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Hemiparasite abundance in an alpine treeline ecotone increases in response to atmospheric CO_2 enrichment

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Abstract Populations of the annual hemiparasites *Melampyrum pratense* L. and *Melampyrum sylvaticum* L. were studied at the treeline in the Swiss Alps after 3 years of in situ CO_2 enrichment. The total density of *Melampyrum* doubled to an average of 44 individuals per square meter at elevated CO_2 compared to ambient CO_2. In response to elevated CO_2, the height of the more abundant and more evenly distributed *M. pratense* increased by 20%, the number of seeds per fruit by 21%, and the total seed dry mass per fruit by 27%, but the individual seed size did not change. These results suggest that rising atmospheric CO_2 may stimulate the reproductive output and increase the abundance of *Melampyrum* in the alpine treeline ecotone. Because hemiparasites can have important effects on community dynamics and ecosystem processes, notably the N cycle, changing *Melampyrum* abundance may potentially influence the functioning of alpine ecosystems in a future CO_2-rich atmosphere.

Keywords Elevated CO_2 · *Melampyrum pratense* · Reproduction · Plant growth · Swiss Alps

Introduction

One of the most important direct influences of the rising atmospheric CO_2 concentration on ecosystem properties is the species-specific growth stimulation of co-occurring plants, leading to altered community composition, and potentially strong cascading effects on ecosystem functioning (Körner 2000, 2003). In the Mojave Desert, for example, the invasive annual grass *Bromus madritensis* ssp. *rubens* showed a much stronger CO_2 response in biomass and seed production than native annuals (Smith et al. 2000). Smith and coworkers concluded that the CO_2-induced increasing dominance of the invasive *Bromus* will accelerate the fire cycle, and thus, may reduce biodiversity and fundamentally change ecosystem functioning in North American deserts. Certain plant functional groups may respond particularly strongly to elevated CO_2. For example, some laboratory experiments suggest a high growth stimulation of annual root hemiparasites exposed to elevated atmospheric CO_2 concentrations (Hättenschwiler and Körner 1997; Matthies and Egli 1999; Grünzweig and Körner 2001). However, it is difficult to predict whether or not laboratory results reflect the situation in the field, because hemiparasite performance is highly context dependent (Press 1989), i.e., is influenced by the diversity and abundance of host species, their growth conditions, and general environmental conditions which are all difficult to simulate in the laboratory.

Although parasitic plants rarely contribute significantly to community biomass in natural ecosystems, they have strong effects on the structure and function of plant communities (see review by Phoenix and Press 2005). They can substantially reduce the growth of their hosts (Matthies 1997; Joshi et al. 2000), mediate the competitive balance among host plants (Gibson and Watkinson 1991; Matthies 1996), and determine species composition and community structure to a great extent (Davies et al. 1997; Callaway and Pennings 1998; Marvier 1998; Joshi et al. 2000; Westbury and Dunnett 2000). Hemiparasite dependence on host plants is primarily for water and inorganic nutrients, but they also commonly constitute a sink for host derived organic carbon compounds to a considerable degree (Press et al. 1987; Press 1989; Tennakoon and Pate 1996). Experiments with elevated CO_2 frequently show that plants allocate most of their surplus carbon gain in a CO_2-

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enriched atmosphere to belowground sinks (Hättenschwiler and Körner 1996; Hungate et al. 1997). Such enhanced belowground carbon allocation in host plants provides a mechanism for the observed strong CO_2 response in root hemiparasites, which may profit from both their own increased autotrophic and the host derived heterotrophic carbon uptake.

In the present study we test the hypothesis that elevated CO_2 increases the population density of root hemiparasites under field conditions in a natural treeline ecotone (2,180 m a.s.l.) of the Swiss Central Alps after 3 years of CO_2 enrichment. The two annual species *Melampyrum pratense* and *Melampyrum sylvaticum* are a typical and abundant component of the ericaceous dwarf shrub dominated plant community at treeline which was exposed to an elevated CO_2 concentration (target value of 560 mol mol^{-1}) using free air CO_2 enrichment (FACE) technology.

