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Effects of elevated CO$_2$ and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland

Abstract We investigated the effects of elevated CO$_2$ (600 µl l^{-1} vs 350 µl l^{-1}) and phosphorus supply (1 g P m^{-2} year^{-1} vs unfertilized) on intact monoliths from species-rich calcareous grassland in a greenhouse. Aboveground community dry mass remained almost unaffected by elevated CO$_2$ in the first year (+6%, n.s.), but was significantly stimulated by CO$_2$ enrichment in year two (+26%, $P < 0.01$). Among functional groups, only graminoids contributed significantly to this increase. The effect of phosphorus alone on community biomass was small in both years and marginally significant only when analyzed with MANOVA (+6% in year one, +9% in year two, $0.1 \geq P > 0.05$). Belowground biomass and stubble after two seasons were not different in elevated CO$_2$ and when P was added. The small initial increase in aboveground community biomass under elevated CO$_2$ is explained by the fact that some species, in particular *Carex flacca*, responded very positively right from the beginning, while others, especially the dominant *Bromus erectus*, responded negatively to CO$_2$ enrichment. Shifts in community composition towards more responsive species explain the much larger CO$_2$ response in the second year. These shifts, i.e., a decline in xerophytic elements (*B. erectus*) and an increase in mesophytic grasses and legumes occurred independently of treatments in all monoliths but were accelerated significantly by elevated CO$_2$. The difference in average biomass production at elevated compared to ambient CO$_2$ was higher when P was supplied (at the community level the CO$_2$ response was enhanced from 20% to 33% when P was added, in graminoids from 17% to 27%, in legumes from 4% to 60%, and in *C. flacca* from 120% to 298% by year two). Based on observations in this and similar studies, we suggest that interactions between CO$_2$ concentration, species presence, and nutrient availability will govern community responses to elevated CO$_2$.

Introduction

The complexity of species-rich natural or seminatural vegetation is a challenge for global change research. Species differ greatly in their photosynthetic and growth responses to CO$_2$ (Hunt et al. 1991; Poorter et al. 1996), but elevated CO$_2$ is also likely to affect interactions among species and to induce population-level processes with unknown feedbacks at the ecosystem level (Bazzaz 1990; Woodward et al. 1991; Körner and Bazzaz 1996). In mixed communities, species-specific responses to elevated CO$_2$ strongly depend on factors such as nutrients, water availability, temperature, and light as well as on biotic interactions, including microbial ones (Sanders 1996). Given current knowledge, it seems difficult to predict shifts in species composition and their consequences for ecosystem processes under elevated CO$_2$ from data obtained from individually grown plants with abundant nutrient or water supply. Hence, there is a need for CO$_2$ enrichment studies that allow, on the one hand, control and manipulation of some important environmental factors while at the same time ensuring that biological interactions, particularly those belowground are not disrupted (Körner 1995a).

The few studies with vegetation in undisturbed low-fertility soils have shown that the direct responses of community biomass to elevated CO$_2$ are usually much smaller than in agro-ecosystems, in some cases even zero (Owensby et al. 1993; Jackson et al. 1994; Navas et al. 1995; Wolfenden and Diggle 1995; Leadley and Körner 1996; Schäppi and Körner 1996). Results from studies with species-rich model ecosystems indicate that community responses to elevated CO$_2$ may be low because highly positive responses of some species are dampened

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by small and sometimes negative responses of other species (Leadley and Stöcklin 1996; Roy et al. 1996; Stöcklin et al. 1997).

Monoliths of extensively managed, unfertilized calcareous grassland are an ideal tool to explore the CO_2 response of highly diverse ecosystems under standardized conditions. These systems are among the species-richest types of vegetation in Europe and are of high conservation value (Zoller 1954; Willems 1992; Baur et al. 1996; Fischer and Stöcklin 1997). Their productivity and species richness is determined by low nitrogen and phosphorus availability, shallow soil, and regular topsoil desiccation during summer (Gigon 1968; Leuschner 1989). As in many ecosystems, the presence of legumes in such grasslands significantly adds to their nitrogen supply (Cole and Heil 1981; Crews 1993; Niklaus et al. 1997) and a common agricultural practice for promoting legume abundance and increasing overall productivity is phosphorus fertilization (Klapp 1971; Williams 1978; Van Hecke et al. 1981). In contrast to N fertilization, moderate P fertilization usually does not decrease the species richness of such communities (Bobbink 1991).

