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## Is palatability of a root-hemiparasitic plant influenced by its host species?

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**Abstract** Palatability of parasitic plants may be influenced by their host species, because the parasites take up nutrients and secondary compounds from the hosts. If parasitic plants acquired the full spectrum of secondary compounds from their host, one would expect a correlation between host and parasite palatability. We examined the palatability of leaves of the root-hemiparasite *Melampyrum arvense* grown with different host plants and the palatability of these host plants for two generalist herbivores, the caterpillar of *Spodoptera littoralis* and the slug *Arion lusitanicus*. We used 19 species of host plants from 11 families that are known to contain a wide spectrum of anti-herbivore compounds. Growth of *M. arvense* was strongly influenced by the host species. The palatability of the individual host species for the two herbivores differed strongly. Both *A. lusitanicus* and *S. littoralis* discriminated also between hemiparasites grown with different host plants. There was no correlation between the palatability of a host species and that of the parasites grown on that host, i.e., hemiparasites grown on palatable host species were not more palatable than those grown on unpalatable hosts. We suggest an interacting pattern of specific effects of chemical anti-herbivore defences and indirect effects of the hosts on herbivores through effects on growth and tissue quality of the parasites.

**Keywords** *Melampyrum arvense* · Herbivory · Host–parasite interactions · Secondary compounds

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### Introduction

Parasitic plants attack shoots or roots of other plants and take up water, nutrients and solutes from the hosts by means of specialized contact organs (haustoria, Kuijt 1969). About 1% of all plants are parasitic and parasitic plants are common components of many plant communities (Molau 1995). The majority of parasitic plants are actually hemiparasites that have green leaves and are able to photosynthesize (Kuijt 1969). Parasitic plants can drastically reduce the growth of their host plants and some are important agricultural pests (Parker and Riches 1993; Pennings and Callaway 2002). Because parasitic plants are to a certain degree host-specific, they may mediate competitive interactions between different host plants and thus influence community structure (Matthies 1996; Joshi et al. 2000; Pennings and Callaway 2002; Pywell et al. 2004).

The parasitic way of life may have other benefits for the parasites apart from providing access to resources like water, nutrients and carbohydrates from the host plant. Parasitic plants can also take up secondary compounds produced by their hosts that act as anti-herbivore defences (Schneider and Stermitz 1990; Boros et al. 1991). Several studies of specific host–parasite pairs found that these compounds are taken up by the parasite and reduce its herbivory levels (Harvey 1966; Marvier 1996; Adler et al. 2001; Adler 2002, 2003). For example, quinolizidine alkaloids taken up by the root hemiparasite *Castilleja indivisa* from high-alkaloid *Lupinus albus* reduced herbivory levels and increased lifetime seed set of the parasites in comparison to parasites grown with low-alkaloid lupines (Adler 2000). Insect larvae suffered higher mortalities when fed with fruits of the root hemiparasite *Santalum acuminatum* that had grown near the host *Melia azedarach* than when fed with fruits from parasites growing away from *M. azedarach* (Loveys et al. 2001).

However, no attempt has been made to study the effect of a wide range of hosts on the palatability of a parasitic plant. If parasitic plants take up indiscrimi-

nately a wide spectrum of secondary compounds from their host plant, the palatability of a parasite and its host should be correlated. We studied the influence of hosts from 11 plant families, most of them known to produce secondary compounds that may deter herbivores, on the palatability of the root hemiparasite *Melampyrum arvense* L. for two generalist herbivores, the slug *Arion lusitanicus* and the caterpillar of *Spodoptera littoralis*. We addressed the following specific questions: (1) Do the different host species influence the palatability of the parasitic plant for generalist herbivores? (2) Is the palatability of the hemiparasite correlated with that of its host?

## Materials and methods

*M. arvense* (Scrophulariaceae) is an obligate root hemiparasite that without a host dies during the early stages of development (Matthies 1995). The annual species was formerly a noxious weed of cereal fields in Europe but has become rare due to changes in agricultural practices. Today, *M. arvense* is a plant of calcareous grasslands and field margins (Matthies 1986).

