials by having access to nutrients and water obtained from the host while sparing resources otherwise needed for root system development (Karlsson 1974; Strykstra et al. 2002). The annuality have evolved independently in a number of temperate root-hemiparasitic genera (Těšitel et al. 2010) indicating an advantage of annuality in hemiparasites probably connected to a more effective resource acquisition (Ehleringer & Marshall 1995). Many hemiparasitic species have nonetheless become rare or even endangered which was caused by meadow fertilization and abandonment of traditional meadow management (mowing), i.e. factors increasing competitive pressure in the communities (Štech 2000; Svensson & Carlsson 2005; Ramsay & Fotherby 2007). Numerous annual hemiparasites are on the other hand still widespread and display broad ecological niches, some taxa even being successful invaders (van Hulst et al. 1987; Pate & Bell 2000).

Melampyrum pratense presents an example of such exceptionally successful hemiparasitic species. It displays a broad ecological niche and a wide geographical range growing in most of the forest types and several other types of herbaceous and shrubby communities of western Eurasia and central Siberia (Meusel et al. 1978). In Central Europe, it presents the most common root-hemiparasitic species (with 990 occurrences in the geographically stratified version of the Czech National Phytosociological Database; Chytrý & Rafajová 2003) occurring in forests from lowlands to the subalpine level but also common in open habitats such

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* Present address: Institute of Botany, Academy of Sciences of the Czech Republic, Section of Plant Ecology, Dukelská 135, 379 82 Třeboň, Czech Republic
** corresponding author

as dwarf-pine vegetation, alpine grasslands and peatbogs (Štech 1998, 2000). This broad ecological range is likely enabled by the ability to develop ecotypes adapted to contrasting conditions (length of growing season, nutrient availability, moisture etc.) in different environments (Wettstein 1895; Jalas 1967; Karlsson 1974; Štech 1998).

The most remarkable features of the life history of *M. pratense* comprise strict annuality, a complete lack of vegetative reproduction and the production of few heavy, resource-rich seeds (Masselink 1980; ter Borg 1985). Germination takes place in the autumn and the plant overwinters in epicotyl dormancy (i. e. partially germinated seedling with dormant epicotyl and emerged hypocotyl; Masselink 1980), which is broken in the spring when green cotyledons start to emerge. Existence of a persistent but rather short-lived seed bank has been reported in *M. pratense,* with seeds keeping their germination ability for up to several years (Masselink 1980; Heinken 2004) but these observations are largely ignored in ecological trait databases and general literature widely used as data sources by ecologists; the LEDA traitbase (Kleyer et al. 2008) and Grime et al. (2007) report a lack of seed bank and only transient seed bank with synchronous germination in spring and no long term persistence of seeds in soil respectively. *M. pratense* shares this general life history picture with numerous other temperate hemiparasitic Orobanchaceae (Těšitel et al. 2010). Bekker & Kwak (2005) compared life history traits of rare and common species in the Netherlands revealing *M. pratense* as a putative member of the rare species group, similarly to most of the other analysed hemiparasitic Orobanchaceae. This however contrasted with its rather common occurrence in the country. *M. pratense* therefore presents an interesting example of a species that is successful despite displaying traits predetermining it to be rare.

Several recent studies dealing with population ecology of *M. pratense* focused mainly on demography (Ramula 2008), seed dispersal (Heinken 2004; Winkler & Heinken, 2007) and compensatory response after damage (Lehtilä & Syrjänen 1995). Our study aims to complement this present knowledge of *M. pratense* biology by a detailed observation of development of a natural population of the species throughout the growing season. An individual-based observation allowed identification of demographic characteristics (vegetative biomass production, phenology, lifespan) affecting reproductive output, which is a fundamental component of fitness in these annual plants. Repeated observations of individuals during the season provided an opportunity to track the causes of differential reproductive output realized in late summer back to the spring, which is important in these relatively long-lived annuals. An analysis of the dynamics of the spatial distribution pattern within a population provided the study by a context of the interactions among the individuals, in particular the intraspecific competition. In addition, the natural occurrence of damage by herbivores and its influence on the reproductive output was analysed as one of the most apparent external factors affecting *M. pratense* populations. The outcomes of our study are further combined with the available literature data in order to draw an updated picture of population biology of *M. pratense.*

Material and methods

Study sites

Growth and development of *Melampyrum pratense* individuals was recorded on two nearby study sites during the whole growing season of 2009 (end of April to end of August). These sites were located in an acidophilous oak forest in Budějovice Basin in the vicinity of České Budějovice city, Czech Republic (exact geographical positions were as following: site 1: N48°57′40.0″, E14°24′29.1″, 440 m a.s.l., site 2: N48°57′27.4″, E14°23′21.8″, 440 m a. s. l.. Both sites were visited once in *ca* one month intervals (five visits in total) in order to record the growth characteristics of plants under study and obtain samples of biomass.

Design of the observations and data collection

Fifty individuals of *M. pratense* were selected at random at each of the study sites at the time of the first observation (April 23rd). These plants were marked with a tape with a unique code at the base of their stem and used for the individual-based analyses of growth and generative reproduction. The following morphological characteristics were recorded for each of these plants at each sampling date.