To study the interactive effects of phosphorus and CO_2 we undertook the present monolith experiment in a greenhouse. This study parallels a long-term field experiment of the response of calcareous grassland to elevated CO_2 as the only treatment (Körner 1995b; Leadley and Körner 1996). The use of monoliths in a greenhouse permitted large microplot replications in conditions of reduced environmental variability. Monoliths also allow destructive harvest of all belowground biomass, a procedure which would have terminated the long-term field experiment. We expected that such grassland swards will undergo changes in species composition in response to both increased nutrient availability (Bornkamm 1958; Bobbink and Willems 1988; Stöcklin and Gisi 1989; Hillier et al. 1990) and elevated CO_2 (Hunt 1991; Ferris and Taylor 1993; Leadley and Stöcklin 1996; Lauber and Körner 1997; Stöcklin et al. 1997). Whether biomass production under elevated CO_2 alone would increase significantly could not be predicted with any confidence, because the literature in this respect is conflicting (Wolfenden and Diggle 1995; Leadley and Körner 1996 and references above). We hypothesized that, by stimulating legumes, the phosphorus treatment should increase the ecosystem N pool without affecting species diversity but would enhance the CO_2 sensitivity of biomass production.

Materials and methods

Twenty-four 26 cm × 36 cm × 21 cm deep monoliths with intact vegetation and the complete undisturbed A soil horizon were transferred from a calcareous grassland site 20 km south of Basel, Switzerland (Nenzlingen, 500 m altitude) on 4 April 1995. The site is representative for south-facing species-rich meadows and pastures ('Mesobromion') in the foothills of the Swiss Jura. The soil is a Para-Rendzina with a 15-cm silty clay loam top horizon (pH 6.5, bulk density 1.1 g cm^{-3}) of high humus content underlain by calcareous debris. Monoliths were taken in groups of eight from three different locations. On average, each monolith contained 15 species (a total of 50 plant species across all monoliths). On average, graminoids were represented with 8 species (85% of aboveground biomass), non-legume forbs with 5 species (7%), and legumes by 3 species (8%). The dominant grass *Bromus erectus* was present in all 24 monoliths. *Carex flacca* was present in 22 of 24 monoliths, *Sanguisorba minor* in 21 and *Trifolium repens* in 19 monoliths, with most other species present only at a low frequency. Monoliths were tightly fitted into polyethylene containers with a 4-cm marl layer and a 2-cm drainage mat placed at the bottom.

