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The effect of host mycorrhizal status on host plant–parasitic plant interactions

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Abstract Two pot experiments were conducted to examine three-level interactions between host plants, mycorrhizal fungi and parasitic plants. In a greenhouse experiment, *Poa annua* plants were grown in the presence or absence of an AM fungus (either *Glomus lamellosum* V43a or *G. mosseae* BEG29) and in the presence or absence of a root hemiparasitic plant (*Odontites vulgaris*). In a laboratory experiment, mycorrhizal infection (*Glomus claroideum* BEG31) of *Trifolium pratense* host plants (mycorrhizal versus non-mycorrhizal) was combined with hemiparasite infection (*Rhinanthus serotinus*) of the host (parasitized versus non-parasitized). Infection with the two species of *Glomus* had no significant effect on the growth of *P. annua*, while hemiparasite infection caused a significant reduction in host biomass. Mycorrhizal status of *P. annua* hosts (i.e. presence/absence of AM fungus) affected neither the biomass nor the number of flowers produced by the attached *O. vulgaris* plants. Infection with *G. claroideum* BEG31 greatly increased the biomass of *T. pratense*, but hemiparasite infection had no effect. The hemiparasitic *R. serotinus* plants attached to mycorrhizal hosts had higher biomass and produced more flowers than plants growing with non-mycorrhizal hosts. Roots of *T. pratense* were colonized by the AM fungus to an extent independent of the presence or absence of the hemiparasite. Our results confirm earlier findings that the mycorrhizal status of a host plant can affect the performance of an attached root hemiparasite. However, improvement of the performance of the parasitic plant following attachment to a mycorrhizal host depends on the extent to which the AM fungi is able to enhance the growth of the host.

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Introduction

A symbiotic association between plants and mycorrhizal fungi can be beneficial for the plant associate, for example, through enhanced uptake and transport of nutrients and water (Harley and Smith 1983; Allen 1991) and reduced pathogenic infection (Newsham et al. 1995). Through their positive influence on plant growth, mycorrhizal fungi can play an important role in mediating interactions between their plant associates and other organisms. Indeed, the importance of fungi has been shown, for example, in the interaction between two plants (Perry et al. 1989; Hartnett et al. 1993; Moora and Zobel 1996; West 1996), between plants and herbivores (Gange and West 1994; Gehring and Whitham 1994; Larsen and Jakobsen 1996; Borowicz 1997) and between plants and soil pathogens (Newsham et al. 1995). The importance of mycorrhiza has been demonstrated also for the tripartite interaction between parasitic plants, mycorrhizal fungi and their common hosts (Gehring and Whitham 1992; Sanders et al. 1993; Davies and Graves 1998; Salonen et al. 2000). In a field experiment, Sanders et al. (1993) found that successful shoot parasitism by the holoparasitic *Cuscuta pentagona* on *Abutilon theophrasti* plants occurred almost exclusively when the host roots were colonized by mycorrhizal fungi. They also found under controlled conditions that colonization of host roots by mycorrhizal fungi increased the growth rate of *C. pentagona* 3.4-fold relative to the rate on non-mycorrhizal plants. So far, only two studies have examined the influence of host mycorrhizal status on performance of root hemiparasites, one giving an example of an endomycorrhizal association (Davies and Graves 1998) and the other of an ectomycorrhizal association (Salonen et al. 2000).

The root hemiparasites in the Scrophulariaceae family are common members of several types of plant com-

munity. At sites with abundant hemiparasites, other members of the community may readily become infected, since most root hemiparasites are generalists with respect to host plants. For example, the host range of *Rhinanthus minor* extends to at least 50 species from 18 different families (Gibson and Watkinson 1989). Given that the vast majority of potential host plants are mycorrhizal (Harley and Harley 1987; Newman and Reddell 1987), the attachment of a parasitic plant to a host plant usually leads to a tripartite system within which nutrients, water and carbohydrates flow from one associate to another.