– number of vegetative internodes (i. e. internodes between the cotyledon node and the uppermost node bearing a pair of branches; this number is equal to the number of vegetative nodes – 1 if the cotyledon node producing branches in some cases is included in the vegetative node number)

– number of intercalary internodes (i. e. internodes between the highest pair of branches and the basalmost flowers; this number equals intercalary nodes + 1)

– number of leaves on the main stem axis

– number of abscised leaves on the main stem

– number of leaves on branches

– number of branches (first and second order) bearing at least one pair of leaves

– number of capsules on the main stem axis (incl. those from which ripe seeds had fallen out)

– number of capsules on branches (incl. those from which ripe seeds had fallen out)

Damage caused by herbivores and survival were recorded in addition to growth characteristics. These plants were finally sampled for measurements of dry weight of their biomass on August 29th when the last observation was conducted. Another independent dataset consisted of 20 randomly selected plants that were sampled at the time of each observation (except August 29th). The same morphological characteristics were recorded for each of them as in the first dataset but in addition, the dry weight of their biomass was also determined. Therefore, this second dataset could be used to calibrate the biomass production of the plants which were monitored during the whole season. Vegetative and generative biomass (fruits and flowers) were separated before further processing during the flowering and fruiting season. All biomass samples were dried at 80 °C for 24 hours and weighed immediately after drying.

A permanent plot was established on the study site 1 based on sampling of *M. pratense* individuals within randomly positioned 30×30 cm quadrats. Prior to sampling, a permanent study area with an orthogonal coordinate system of 8×10 meters was set up. Location of the sampling squares was then determined by a random generation of coordinates. Ten samples with *M. pratense* were sampled at each of the five visits of the study site 1. Zero occurrences of the species were also noted and used in the analyses of spatial distribution pattern (nonetheless, only three such samples were recorded in the first sampling on April 23$^{\mathrm{rd}}$). Dry weight of above ground vegetative biomass of all sampled plants was determined and number of produced seeds was counted.

Calibration of biomass production

Biomass production in the plants observed throughout the growing season (calibrated data-set) was estimated on the basis of their morphological characteristics obtained by non-destructive observation. The calibration between these traits and the dry-weight of biomass was conducted at each sampling date using the 20 plant calibration data-set. A multiple linear regression model including log-transformed dry weight as response and the morphological characteristics as predictors was used for this purpose. A backward selection procedure was used to select the optimal model and the Akaike Information Criterion (AIC) was employed as the quality parameter of the model. Some of the calibration models therefore included also few predictors for which partial effects were not statistically significant (when tested by an F-test). Nonetheless, this small redundancy does not introduce any bias in the results since the only purpose of the model was to acquire the best estimation of dry biomass of the calibrated data-set. The regression model was subsequently cross-validated by a jacknife procedure. 25% of data for each of the model was removed for the initial fitting of the model which was subsequently used to predict expected values of the omitted 25% of observations. This calculation was repeated 500×. The deviation between the predicted and observed values of the log-transformed dry-weight of biomass was recorded. Mean value of this deviation demonstrates the quality of the estimate. Regression coefficients obtained from the calibration data-set analysis were subsequently used for the estimation of the dry biomass of the calibrated data-set.

Reproductive output of individual plants was estimated on the basis of mean number of seeds per capsule and subsequent multiplication of this number by the number of capsules found on the plant. The mean number of seeds per capsule was estimated from a sample of 50 capsules chosen at random on July 29$^{\mathrm{th}}$. Open capsules from which seeds have fallen out remained on the plants which allowed calculation of the cumulative number of seeds produced. Therefore, its maximal recorded value could be used as a proxy measure of total seed output cross the whole growing season. In addition to seed number, their mass was also estimated based on the basis of weighing of 18 randomly chosen ripe seeds (dried at 80 ℃ for 24 h).

Statistical analyses

Linear regression models were used to analyse dependence of total seed production on amount of the vegetative biomass, other vegetative characteristics, survival and herbivory damage. Decadic logarithm of dry mass in milligrammes entered these calculations in case of both the response variable and the vegetative biomass-based predictors. Both marginal and forward selection-based partial effects of the predictors were calculated and reported.

Spatial distribution of plants was assessed by comparisons between means and variances of number of plants in sampling quadrats and by calculation of the Lloyd's index of patchiness (Lepš 1993):

$$L = 1 + \frac{\frac{var}{\bar{x}} - 1}{\bar{x}}$$

where *var* denotes variance and $\bar{x}$ mean number of individuals in a quadrat. Not only did these calculations provide information on the character of the spatial distribution of individuals, but also allowed to infer the nature of intraspecific competition in the population under study (if individuals are removed from a population at random, then the value of L does not change; decrease in L means density dependent mortality). Correlations between the number of plants per sampling square and the mean amount of vegetative/reproduction-allocated biomass of one of the sampled plants furthermore supplemented the analyses of spatial distribution.

Package R, version 2.10.1 (R Core Development Team 2009) was used for all statistical analyses.