Materials and methods

Study site

The study site was chosen within the long-term research site at Stillberg, Davos in the Swiss Central Alps at 2,180 m a.s.l. (47°28′N, 7°30′E), representative of, or slightly above, the actual natural treeline. The long-term average annual precipitation at the NE-exposed study site is 1050 mm with a mean maximum snow depth of 1.46 m, an average temperature of –5.8°C in January, and 9.4°C in July (Schönenberger and Frey 1988). The soil (classified as Ranker/Lithic Haplumbrept) consists typically of a 10 cm-deep organic top layer on siliceous (Paragneis) bedrock (Schönenberger and Frey 1988).

The vegetation is dominated by ericaceous dwarf shrubs with *Vaccinium myrtillus, Vaccinium uliginosum*, and *Empetrum hermaphroditum* as the most abundant species. Herbaceous plants contributing only a little to total plant cover and biomass are represented by a total of 24 species with *Avenella flexuosa*, *Homogyne alpina, Leontodon* sp., *Gentiana punctata*, and *M. pratense* as the most common and abundant species. Widely spaced individuals of two tree species (*Larix decidua, Pinus uncinata*) form an open tree canopy.

Experimental design

Across an area of approximately 2,500 m^2, a total of 40 plots each of 1.1 m^2 surface area and with one tree (20 of each of the two species *L. decidua* and *P. uncinata*) in the plot center was established, beginning with snowmelt on June 12, 2001. Using a split-plot approach, the 40 plots were assigned to ten blocks of four neighboring plots in order to facilitate logistics of CO_2 distribution and regulation. Half of these blocks were subsequently exposed to an elevated CO_2 atmosphere over three growing seasons using the pure CO_2 release technology (see Hättenschwiler et al. 2002), while the remaining blocks served as controls at ambient CO_2 concentration (ca 367 μmol mol^{-1}). Plots were delimited by three wooden posts and a hexagonal stainless steel frame. From each frame, 24 laser-punched drip irrigation tubes (inner diameter of 4.3 mm, laser holes of 0.5 mm every 15 cm; Drip Store Inc., Escondido, CA, USA) were hung vertically around the ring (15 cm apart from each other) and weighted with a 3 mm stainless steel rod (to maintain rigidity). Each plot was fed by four supply tubes of pure CO_2 (attached in the four cardinal directions in the inner circumference of the frame). CO_2 concentrations were continuously measured and kept constant by means of a monitoring and regulating system (Hättenschwiler et al. 2002). The CO_2 enrichment treatment was applied in the growing season (ca 15 June to 15 September in 2001 to 2003) during daylight hours when weather conditions were suitable. Under highly suboptimal weather conditions (i.e., PPFD < 100 μmol m^{-2}s^{-1}, wind speeds > 75 km/h, temperatures < 5°C, snow, or sleet), we interrupted CO_2 release because of the high costs of CO_2 and helicopter gas transport. Technical failure (< 5%) or weather conditions meant that plots received CO_2 enrichment for 75, 81, and 73% of the respective 2001–2003 growing seasons. Seasonal averages (2001–2003; ± SD) were 566 ± 42, 582 ± 35, and 579 ± 52 μmol CO_2 mol^{-1}.

Plant sampling and data analysis

Vascular plant species were identified and cover/abundance estimates were made for each species in each individual plot at the onset of the first experimental summer in 2001. The first seed cohort of *Melampyrum* produced under treatment conditions germinated in 2002, and the 2003 populations represented the first generation that descended from completely treatment-influenced mother plants (including seed origin for mothers). All individuals of *M. pratense* and *M. sylvaticum* were counted within each of the 40 experimental plots at the beginning of the flowering period (July 10) when the aboveground seedling establishment phase was completed in 2003. All plots were visited again towards the end of the growing season in August 2003 to measure total plant height, and fruits were collected in the more common *M. pratense*. Three individuals within each plot were chosen randomly for height measurements and fruit collection. Plant height is defined as the total length of the main stem from the soil surface to the plant top. The two lowermost fruits along the plant stem were collected from each individual when ripe (i.e., carpels were dry and ready to open and release seeds), seeds were counted, oven-dried at 80°C, and weighed. The two lowermost fruits were chosen to standardize measurements because *M. pratense* continues to produce fruits until the end of the growing season, and many of them do not commonly fully mature.