Two randomly selected monoliths from each of the three excavation plots (a total of six) were assigned to the four treatment combinations described below. Twelve monoliths were exposed to ambient (ca. 350 μl l^{-1}) and twelve to elevated (ca. 600 μl l^{-1}) CO_2. Six of the monoliths at each CO_2 level received phosphorus fertilization of 1 g P m^{-2} year^{-1}, and six remained unfertilized. The fertilizer was provided as dry super phosphate (Triple-Super phosphate 46%, Landor, Birsfelden, Switzerland) in five equal portions during the growing season. Monoliths assigned to these treatments were then allocated equally to four naturally lit, air-conditioned greenhouses (two for each CO_2 level). In each house, containers were placed on trolleys which were rotated within greenhouses weekly. Positions on each trolley were randomized monthly and trolleys were switched between greenhouses every 2 months. All monoliths were watered equally, but only every 3rd–7th day (depending on the weather) with 5–10 mm of rainwater, annual sums corresponding to field conditions. However, shallow rooting depth of monoliths required a more regular watering regime compared to natural precipitation patterns in the field. In the greenhouse, topsoil moisture desiccation during hot summer periods lasted only 2–3 days and was less severe (soil moisture 35–43% vol.) than in the field where several dry periods >10 days with soil water content drooping to 20% vol. occurred in 1995 and 1996 (P. Niklaus, oral communication). In the greenhouse, means of atmospheric water vapor deficit during daytime (11:00 a.m.–16:00 p.m.) were between 5–10 mbar; daily maxima rarely exceeding 12 mbar. At the field site, water vapor deficits frequently reach 17 mbar. Thus, climatic conditions in the greenhouse were more mesic than at the field site. The temperature regime in the greenhouses was maintained close to conditions outside the greenhouse using air conditioners. The reduction of solar radiation in the greenhouse was partly compensated by additional light provided by two 1000-W daylight halogen lamps mounted above each 7-m^2 chamber, which were activated automatically when ambient photon flux density dropped below about 180 μmol m^{-2} s^{-1} during the natural photoperiod. At canopy level, photon flux densities ranged from 600 to 1100 μmol m^{-2} s^{-1} at midday on sunny days.

The treatment began on 11 April 1995. On this date, and then twice every year (12 June and 15 October 1995, 15 June and 15 October 1996), aboveground biomass of all monoliths was harvested 5 cm above soil level. The June and October harvest dates corresponded to the time of mowing or grazing at our field site. We sorted biomass of individual species for *B. erectus*, *C. flacca*, mesophytic grasses (*Cynosurus cristatus*, *Danthonia decumbens*, *Koeleria pyramidata*, *Agrostis tenuis*, *Briza media*, *Anthoxantum odoratum*, *Dactylis glomerata*, *Poa pratensis*, *Festuca pratensis*) and of functional groups for graminoids, non-legume forbs, and legumes. The number of inflorescences was counted for *B. erectus*, *C. flacca*, and legumes. After two complete seasons, a soil block including stubble of about one-third of each rectangular monolith was sampled after harvesting aboveground biomass in October 1996. From this soil block, belowground biomass (roots and rhizomes) and stubble (stem and leaf bases of the bottom 0–5 cm layer) were assessed. To account for possible border effects within the monoliths, we analyzed the core part of this soil block and its border slices (4 cm) separately. Roots and rhizomes were separated from the soil by wet sieving. Plant material from the 0–5 cm layer was separated into living biomass, standing dead plant material, and moss. Above 5 cm, biomass was separated into green leaves, stems, inflorescences, and standing dead. All material was dried at

80°C for 48 h before weighing. During winter, from 20 November 1995 to 14 March 1996, the monoliths were placed in an outdoor soilbed and experienced natural midwinter climate, including frost. No growth occurs during this time and swards are largely brown.

For statistical analysis, the monoliths were treated as replicates ($n = 6$ in each treatment combination). Here we present annual sums of aboveground dry matter per container only; i.e., dry weights from the June and October harvest of each year were added. The dependent variables were analyzed first with repeated-measure analyses using the MANOVA procedure of JMP, version 3.1 (SAS Institute, Cary, N.C.) to assess the effects of CO_2, P fertilization, and their interaction. For total aboveground dry weight, the interaction of CO_2 with time was significant, and results from each year were analyzed separately using ANOVA. If necessary, data were transformed to correct for non-normal distribution or non-homogeneity of variance.

Results

Effects of elevated CO_2 alone

Aboveground biomass from both harvests per season (>5 cm) accumulated to 330 g m^{-2} in 1995 and 362 g m^{-2} in 1996 under ambient CO_2 and to 348 g m^{-2} (+6%, n.s., ANOVA, 1995) and 457 g m^{-2} (+26%, $P < 0.01$, ANOVA, 1996) under elevated CO_2. The overall effect of CO_2 on total aboveground biomass (data of both years included) was significant ($P < 0.01$, MANOVA), but there was also a highly significant difference in the CO_2 response between the two years (Table 1, Fig. 1). The positive CO_2 effect resulted from positive responses of leaf biomass and standing dead plant mass only, whereas biomass of stems and inflorescences remained unaffected (Table 1). At the level of functional groups (Table 1, Figs. 2, 3), biomass production of graminoids increased significantly under elevated CO_2 by 10.5% in 1995, and by 22.1% in 1996 ($P < 0.01$, MANOVA). The contribution of non-legume forbs and legumes to aboveground biomass production did not differ under ambient and elevated CO_2 in both years. There were differences among

