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REGULAR PAPER

Response of two hemiparasitic Orobanchaceae species to mowing dates: implications for grassland conservation and restoration practice

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Background and aims – *Rhinanthus major* (= *R. angustifolius*) and *Melampyrum nemorosum* are very sensitive to mowing date. As they are annuals without a long-term persistent seed bank and with a poor long-distance dispersal ability, seed loss caused by an unsuitable mowing date could lead to rapid population decline. Since their populations have disappeared from productive grasslands, they have become a focus of conservational management. *Rhinanthus* is also used in restoration projects as a treatment for reducing biomass, where its permanent populations are desired. We aimed to determine the earliest suitable mowing date for these species in White Carpathians Protected Landscape Area to support its administration to plan the management.
Methods – We conducted a mowing experiment with plots mown on 7 and 18 June and 5 July 2012. The number of parasites was counted in central plots before mowing and in the following growing season. The phenology of hemiparasites and co-occurring species was recorded to better understand the effects of mowing date.
Key results – *Melampyrum* showed a significant population decrease after mowing on 7 and 18 June, while the 5 July mowing did not inflict any significant change. The effect on *Rhinanthus* was not significant, as it was probably obscured by seed dispersal from the close surroundings.
Conclusions – Mowing in July is suitable for both species, while June mowing leads to population declines. Mosaic mowing (which includes early mowing in some parts of a site), could therefore gradually eradicate *Melampyrum*. *Rhinanthus* metapopulation could compensate for the seed loss by seed dispersal from neighbouring parts, but careful monitoring is necessary. When using *Rhinanthus* in restoration experiments, postponed mowing is essential to keep its population permanent. Our conclusions are widely applicable, but the particular mowing date must be determined separately for each region, species and ecotype.

Key words – Agri-environmental schemes, Yellow rattle, Wood cow-wheat, hemiparasite, differential mowing, delayed mowing, grassland restoration, White Carpathians, conservation, endangered species.

INTRODUCTION

Hemiparasitic plants of the family Orobanchaceae are represented in temperate European grasslands mainly by the genera *Rhinanthus*, *Melampyrum*, *Odontites*, *Pedicularis* and *Euphrasia* (Těšitel et al. 2010). They are considered ecosystem engineers because of their ability to modify competitive relations and mineral nutrient cycling in ecosystems (ter Borg 1985, Matthies 1996, Ameloot et al. 2005, Press & Phoenix 2005, Bardgett et al. 2006, Mudrák & Lepš 2010, Demey et al. 2013, 2014). Despite being very common in the past, they persisted mainly in non-intensive grasslands after the intensification of agricultural practices (ter Borg 1972, 1985, Linusson et al. 1998, Petrů & Lepš 2000, Westbury 2004, Ameloot 2007). As a result, there is a rising concern about conservation of these species (Matthies et al. 2004, Bekker & Kwak 2005, Grulich 2012) and their ecological requirements should be taken into account in conservation management planning.

The decline in the distribution of the hemiparasitic species in grasslands has been driven by intensive agricultural practices, mainly by fertiliser application and an increase of mowing frequency. Fertilizer application increases biomass production and is known to increase competition for light (Hautier et al. 2009). This decreases the establishment of hemiparasite seedlings and also the densities of their populations (van Hulst et al. 1987, Karlsson 1984, Matthies 1995, Fibich et al. 2010, Hejcman et al. 2011, Těšitel et al. 2013).

By contrast, the effect of mowing regime on hemiparasitic species has received much less attention. Populations of hemiparasites were shown to be seriously harmed if mowing is applied during flowering (Smith et al. 2000, Blahník 2013, Blažek & Lepš 2015), but the problem is more complex. There is a variety of morphological types within each species differing in the onset of flowering (vernal, aestival, autumnal types), the length of basal internodes and branching frequency, affecting regeneration potential (ter Borg 1972, 1985, Zopfi 1993, 1998, Štech 2000, Westbury 2004, Blažek & Lepš 2015). These ecotypes react differently to the same mowing dates, so the most suitable mowing date must be determined separately for each species and its ecotypes.

