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Response of a root hemiparasite to elevated CO₂ depends on host type and soil nutrients

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Abstract Although elevated CO₂ may affect various forms of ecological interactions, the effect of elevated CO₂ on interactions between parasitic plants and their hosts has received little attention. We examined the effect of elevated CO₂ (590 µl l⁻¹) at two nutrient (NPK) levels on the interactions of the facultative root hemiparasite *Rhinanthus alectorolophus* with two of its hosts, the grass *Lolium perenne* and the legume *Medicago sativa*. To study possible effects on parasite mediation of competition between hosts, the parasite was grown with each host separately and with both hosts simultaneously. In addition, all combinations of hosts were grown without the parasite. Both the parasite and the host plants responded to elevated CO₂ with increased growth, but only at high nutrient levels. The CO₂ response of the hemiparasite was stronger than that of the hosts, but depended on the host species available. With *L. perenne* and *M. sativa* simultaneously available as hosts, the biomass of the parasite grown at elevated CO₂ was 5.7 times that of parasites grown at ambient CO₂. Nitrogen concentration in the parasites was not influenced by the treatments and was not related to parasite biomass. The presence of the parasite strongly reduced both the biomass of the hosts and total productivity of the system. This effect was much stronger at low than at high nutrient levels, but was not influenced by CO₂ level. Elevated CO₂ did not influence the competitive balance between the two different hosts grown in mixture. The results of this study support the hypothesis that hemiparasites may influence community structure and suggest that these effects are robust to changes in CO₂ concentration.

Key words Competition · *Lolium* · *Medicago* · *Rhinanthus* · Root hemiparasites

Introduction

A rise in the concentration of CO₂ in the atmosphere can directly affect the physiology of plants. Frequently observed effects of elevated CO₂ include higher rates of photosynthesis and increased water use efficiency (Bazzaz 1990; Eamus 1991; Körner 1993). However, the indirect effects of elevated CO₂ through changes in the interactions between plants and other organisms may be more important than direct physiological changes. Interactions that have been found to be influenced by CO₂ concentration include competition (Bazzaz and Garbutt 1988; Stewart and Potvin 1996), herbivory (Williams et al. 1994; Bezemer and Jones 1998), and the relations between plants and their fungal and bacterial mutualists and parasites (Masterson and Sherwood 1978; Sanders 1996; Jongen et al. 1996). Little attention has been paid, however, to the possible influence of elevated CO₂ on interactions between parasitic plants and their hosts, although several features of plant parasitism may be affected (Watling and Press 1997). Elevated CO₂ might change the physiology (e.g. rates of photosynthesis) of both parasite and hosts, it might affect “food quality” (e.g. availability of nitrogen) for the parasite through an effect on the C/N ratio of host tissue (Williams et al. 1994), and it could influence the transpiration rates of parasite and host.

Most parasitic plants are in fact hemiparasites and capable of photosynthesis, but extract water, inorganic and organic solutes via specialized contact organs (haustoria) from their hosts (Press et al. 1990). A consistent feature of hemiparasites is a transpiration rate that far exceeds that of their hosts (Press et al. 1990). Increased water use efficiency of the parasite and the host under elevated CO₂ could thus reduce the negative effects of parasitism on the host. However, if parasite growth were

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strongly stimulated by elevated CO₂, the effects of increased water use efficiency could be easily outweighed by increased demand from the parasite.

Although hemiparasites are usually not host-specific, their growth and reproduction can be strongly influenced by the type of host species (e.g. Matthies 1996; Marvier 1996) and by host condition (Salonen and Puustinen 1996). Hemiparasites growing with nitrogen-rich hosts (e.g. legumes) often have greater concentrations of nitrogen, higher rates of photosynthesis and better growth than those growing with nitrogen-poor hosts (Seel and Press 1993; but see Marvier 1996). The loss of water and solutes to a hemiparasite can strongly reduce the growth of the host plants, especially when nutrients are limiting (Malcolm 1964; Gibson and Watkinson 1991). Because parasitic plants may reduce the productivity of vegetation (Matthies 1995) and mediate competition between different host species they may affect the structure and composition of their communities (Gibson and Watkinson 1991; Matthies 1996; Pennings and Callaway 1996). In addition to direct effects on parasitic plants and their hosts, elevated CO₂ could therefore also have indirect effects on community composition, mediated by the parasites.