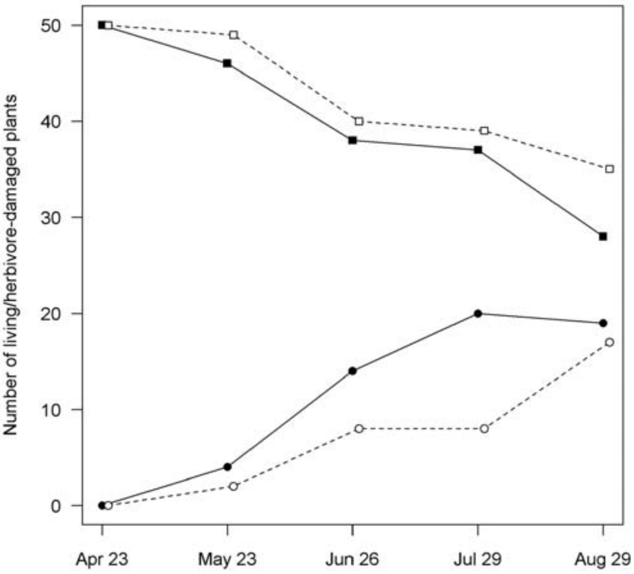

Fig. 1. Survival of observed plants and damage (stem clipping) by herbivores during the growing season. Boxes indicate number of living plants of the monitored dataset found on sites during the growing season while circles indicate how many of these were damaged by herbivores. Data of site 1 are depicted by filled symbols while open symbols represent site 2. The total starting number of individuals was 50 on each site (on April 23$^{\mathrm{rd}}$).

Results

Individual-based observation of the ontogeny and reproduction

More than one half of the labelled plant individuals survived until the end of the growing season on both study sites (Fig. 1). The highest values of mortality were recorded in the late spring between the end of May and the end of June and in the end of the season in August. This pattern was consistent at both study sites. A substantial part of the studied plants was damaged by stem clipping inflicted by grazing deer, which however mostly did not cause death of affected plants.

The calibration model of vegetative biomass production in the individual-based observations (Table 1)

Table 1. Calibration table summarizing linear models used for the calculation of vegetative dry mass of plants under study. The influence of individual morphological traits on the biomass weight is indicated by regression slopes. Statistical significance of model terms is displayed using following symbols +: p = 0.05–0.11; *: $p < 0.05$; **: $p < 0.005$). Df 1 – model degrees of freedom. Df 2 – residual degrees of freedom). Mean deviation from the calculated value of vegetative dry mass is based on the cross-validation procedure.

	Number of 1st order branches	Number of 2nd order branches	Number of leaves	Number of leaves on the main stem axis	Number of leaves abscissed from the main stem axis	Number of leaves on branches	Intercept	Adjusted r^2	F	Df 1	Df 2	p	Mean deviation (mg)
Site 1													
April 23			0.1313**				0.5295	0.462	17.34	1	18	<**0.001**	2.62
May 23			0.1214**				0.2459	0.491	19.33	1	18	<**0.001**	3.25
June 26	0.0949**	0.0381+		−0.0446*	−0.0735*		1.4722	0.855	29.03	4	15	<**0.001**	1.98
July 29	0.0448**			−0.0251*		0.0073**	1.5449	0.805	27.18	3	16	<**0.001**	1.98
Site 2													
April 23			0.1417**				0.5399	0.729	49.56	1	17	<**0.001**	2.23
May 23			0.1268**				0.3402	0.697	44.83	1	18	<**0.001**	4.14
June 26	0.0394**			−0.0598*	−0.0628*	0.008*	1.7327	0.758	15.88	4	15	<**0.001**	3.24
July 29	0.1233**	0.0433+		−0.1165*	−0.1124**	0.0042*	1.9151	0.817	17.98	5	14	<**0.001**	3