Hemiparasites are mostly found at sites where mowing is applied in summer as a conservation management measure (Isselstein et al. 2005, Humbert et al. 2012). In recent years, a mosaic mowing regime has received substantial popularity in nature conservation. Under this regime, various mowing dates are applied to different plots within the same site, and the assignment of a plot to individual mowing dates is changed each year. This is especially important for arthropods, which require constant availability of plant resources (Konvička et al. 2008, Čížek et al. 2012, Buri et al. 2013), and also for those plant species for which the single uniform mowing date is considered not suitable (Humbert et al. 2012, Valkó et al. 2012). However, some plots under the mosaic mowing regime are inevitably mown early. This might be an issue since some plant species may react negatively to early mowing (Humbert et al. 2012). This applies in particular to those species with a short life span, without a persistent seed bank or without an efficient dispersal mechanism, which would help the metapopulation to compensate for an occasional decrease in some plots. Unfortunately, the hemiparasitic Orobanchaceae display a combination of all these traits (to an extent depending on the species) making them especially sensitive to early mowing (Westbury 2004, Bekker & Kwak 2005, Bullock & Pywell 2005, Kleyer et al. 2008, Těšitel et al. 2010).

The mowing regime is not only a concern at sites where a current population of hemiparasites exists. Maintaining metapopulation dynamics requires the occurrence of suitable unoccupied sites where plants can establish (Hanski 1998, 1999). Therefore, the mowing regime allowing existence of populations of hemiparasites should be applied also to sites where their populations are currently absent, but their occurrence would be plausible or desirable from a conservation perspective. This, however, raises the question how to choose a suitable mowing regime at such sites where the phenology of hemiparasitic species cannot be taken as a guideline and individual sites within a region can notably differ in climatic conditions resulting in shifts in plant phenology (Blažek & Lepš 2015). We suggest instead to use the phenology of co-occuring species as a useful indicator for suitable mowing dates.

Rhinanthus species are also used in projects where species-rich grasslands are being restored on formerly ameliorated grasslands or arable fields to help with lowering the community biomass (Bullock & Pywell 2005, Westbury et al. 2006, Pywell et al. 2007, Westbury & Dunnett 2007). To keep permanent populations in such sites, a suitable mowing date should be used.

Here, we aim to determine a suitable mowing date for two annual hemiparasitic species in the Orobanchaceae. Our study is based on an experimental application of mowing on different dates, and on monitoring the phenology of both target species and co-occurring perennial species.

MATERIALS AND METHODS

Study species and study site

Annual hemiparasites *Rhinanthus major* L. (referred to in some ecological papers using the synonyms *R. angustifolius* C.C.Gmel. and *R. serotinus* (Schönh.) Oborny, hereafter referred to as *Rhinanthus*) and *Melampyrum nemorosum* L. (hereafter referred to as *Melampyrum*) were used for this study. Both species have rather scattered distributions in central Europe. Although they may be still quite common in some regions, they both have undergone a substantial decline. Moreover, in case of *Melampyrum*, our study deals with its variety *M. nemorosum* var. *praecox* Štech, which is included in the Red List of vascular plants of the Czech Republic and considered critically endangered (Štech 2000, Grulich 2012). The studied populations of both species belong to the respective vernal ecotypes with peak flowering in the first half of June (table 1).

The study was conducted in the Čertoryje National Nature Reserve, White Carpathians (Bílé Karpaty) Protected Landscape Area (hereafter PLA), Czech Republic. The reserve is mainly formed by regularly mown dry to mesic meadows. Grasslands form a mosaic with single or grouped trees or small forests (Jongepierová 2008). It is one of the most valuable grassland reserves in the Czech Republic, which is famous also for several world records in vascular plant species richness in plots sized between 16 and 49 m^2 (Merunková et al. 2012, Michalcová et al. 2014, Chytrý et al. 2015). Due to the high species richness and occurrence of many rare and protected species, the PLA administration tries to apply the best management considering also the requirements of arthropods (Čížek et al. 2012). The mosaic mowing might however be in conflict with the requirements of the hemiparasitic species growing on multiple sites in the reserve. In addition, extensive grassland restoration projects are conducted in the Čertoryje surroundings using mainly regional seed mixtures (Prach et al. 2015) and *Rhinanthus* population in the Čertoryje reserve can be used as a local seed source for facilitating grassland restoration using this hemiparasite.