graminoids in their CO_2 response, including both significant positive and significant negative responses. In both years, biomass production of *B. erectus* was reduced under elevated CO_2, and in 1996 this reduction was reflected by a significantly lower number of inflorescences (65 m^{-2} at ambient and 27 m^{-2} at elevated CO_2, $P < 0.05$). In contrast, biomass production of mesophytic grass species and of *C. flacca* increased under elevated CO_2 (for *C. flacca* +204% in 1995 and +209% in 1996). *C. flacca* was the most strongly responding species and contributed most to community-level biomass gains under elevated CO_2.

Independent of treatments, aboveground community biomass of the monoliths and most of its components
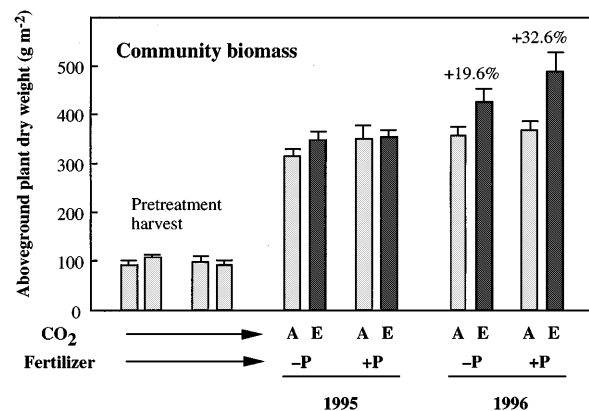

Fig. 1 Aboveground community phytomass at the beginning of the experiment and components of community productivity in two consecutive years (1995, 1996) for two CO_2 levels (ambient *A*, elevated *E*), and P fertilization (0, 10 kg ha^{-1} year^{-1}). Values are means with standard error bars for total community biomass 5 cm above soil level from pooled harvests from June and October of each year. For 1996, percent differences due to CO_2 level within fertilizer treatments are indicated (for 1995 the effect of CO_2 was n.s.). Values for community biomass at the beginning of the experiments are means for the microcosms later assigned to the four treatments

Table 1 F-values and significance levels of repeated-measures MANOVAs with aboveground dry weight data from harvests in 1995 and 1996 for the effects of CO_2 (350, 600 μ l^{-1}), P fertilization (0, 10 kg l ha^{-1} year^{-1}), the interaction $CO_2 \times$ P, year to year differences, and the interaction $CO_2 \times$ year ($n = 6$ microcosms per treatment, total 24). Levels of significance: *$P < 0.05$; **$P \leqslant 0.01$; ***$P < 0.001$; P-values >0.1 are tabulated as *n.s.* With the exception of *Bromus erectus*, all significant effects due to CO_2 were positive (the interaction $CO_2 \times$ year is a measure for differences of the effect of CO_2 between years)