We examined the effect of elevated CO₂ at two nutrient levels on the interactions of the facultative hemiparasite *Rhinanthus alectorolophus* with two of its hosts, the grass *Lolium perenne* and the legume *Medicago sativa*. To study possible effects on the competitive balance between these two host species, the parasite was grown with each host separately and with both hosts simultaneously. We address the following specific questions:

1. Does CO₂ concentration influence the growth of the hemiparasite, and does this effect depend on nutrient level and on the hosts available?
2. Does the effect of the parasite on host biomass and total productivity depend on CO₂ concentration and nutrient level?
3. Do the levels of CO₂ and nutrients affect a possible mediation of competition between different host species by the parasite?

Materials and methods

The annual hemiparasite *R. alectorolophus* is widely distributed throughout Central Europe. Typical habitats of the plant include calcareous grasslands, meadows and waysides, but the species was also formerly a weed of arable fields (Hartl 1974). *Rhinanthus* occurs on both nutrient-rich and nutrient-poor soils. Like other hemiparasitic Scrophulariaceae, *Rhinanthus* has a wide host range that includes both grasses and dicots (Hartl 1974). *Lolium perenne* (perennial rye-grass) and *Medicago sativa* (alfalfa), the host species selected for this study, are widespread species that frequently occur together with *Rhinanthus*. The study species are hereafter referred to by genus.

Seeds of *Rhinanthus* were germinated on moist filter paper in petri dishes at 5°C. On 27 March 1996 the seedlings were transplanted into pots (10 cm diameter) filled with nutrient-poor commercial potting soil (NPK each 150 mg l⁻¹, pH 5.8). At the same time seeds of the designated host plants *Lolium* and *Medicago* were

sown into part of the pots. The following host treatments were set up: (1) 1 *Rhinanthus* without a host, (2) 1 *Rhinanthus* + 2 *Lolium* as hosts, (3) 1 *Rhinanthus* + 2 *Medicago*, (4) 1 *Rhinanthus* + 1 *Lolium* + 1 *Medicago*. To investigate the effect of the hemiparasite on the hosts, all host combinations were also set up without the parasite. There were 50 replicates for each combination of plants. The plants were kept on benches in the experimental garden at Zürich and were watered if necessary. On 24 April, 32 replicate pots in which all plants had survived were selected randomly for each combination of plants and transported to the CO₂ enrichment facility of the Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft (WSL) at Birmensdorf near Zürich. This facility consists of 16 open-top chambers, half of which are run at ambient CO₂ (374 µl l⁻¹) and the other half at elevated CO₂ (590 µl l⁻¹). Light intensity in the chambers was c. 60% of full daylight. Two replicate pots for each combination of plants (i.e. 14 pots) were placed in each of the chambers. One replicate set of pots in each chamber received 60 ml of a nutrient solution prepared with a commercial fertilizer (Wuxal, Maag, Switzerland) containing 400 mg N l⁻¹, 400 mg P l⁻¹ and 300 mg K l⁻¹ (high-nutrient treatment). The other set received the same amount of water (low-nutrient treatment). To prevent contamination with fertilizer the pots were placed on saucers. To maintain the differences between the nutrient treatments, the high nutrient plants received another 30 ml of the same nutrient solution on 23 May and 4 June. The plants were watered every 2nd day and randomized within each chamber every 2 weeks. Because the chambers were covered automatically by transparent roofs at the onset of rain, the plants received no precipitation.

On 24 June 1996 the height of each parasite was measured. The above-ground parts of the parasites were harvested and partitioned into vegetative (stems and leaves) and reproductive structures (flowers and capsules). The above-ground parts of the host plants were also harvested. An inspection of the root systems showed that the roots of the legume were well nodulated. No roots were harvested, because annual root hemiparasites like *Rhinanthus* allocate very little of their biomass to roots (Matthies 1995), and treatment effects on above-ground biomass and reproduction were therefore most interesting. Moreover, the root systems of the two different host species could not have been separated.

All plant parts were dried for 48 h at 80°C and weighed. The parasites were milled and element concentrations were determined with a CHN-analyser (Leco, St. Joseph, Mich., USA).

The data were analysed by ANOVA. To achieve normally distributed residuals and homoscedasticity, biomass data were log-transformed prior to analysis. Because of the hierarchical design the main effect of CO₂ level was tested against the residual mean square among chambers, whereas all other main and interaction effects were tested against the residual mean square among pots. For the same reason sequential sums of squares (type 1 sums of squares, Shaw and Mitchell-Olds 1993) were used in the analyses. Single degree of freedom contrasts were used to test specific hypotheses. All results were robust; changing the order in which effects were fitted did not change the results qualitatively.