Experimental design and data analysis

We selected plots with visually even distribution of individuals of one or both study species for our study in summer 2012. We established two blocks with *Rhinanthus*, two blocks with *Melampyrum* and three blocks containing both species (i.e. five blocks per species; 48°51′22″–48°51′47″N, 17°24′48″–17°25′11″E). Each block consisted of four permanent plots 1.5 m × 1.5 m, where parasite individuals were counted on 1 to 3 June. Three of the plots, together with the buffer zone (fig. 1), were mown on 7 and 18 June and 5 July,

Table 1 – Phenology of hemiparasites and of co-occuring species on the mowing dates.
Species showing no or weak trend were omitted. If two values are shown, it is a difference between NE and SW slopes. Target species of restoration projects are classified to sown, spontaneously established and other target species (Jongepierová et al. 2007, Prach et al. 2015). Red List classification is also indicated (CR = critically threatened taxa, EN = endangered taxa, VU = vulnerable taxa, NT = lower risk – near threatened, Grulich 2012). Nomenclature: Danihelka et al. (2012).

Code	Description
0	sterile plants without visible flower buds
1a	flower buds start to appear
1b	clearly visible but small flower buds
1c	flower buds just before flowering, some individuals could start flowering
2a	most individuals started flowering
2b	peak of flowering
2c	end of flowering
3a	most plants just finished flowering (some plants or parts of inflorescence can still have some flowers)
3b	plants after flowering with almost ripe fruits
3c	plants with fruits, seeds fall out

Species	Red List	Target	7 June	18 June	5 July
Agrostis capillaris			NA	2a	3b
Agrostis vinealis		other	NA	2b	3b
Allium carinatum	VU	other	NA	NA	1c
Anthericum ramosum	NT	spont.	NA	NA	2a
Arrhenatherum elatius		sown	2c	3b–3c	3c
Asperula tinctoria			2b	2b	3a
Astrantia major		other	1c	2a	2b
Avenula pubescens		spont.	3b	3c	3c
Betonica officinalis		sown	1b	1c	2b
Briza media		sown	2b	3b	3c
Bromus erectus		sown	3b	3c	3c
Calamagrostis arundinacea			1b	2b	3c
Centaurea jacea		sown	1a	1b	2a
Centaurea scabiosa		sown	1a	1c	2a
Centaurea stenolepis			0	0	1c
Cirsium pannonicum	VU	sown	2a	2a	3a
Dianthus carthusianorum		sown	2a	2b	3a
Digitalis grandiflora			1c	2b	3a
Elymus hispidus			NA	1c	2b–2c
Galium verum		sown	1a	1b	2b
Geranium sanguineum	NT	other	2b	2b	3a
Inula salicina		spont.	0	1b	2b
Iris variegata	EN		2b	3a	3b
Knautia kitaibelii	NT	sown	2a	2b	3a
Lathyrus niger		other	2b	3a	3b
Melampyrum nemorosum* var. *praecox	**CR**	**other**	**2b**	**2b–2c**	**3a**
Molinia arundinacea		other	NA	NA	1c
Orobanche alba	VU		NA	2a	2c
Peucedanum cervaria	NT	spont.	NA	1a	2a
Phleum phleoides		other	1c	2b	3b
Prunella grandiflora	VU	other	NA	NA	2a
Rhinanthus major			**2b**	**2c**	**3a**
Scorzonera hispanica	VU	other	2a	3b	NA
Serratula tinctoria		spont.	1a	1b	1c
Stachys recta		other.	2b	2b	2c
Tanacetum corymbosum		sown	1b	2b	2c
Thalictrum simplex subsp. *galioides*	CR		0	1c–1a	2b
Thesium linophyllon	VU	spont.	2b–2c	2c–3a	3a
Trifolium alpestre		spont.	2b–2a	2b–2c	3b
Trifolium montanum		sown	2a	2b	2c
Trisetum flavescens		sown	2b	3b–3c	3c
Valeriana stolonifera subsp. *angustifolia*	NT	spont.	2c–2b	3b	3c
Vicia tenuifolia			2b	3a	3b

respectively, and hay was dried on site. The control plot was not mown on any of these days and it was located further away, so it was not influenced by the experimental mowing. The plots were mown once more in late July, when the whole area was mown by tractor-mounted machinery. The parasite plants were counted again between 31 May and 3 June 2013.