Dependent variable	CO_2 level	P fertilization	Interaction $CO_2 \times$ P	Year to year differences	Interaction $CO_2 \times$ year
Aboveground community biomass	9.5**	3.5, $P = 0.08$	0.1 n.s.	23.8***	7.2**
Litter	4.8*	0.4 n.s.	0.1 n.s.	n.s.	n.s.
Leaves	7.2*	2.1 n.s.	0.01 n.s.	n.s.	7.5*
Stems	2.1 n.s.	0.3 n.s.	0.2 n.s.	36.2***	n.s.
Inflorescences	0.9 n.s.	0.8 n.s.	0.03 n.s.	21.8***	n.s.
Graminoids	8.2**	0.4 n.s.	0.01 n.s.	10.4**	1.6 n.s.
Non-legume forbs	0.1 n.s.	1.6 n.s.	0.3 n.s.	24.9***	1.2 n.s.
Legumes	0.7 n.s.	0.3 n.s.	1.8 n.s.	44.2***	3.7, $P = 0.08$
Bromus erectus	4.6**	0.4 n.s.	0.01 n.s.	99.1***	0.1 n.s.
Mesophytic grasses	9.4**	0.2 n.s.	0.01 n.s.	14.1**	2.8, $P = 0.1$
Carex flacca	15.0***	1.9 n.s.	3.1, $P = 0.09$	0.1 n.s.	0.4 n.s.

were significantly different between 1995 and 1996 (Table 1). Averaged over all treatments, graminoids decreased, and forbs, especially legumes, increased their contribution to community biomass (Fig. 2). Among graminoids *B. erectus* was partially replaced by mesophytic grasses (Fig. 3). As mentioned above, this trend was enhanced by CO_2 enrichment. The contribution of
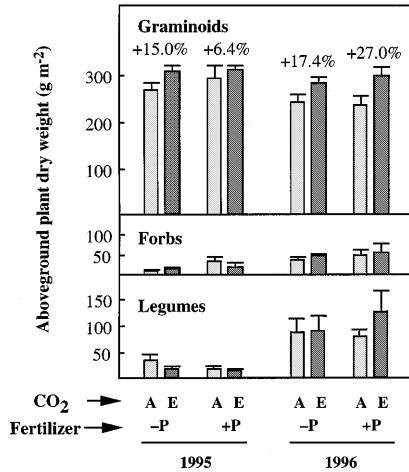

Fig. 2 Total aboveground phytomass of functional groups (graminoids, non-legume forbs, legumes) in two consecutive years (1995, 1996) for two CO_2 levels (ambient *A*, elevated *E*), and P fertilization (0, 10 kg ha^{-1} year^{-1}). Values are means with standard error bars for total aboveground biomass 5 cm above soil level from harvests in June and October of each year. For graminoids, percent differences due to CO_2 level within fertilizer treatments are indicated ($P < 0.01$ for CO_2 level, year-to-year differences n.s.; see Table 1 for details)
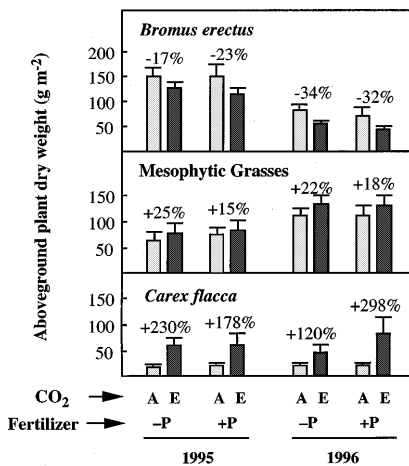

Fig. 3 Total aboveground phytomass (> 5 cm) of *Bromus erectus*, mesophytic grasses, and *Carex flacca* in two consecutive years (1995, 1996) for two CO_2 levels (ambient *A*, elevated *E*), and P fertilization (0, 10 kg ha^{-1} year^{-1}). Values are means with standard error bars for the pooled harvests in June and October of each year. Percent differences due to CO_2 concentration within fertilizer treatments are indicated (significant *P*-values for CO_2 level, year-to-year differences n.s.; see Table 1 for details). Mesophytic grasses include (in decreasing order of abundance): *Cynosurus cristatus, Danthonia decumbens, Koeleria pyramidata, Agrostis tenuis, Briza media, Anthoxantum odoratum, Dactylis glomerata, Poa pratensis,* and *Festuca pratensis*

C. flacca to community biomass did not differ among years (Table 1).

Effects of P fertilization alone

P fertilization increased aboveground biomass production of monoliths by 6.3% in 1995 and by 9.3% in 1996 and the effect was marginally significant ($P = 0.08$) when the excavation location of monoliths was treated as a cofactor in MANOVA. Components of aboveground community biomass (functional groups, *B. erectus*, mesopytic grasses, *C. flacca*) were not affected by P fertilization, but legume biomass increased substantially between 1995 and 1996 without fertilization and even more when P was added ($P < 0.05$, ANOVA with log-transformed data). In 1996, the number of flowers in legume species was significantly increased ($+80\%$, $P < 0.01$, data not shown) in monoliths with P fertilizer.