Two generalist herbivores were used in our study. The cotton leafworm *S. littoralis* (Boisduval) (Lepidoptera: Noctuidae) is a serious pest of several crops in North Africa, the Mediterranean and the Middle East (Sadek 2003). The caterpillars of this moth attack host plants belonging to at least 40 plant families (Brown and Dewhurst 1975). The species was bred under laboratory conditions on lettuce and welled white beans. The slug *Arion lusitanicus* (Mollusca: Agriolimacidae) is a widespread invasive herbivore introduced from Southern Europe. In Central Europe, the slug feeds on a wide range of plant species (Briner and Frank 1998). Slugs were sampled in the surrounding of the institute in Marburg in the mornings

of the days when the feeding trials were conducted. While *S. littoralis* is a standard test organism in palatability trials and does not occur together with *M. arvense*, *A. lusitanicus* may be regarded as a potential herbivore of this species in the field.

We selected a total of 19 host plant species from 11 families (Table 1). These included plants known to contain a wide spectrum of secondary compounds that may negatively affect generalist herbivores and some species that are not or poorly defended by secondary compounds (Poaceae, some Fabaceae). Seeds of the host species were sown in standard potting soil (TKS 1, Floragard, Oldenburg/Germany, 110 mg l<sup>-1</sup> N, 130 mg l<sup>-1</sup> P<sub>2</sub>O<sub>5</sub>, 180 mg l<sup>-1</sup> K<sub>2</sub>O) in October 2002. Seedlings were transplanted into individual pots (9 cm×9 cm×9.5 cm) filled with the same soil in January 2003. The temperature in the glasshouse was 20–30°C during the day and 15–20°C at night. Day length was maintained at 14 h, with additional light supplied by high-pressure sodium lamps (Philips, Son-T Agro, 400 W). Thirty to 40 replicates were prepared for every host species. Once per week, a 0.2% solution of an NPK-fertilizer (8-8-6, Wuxal super, Aglukon Düsseldorf) was applied to the plants.

Seedlings of *M. arvense* were germinated at the beginning of December 2002 in Petri dishes on moist filter paper in a climate chamber at 4°C to break dormancy. After 3 weeks, the temperature was raised to 8°C. When the parasites had fully developed their cotyledons in March 2003, two individuals of *M. arvense* were planted into half of the pots with the host species. During the following 2 weeks, pots with hemiparasites were placed in a climate chamber at 18°C/15°C (day/night) and a day length of 16 h to facilitate the establishment of seedlings. During this time, dead hemiparasites were replaced by new seedlings before pots were brought back to the glasshouse. In mid-April 2003, all pots were moved to a flowerbed in the Botanical Gar-

**Table 1** List of host plant species used in the experiments with information on important secondary compounds known to occur in the plant tissue (taken from Hoppe 1958; Roth et al. 1994, and the toxicological data base of the University of Zürich at <http://www.vetpharm.unizh.ch>). Taxonomy of plants follows Schmeil and Fitschen (1996) and Roth et al. (1994). Species are in alphabetical order