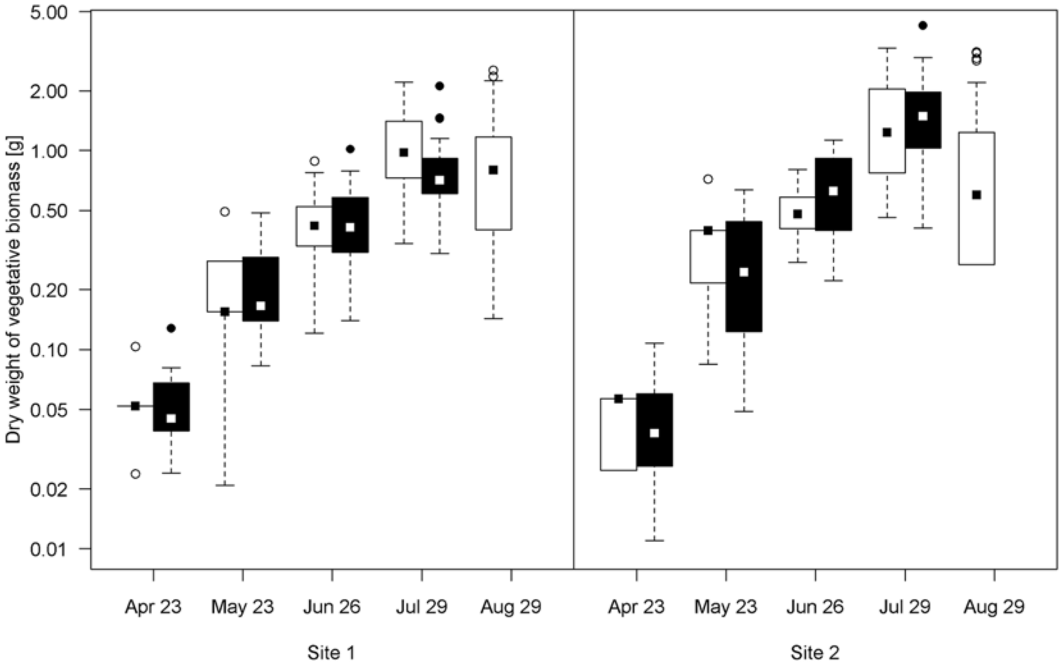

Fig. 2. Dynamics of estimated and measured vegetative dry mass of individual plants during the growing season at the two study sites. Values for the calibration dataset are displayed by black box-and-whisker plots while data for calibrated dataset are displayed by white box-and-whisker plots (displaying median, interquartile range, adjacent extremes, and outliers). The values reported on August 29 are based on direct measurements of the calibrated dataset. Note the log scale of y-axis.

provided accurate and realistic estimates of biomass production throughout the growing season. The model achieved generally high values (up to *ca* 80%) of explained variability, particularly for the June and July data collections. The mean deviation detected by the cross-validation procedure mostly reached only few percent of absolute biomass production (cf. Table 1 and Fig. 2). In addition, estimated dry mass generally agreed with values obtained by direct weighing of the calibration data-set.

Calibration functions of the relationships between the amount of dry mass and morphological characteristics were closely similar on both study sites. The total number of leaves was shown to be the only predictor with a significant effect in the beginning of the growing season. Later, in June and July, the number of branches

Table 2. Marginal effects of individual explanatory variables on total seed production based on individual regressions fitted separately for each of the predictors at sites 1 and 2. NAs stand for an invariable predictor (i.e. no stem clipping occurred on this site in July) for which no model could be fitted. Statistically significant regression results ($p < 0.05$) are displayed in bold. Number of residual degrees of freedom was 35 and 38 in each of the individual tests in site 1 and 2 respectively.

Explanatory variable	r^2	F	Df	p	Effect direction
Site 1					
Number of vegetative internodes	0.04	1.33	1,35	0.257	
Flowering in June	0.03	1.12	1,35	0.297	
Alive in August	0.28	13.32	1,35	**0.001**	+
Stem clipping by herbivores – June	0.01	0.27	1,35	0.606	
Stem clipping by herbivores – July	0.06	2.20	1,35	0.147	
Stem clipping by herbivores – August	0.02	0.75	1,35	0.393	
Dry weight of vegetative biomass – April	0.06	2.18	1,35	0.149	
Dry weight of vegetative biomass – May	0.17	7.09	1,35	**0.012**	+
Dry weight of vegetative biomass – June	0.24	11.35	1,35	**0.002**	+
Dry weight of vegetative biomass – July	0.32	16.72	1,35	< **0.001**	+
Dry weight of vegetative biomass – August	0.40	23.28	1,35	< **0.001**	+
Site 2					
Number of vegetative internodes	0.02	0.85	1,37	0.362	
Flowering in June	0.07	2.96	1,37	0.094	
Alive in August	0.27	13.92	1,37	**0.001**	+
Stem clipping by herbivores – June	0.04	1.40	1,37	0.245	
Stem clipping by herbivores – July	NA	NA	0	NA	
Stem clipping by herbivores – August	0.11	4.72	1,37	**0.036**	–
Dry weight of vegetative biomass – April	0.24	11.62	1,37	**0.002**	+
Dry weight of vegetative biomass – May	0.08	3.44	1,37	0.072	
Dry weight of vegetative biomass – June	0.07	2.90	1,37	0.097	
Dry weight of vegetative biomass – July	0.26	13.12	1,37	**0.001**	+
Dry weight of vegetative biomass – August	0.52	39.42	1,37	< **0.001**	+

had the most pronounced effect and the dependence on the number of leaves was more complex (Table 1).

The ontogeny of the plants was fairly similar on both study sites. Cotyledons and 0–2(–4) stem leaves were developed at the moment of the first observation on April 23rd. By May 23rd, most of the plants had developed branches some of which grew from the cotyledon node. The highest values and variability of dry-weight of vegetative biomass were recorded in July (Fig. 2). Abscission of senescent leaves started in the end of July, nonetheless its intensity was highest in the end of the growing season when it caused most of the decline of biomass weight estimate between July and August data collection (Fig. 2).

Flowering was first noted on the main plant axis during the observation on June 26th and the fruiting season started at around the July observation when first ripe capsules with fully developed seeds were recorded. We counted 121 seeds in a sample of 50 randomly chosen capsules resulting in a mean of 2.42 seeds per capsule and the mean dry-weight of ripe seeds was 4.95 mg (standard deviation 1.22). Seeds started to fall out of the capsules on the main plant axis after having ripened, while flowers on branches started flowering which peaked in the first decade of August. This resulted in the second fruiting period in the end of August captured by the August observation. In general, the month of August can be considered as the key period of the fruiting season during which the number of produced seeds substantially increased (Fig. 3). The total number of seeds in individual plants displayed a positively skewed distribution. Most of the plants produced sub-average or average number of seeds while few of them managed to achieve high reproductive output (Fig. 3). This pattern was particularly pronounced in site 1 where one exceptionally successful plant managed to produce almost 300 seeds (compared to the mean and median seed production of 72.5 and 53.2 seeds per plant respectively).