The performance of hemiparasitic plants has been shown to depend on host species (Snogerup 1982; Matthies 1996). Several studies have shown that hemiparasites perform best when attached to legumes (e.g. Gibson and Watkinson 1991; Matthies 1996; Tennakoon and Pate 1996), indicating that nitrogen availability is of importance. Just like the increased availability of nitrogen to the host in a symbiosis with nitrogen-fixing bacteria, increased availability of other nutrients and water to hosts as an outcome of mycorrhizal symbiosis could increase the growth and reproduction of hemiparasites. Indeed, Salonen et al. (2000) found that symbiosis with ectomycorrhizal (EM) fungi increased host (*Pinus sylvestris*) growth and phosphorus content in host tissue in ways that enhanced the growth and flower production of the attached hemiparasitic plants (*Melampyrum pratense*). Likewise, Davies and Graves (1998) found enhanced performance of a root hemiparasite (*Rhinanthus minor*) growing with a mycorrhizal host (*Lolium perenne*), even though the mycorrhizal colonization had no significant effect either on phosphorus and nitrogen status or biomass and photosynthetic rate of hosts. Growth and reproductive output of *R. minor* rose by 58% and 47%, respectively, when the hosts were mycorrhizal. Infection by the root hemiparasite also resulted in a significant decline in the mycorrhizal colonization of host roots.

We conducted two experiments, one in a greenhouse and another in the laboratory, in which seedlings of two host species, the grass *Poa annua* L. and the leguminous herb *Trifolium pratense* L. cv Bjursele, were grown in the presence or absence of the root hemiparasite *Odontites vulgaris* Moench or *Rhinanthus serotinus* (Schönh.) Oborny and in the presence or absence of endomycorrhizal *Glomus* species. We hypothesized that host mycorrhizal status would affect performance of the hemiparasite. We predicted that mycorrhizal association would be advantageous for host plants, even though in some cases AM fungal colonization of plants can lead to reduced rather than enhanced growth (Johnson et al. 1997). As a consequence of enhanced host growth and photosynthetic capacity, the growth and flower production of the parasitic plant should be stimulated more following attachment to a mycorrhizal than to a non-mycorrhizal host.

Materials and methods

Experiment with *Poa annua* and *Odontites vulgaris*

Seeds of *P. annua* (commercially available material) were sown on 1 April 1996 and precultivated in a mixture of sterilized B2 peat (Vapo Oy, Finland) and sand (1:1) for 2 weeks in a growth chamber at 17/15°C (day/night), 50–60% relative humidity, under warm white artificial light (approximately 120 µmol $m^{-2}s^{-1}$) and a day-length of 14 h. Seeds of *O. vulgaris*, collected on 31 August 1995 from several wild plants in a single population in Turku, southern Finland were first stored in paper bags (at room temperature) for several months and then incubated between moist filter papers at 3–5°C for about 2.5 months to break dormancy.

Two weeks later, on 16 April 1996, the experiment was started in a greenhouse with natural light by transplanting a total of 60 uniform *P. annua* seedlings individually into 0.25-l plastic pots (Vefi A/S, Norway) inoculated or not with an AM fungus. At the same time, cotyledon-stage *O. vulgaris* seedlings, each with a root 1–1.5 cm long, were transplanted two per pot. In order to promote the establishment of haustorial connections, the hemiparasite seedlings were planted very close to the host (distance about 1 cm). On 24 April, transplantation of the hemiparasite seedlings was repeated if the first transplantation had failed; where two seedlings successfully established, one was removed. The growth substrate was a mixture (3:1:1) of natural peat (B0, Vapo Oy, Finland), sand (from a nearby sand ridge) and vermiculite (3-V, Vermipu Oy, Finland). The peat and the sand were steam-sterilized three times (2 h per time) on successive days. After sterilization, the peat was limed with 8 g l^{-1} Dolomite lime (Saxo Oy, Finland) to give an approximate pH of 6.0 and fertilized with 0.5 g l^{-1} controlled-release fertilizer Osmocote Plus (for 9 months, 16N-3P-10K, Sierra Chemical Europe B.V., Heerlen, The Netherlands).

Mycorrhizal inoculation (5% of the growth substrate by volume) was carried out just before transplanting the grass and parasite seedlings. Two fungal strains originating from Finnish agricultural soil were used: *Glomus lamellosum* Dalpe, Koske & Tews V43a and *G. mosseae* (Nicol. & Gerd.) Gerdemann & Trappe BEG29. The inocula consisted of a mix of colonized roots, spores, hyphae and substrate. Seedlings not given a mycorrhizal treatment were inoculated with a similar substrate lacking the mycorrhizal fungus. The mycorrhizal and non-mycorrhizal inocula were produced in the roots of micropropagated strawberry (*Fragaria* × *ananassa* Duch. cv Nora) between 26 April and 15 October 1995. The substrate was a mixture of steam-sterilized natural peat (B0 peat, Vapo Oy, Jyväskylä, Finland) and vermiculite (Vermipu Oy, Finland) (3:1). The vermiculite was washed thoroughly in running water before mixing with sand. The peat-substrate mix was limed with 3 g l^{-1} of dolomite (Saxo Oy, Finland) and the whole mixture was fertilized with 2 g l^{-1} of bone meal (7N-7.9P-K, Kemira-Agro Oy, Helsinki, Finland). The inocula were stored at 8°C prior to use. This experiment was run for 20 weeks (counting from transplantation of the hemiparasite seedlings). The pots were placed in random order and their positions changed randomly during the experiment.