Host species	Family	Secondary compounds	Longevity
<i>Achillea millefolium</i>	Asteraceae	Sesquiterpenic lactones	Perennial
<i>Agrostemma githago</i>	Caryophyllaceae	Steroid saponins	Annual
<i>Arrhenatherum elatius</i>	Poaceae	No defensive compounds known	Perennial
<i>Atropa belladonna</i>	Solanaceae	Alkaloids (atropin)	Perennial
<i>Chelidonium majus</i>	Papaveraceae	Alkaloids	Perennial
<i>Cicuta virosa</i>	Apiaceae	Cicutoxin	Perennial
<i>Conium maculatum</i>	Apiaceae	Alkaloids (e.g., coniin)	Biennial
<i>Digitalis purpurea</i>	Scrophulariaceae	Glucosides	Biennial
<i>Euphorbia platyphyllos</i>	Euphorbiaceae	Triterpene saponines, Euphorbon	Annual
<i>Genista germanica</i>	Fabaceae	Alkaloids	Perennial
<i>Lobelia inflata</i>	Campanulaceae	Alkaloids	Annual
<i>Lotus corniculatus</i>	Fabaceae	Cyanogenic glucoside	Perennial
<i>Lupinus angustifolius</i>	Fabaceae	Alkaloids	Annual
<i>Lupinus luteus</i>	Fabaceae	None (low-alkaloid line)	Annual
<i>Melilotus alba</i>	Fabaceae	Coumarine-glucoside, Cyanogenic glucoside	Annual, biennial
<i>Nicotiana tabacum</i>	Solanaceae	Alkaloids (nicotin)	Annual
<i>Ricinus communis</i>	Euphorbiaceae	Proteins	Annual
<i>Sinapis alba</i>	Brassicaceae	Glucosinolates (sinalbin)	Annual
<i>Trifolium repens</i>	Fabaceae	Cyanogenic glucosides	Perennial

den, where light conditions and temperatures were more favourable for the growth of the parasites. After one month of growth, the height, number of leaves and the length and width of the longest leaf were determined for each hemiparasite. In addition, the water content was determined for 80 leaves of *M. arvense* and 20 leaves of every host species. Leaves were weighed, dried at 80°C to weight constancy and weighed again. Water content was defined as proportional weight loss.

For the feeding trials with the slug, leaves of *M. arvense* were harvested in each pot and placed into moistened Petri dishes. Since the establishment success of *M. arvense* differed between host species, the number of replicates (i.e., pots with *M. arvense*) varied between 3 and 17. Approximately 300 mg fresh weight (equivalent to ca 9 cm<sup>2</sup>) of leaves from each pot was weighed and then placed together with an individually weighed slug into a plastic container (9-cm diameter, 15-cm height). The containers were placed top-down into large boxes that were covered with a plastic foil and lined with moist cloth to maintain a high humidity. The boxes were stored outdoors in a shady place. After 36 h, the slugs were removed and the remaining leaf material was dried at 80°C for 24 h and weighed. To study the palatability of the leaves of the host plants, a similar test was carried out using leaves from ten pots per species.

For the feeding trials with *Spodoptera littoralis*, ca 70 mg of parasite leaf material from each pot was weighed. For these trials, no leaf material from parasites grown with *Trifolium repens* was available. Two to three second-instar larvae (ca 2 weeks old) were weighed individually and added to each leaf sample in a Petri dish containing moist filter paper and kept for 24 h at 23°C. The remaining leaf material was dried and weighed. To study the palatability of the leaves of the host plants, an analogous test was carried out using leaves from eight pots for each species.

### Statistical analysis

Data for vegetative traits of *M. arvense* were log-transformed to obtain normally distributed residuals. The effect of the host species on these traits was analysed by one-way MANOVA, followed by separate ANOVAs for every trait. Consumed dry mass was calculated as the difference between initial dry mass (calculated as fresh mass × [1 – water content]) and remaining dry mass at the end of the experiment. As a measure of palatability, we used the consumed dry mass adjusted for the effect of herbivore mass. This is a better measure of palatability than conventional palatability indices when herbivore mass varies (Raubenheimer and Simpson 1992; Horton and Redak 1993).

To analyse the effect of host species on palatability, we carried out an ANCOVA of consumed dry mass with the herbivore mass as a covariate. For the palatability of *M. arvense*, plant height of the hemiparasite was included as an additional covariate. By using type I sums of

squares in the analyses, the effect of host species on feeding was analysed after removing the possibly confounding influence of individual herbivore size, and size and nutritive status of the hemiparasite.