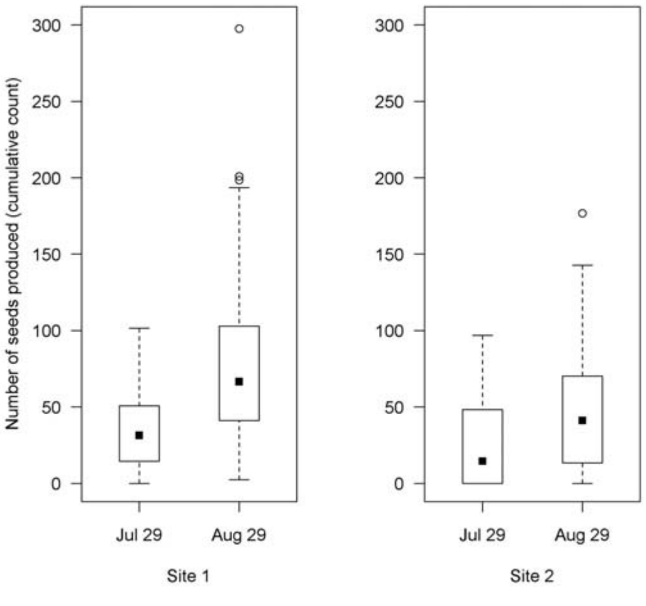

Fig. 3. Cumulative counts of seeds produced by an individual plant in the indicated moments of the fruiting season.

The amount of seeds produced was predominantly connected with the vegetative dry mass (Table 2). In addition, survival till August was another universal factor strongly increasing the reproductive output. Sur-

Table 3. Summary of the linear model describing dependence of total seed production on vegetative traits and survival variables in sites 1 and 2. Individual terms entering the model were selected by the forward selection procedure. Whole models summaries – site 1: adjusted $r^2 = 0.615$, $F_{(4,32)} = 15.4$, $p < 0.001$, site 2: $r^2 = 0.704$, $F_{(4,34)} = 23.56$, $p < 0.001$.

Explanatory variable	Regression slope	Df	Sum Sq.	F	p
Site 1					
Dry weight of vegetative biomass – July	0.34	1	3.99	30.26	< 0.001
Dry weight of vegetative biomass – August	1.10	1	2.25	17.08	< 0.001
Alive in August	−2.47	1	1.19	9.02	0.005
Flowering in June	0.32	1	0.69	5.23	0.029
Residuals		32	4.22		
Site 2					
Dry weight of vegetative biomass – August	0.77	1	7.42	66.14	< 0.001
Stem clipping by herbivores – August	−0.36	1	1.84	16.42	< 0.001
Flowering in June	0.32	1	0.81	7.23	0.011
Alive in August	−1.04	1	0.50	4.43	0.043
Residuals		34	3.81		

Table 4. Mean and variance of the number of plant individuals per sampled square and the Lloyd's index value in the course of the growing season.

Sampling date	Mean number of plants per square	Variance	Lloyd's index
April 23	1.8	2.808	1.282
May 23	4.0	5.556	1.097
June 26	3.4	1.156	0.806
July 29	2.3	1.789	0.903
August 29	1.4	0.489	0.535

prisingly, only a small negative effect of stem clipping by herbivores was detected, and just in site 2. Complete models describing the dependence of reproductive success on morphological and phenological characteristics (Table 3) identified vegetative biomass in the second half of the growing season (July, August) as the most influential predictors. Early flowering (detection of flowers in the end of June) had an additional positive effect on the number of seeds. Survival in August had on the contrary a strong negative partial effect which is in a clear disagreement with its positive marginal effect. This can be however explained as an artifact introduced by the character of the August vegetative biomass variable which contained zeros for plants that died before August 29th. A slight negative partial effect of herbivory was again detected only in site 2.

Dynamics of spatial pattern and density dependence of growth

The mean number of plants per sampling square, the variance of this value and Lloyd's index first increased between the first two observations focused on the development of spatial structure of the population (Table 4). All these values however showed a negative trend in the course of the rest of the growing season indicating a gradual density-dependent mortality of plants and a shift from an aggregated to a regular spatial distribution of individuals. Particularly pronounced declines of the Lloyd's index were recorded on June 26th and August 29th corresponding with the peaks of mortality of the individuals which we tracked (Fig. 1).

The relationship between the number of individuals sampled in a sampling square and the mean dry mass per plant within the sampling square displayed only slight and statistically non-significant negative tendencies across the whole reproductive season (April 23rd: $r = -0.155$, $p = 0.669$, May 23rd: $r = -0.437$, $p = 0.207$, June 26th: $r = -0.258$, $p = 0.472$, July 29th: $r = -0.147$, $p = 0.685$, August 29th: $r = -0.370$, $p = 0.292$). A similar negative non-significant dependency was observed between mean fecundity and number of plants within the square during the fruiting season (July 29th: $r = -0.239$, $p = 0.507$, August 29th: $r = -0.479$, $p = 0.162$).