Results

The biomass of the hemiparasite *Rhinanthus* depended strongly on host presence and host combination (Fig. 1, Table 1). The availability of a host increased parasite biomass on average 5-fold ($F = 34.6$, $P < 0.001$). Parasites grown with two different hosts simultaneously did not produce more biomass than parasites grown with only one species of host ($F = 0.8$, $P > 0.2$). Of the two host species, the grass *Lolium* was a far better host for *Rhinanthus* than the legume *Medicago* ($F = 6.7$, $P < 0.05$). Mean biomass of the parasite was 74% higher with *Lolium* than with *Medicago*.

Parasites grown at high nutrient levels produced twice the biomass of parasites grown at low nutrient levels. The effect of elevated CO₂ depended on nutrient level (Table 1, significant CO₂ × nutrient interaction). While elevated CO₂ at low nutrients slightly decreased parasite biomass (−16%), it strongly increased parasite biomass at high nutrients (+123%). However, the effect of elevated CO₂ depended not only on nutrient level, but also on the host treatment (Table 1, significant CO₂ ×

nutrient × host interaction): elevated CO₂ had the strongest effect (5.7-fold increase in biomass) on parasites grown at high nutrients and with both hosts simultaneously. In contrast, the ratio between parasite biomass at elevated CO₂ and ambient CO₂ at high nutrient levels was only 2.7 with *Medicago* as host, 0.9 with *Lolium*, and 1.4 without a host. The height of the parasites was highly correlated with their biomass ($r = 0.94, P < 0.001$) and the different treatments affected parasite height similarly to biomass.

For an annual plant like *Rhinanthus* reproduction is more important than biomass accumulation. Reproduction of the parasite was much higher at high than at low nutrient levels (Table 1). Nutrient availability also influenced strongly the effect of CO₂ level (Table 1, significant CO₂ × nutrient interaction). While at low nutrient levels the number of flowers produced was lower (−44%) at elevated than at ambient CO₂, at high nutrients elevated CO₂ strongly increased reproduction of the parasite (+88%). However, neither CO₂ nor nutrient level influenced the phenology of the parasite, as indicated by the proportion of plants flowering at the time of harvest (χ^2 -test, $P > 0.5$).

The nitrogen concentration of the parasite (2.0% on average) was not related to biomass ($r = -0.14, P = 0.22$), and neither the nitrogen concentration ($P = 0.12$ for the effect of nutrient level, $P > 0.5$ for all other effects) nor the C/N ratio (21.1% on average) of the parasite tissue was significantly influenced by any of the treatments ($P > 0.5$ for all effects).

The biomass produced by the host plants depended on the host combination (Fig. 2, Table 2). In particular, both host combinations containing the grass *Lolium* had a much higher biomass than the combination consisting of two *Medicago* plants. Host biomass was much higher at high nutrient levels, but there was no main effect of CO₂ level. However, there was a significant interaction between the effects of nutrient and CO₂ level. At low nutrients, elevated CO₂ decreased host biomass by 18%, whereas at high nutrients it increased host biomass by 29%. The nutrient effect varied among the host treat-