Table 1 Analyses of covariance (mean vegetation height as covariable) to test for effects of CO_2 concentration on hemiparasite abundance, growth, and seed production. The CO_2 effect was tested at the block level according to the split plot design

Variable	Source of variance	*Df*	Mean square	*F*-value	*P*-value
Total density of	Vegetation height	1	5.16	9.77	0.004
Melampyrum individuals	CO_2	1	6.38	12.75	0.007
	Residual	8	0.50		
Density of	Vegetation height	1	6.91	12.75	0.001
M. pratense individuals	CO_2	1	4.91	17.09	0.003
	Residual	8	0.29		
M. pratense	Vegetation height	1	5.11	1.26	0.27
plant height	CO_2	1	17.72	9.93	0.014
	Residual	8	1.79		
M. pratense	Vegetation height	1	0.31	1.41	0.26
seed number	CO_2	1	2.42	6.37	0.036
	Residual	8	0.38		
M. pratense	Vegetation height	1	6.60	1.15	0.32
total seed mass per fruit	CO_2	1	159.6	27.86	0.001
	Residual	8	5.72		
M. pratense	Vegetation height	1	0.11	0.06	0.81
individual seed mass	CO_2	1	1.69	0.97	0.35
	Residual	8	1.74		

Data were analyzed by analysis of covariance (ANCOVA) using a full factorial split-plot model to test for effects of CO_2 concentration (elevated and ambient) and tree species presence (larch and pine in the center of the plot, $n = 10$ plots). However, neither tree species identity nor the interaction term of tree species identity, and CO_2 treatment explained a significant amount of variation in any of the variables measured, and the factor ''tree species'' was consequently removed from the statistical model. The mean height of the understory plant community of each plot (measured at five random points within each plot) was entered as a covariable into the statistical model because aboveground competition for light might influence establishment success and growth of *Melampyrum* seedlings. Depending on the composition of the dwarf shrub community, experimental plots varied between 7.6 ± 1.1 cm and 30.4 ± 3.4 cm in mean understory height. The variation in understory vegetation height explained a significant portion of variability in *Melampyrum* population density. Understory vegetation height as such, however, was not different between plots of contrasting CO_2 treatments (see also Fig. 1). To meet the requirement of normally distributed residuals, data of plant densities were log-transformed prior to analyses.

Results

Melampyrum abundance

Melampyrum spp. was present in 34 of the 40 study plots at the beginning of the experiment in 2001, and in all 40 plots in 2003 (data not shown). Both *Melampyrum* species were equally distributed between ambient and elevated CO_2 treatments (data not shown).

The density of established *Melampyrum* individuals at the onset of the flowering period in 2003 was significantly higher in elevated CO_2 plots than in ambient CO_2 plots (Table 1). Across species, we counted a total of 44 ± 8 individuals per square meter of ground in elevated CO_2 plots compared to 22 ± 4 individuals in ambient CO_2 plots. There were 27 ± 4 individuals per square meter of ground in elevated CO_2 plots, and 20 ± 4 individuals in ambient CO_2 plots from the more common and evenly distributed *M. pratense*. However, *Melampyrum* density was significantly lower in taller understory vegetation (Table 1, Fig. 1). Separate regression analyses within CO_2 treatments revealed that the negative relationship between *M. pratense* abundance and vegetation height was more pronounced at ambient than at elevated CO_2, with actually a rather poor ($r^2 = 0.1$) and not significant ($P = 0.18$) relation under elevated CO_2 (Fig. 1).