The phenology of the hemiparasites together with co-occurring species was recorded to allow for a generalization of the mowing-date recommendations between years and sites within the region. Since there is no single dominant species, we monitored fifty subdominant species. Only species which were found on most dates and showed a reasonable trend are presented. Some of these are also used in local restoration projects as sown or target species (Jongepierová et al. 2007, Prach et al. 2015).

Population change between years (i.e. count in 2013 / count in 2012) was used as the response. It was log-transformed before computations, back-transformed values are presented in figures. The effect of treatment on species response was tested for each species separately using an analysis of variance (ANOVA) with mowing date and block identity as the main effects. When the effect of mowing date was significant, the Tukey test was performed to determine significantly different pairs of dates. As the population size of most hemiparasites is prone to large inter-annual fluctuations (de Hullu et al. 1985, Ameloot et al. 2006), the comparison of the population change in treated plots with the change in control plots is of the main interest, not the absolute change.

RESULTS

The number of *Melampyrum* individuals mostly decreased between years in control plots, while there was no change on average in the *Rhinanthus* population (table 2, fig. 2). The response of *Melampyrum* differed significantly among treatments ($F_{3,12} = 12.1$, $p = 0.001$; fig. 2). Whereas the early mowing dates (7 and 18 June) resulted in a significant decrease in population size by 90.3% and 80.5%, respectively, when compared to the control plots, the population change in the plots mown on 5 July was not different from the control (pairwise comparisons using Tukey test: 7 June vs. control: $p = 0.003$, 18 June vs. control: $p = 0.032$, 5 July vs. control: n.s.). The effect of mowing date on the *Rhinanthus* population was not significant ($F_{3,12} = 0.22$, n.s.; fig. 2).

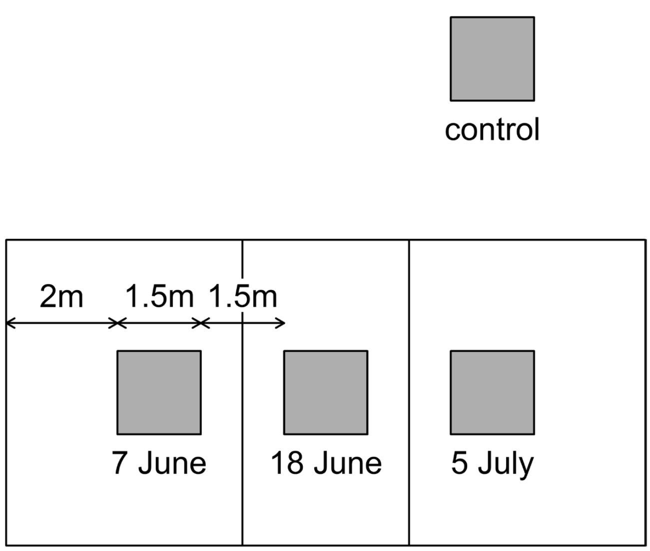

Figure 1 – Arrangement of the experimental plots. Mowing was done in the whole plot (white) on the specified dates, hemiparasites were counted only in the central plots (grey). There were two such blocks for *Melampyrum*, two for *Rhinanthus* and three for both species combined. The position of the control plot varied.

Table 2 – Summary of plant counts per plot.
Median and range is shown. There were five replicates per species and treatment.