Discussion

Survival and growth

The investigated population of *Melampyrum pratense* was characterized by a rather high survival of individuals with most of the plants reaching maturity. This agrees with conclusions of other population studies (Masselink 1980; Eliáš 1986; Heinken 2004; Ramula 2008) conducted on various sites across Europe (and also with those dealing with other *Melampyrum* species, Matthies 1991) and can be hence considered as a general characteristic of the population biology of the species. Although a thinning experiment would be required to draw a complete picture of competitive relationships among *M. pratense* individuals, the present data clearly suggest presence of density dependence in its populations. The intraspecific competition however appears to act by an increase of mortality rather than by decrease of plant growth rate, which was also observed in populations of other hemiparasites, *Rhinanthus minor* (Mudrák & Lepš 2010) and *R. angustifolius* (de Hullu et al. 1985). This effect of competition can be hypothesized to be related with lack of resource storage organs; instead, the resources are rapidly invested into growth (or reproduction) in these hemiparasites.

The population of *M. pratense* under study displayed an effective temporal exploitation of the growing season with the peak of vegetative growth in July and highest offspring production following in August just before the death of plants in the end of August/beginning of September. The long period of vegetative growth allowed plants to build rather large leaf area producing resources that can be used for seed production. In addition, the autumn germination and epicotyl dormancy (Masselink 1980) allows a rapid development of the seedlings in spring, which is particularly beneficial for populations of deciduous forests (such as the population under study) taking advantage of full light irradiation before the development of leaves of the canopy trees. The long lifespan (for an annual) and late reproduction can nonetheless be a risky strategy since an eventual premature death can prevent plants from producing any offspring at all, particularly in the case of delicate plants whose ability of vegetative regrowth after damage is fairly limited (Klimešová & Klimeš 2007). Despite the high prevalence of damage by grazing herbivores (deer), this rarely led to death of the plants. Moreover, the generally low influence of herbivory on fecundity suggests that the plants were able to compensate for the inflicted losses of biomass and reproductive organs by an increased development of lateral branches. On the other hand, a really intense herbivory pressure could be hypothesised to have a more detrimental effect on the population (ter Borg, 1985; Lehtilä & Syrjänen, 1995).

Generative reproduction

Fecundity of the observed plants was rather low in terms of count of seeds produced. On the other hand, the reproductive output appears fairly high if the heavy weight (*Melampyrum* seeds are the heaviest among related genera; Matthies 1991; Těšitel et al. 2011) of the seeds is considered. Seed production is closely linked to the size of the vegetative part of plant individuals depending closely on the dry mass during the late summer fruiting season. However, plant size in spring also had a significant positive effect on seed production (Table 2), although this effect was not included in the final models due to colinearity with the vegetative plant size in summer. This suggests that the total reproductive output and hence also fitness is dependent on vegetative growth across the whole lifespan. In this respect, it is quite likely that differential rate of early development are underpinned by quality of attachment to the host (Cameron & Seel 2007) since otherwise all individuals occur on the same site and the intensity of competition for light potentially affecting the seedlings in the spring period (Těšitel et al. 2011) is minimal due to the very open forest understory.

Fig. 4. Dormant seeds recovered at the study site 1, May 9th 2010.

If more or less stable population census is assumed in the population under study (which is quite realistic since *M. pratense* is a well-established omnipresent species in local woodlands), a substantial seed overproduction becomes apparent. Transition from the stage of seed to an emerged seedling must be hence the most critical stage of life of *M. pratense* given the rather low mortality of emerged plants. It is quite likely that resource rich seeds are predated by various animals, e.g. rodents as observed by Masselink (1980) and Gibson (1993). Presence of a substantial persistent (at least one year) seedbank was however also detected, which is in agreement with earlier studies (Masselink 1980; Heinken 2004; Ramula 2008). During a soil surface investigation in the spring following the season when the observations took place, a cluster of non-germinated yet apparently viable seeds was recovered in the leaf litter at the base of several *M. pratense* seedlings (Fig. 4). These seeds were subsequently transferred on moist filter paper in a Petri dish and incubated at 4℃ resulting in their germination 2.5 months later. The evidence for a persistent seed bank in *M. pratense* now comes from a number of localities (Masselink 1980; Heinken 2004) suggesting that it is a universal trait of the species (as well as many of its congeners; Curtis & Cantlon 1968; Matthies 1991; Dalrymple 2007), which should be established in ecological databases and general literature. A seed bank that is viable for several years certainly presents an important feature preventing local extinctions of the species under adverse conditions, e.g. extreme summer drought (Eliáš 1986). On the other hand, we can expect that the large nutritious seeds will be target of predation, and the seed bank, if not amended with new seeds, will undergo rather fast exponential decline. However, the chance that two or even more subsequent years are extremely adverse is rather low, and the persistence of seed bank is undoubtedly sufficient to overcome a single extreme year.