Since phylogenetically related taxa often contain similar secondary compounds (Hendriks et al. 1999), we further used a phylogenetically controlled analysis to disentangle phylogenetic from functional relationships (Harvey and Pagel 1991). When available, molecular-based phylogenies were used. In the cases where no molecular phylogenies were available within families, we used traditional taxonomy on the level of tribes, subtribes, genera, sub-genera, sections, sub-sections, series and aggregates, which were interpreted as phylogenetic clades (Tutin et al. 1964). Branch lengths were set to 1 and phylogenetically independent contrasts were tested using regression through the origin (Harvey and Pagel 1991), using the program CAIC 2.0 (Purvis and Rambaut 1995).

## Results

### Growth of *M. arvense*

All studied traits of *M. arvense* were significantly affected by the host plants (MANOVA and separate ANOVAs: all  $P < 0.001$ ). *M. arvense* performed best with *Lupinus angustifolius*, *L. luteus*, *Nicotiana tabacum* and *Lobelia inflata* as hosts (height > 20 cm). Parasites were smallest when grown with *Trifolium repens*, *Atropa belladonna*, *Agrostemma githago*, *Arrhenatherum elatius*, *Cicuta virosa*, *Digitalis purpurea* and *Genista germanica* (height < 10 cm).

### Feeding preferences

The palatability of the different host species for the two herbivores varied strongly (Fig. 1, Table 2). However, the palatability of the individual plant species for the two herbivores was not correlated ( $r = 0.12$ ,  $P > 0.6$ ). While, for instance, *Lupinus angustifolius* ranked second in palatability for *A. lusitanicus*, it was one of the least palatable species for *S. littoralis*. However, a few species ranked similar in palatability for both species. *Lobelia inflata* was the most palatable plant and *Digitalis purpurea* was among the most unpalatable plants for both herbivores.

For *A. lusitanicus*, the leaves of the hosts were more palatable than those of the parasite ( $F_{1,18} = 5.7$ ,  $P < 0.05$ , ANCOVA with herbivore mass as covariate), whereas for *S. littoralis*, the leaves of the parasite were far more palatable than those of the host plant on which the parasite was grown ( $F_{1,17} = 55.0$ ,  $P < 0.001$ ; ANCOVA). With increasing plant size, the palatability of the leaves of *M. arvense* decreased for *S. littoralis* (see Table 2). The host on which the parasites had been grown significantly influenced the feeding of both the slug *A. lu-*



*sitanicus*, and that of the caterpillars of *S. littoralis* (Fig. 1, Table 2). Plants of *M. arvense* grown with *Conium maculatum*, *Chelidonium majus* and *Lupinus luteus* were rather palatable for the slug, whereas hemiparasites grown with *Ricinus communis* and *Lobelia inflata* were rather unpalatable. As for the host plants, the palatability of the hemiparasite leaves for the two herbivores was not correlated ( $r = 0.37$ ,  $P = 0.14$ ).

Contrary to our expectation, we found for both herbivore species no significant correlation between the palatability of a host species and that of hemiparasites grown with that host (Fig. 2). The use of phylogenetically independent contrasts did not change these results qualitatively.

## Discussion

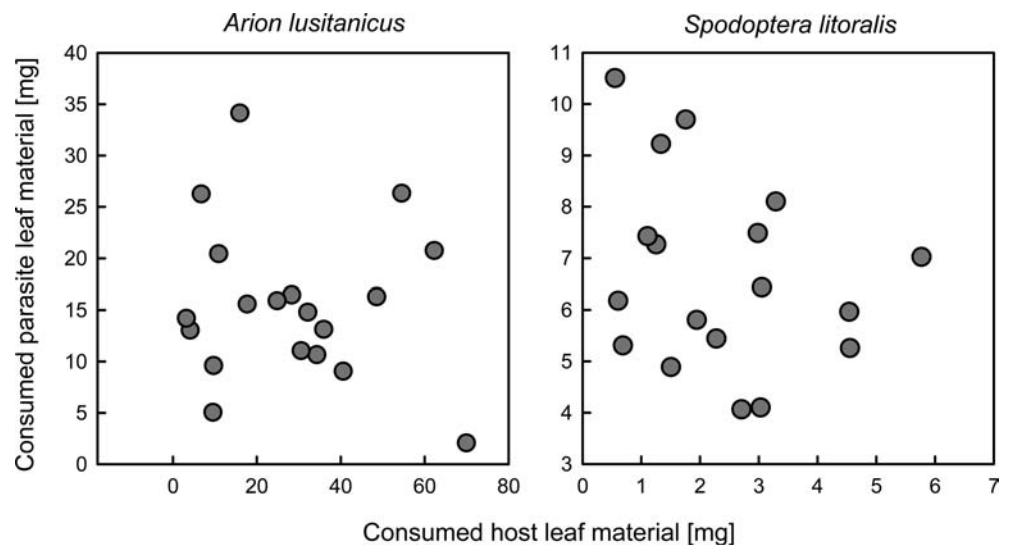
### Host effects on the growth of *M. arvense*