Growth and seed production in *M. pratense*

Individuals of *M. pratense* were significantly taller at elevated than at ambient CO_2 (Fig. 2, Table 1). The average number of seeds of the two largest and fully mature fruits of each individual plant was higher in elevated CO_2 plots than in ambient CO_2 plots (Fig. 2, Table 1). Accordingly, elevated CO_2 also increased total seed mass per fruit, but the mass per seed was unaltered by CO_2 enrichment (Fig. 2, Table 1), indicating a greater number of seeds of a similar size at elevated CO_2. Although there was no apparent overall effect of understory vegetation height on individual plant performance in *M. pratense* (Table 1), individual plant height and seed mass tended to negatively correlate with vegetation height at ambient CO_2; however, there was no such negative relationship at elevated CO_2 (Fig. 1).

Discussion

The data presented here provide strong evidence for a substantial population-level response of the annual root hemiparasites *M. pratense* and *M. sylvaticum* after three

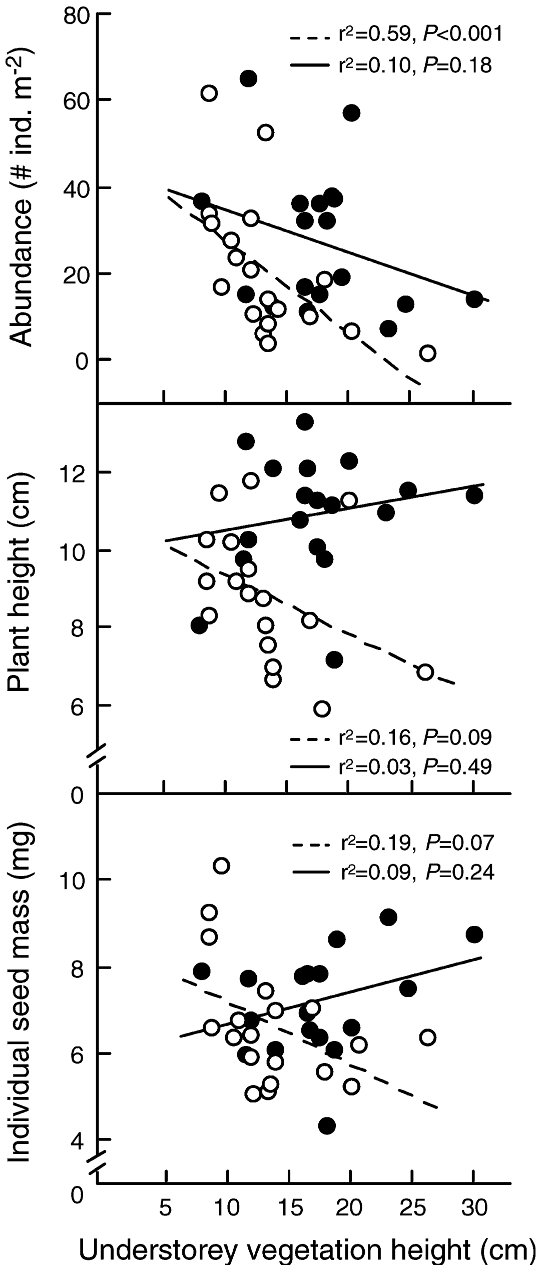

Fig. 1 Abundance, average plant height, and average mass per seed of *M. pratense* as a function of plot-specific understory vegetation height. Each *circle* represents the mean value of one experimental plot. *Open circles* and *dashed regression lines* represent plots maintained at current ambient CO_2, while *black circles* and *solid lines* are used for CO_2-enriched plots. Coefficients of determination (r^2) and error probabilities for regression slopes significantly differing from zero are indicated within panels

growing seasons of CO_2 enrichment in an otherwise undisturbed treeline ecotone. Densities of established individuals were significantly higher in both species in elevated CO_2 plots compared to ambient CO_2 plots. A higher abundance of *Melampyrum* in a CO_2-enriched atmosphere could have resulted from higher seed production, and/or from improved seed and seedling survival. Data at the individual plant level of *M. pratense*