	Rhinanthus	*Melampyrum*
2012		
Control	54 (45–550)	114 (42–350)
All treatments	57 (36–305)	157 (51–350)
2013		
Control	117 (42–136)	67 (30–89)
Mown on 7 June	68 (37–164)	6 (2–11)
Mown on 18 June	111 (68–112)	14 (8–44)
Mown on 5 July	103 (44–153)	78 (56–168)

Both *Rhinanthus* and *Melampyrum* were in a flowering stage on the June mowing dates, possibly with small unripe fruits. Most individuals already finished flowering in July, with almost ripe fruits able to ripen during drying of the hay, or even sporadically with some ripe fruits (table 1). In unoccupied sites, plants that finished flowering at the same time can be used as good indicators of suitable mowing dates, such as *Cirsium pannonicum*, *Dianthus carthusianorum*, *Digitalis grandiflora*, *Geranium sanguineum*, *Knautia kitaibelii*, *Thesium linophyllon*, as well as other plants that develop their flowers or fruits during this time period (table 1).

DISCUSSION

We have demonstrated that the survival of *Melampyrum* growing in the Čertoryje meadows is strongly affected by mowing date. Its population size changed similarly to the control treatment after the July cut, but it was strongly reduced in the plots mown in June (fig. 2), when the fruits were not ripe yet (table 1). We expected similar trends for *Rhinanthus*, because it was shown in a previous study that it is harmed by early mowing (Blažek & Lepš 2015) and its phenology was very similar to *Melampyrum* (table 1), but there was no such trend in our data (fig. 2).

The lack of the treatment effect on *Rhinanthus* can be attributed to the "safety mechanisms" which annual plants use to compensate for occasional seed loss: seed dormancy and dispersal. The data on seed dormancy are scarce for both species, but they are considered to form only a transient seed bank (the seeds remain dormant to the first autumn or early spring) or a very scarce short-term persistent seed bank (ter Borg 1985, Pons 1991, Thompson et al. 1997). There are also sporadic observations of good *Rhinanthus* spp. population establishment with a one-year delay and it was suggested that this is caused by environmental conditions. An insufficiently long period of cold stratification or dry weather in early spring may prevent some seeds from germination, which then remain dormant (Kelly 1989, ter Borg 2005, Mudrák et. al. 2014). This could also have been the case in our experiment, as there was a dry spring in the first year (precipitation from February to April 2012 reached only 38% of the long-term mean in the region), and we observed *Rhinanthus* establishment to be postponed by one year also in a seed-sowing experiment on restored grasslands nearby.

Melampyrum seeds are ant-dispersed and *Rhinanthus* seeds wind-dispersed, but for both species, the natural dispersal distance is usually shorter than 1 or 2 m (Adamec 2012, Coulson et al. 2001). *Rhinanthus* dispersal can however be largely enhanced by mowing machinery within a site (Strykstra et al. 1996, 1997, Bullock et al. 2003). When the whole meadow was mown in the end of July including our plots, the heavy seeds of *Melampyrum* were not able to surpass the buffer zone, while the much lighter, winged *Rhinanthus* seeds from the surroundings might have been able to reach the central plots. Smith et al. (2000) also reported the spread of *Rhinanthus* between experimental plots. Although *Rhinanthus* was able to compensate for the local seed loss in our small-scale experiment, early mowing still presents a threat to species persistence as the species cannot rely on irregular seed dormancy, and seed dispersal is still limited to several meters within a mown area.