Similarly to most of its relatives of the Rhinanthoid clade of Orobanchaceae, *M. pratense* displays so called seasonal variation, i.e. genetically-based variation in plant architecture that is closely linked with phenology of the plants (in particular timing of reproduction period). The seasonal variation is likely to present the key feature underpinning the broad ecological niche of the species since populations occurring in different habitats tend to differ in their seasonal morphological characters, namely the number of vegetative internodes and the closely related number of branches (Štech 1998), just like in other related species (e.g. *Melampyrum sylvaticum*, Těšitel 2005; *Rhinanthus glacialis,* Zopfi 1995; *Euphrasia rostkoviana* Zopfi 1998; various *Euphrasia* species, Karlsson 1974). Most of the studies dealing with seasonal variation focused on various biotic and abiotic factors limiting the values of seasonal characters mostly concluding on the key roles of the length of growing season and presence of disturbance (e.g. mowing, grazing of grasslands) in this respect. In this study, we investigated a population that is not affected by any detrimental disturbance that could substantially increase mortality rate and grows at sites with rather long growing season. We have demonstrated the effect of the seasonal characters on fecundity within a particular population of *M. pratense* by revealing the link among seed production, vegetative growth of a plant and its architecture, in particular number of branches. The production of lateral inflorescences on branches has several apparent advantages increasing the reproductive output. i) It allows parallel production of multiple fruits, which is fairly restricted on a single inflorescence due to developmental constrains. ii) Branches provide an excellent backup if the main inflorescence is clipped by herbivory. iii) Branches allow better exploitation of space and hence more effective sunlight exposition of leaves. Furthermore, large plants with many branches have a greater chance to produce several times more seeds compared to the average due to the positively skewed seed production (Fig. 3; also observed in other *Melampyrum* species, Matthies 1986). Although we did not detect any direct effect of the number of vegetative internodes on fecundity this parameter underpins the upper limit for the number of first order branches, which is the plant characteristics most closely linked with vegetative biomass production during the summer flowering and fruiting period (Table 1). Apparently, this is why populations of *M. pratense* (and other hemiparasites) growing on sites with stable favourable conditions across the whole growing season tend to have higher numbers of internodes and branches (ter Borg 1972; Zopfi 1995; Štech 1998; Zopfi 1998; Těšitel 2005) despite the moderate risk of premature death and no offspring production due to delayed flowering.

Conclusion

This study presents principal features of population biology of *Melampyrum pratense* growing under undisturbed conditions in a site with long growing season. These include rather low premature mortality rate of successfully established seedlings, tight relationship between vegetative growth and seed production and positively skewed distribution of total seed production per plant. Observed moderate herbivory pressure appeared rather well compensated by increased branch growth. Performance of individuals was more limited by intraspecific competition manifesting itself as increased premature mortality. *M. pratense* displayed an optimal temporal exploitation of the growing season gathering resources and building photosynthetically active area in its beginning, which was subsequently used for generative reproduction in its second half. Therefore, despite being an annual, *M. pratense* appears well-adapted to the life in perennial-dominated forest communities which is also underpinned by its hemiparasitic strategy providing essential resources and allowing to avoid below-ground competition.

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References

Bekker R.M. & Kwak M.J. 2005. Life history traits as predictors of plant rarity, with particular reference to hemiparasitic Orobanchaceae. Folia Geobot. **40:** 231–242.

Cameron D.D. & Seel W.E. 2007. Functional anatomy of haustoria formed by *Rhinanthus minor*: linking evidence from histology to isotope tracing. New Phytol. **174:** 412–419.

Chytrý M. & Rafajová M. 2003. Czech National Phytosociological database: basic statistics of the available vegetation-plot data. Preslia **75:** 1–15.

Curtis E.J.C. & Cantlon J.E. 1968. Seed Dormancy and Germination in *Melampyrum lineare*. Am. J. Bot. **55:** 26–32.

Dalrymple S.E. 2007. Biological flora of the British Isles: *Melampyrum sylvaticum* L. J. Ecol. **95:** 583–597.

de Hullu E., Brouwer T. & ter Borg S.J. 1985. Analysis of the demography of *Rhinanthus angustifolius* populations. Acta Bot. Neerl. **34:** 5–22.

Ehleringer J.R. & Marshall J.D. 1995. Water relations, pp. 125–140 In: Press M.C. & Graves J.D. (eds), Parasitic plants. Chapman & Hall, London.

Eliáš P. 1986. Effects of drought on population dynamics of *Melampyrum pratense* L. Biologia **41:** 57–86.

Gibson W. 1993. Selectivity advantages to hemiparasitic-annuals, genus *Melampyrum*, of seed-dispersal mutualism involving ants: II. Seed predator avoidance. Oikos **67:** 345–350.

Grime JP., Hodgson J.G. & Hunt R. 2007. Comparative plant ecology, a functional approach to common British species, second edition. Castlepoint Press, Colvend Dalbeattie.

Heinken T. 2004. Migration of an annual myrmecochore: a four year experiment with *Melampyrum pratense* L. Pl. Ecol. **170:** 55–72.

Jalas J. 1967. Populationsstudien an *Melampyrum pratense* L. in Finnland. III. Merkmalsverbreitung und Taxonomie. Ann. Bot. Fenn. **4:** 486–536.

Karlsson T. 1974. Recurrent ecotypic variation in Rhinanthae and Gentianaceae in relation to hemiparasitism. Bot. Notiser **127:** 527–539.

Kleyer M., Bekker R.M., Knevel I.C., Bakker J.P, Thompson K., Sonnenschein M., Poschlod P., van Groenendael J.M., Klimeš L., Klimešová J., Klotz S., Rusch G.M., Hermy M., Adriaens D., Boedeltje G., Bossuyt B., Dannemann A., Endels P., Götzenberger L., Hodgson J.G., Jackel A-K., Kühn I., Kunzmann D., Ozinga W.A., Römermann C., Stadler M., Schlegelmilch J., Steendam H.J., Tackenberg O., Wilmann B., Cornelissen J.H.C., Eriksson O., Gernier E. & Peco B. 2008. The LEDA Traitbase: A database of life-history traits of Northwest European flora. J. Ecol. **96:** 1266–1274.