Experiment with *Trifolium pratense* and *Rhinanthus serotinus*

Seeds of *T. pratense* were pregerminated on sterile, moist filter paper for 2 days at 27°C. A total of 100 seedlings with approximately 1-cm-long hypocotyls were transplanted, two each into 0.4-l plastic pots (6×8×7.5 cm; Cookson, Plantpak Limited, Flower Pot, UK). At transplantation, all *T. pratense* seedlings were inoculated with a suspension of *Rhizobium* sp. (provided by P. Leinonen, MTT, Juva, Finland), 2×10^6 bacteria per pot. The pots were filled with a sand and perlite (Nordisk Perlite-APS, Copenhagen, Denmark) substrate (9:1) steam-sterilized three times for 2 h on successive days at 100°C. The substrate was limed with 5 g l^{-1} of dolomite (Saxo Oy, Finland) and fertilized with 2 g l^{-1} of bone meal (7N-7.9P-0K, Kemira-Agro Oy, Helsinki, Finland). Two weeks after transplantation, one of the two seedlings was re-

moved. Seeds of *R. serotinus* were collected on 30 August 1996 from several plants in a population located in Konnevesi, central Finland and stored in paper bags (at room temperature) for several months. The seeds were incubated between moist filter papers at 3–5°C for about 3.5 months to break dormancy. In the two treatments with hemiparasites, two cotyledon-stage *R. serotinus* seedlings per pot (each with a root 1–1.5 cm long) were transplanted in close vicinity to the hosts a week later than the *T. pratense* seedlings. The experiment was run for 13 weeks in a growth-room with 20/18°C (day/night), 50–60% relative humidity, under cool white artificial light (approximately 80 µmol $m^{-2}s^{-1}$) (Oy Airam Ab, Finland) and a daylength of 14 h.

The *T. pratense* seedlings were inoculated with *G. claroideum* Schenck & Smith emend Walker & Vestberg BEG31 by placing approximately 1 ml of inoculum in the planting hole prior to transplanting. The inoculum consisted of a mix of colonized roots, spores, hyphae and substrate. Seedlings not given a mycorrhizal treatment were inoculated with a similar substrate lacking the mycorrhizal fungus. The mycorrhizal and non-mycorrhizal inocula were produced in the roots of micropropagated strawberry (*F.* × *ananassa* cv Nora) between 25 June and 15 December 1996. The substrate was a mixture of steam-sterilized sand and vermiculite (Vermipu Oy, Finland) (1:1). The vermiculite was washed thoroughly in running water before mixing with sand. The substrate mix was limed with 5 g l^{-1} of dolomite (Saxo Oy, Finland) and fertilized with 2 g l^{-1} of bone meal (7N-7.9P-0K, Kemira-Agro Oy, Helsinki, Finland). The inocula were stored at 8°C prior to use.

Experimental design and data analysis

The experiment with *P. annua* and *O. vulgaris* had a 3×2 design with mycorrhizal infection of the host plant (non-mycorrhizal, infected with *G. lamellosum* V43a, infected with *G. mosseae* BEG29) combined with hemiparasitic infection of the host (parasitized versus non-parasitized). There were thus six treatments in this experiment, each replicated 10 times: (1) a host plant infected with *G. lamellosum* V43a growing alone, (2) a host plant infected with *G. mosseae* BEG29 growing alone, (3) a non-mycorrhizal host plant growing alone, (4) a host plant infected with *G. lamellosum* V43a and with one hemiparasite seedling, (5) a host plant infected with *G. mosseae* BEG29 and with one hemiparasite seedling, (6) a non-mycorrhizal host plant infected with one hemiparasite seedling.