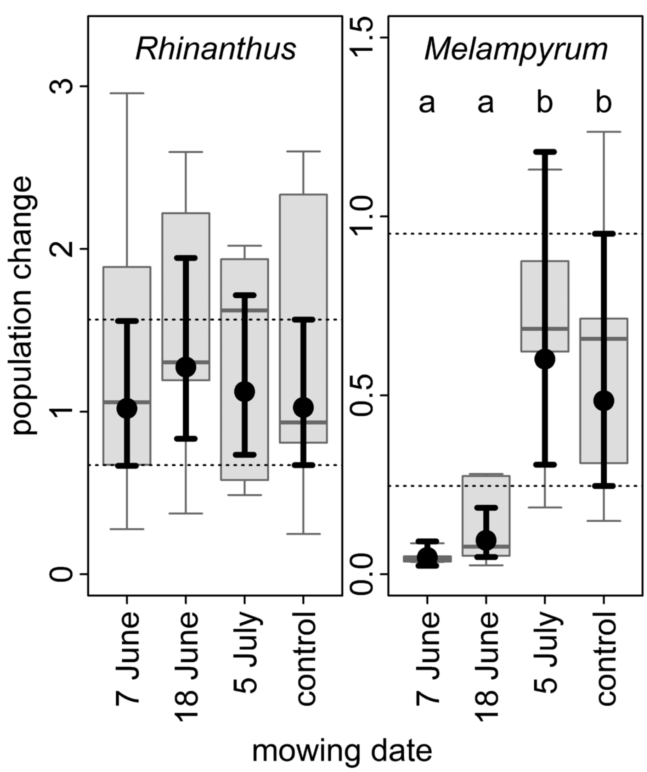

Figure 2 – Response of *Rhinanthus* and *Melampyrum* to mowing date, expressed as the relative population change from the first to the second year (one means no change). Grey boxplots show median, quartiles and range of original data. Points and thick bars show means and 95% confidence intervals based on ANOVA models for log-transformed data and back-transformed for plotting. Letters indicate groups which differed significantly in Tukey tests. There were five replicates in each group.

Until recently, postponed mowing (after 15 July) was mostly applied in Čertoryje meadows, because it is supported by agri-environmental measures (Ministry of Agriculture of the Czech Republic 2013). This was favourable for the populations of both studied species, which form stable populations in the reserve. However, the PLA administration has recently introduced a mosaic mowing scheme to preserve continual resource availability for arthropods (Konvička et al. 2008, Čížek et al. 2012). As a result, some sections of the reserve are mown early in the season and the early mowing is applied to various sections each year to maintain management heterogeneity. A possible adverse impact of this management could however be a gradual decline of hemiparasites, because of the seed loss on early-mown parts. *Rhinanthus* would be probably able to compensate for occasional seed loss and keep a persisting metapopulation, but the effect on *Melampyrum*, whose population decreased by 80–90% in the June-mown plots in our experiment, would be detrimental. We suggest, therefore, that plots with *Melampyrum*, which is more susceptible and has higher conservational priority (the vernal ecotype is considered critically endangered, Grulich 2012), should never be assigned the early cut, so they will always be mown after the beginning of July. *Rhinanthus* probably does not require special treatment, but it needs to be carefully monitored. Some of the unoccupied patches suitable for the establishment of hemiparasites should be also treated in the same way to allow for their potential spread. Proper mowing dates can be identified using the phenology of other species (table 1) in such patches.

While the continuity of grasslands in the Čertoryje reserve was not interrupted, many semi-natural grasslands in the surroundings were destroyed by agricultural improvement or conversion to arable fields in the second half of the 20th century, and they are now being restored (Jongepierová et al. 2007, Jongepierová 2008, Prach et al. 2013, 2014, 2015). *Rhinanthus* species were shown to help in such projects, because they can lower the community biomass, mainly by suppressing grasses (Bullock & Pywell 2005, Westbury et al. 2006, Pywell et al. 2007, Westbury & Dunnett 2007). After the establishment of a sown *Rhinanthus* population (Mudrák et al. 2014), it is desirable to keep the population permanent. If seed from the studied area is used, the restored areas should be mown after the beginning of July. In addition, a finer adjustment of mowing date can be achieved on the basis of the phenology of *Rhinanthus* or the correlation with co-occuring species on the target site (table 1) even before sowing of *Rhinanthus* in the target plots. In contrast to permanent populations, no recovery from seed bank or by natural spread from surroundings can be expected, because there are no seeds in the soil and the long-distance dispersal of *Rhinanthus* is poor (Bullock et al. 2003).

Not only are our results useful for the local nature conservation authorities, but they can also be used as a guideline case study elsewhere. The described problems and biological principles are general, only the recommended mowing date will undoubtably differ among regions with different climates and among species and their ecotypes with different phenologies (Svensson & Carlsson 2005). To compensate for this and for the variable and changing climate, which affects the phenology of hemiparasites, the phenological data on the host vegetation (table 1) can provide a reasonable guideline for a precise setting of the mowing regime. We encourage people in charge of management planning either to at least check the hemiparasites' phenology (Svensson & Carlsson 2005, Blažek & Lepš 2015) or even to arrange a similar simple experiment as in this study to determine the earliest possible mowing date, so that a proper conservation management for hemiparasites can be applied.

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