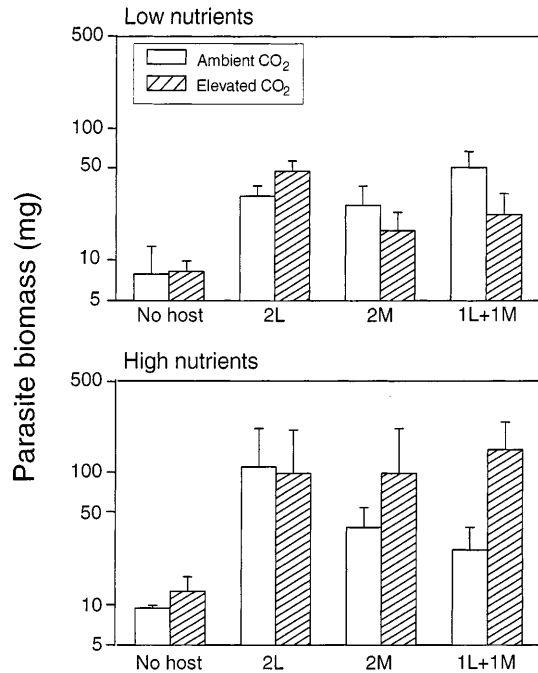


Fig. 1 The effect of CO₂ and nutrient level on above-ground biomass of the hemiparasite *Rhinanthus alectorolophus* grown with different hosts. The parasite was grown without host (*no host*), with two individuals of the grass *Lolium perenne* (*2L*), with two individuals of the legume *Medicago sativa* (*2M*), and with one individual each of *Lolium* and *Medicago* (*1L + 1M*). Vertical bars denote 1 SE. Note log-scale for biomass. Means and SEs were calculated from log-transformed data, and SEs are therefore symmetrical around the mean

Table 1 Summary of analyses of variance of the effects of CO₂ level, nutrient level and host combination on biomass, height and reproduction of the hemiparasite *Rhinanthus alectorolophus*. The parasite was grown with either two individuals of *Lolium perenne* or

Medicago sativa, or with one individual of *Lolium* and *Medicago* each. The effect of CO₂ level was tested against the residual variation among chambers, all other effects against the residual among pots

Source of variation	df	F-value		
		Biomass	Plant height	Number of flowers
CO ₂ level	1	0.4	0.8	0.3
Chamber within CO ₂ level	14	1.9	1.3	1.0
Nutrient level	1	14.4***	15.8***	13.5***
Host combination	3	12.7***	7.8***	5.1**
CO ₂ × nutrient level	1	6.1*	4.5*	5.7*
CO ₂ × host combination	3	<0.1	0.2	0.4
Nutrients × host combination	3	0.7	1.1	0.1
CO ₂ × nutrients × host combination	3	3.0*	2.7	0.1
Residual	43			

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

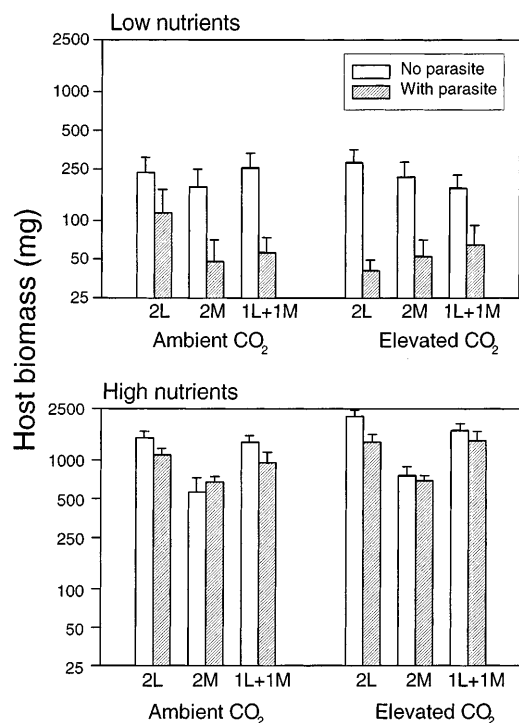


Fig. 2 The effect of nutrient level, CO₂ concentration and parasitization by the hemiparasite *R. alectorolophus* on above-ground biomass of different combinations of host plants. Host combinations were two individuals of *L. perenne* (2L), two individuals of *M. sativa* (2M), and one individual of *Lolium* and *Medicago* each (1L + 1M). Vertical bars denote 1 SE. Note log-scale for biomass. Means and SEs were calculated from log-transformed data, and SEs are therefore symmetrical around the mean

Table 2 Summary of analyses of variance of the effects of CO₂ level, nutrient level, different host combinations and the hemiparasite *R. alectorolophus* on the biomass of the host species and on total biomass per pot. The parasite was grown with either two individuals of *L. perenne* (2L) or *M. sativa* (2M), or with one individual of *Lolium* and *Medicago* each (1L/1M). The effect of CO₂ level was tested against the residual variation among chambers and all other effects against the residual. All three- and four-way interactions were not significant and were pooled with the residual