The experiment with *T. pratense* and *R. serotinus* had a 2×2 design with mycorrhizal infection of the host plant (mycorrhizal versus non-mycorrhizal) combined with hemiparasitic infection of the host (parasitized versus non-parasitized). Thus there were four treatments in this experiment: (1) a mycorrhizal host plant growing alone, (2) a non-mycorrhizal host plant growing alone, (3) a mycorrhizal host plant growing with one hemiparasite seedling, (4) a non-mycorrhizal host plant growing with one hemiparasite seedling, replicated 12 times.

In the experiment with *P. annua* and *O. vulgaris*, the number of panicles produced by hosts and the number of flowers produced by hemiparasites were counted. Only aboveground biomass of plants was analysed. Both the host plant and the parasitic plant were cut off at the base and oven-dried (80°C, 48 h) before weighing. In the experiment with *T. pratense* and *R. serotinus*, roots of each experimental plant were washed free of debris and the occurrence of haustoria in the two treatments with parasitic plants was verified microscopically. Dry biomass (80°C, 48 h) of both roots and aboveground parts was determined by weighing each plant. The number of flowers produced by the hemiparasite was counted.

In both experiments, a small sample of roots from each host seedling was taken to ascertain that the non-mycorrhizal host plants had remained uninfected with fungi and to evaluate root colonization of the mycorrhizal plants. The roots were bleached in 10% KOH overnight and acidified in 1% HCL before staining at 90°C for 1 h with 0.01% methyl blue (Phillips and Hayman 1970; Grace and Stribley 1991). Root colonization was estimated under a dissecting microscope on the following rating scale: 0, 0–1, 2–5, 6–10, 11–20, 21–30, ... 91–100%.

All statistical analyses were performed using SPSS for Windows. Data sets for the host responses were analysed using two-way ANOVA and data for the parasite responses by *t*-test for two independent samples. After unsuccessful trials to transform the data so as to reach the requirements for a parametric test, one variable (biomass of *R. serotinus*) was analysed with the non-parametric Mann-Whitney *U*-test. Host plants in replicates from which the parasitic plant had died during the experiment were excluded from the statistical analyses.

Results

Host AM root colonization

The roots of *P. annua* did not stain very well, or the internal infection was very low, and root colonization could not be estimated for this host. Observation of roots under the dissecting microscope, however, revealed newly formed spores of both *G. lamellosum* V43a and *G. mosseae* BEG29 in all pots inoculated with these fungi. No spores were detected in samples from the non-inoculated pots. In the experiment with *T. pratense*, the roots of the host plant were similarly colonized by *G. claroideum* BEG31 (t=1.002, df=19, P=0.329) irrespective of the presence (mean 58.9% colonization) or absence (mean 50% colonization) of the hemiparasite.

Host growth responses

Infection with the two species of *Glomus* fungi had no significant effect on the biomass of *P. annua* (Table 1). The non-mycorrhizal *P. annua* plants produced 11% (unparasitized) and 10% (parasitized) less biomass than *P. annua* plants infected with *G. lamellosum* V43a. Corre-

Table 1 ANOVA results showing the effects of infection by a root hemiparasitic plant (host parasitized by one *Odontites vulgaris* plant versus unparasitized) and host mycorrhizal status (infected with *Glomus lamellosum* V43a versus infected with *G. mosseae* BEG29 versus non-mycorrhizal) on host (*Poa annua*) biomass and panicle production

	Biomass				Number of panicles			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Parasite	1	2.619	33.604	<0.001	1	807.978	6.427	0.015
Mycorrhiza	2	0.182	2.334	0.109	2	16.082	0.128	0.880
Parasite×mycorrhiza	2	0.006	0.083	0.921	2	105.627	0.840	0.439
Error	43	0.078			43	125.720		

spondingly, the biomass of non-mycorrhizal *P. annua* plants was only 5% (unparasitized) and 2% (parasitized) lower than the biomass of *P. annua* plants infected with *G. mosseae* BEG29. In contrast to the *P. annua–O. vulgaris* system, infection with *G. claroideum* BEG31 greatly increased the growth of *T. pratense* (Table 2), the biomass of non-mycorrhizal *T. pratense* plants being 72.6% (unparasitized) and 73.3% (parasitized) lower than that of the mycorrhizal plants.