*M. arvense* proved to be not very host-specific. Individuals of *M. arvense* grew with a wide range of host species from different families, many of which are not among the natural hosts of *M. arvense*, e.g., *Ricinus communis* and *Atropa belladonna*. As in other studies (Atsatt and Strong 1970; Matthies 1995), the growth of the hemiparasite was strongly affected by the host species. The suitability of a species as a host for hemiparasites is determined by various plant traits like root architecture, nutrient content and shading by the shoot (Marvier and Smith 1997). Legumes are often considered to be particularly good hosts for parasitic plants (Atsatt and Strong 1970; De Hullu 1984; Press et al. 1993; Matthies 1996; but see Matthies 1998). This was only partly confirmed by our study. We found that *M. arvense* performed well with the *Lupinus* species, but not with *Trifolium repens*, whereas the four other legumes were hosts of moderate suitability. Regular fertilization in our experiment may have reduced the advantages of growing with legumes.

### Palatability of hosts and hemiparasites to generalist herbivores

The different host species influenced the palatability of leaves of the hemiparasite *M. arvense* for both studied generalist herbivores, the slug *A. lusitanicus* and the caterpillars of *S. littoralis*. Host plants may affect the palatability of parasitic plants in several ways. Firstly, host plants may influence the growth of hemiparasitic plants (Snogerup 1982; De Hullu 1984; Matthies 1995, 1996, 1997; Marvier 1998) and as a consequence also the quality of their tissues, e.g., foliar nitrogen concentrations (Seel et al. 1993). Secondly, parasitic Scrophulariaceae like *M. arvense* produce themselves iridoid glycosides (Hartl 1974; Stermitz et al. 1993) that may influence herbivores. The production of these defensive compounds may depend on parasite size and nutrition, which in turn is strongly influenced by host quality. The observed decrease in the palatability of *M. arvense* for both herbivores with increasing plant size could be due to one of these two mechanisms. Moreover, the palatability of parasite species for herbivores may be influenced by other leaf traits, like leaf toughness and leaf hairiness (Jennings and Barkham 1975; Dirzo 1980) that could be affected by the host species. Thirdly, parasites may take up secondary compounds produced by their hosts that may affect tissue palatability for herbivores. This has been shown for *Castilleja*, *Pedicularis* and *Orthocarpus* parasitic genera of the Scrophulariaceae closely related to *Melampyrum* (Stermitz and Harris 1987; Stermitz et al. 1989; Boros et al. 1991; Mead et al. 1992; Marvier 1996; Adler 2002). Marko and Stermitz (1997) found a similar spectrum of alkaloids in *Delphinium* and its parasite *Castilleja*, suggesting a non-selective uptake of these compounds. However, in our study there was no positive correlation between the palatability of the leaves of a host and those of the parasite grown on that host. Previous studies have tested the effect of compounds from specific host species on herbivore activity (e.g., Stermitz et al. 1989; Boros et al. 1991; Adler 2003). In

**Fig. 2** Relationship between the consumed leaf mass of the host species and of the hemiparasite *M. arvense* growing with these species for the two generalist herbivores *Spodoptera littoralis* ( $r = -0.26$ ,  $P = 0.29$ ) and *Arion lusitanicus* ( $r = 0.14$ ,  $P = 0.58$ ). Consumed host leaf mass was adjusted for the effect of individual herbivore mass, and consumed parasite leaf mass for the effect of individual herbivore mass and parasite height



contrast, we tested the effect of a large number of host plants from different families that produce different compounds on parasite palatability.