Source of variation	df	F-value	
		Host biomass	Total biomass
CO ₂ level	1	0.22	0.46
Chamber within CO ₂ level	14	1.87*	2.04
Nutrient level	1	584.6***	605.0***
Parasite presence	1	66.8***	34.4***
Host combination	2	12.1***	18.5***
2L,1L/1M vs. 2M	1	22.9***	35.6***
CO ₂ × parasite	1	0.94	0.72
CO ₂ × nutrients	1	4.30*	5.33*
CO ₂ × host combination	2	0.45	0.01
Parasite × nutrients	1	35.5***	18.6***
Parasite × host combination	2	0.33	0.16
Nutrients × host combination	2	3.76*	2.92
Nutrients × 2L,1L/1M vs. nutrients × 2M	1	7.49**	5.83*
Residual	163		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

ments. Both host combinations containing the grass responded more strongly (11-fold increase) to increased nutrient supply than two legumes (7-fold increase). In contrast, the effect of elevated CO₂ did not depend on the host combination (see Table 2).

Parasitization reduced average host biomass by 53%. However, the negative effect of the parasite on the hosts depended strongly on nutrient level (Table 2, nutrient × parasite interaction). While the parasite reduced host biomass at low nutrients by 73%, it only reduced host biomass by 19% at high nutrients. In contrast, CO₂ level did not influence the effect of the parasite on the hosts (Table 2, interaction parasite × CO₂ level). None of the treatments influenced the competitive balance between *Lolium* and *Medicago* (measured as coefficient of variation of the biomass of the two hosts in a pot) in the mixed host treatment ($P > 0.1$ for all effects).

Treatment effects on total biomass per pot (parasite + hosts) showed a similar pattern as effects on host biomass (Fig. 3, Table 2). Thus, elevated CO₂ slightly decreased total biomass at low nutrients (−11%), but increased it at high nutrients (+31%). The presence of the parasite reduced total productivity per pot on average by 39%. However, the reduction was much stronger at low nutrients (−58%) than at high nutrients (−12%).

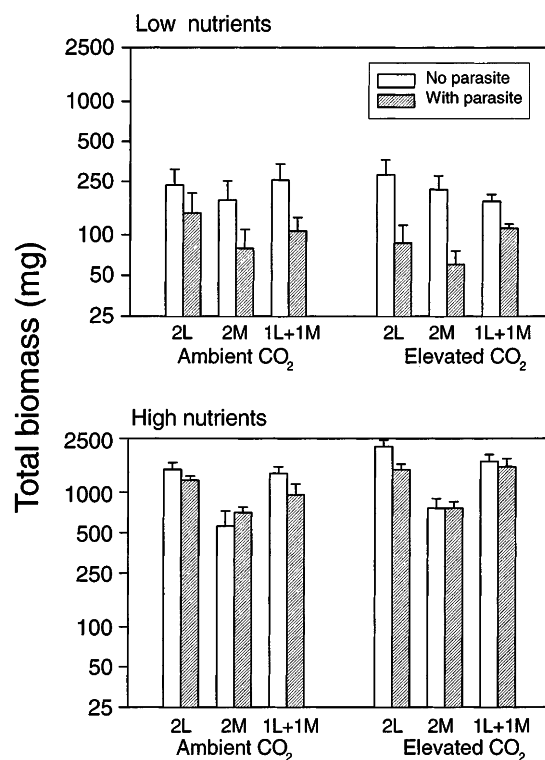


Fig. 3 The effect of nutrient level, CO₂ concentration and parasitization by the hemiparasite *R. alectorolophus* on total biomass per pot (parasite + host). Host combinations were two individuals of *L. perenne* (2L), two individuals of *M. sativa* (2M), and one individual of *Lolium* and *Medicago* each (1L + 1M). Vertical bars denote 1 SE. Note log-scale for biomass. Means and SEs were calculated from log-transformed data, and SEs are therefore symmetrical around the mean

Discussion

Both the parasite *Rhinanthus* and the host plants responded with increased growth to elevated CO₂, but only at high nutrient levels. Other studies have also found that the responsiveness of plants to CO₂ enrichment is stronger at high nutrient levels (Larigauderie et al. 1988; McConnaughay et al. 1993). However, the response of the hemiparasite, measured as the ratio between biomass at elevated CO₂ and ambient CO₂ (mass ratio, e.g. Poorter 1993), was much stronger (mean mass ratio 2.23) than the response of the hosts (mass ratio 1.29). Especially remarkable was the response of the hemiparasite at high nutrients grown with both hosts simultaneously (mass ratio 5.7), which was stronger than that of any of the 250 species reviewed by Poorter et al. (1996). Root hemiparasites obtain not only water and nutrients, but also some carbon from their host (Govier and Harper 1965; Press et al. 1990). The parasite may therefore have benefited from elevated CO₂ both directly through increased own carbon fixation and indirectly through increased carbon uptake from the hosts. However, the response of *Rhinanthus* to elevated CO₂ depended strongly on the host treatment, indicating that the response of parasitic plants to changes in ecological conditions may differ depending on the type and number of host species available. Recently, it has been shown that hemiparasites may profit from a "mixed diet", i.e. several host species simultaneously (Marvier 1998). The number of flowers produced by *Rhinanthus* was influenced in a similar way as parasite biomass by the treatments indicating that the effects on biomass will be translated into evolutionary important effects on the fitness of these annual hemiparasites.