Hemiparasite infection significantly reduced the biomass of *P. annua* (Table 1), but had no significant effect on the biomass of *T. pratense* (Table 2). The parasitized *P. annua* plants produced 22% (when infected with *G. lamellosum* V43a), 23% (when infected with *G. mosseae* BEG29), and 21% (when non-mycorrhizal) less biomass than the respective unparasitized plants. The parasitic infection caused only a 2.9% (mycorrhizal plants) and 5.5% (non-mycorrhizal plants) reduction in the biomass of *T. pratense*. The parasitic plants also reduced the number of panicles produced by the *P. annua* hosts, while the mycorrhizal infection had no effect (Table 1). The parasitized *P. annua* plants produced 12% (when infected with *G. lamellosum* V43a), 11% (when infected with *G. mosseae* BEG29), and 28% (when non-mycorrhizal) fewer panicles than the respective unparasitized plants.

Hemiparasite responses

In the experiment with *P. annua*, a total of 11 *O. vulgaris* plants (out of 30) apparently failed to produce haustorial connections to their hosts. The growth of these plants ceased early and they turned yellowish in colour and died before the end of the experiment. In the experiment with *T. pratense*, three *R. serotinus* plants (out of 24) died during the experiment. The early development of these *R. serotinus* plants was very similar to that of plants growing in identical conditions but without a host plant in the pot.

Mycorrhizal status of *P. annua* hosts affected neither the biomass (0.218±0.065 g for non-mycorrhizal hosts, 0.206±0.065 g for hosts with *G. lamellosum* V43a, 0.293±0.055 g for hosts with *G. mosseae* BEG29; $F_{2,16}$=0.623, P=0.549) nor the number of flowers produced by the attached *O. vulgaris* plants (29.17±7.10 for non-mycorrhizal hosts, 27.83±10.68 for hosts with *G. lamellosum* V43a, 31.14±6.29 for hosts with *G. mosseae* BEG29; $F_{2,16}$=0.044, P=0.957). In the experiment with *T. pratense*, the *R. serotinus* plants attached to mycorrhizal hosts had higher biomass than those growing with non-mycorrhizal hosts (U=18.5, P=0.017) (Table 3). The number of flowers produced by *R. serotinus* plants hosted by mycorrhizal *T. pratense* plants was also higher than that of plants growing with non-mycorrhizal *T. pratense* plants (t=2.885, df=18, P=0.010) (Table 3). Roots of *R. serotinus* were not colonized by *G. claroideum*.

Table 2 ANOVA results showing the effects of infection by a root hemiparasitic plant (host parasitized by one *Rhinanthus serotinus* plant versus unparasitized) and host mycorrhizal status (infected with *G. claroideum* BEG31 versus non-mycorrhizal) on host (*Trifolium pratense*) biomass (data log-transformed prior to analysis)

	df	MS	*F*	*P*
Parasite	1	0.006	0.469	0.497
Mycorrhiza	1	3.516	287.787	<0.001
Parasite×mycorrhiza	1	0.0003	0.027	0.870
Error	39	0.012		

Table 3 Mean (SE) aboveground biomass (g dry wt.) and number of flowers produced by *R. serotinus* hemiparasites attached to *T. pratense* hosts differing in mycorrhizal status (non-mycorrhizal versus infected with *G. claroideum* BEG31)

Host mycorrhizal status	Biomass	Number of flowers
Non-mycorrhizal	0.012 (0.001)	0.40 (0.16)
Mycorrhizal	0.019 (0.002)	1.10 (0.18)

Discussion

In the present study, two host-parasite associations were examined and two types of response by the parasite associates to the mycorrhizal status of hosts were found. The performance of the parasitic plant was found to be higher when associated with a mycorrhizal host in one case (*T. pratense–R. serotinus* system). In contrast, the host mycorrhizal status had no influence on parasite performance in another case (*P. annua–O. vulgaris* system). With *T. pratense–R. serotinus*, the performance of the parasitic plants was either poor (when attached to mycorrhizal hosts) or very poor (with non-mycorrhizal hosts). We believe that a major reason for the poor growth of *R. serotinus* was the very harsh soil conditions. Before the establishment of haustorial connections to host roots, the life of all root hemiparasitic plants is completely autotrophic. Here, the phase of autotrophic life was extended for all *R. serotinus* seedlings by the unproductivity of the soil used. Despite the small size of the *R. serotinus* plants, however, our results are robust and show that both growth and reproduction of the parasite were improved more following a haustorial connection to a mycorrhizal than to a non-mycorrhizal host. Connected to a mycorrhizal host, the parasite obtained access to a root system much larger and more effective in gathering resources from the nutrient-poor soil. Moreover, compared with the parasites growing on non-mycorrhizal hosts, those with mycorrhizal hosts may have benefited from attachment to hosts with higher aboveground biomass and thus increased photosynthetic capacity.