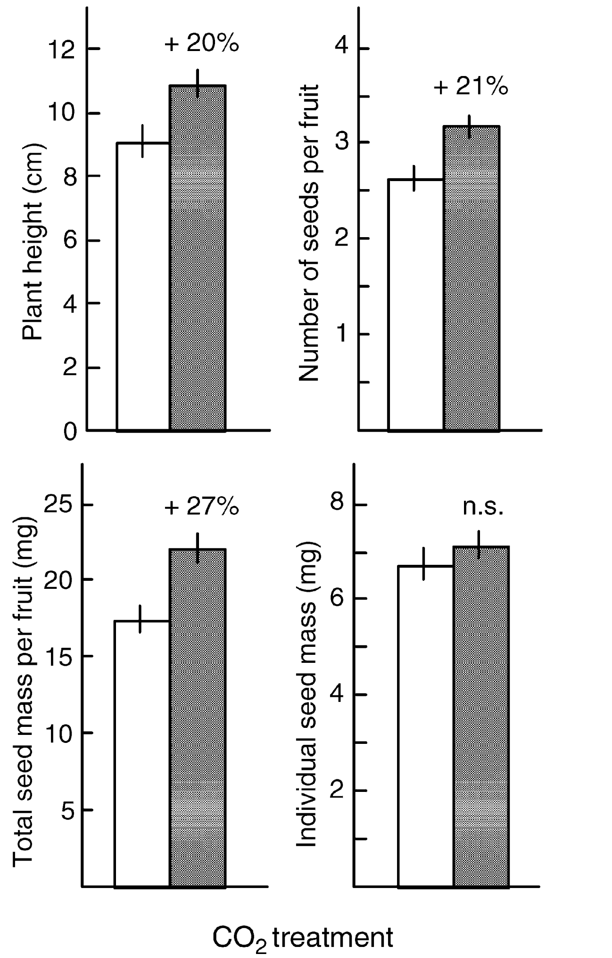

Fig. 2 *Melampyrum pratense* grown at ambient or elevated CO_2 ($n = 20$ plots). Average plant height, average number of seeds per fruit, average mass of seeds per fruit, and average mass per seed of three individuals per plot are shown. *Open* and *shaded bars* represent mean values for ambient and elevated CO_2 treatments, respectively

suggest a 21% higher seed production at elevated CO_2. *Melampyrum*, thus, might be seed limited at the site, and the increased seed production could explain the larger number of mature plants under elevated CO_2. An altered seed/seedling survival appears less likely because of similar seed sizes, and therefore unchanged seed reserves, in both CO_2 atmospheres.

Plant populations have rarely been studied in response to elevated CO_2 under field conditions. In a study of alpine grassland, Schäppi (1996) reported no change in seed number in two abundant perennial plant species, but an increased seed mass in the dominant *Carex curvula* in response to in situ CO_2 enrichment. Community level seed production in a species-rich calcareous grassland after 5 years of CO_2 enrichment increased by 29% (Thürig et al. 2003), but there were highly distinct responses among functional groups and among species. Species-specific CO_2 responses in seed production suggest changes in seedling establishment and community composition in the long term, but this is difficult to demonstrate in communities dominated by perennial species within the common experimental duration of 3–5 years. In annual plants, however, a stimulation of seed production and plant recruitment has immediate consequences for population dynamics. In an earlier field experiment, Smith et al. (2000) reported a substantial increase in seed production and biomass growth in the exotic annual grass *B. madritensis* spp. *rubens* when exposed to elevated CO_2 in the Mojave Desert. In contrast, three species of native annuals did not significantly change their reproductive output. Similarly, in the annual plant dominated Californian grassland, only the dominant species showed increased seed production with no or much smaller CO_2 responses in some less abundant annuals, suggesting potential losses of rare species with increasing atmospheric CO_2 concentration (Jackson et al. 1994). In fact, Fischer et al. (1997) reported a strong negative impact of elevated CO_2 on the survival of the rare species *Gentianella germanica*.