The observed strong response of *Rhinanthus* to elevated CO₂ at high nutrient levels is in contrast to the results of other studies on the effects of CO₂ level on root hemiparasites. No effect of elevated CO₂ or increased nitrogen deposition on parasite biomass was found in the related hemiparasite *Melampyrum sylvaticum* (Hättenschwiler and Körner 1997) and the holoparasite *Orobanche minor* (Dale and Press 1998). The biomass of the tropical root hemiparasites *Striga hermonthica* and *S. asiatica* was actually lower at elevated than at ambient CO₂, although host biomass was higher (Watling and Press 1997).

There was no consistent best host or host combination for *Rhinanthus*. Instead, there was a complex interaction between host type, nutrient level and CO₂ level. This may be related to the fact that there were no consistent effects of the different hosts on the nitrogen concentration of the parasite. In contrast, strong stimulation of parasite growth by legumes has been found for a number of hemiparasites and been related to greater availability of nitrogen in leguminous hosts (Govier et al. 1967; Seel and Press 1993; but see Marvier 1996). Nitrogen concentration of the parasite was also not significantly increased by high nutrient levels.

However, parasite growth was strongly stimulated by nutrients, and growth may have been so rapid that tissue nitrogen concentrations did not rise. Similar responses have been observed in autotrophic species (Fitter 1986).

Like other root hemiparasites (Gibson and Watkinson 1991; Matthies 1995), *Rhinanthus* strongly reduced the biomass of the hosts. Host damage by the parasite was much stronger at low than at high nutrient levels, suggesting that the influence of *Rhinanthus* on the hosts was mainly through competition for nutrients. This mechanism could also explain why the different CO₂ concentrations did not influence the effect of the parasites on the host: the growth of both parasite and hosts was more strongly influenced by CO₂ concentration at high nutrient levels, i.e. when effects of parasitism on the hosts were small. However, interactions between root hemiparasites and their hosts might also be generally insensitive to CO₂ concentration. In a study with the tropical root hemiparasites *Striga hermonthica* and *S. asiatica* the relative impact of the parasites on their host was also very similar under ambient and elevated CO₂ concentrations (Watling and Press 1997). In contrast, the negative effect of the holoparasite *Orobanche minor* on its host *Trifolium repens* was smaller under elevated CO₂ (Dale and Press 1998).

The reduction in host biomass due to the parasite was not compensated by its own biomass, resulting in a reduction of total productivity. Like other root hemiparasites (Gibson and Watkinson 1991; Matthies 1995; Davies et al. 1997), *Rhinanthus* may therefore potentially influence the structure and functioning of its communities, particularly in nutrient-poor habitats (Fig. 3). In contrast to nutrient levels, the CO₂ concentration did not influence the effect of the parasite on productivity. Moreover, elevated CO₂ did not influence the competitive balance between the two different hosts grown in mixture; neither directly, nor indirectly via the parasite. Actually, there was even no evidence for mediation of competition between the hosts by the parasite. This is in contrast to results of an earlier study (Matthies 1996) with the same hosts and the related parasite *Melampyrum arvense*, in which in mixtures of hosts *Medicago* suffered more from parasitization than *Lolium*. However, the interactions between pairs of host and parasite species can be very specific, and even closely related parasitic plant species can have very different effects on the same host (Matthies 1997).

In conclusion, the results of this study suggest that hemiparasites, when growing with certain combinations of hosts, may respond much more strongly than autotrophic plants to increased atmospheric CO₂. This stimulation of parasite growth, however, may not necessarily result in increased damage to their host plants. The results support the hypothesis that hemiparasites may influence community structure, because they reduce productivity, but do not provide evidence that this effect may be influenced by CO₂ concentration.

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