In contrast to *R. serotinus*, the *O. vulgaris* plants performed very well irrespective of host mycorrhizal status. *P. annua*, the host of *O. vulgaris* in this study, is known to form mycorrhizal associations (Gange et al. 1999), but here the presence of mycorrhiza increased the growth

of *P. annua* by only about 10% in one association (*G. lamellosum* V43a) and even less in another (*G. mosseae* BEG29G). It seems that fungal association did not improve the quality of the mycorrhizal *P. annua* hosts sufficiently to allow support of attached *O. vulgaris* hemiparasites.

The response of *R. serotinus* to the *T. pratense–Glomus claroideum* BEG31 association was very similar to that found for *Rhinanthus minor* hosted by mycorrhizal *Lolium perenne* (Davies and Graves 1998). In that study, mycorrhizal colonization of host roots by AM fungi stimulated the growth and reproduction of the attached root hemiparasite. An increase in both *R. minor* biomass and number of flowers was found, even though mycorrhizal infection of host roots affected neither the growth nor the nutritional status of the host. In our study, infection of *T. pratense* by *G. claroideum* BEG31 clearly stimulated growth of the host. We did not investigate the influence of mycorrhizal colonization on the nutrient status of host tissue, but assume that the enhanced host growth was due mainly to enhanced access to soil nutrients, phosphorus in particular. The results from the *T. pratense–R. serotinus* system are also consistent with the results of a recent study (Salonen et al. 2000) in which EM infection was found to increase the growth of *Pinus sylvestris* plants, while infection by the root hemiparasitic *Melampyrum pratense* significantly decreased their biomass. In that study, *M. pratense* plants attached to mycorrhizal pines had higher biomass and produced more flowers than those growing with non-mycorrhizal pines. The stimulation of parasite performance in the presence of EM fungi was attributed to enhanced phosphorus availability to the hosts and to the increased photosynthetic capacity resulting in increased aboveground biomass.

The influence of mycorrhizal infection on host growth was much stronger for *T. pratense* than for *P. annua*. There are several possible explanations for this difference, bearing in mind that an AM effect on plants is the resultant of plant dependence on AM, AM fungus community size and structure, soil and climatic conditions, and the compatibility of these factors (Kahiluoto et al. 2000). Plant species may differ greatly in response to colonization by AM fungi. *Trifolium* spp., as most members of the family Fabaceae, are known to be very responsive to AM, whereas *P. annua* is considered to be only weakly mycorrhizal (Harley and Harley 1987). In fact, the growth of grasses from temperate regions is often not increased by AM inoculation (Hall et al. 1984; Sanders and Fitter 1992; Newsham et al. 1995). It has been suggested that AM fungi function in other ways in grasses, for example by protecting the roots against soil pathogens (Newsham et al. 1995). The influence of a mycorrhizal association on plant growth is always conditional on the availability of soil nutrients, especially phosphorus (Pearson and Jakobsen 1993; Marschner and Dell 1994). Thus the observed differences in plant response to mycorrhiza may have resulted from a difference in productivity of the soil used in the two experiments. In order to assure a heavy mycorrhizal infection, the substrate in our *T. pratense–R. serotinus* system was very nutrient-poor, while the substrate used in the *P. annua–O. vulgaris* system had a much higher content of organic matter and was thus much more productive. In this substrate, phosphorus was not the limiting factor for optimal growth of *P. annua*.

In our growth-room experiment, parasitism (by *R. serotinus*) was found to have no effect on host (*T. pratense*) mycorrhizal colonization. This result contrasts with that obtained by Davies and Graves (1998) who found that infection by *R. minor* resulted in a significant decline in the mycorrhizal colonization of *L. perenne*. In our study, the *R. serotinus* plants caused no significant reduction in biomass of the *T. pratense* hosts. Consequently, the size of the carbon pool available to the AM fungus was very similar with or without parasites. In agreement with our results, Puustinen et al. (2001) found no reduction in growth of *T. pratense* following *R. serotinus* infection. Similarly, Matthies (1998) found no negative effects of parasitism by *Euphrasia minima* on growth of *Lolium perenne* or *Medicago sativa*. The fact that the growth of the *T. pratense* host was not reduced by the hemiparasite implies that the host plants were not resource limited, despite a very nutrient-poor soil, and could fully compensate for their losses to the hemiparasites by extra growth.

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