Klimešová J. & Klimeš L.2007. Clo-Pla3 – database of clonal growth of plants from Central Europe. http://clopla.butbn.cas.cz/. (Accessed 10.12.2011)

Lehtilä K. & Syrjänen K. 1995. Compensatory responses of two *Melampyrum* species after damage. Func. Ecol. **9:** 511–517.

Lepš J. 1993. Taylor's power law and measuring variation in the size of populations in space and time. Oikos **68:** 349–356.

Masselink A.K. 1980. Germination and seed population in dynamics in *Melampyrum pratens.* Acta Bot. Neerl. **29:** 451–468.

Matthies D. 1986. Untersuchungen zur Vergesellschaftung und Populationsbiologie von *Melampyrum arvense* L. Tuexenia **6:** 3–20.

Matthies D. 1991. Die Populationsbiologie der annuellen Hemiparasiten *Melampyrum arvense*, *Melampyrum cristatum* und *Melampyrum nemorosum.* Ph.D. thesis, Ruhr-Universität Bochum.

Meusel H., Jäger E., Rauschert S. & Weinert E. 1978. Vergleichende Chorologie der zentraleurpäishen Flora, vol. 2. VEB Gustav Fischer Verlag, Jena.

Mudrák O. & Lepš J. 2010. Interactions of the hemiparasitic species *Rhinanthus minor* with its host plant community at two nutrient levels. Folia Geobot. **45:** 407–424.

Pate J.S. & Bell T.L. 2000. Host associations of the introduced annual root hemiparasite *Parentucellia viscosa* in agricultural and bushland settings in western Australia. Ann. Bot. **85:** 203–213.

R Core Development Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org. (accessed 10.9.2010).

Ramsay P.M. & Fotherby R.M. 2007. Implications of the spatial pattern of Vigur's Eyebright (*Euphrasia vigursii*) for heathland management. Basic Appl. Ecol. **8:** 242–251.

Ramula S. 2008. Responses to the timing of damage in an annual herb: Fitness components versus population performance. Basic Appl. Ecol. **9:** 233–242.

Soó R., Webb D.A. 1972. *Melampyrum* L. pp. 253–257. In: Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (eds), Flora Europaea 3, Cambridge Univ. Press, Cambridge.

Strykstra R.J., Bekker R.M. & van Andel J. 2002. Dispersal and life span spectra in plant communities: a key to safe site dynamics, species coexistence and conservation. Ecography **25:** 145–160.

Svensson B.M. & Carlsson B.Å. 2005. How can we protect rare hemiparasitic plants? Early-flowering taxa of *Euphrasia* and *Rhinanthus* on the Baltic Island of Gotland. Folia Geobot. **40:** 261–272.

Štech M. 1998. Variabilita vybraných druhů sekce *Laxiflora* (Wettstein) Soó 1927 a revize rodu *Melampyrum* L. v České republice. Ph.D. thesis, University of South Bohemia, Faculty of Science.

Štech M. 2000. *Melampyrum* L., pp. 412–429. In: Slavík B. (ed.), Květena ČR, vol. 6, Academia, Praha.

ter Borg S.J. 1972. Variability of *Rhinanthus serotinus* (Schönh.) Oborny in relation to the environment. PhD thesis, University of Groningen.

ter Borg S.J. 1985. Population biology and habitat relations of some hemiparasitic Scrophulariaceae. pp. 463–487. In: White J. (ed.), The population structure of vegetation, Dr W. Junk Publishers, Dodrecht.

Těšitel J. 2005. Variabilita Melampyrum sylvaticum agg. v části Střední Evropy. B.Sc. thesis, University of South Bohemia, Faculty of Science.

Těšitel J., Říha P., Svobodová S., Malinová T. & Štech M. 2010. Phylogeny, life history evolution and biogeography of the Rhinanthoid Orobanchaceae. Folia Geobot. **45:** 347–367.

Těšitel J., Lepš J., Vráblová M. & Cameron D.D. 2011. The role of heterotrophic carbon acquisition by the hemiparasitic plant *Rhinanthus alectorolophus* in seedling establishment in natural communities: a physiological perspective. New Phytol. **192:** 188–199.

van Hulst R., Shipley B. & Thériault A. 1987. Why is *Rhinanthus minor* (Scrophulariaceae) such a good invader? Can. J. Bot. **65:** 2373–2379.

Wettstein R. 1895. Der Saison-Dimorphismus als Ausgangspunkt für die Bildung neuer Arten im Pflanzenreiche. Ber. Dtsch. Bot. Ges. **13:** 303–313.

Winkler E. & Heinken T. 2007. Spread of an ant-dispersed annual herb: An individual-based simulation study on population development of *Melampyrum pratense* L. Ecol. Model. **203:** 424–438.

Zopfi H.J. 1995. Life history variation and infraspecific heterochrony in *Rhinanthus glacialis* (Scrophulariaceae). Plant Syst. Evol. **198:** 209–233.

Zopfi H.J.1998. Life-history variation among populations of *Euphrasia rostkoviana* Hayne (Scrophulariaceae) in relation to grassland management. Biol. J. Linn. Soc. **64:** 179–205.

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