Interactions of elevated CO_2 and P addition

The interaction of the CO_2 response with P fertilization was not significant for aboveground biomass or functional groups in MANOVA. However, in 1996, mean dry weight of aboveground community biomass and some of its components (graminoid species, legumes, and *C. flacca*) at elevated CO_2 was larger when P was added compared to unfertilized monoliths (Figs. 1–3). In 1996, the mean response to elevated CO_2 became enhanced at the community level from 20% to 33% when P was added, in graminoids, the CO_2 response increased from 17% to 27%, in legumes from 4% to 60% and in *C. flacca* from 120% to 298%. For *C. flacca*, this enhancement of the CO_2 response when P was added was marginally significant ($P = 0.09$) when tested with a MANOVA. This consistency of trends might indicate that P fertilization enhanced the effect of CO_2 on dry weight production although this was not statistically significant.

Belowground biomass and stubble at the final harvest

At the final harvest (October 1996), the mean belowground biomass (roots, rhizomes) of monoliths was 770 g m^{-2} and stubble (stem and leaf bases) in the 0–5 cm layer contributed 300 g m^{-2} (Fig. 4). Together these two fractions amount to more than twice the aboveground biomass which was harvested above 5 cm in each year. Differences in belowground biomass and stubble due to treatments (CO_2, P, and their interaction) were small and not significant. However, the trend with CO_2 concentration was consistent with aboveground responses. Under elevated CO_2, belowground biomass was increased by 6% at the final harvest, and stubble in the 0–5 cm layer increased by 7%. With P fertilization
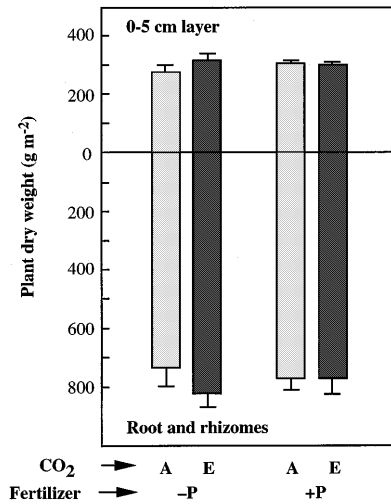
Fig. 4 Final harvest: plant dry matter in the 0–5 cm layer and belowground dry matter of roots and rhizomes (October 1996) for two CO_2 levels (ambient *A*, elevated *E*), and P fertilization (0, 10 kg ha^{-1} year^{-1}). Values are means with standard error bars. Differences due to treatments are not significant

alone, no trend was observed. Border effects, i.e., differences between border slices and the core segment of the monoliths with respect to belowground biomass or stubble, were not found.

Discussion

Our results suggest that the extent of responsiveness to elevated CO_2 in natural plant communities is not a simple function of resource availability, but depends on the presence and abundance of responsive species. We observed a significant increase in aboveground community biomass with elevated CO_2 in the second year only. However, at the level of species, highly significant positive responses (e.g., *C. flacca*) occurred already in the first year but were initially balanced by the decline of other species (i.e., *B. erectus*). Shifts towards more responsive species during the experiment thus considerably increased biomass production of monoliths under elevated CO_2.