In line with the stated hypothesis, elevated CO_2 had a clear positive effect on annual hemiparasites under field conditions. The high CO_2-driven increased carbon gain and growth in *Melampyrum* may not exclusively be related to higher autotrophic carbon assimilation like in other plant functional groups. Photosynthetic capacity is typically poor in hemiparasites (Press et al. 1991), and was particularly low in *M. sylvaticum* studied under different CO_2 concentrations in model ecosystems kept in growth chambers (Hättenschwiler and Körner 1997). Moreover, in this latter study, there was no significant difference in photosynthesis among different CO_2 treatments. A ^{13}C tracer experiment, however, indicated a two to three times larger C transfer from host plants to hemiparasites (R. Siegwolf et al. unpublished) that resulted in a doubled individual plant biomass at high compared to low CO_2 (Hättenschwiler and Körner 1997). A higher carbohydrate flux from hosts to hemiparasites under elevated CO_2 could also explain the observed CO_2 effect on *Melampyrum* in the present study. The findings support that light competition by the tall dwarf shrub community apparently had less influence on *Melampyrum* performance under elevated than at ambient CO_2 (Fig. 1), which can best be explained by a higher independence from autotrophic carbon gain at elevated CO_2. Additionally, increased concentrations of non-structural carbohydrates in *V. myrtillus* and *V. uliginosum* (Asshoff and Hättenschwiler 2005) as the supposed main host plants of the two *Melampyrum* species studied here, increased soil respiration (Hagedorn et al. unpublished), and increased water-extractable soil organic carbon (Hagedorn et al. unpublished) all point in the direction of higher carbohydrate availability and increased C allocation to belowground sinks at elevated CO_2.

Decreasing dependency on autotrophic carbon uptake may enable hemiparasites to avoid competitive exclusion in dense vegetation, as is indicated by the lack of a negative correlation between *M. pratense* abundance and understory vegetation height at elevated CO_2 (Fig. 1). As a consequence, *Melampyrum* may invade tall dwarf shrub communities with rising atmospheric CO_2 where it has previously been absent. Such a shift in hemiparasite occurrence could potentially influence recruitment success of other herbaceous plant species. Community structure and ecosystem processes might additionally be influenced by increasing hemiparasite abundance through intensified competitive imbalance between hosts and non-hosts and through hemiparasite-specific physiological traits (Phoenix and Press 2005). Root hemiparasites have been proposed to accelerate nutrient cycling by producing nutrient-rich litter, thus providing a mechanism for increased nutrient availability and the maintenance of plant species diversity in nutrient-poor ecosystems (Press 1998). In a comparative study involving 72 different sub-arctic plant species, Quested et al. (2003a) showed that litter from root hemiparasites (seven species) had higher nitrogen concentrations and decomposed faster than litter from most co-occurring non-parasitic plants. Three annual hemiparasites, among them *M. sylvaticum*, had particularly high litter N concentrations of 3.1% (Quested et al. 2003a). The high quality and rapid decomposition of hemiparasite litter compared to other species enhanced nutrient uptake and growth of neighbor plant species in a pot experiment (Quested et al. 2003b). These recent results are strong evidence for an important functional role of root hemiparasites in comparatively nutrient-poor arctic and alpine ecosystems. Quested et al. (2003a) estimated a 53% increase in the total annual nitrogen input from litter to the soil across a site with a hemiparasite density of 43 stems per square meter. If *Melampyrum* had a comparable influence at the alpine site studied here, N release from decomposing *Melampyrum* litter could significantly alter N dynamics in a CO_2-enriched atmosphere. The carbon and the nitrogen cycle at the alpine treeline could thus be connected in a particular way with a potentially strong positive feedback of CO_2-induced increased hemiparasite abundance, leading to an enhanced input of N-rich litter, and consequently accelerated N cycling, and possibly further stimulation of plant growth responses to elevated CO_2. Since N availability is known to control dwarf shrub abundance and ecosystem properties in similar ecosystems (Berendse et al. 1994, Bret-Harte et al. 2004), such a positive feedback of an accelerated *Melampyrum* population growth at elevated CO_2 might have important implications for community composition and the functioning of alpine ecosystems.

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