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
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 parasitises.

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 ± l⁻¹) and the other half at elevated CO₂ (590 ± 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 parasitises 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 parasitises 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.