Most studies with undisturbed natural grassland communities under elevated CO_2 have yielded only marginally and frequently not significant increases in community-level biomass (Owensby et al. 1993; Navas et al. 1995; Wolfenden and Diggle 1995). We observed a small increase (+6%) in aboveground community biomass in the first, and a much larger increase (+26%) in the second year of our experiment. In both years, only graminoids including *C. flacca* contributed significantly to this increase. This reflects, first of all, the large contribution of the graminoid fraction to community biomass and should not suggest that there is no positive response of non-legume forbs and legumes to elevated CO_2. Second, the spatial distribution of non-graminoids in these natural swards was heterogeneous, which prob-

ably contributed to the absence of a statistically significant effect in forbs and legumes. In another study with designed grassland communities in which replicates had identical canopy structure and also contained a relative higher forb fraction (including legumes), biomass responses to elevated CO_2 were significant also in non-graminoid species (Stöcklin et al. 1997).

The crucial role of species composition for the CO_2 responsiveness of community biomass is illustrated by the significant and highly positive as well as negative responses within the graminoid fraction of species of the monolith communities. *C. flacca*, the most abundant sedge, showed a consistent and massive, more than three-fold increase under elevated CO_2. As a group, mesophytic grasses also increased in biomass, but the contribution of *B. erectus* to total biomass decreased under elevated CO_2. The negative response of this dominant and most characteristic grass species considerably dampened the overall positive response of the graminoid fraction.

There is no clearcut and obvious explanation for the observed differences among graminoids. First, the overwhelming response of *C. flacca* is consistent with all experimental evidence collected so far both in the field and in the greenhouse either in multispecies assemblages or when this species was grown in isolation (Leadley and Körner 1996; Stöcklin et al. 1997; Leadley et al. unpublished). The positive response in this relatively slow growing sedge does, however, not match Poorter et al.'s (1996) conclusion that among wild herbaceous species, fast growers usually respond much more strongly than slow growers. Results for *B. erectus* are more ambiguous. Under several experimental conditions, this species did not increase its biomass under elevated CO_2 (Leadley and Körner 1996; Steinger et al. 1997; Stöcklin et al. 1997). Leadley and Stöcklin (1996), however, observed significant genetic variation in CO_2 response within this species, including positive- and negative-responding genotypes. In a study by Navas et al. (1995) with monoliths from dry Mediterranean grasslands, growth of *B. erectus* was stimulated under elevated CO_2. Also during the third year of exposure to elevated CO_2 at the site of origin of our monoliths, a moderately positive effect of CO_2 enrichment became apparent in this species, exclusively due to enhanced tillering (Leadley et al. unpublished). These response differences may reflect the specific moisture conditions during the various experiments. In our greenhouse study, growth conditions were more mesic than in the field (see Materials and methods), which may have facilitated the relatively better growth of mesophytic species (including *Carex flacca* and legumes; Oberdorfer 1983) compared to the more xerophytic *Bromus*, independently of any treatment. A second reason for the legume expansion seen in the greenhouse is probably the absence of snails and slugs. In the field, legumes are the preferred food of these animals and grazing pressure is very high (Ledergerber et al. 1997). In both legumes and mesophytic grasses, these changes in abundance over time were clearly more

pronounced under elevated CO_2, hence CO_2 enrichment enhanced the shift in community composition.

The difference in average dry weight production at elevated compared to ambient CO_2 was higher when P was added. However, this interaction was not statistically significant.

Conclusion

From our results we can draw the following conclusions concerning the effects of elevated CO_2 on species-rich calcareous grassland. (1) Overall biomass responses in these communities result from differential responses of species, including positive as well as negative responses, highlighting the species specificity of CO_2 responsiveness. (2) This variability among species produces shifts in community composition under elevated CO_2, which, in the longer term, enhances overall biomass.

It is suggested that similar interactions between CO_2 enrichment, plant species diversity and resource supply will govern CO_2 responses in other complex plant communities. The results of this and other studies suggest little predictive value of experiments with individually grown plants or conventional functional groups with respect to CO_2 responsiveness of species assemblages. Furthermore, CO_2 enrichment studies which do not account for species replacement are of restricted value for understanding the CO_2 responses of plant communities.

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