There are several mutually non-exclusive explanations for the absence of a positive correlation. Firstly, some plants only produce secondary compounds when damaged (Karban and Baldwin 1997). For example, *N. tabacum* which is supposed to be highly poisonous was readily eaten by the herbivores, while some species that are presumably unprotected by anti-herbivore compounds (e.g., *A. elatius*, *A. millefolium*) were rather avoided. Secondly, not all compounds produced by the hosts are necessarily taken up by root hemiparasites. The evidence regarding the extent to which parasites control the solutes taken up from the host is conflicting, but several studies suggest that uptake is selective (see Press 1995 and references therein). Puustinen and Mutikainen (2001) found that the feeding deterrent HCN produced by the host *Trifolium repens* was not taken up by the hemiparasite *Rhinanthus serotinus*. Whether a compound is taken up or not may partly depend on the plant part in which it is synthesized. Secondary compounds that are synthesized in plant roots like nicotine by *Nicotiana tabacum* (Richter 1988) and certain pyrrolizidine alkaloids (Vrieling and van Wijk 1994) should be easily available for root parasites. In contrast, alkaloids produced in the chloroplasts (e.g., by lupines, Richter 1988) might be less accessible to root parasites. However, their uptake by root hemiparasites has been shown by a number of studies (Stermitz and Harris 1987; Boros et al. 1991; Mead et al. 1992; Marvier 1996; Adler et al. 2001). The uptake of secondary compounds from the host species by parasitic plants may thus depend on the identity of the host and the parasite species or even on the specific host–parasite combination. In our study, the leaves of *Conium maculatum* and *Cicuta virosa*, two plant species which are known to contain high amounts of poisonous secondary compounds, were unpalatable to both herbivores, as expected. However, the leaves of parasites grown with these two species as hosts were among the most palatable, suggesting that the compounds may not have been taken up by *M. arvensis*.

Our study specifically focussed on the importance of plant chemistry on leaf palatability, but herbivory is influenced by a number of other factors, in particular various leaf traits. Spines and trichomes are known to be feeding deterrents for many herbivores (Duffey 1986; but see Hendriks et al. 1999; Gutschick 1999). Further, leaf toughness due to thick cell walls and lignification is known to reduce tissue palatability for leaf chewing herbivores (Choong et al. 1992). However, its relative importance as compared to secondary compounds is still a matter of debate (see Kouki and Manetas 2002).

The performance of root hemiparasites in the field is strongly influenced by the identity and the diversity (Joshi et al. 2000) of the host plants they have access to. If herbivore pressure in the field is strong, the presence of compounds in a host that can be taken up by the parasite and deter herbivores may be an important aspect of host

quality for the parasite. Plants of the root hemiparasite *Castilleja miniata* parasitizing the alkaloid-rich host *Lupinus argenteus* experienced reduced herbivory by several groups of vertebrates and invertebrates (Adler 2002). Such a use of plant allelochemicals as a defence against natural enemies is well known from phytophagous insects (e.g., Havill and Raffa 2000; Singer and Stireman 2003). However, secondary compounds will only be effective against generalist herbivores. Many specialist herbivores are adapted to and may even be attracted by the secondary compounds of their host plants (van der Meijden 1996; Karban and Baldwin 1997).

In conclusion, our results suggest that the host does not only influence the growth of root hemiparasites, but also the palatability of their tissue for at least some herbivores. However, the lack of a clear correlation between the palatability of the hosts and the parasites grown on them indicates that the host plants influence parasite palatability not only through the production of secondary compounds that may be taken up by the parasite, but also through effects on growth and tissue quality of the parasites.

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