Photosynthesis and resource allocation of three Mojave Desert grasses in response to elevated atmospheric CO_2

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Abstract

Gas exchange, biomass and N allocation were compared among three Mojave Desert grasses representing different functional types to determine if photosynthetic responses and the associated allocation of resources within the plant changed after prolonged exposure to elevated CO_2. Leaf gas exchange characteristics were measured for *Bromus madritensis* ssp. *rubens* (C_3 invasive annual), *Achnatherum hymenoides* (C_3 native perennial) and *Pleuraphis rigida* (C_4 native perennial) exposed to 360 $\mu mol\ mol^{-1}$ (ambient) and 1000 $\mu mol\ mol^{-1}$ (elevated) CO_2 concentrations in a glasshouse experiment, and tissue biomass and total N pools were quantified from three harvests during development. The maximum rate of carboxylation by the N-rich enzyme Rubisco (Vc_{max}), which was inferred from the relationship between net CO_2 assimilation (A_{net}) and intracellular CO_2 concentration (c_i), declined in the C_3 species *Bromus* and *Achnatherum* across all sampling dates, but did not change at elevated CO_2 for the C_4 *Pleuraphis*. Whole plant N remained the same between CO_2 treatments for all species, but patterns of allocation differed for the short- and long-lived C_3 species. For *Bromus*, leaf N used for photosynthesis was reallocated to reproduction at elevated CO_2 as inferred from the combination of lower Vc_{max} and N per leaf area (NLA) at elevated CO_2, but similar specific leaf area (SLA, $cm^2\ g^{-1}$), and of greater reproductive effort (RE) for the elevated CO_2 treatment. Vc_{max}, leaf N concentration and NLA declined for the perennial *Achnatherum* at elevated CO_2, potentially due to accumulation of carbohydrates or changes in leaf morphology inferred from lower SLA and greater total biomass at elevated CO_2. In contrast, Vc_{max} for the C_4 perennial *Pleuraphis* did not change at elevated CO_2, and tissue biomass and total N were the same between CO_2 treatments. Adjustments in photosynthetic capacity at elevated CO_2 may optimize N allocation of C_3 species in the Mojave Desert, which may influence plant performance and plant-plant interactions of these co-occurring species.

Introduction

Enhancement of net carbon assimilation is often associated with short-term exposure to elevated atmospheric CO_2 concentrations, but downward adjustment of photosynthetic capacity is characteristic of longer-term exposure, especially in plants that use the C_3 photosynthetic pathway. Net assimilation rates increase in C_3 plants exposed to elevated CO_2 because the diffusional limitation of CO_2 into the leaf is reduced and the concentration of CO_2 is enhanced at the site of carboxylation (Sharkey 1985). However, C_3 plants exposed to elevated CO_2 for hours to weeks may reduce the amount and activity of enzymes such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) because increasing leaf carbohydrate supply at elevated CO_2 causes a feedback limitation on the photosynthetic apparatus (Sage 1990). Rubisco is a large, N-rich enzyme and accounts for 30 to 60% of the soluble protein in leaves of C_3 plants and 5 to 20% in C_4 plants (Ku et al. 1979; Schmitt and Edwards 1981; Gutteridge and Key 1985). Thus, the reduction of Rubisco and other enzymes in C_3 plants is often accompanied by reduced N investment in the leaf (Sage et al. 1987, 1989; Sage 1994). This acclimatory response is generally lacking in C_4 plants exposed to elevated CO_2 because CO_2 concentrations at the site of carboxylation in the bundle sheath are already saturated at ambient CO_2 conditions (Osmond et al. 1982; Pearcy and Björkman 1983).

Down-regulation of photosynthesis can be diminished when soil water and N are limited (Huxman et al. 1998a; Huxman and Smith 2001), which may have important consequences for desert grasses whose growth and development typically coincide with rainfall pulses before the onset of water stress (DeFalco 2003). Associated with photosynthetic down-regulation is the potential investment of N away from photosynthetic enzymes into limiting processes over the life of the plant (Sage 1994). Plants optimize survival, growth and reproduction by increasing allocation to organs that will enhance acquisition of resources that are in limited supply (Acock and Pasternak 1986). Thus, under a high CO_2 environment, proportionally more C and N may be allocated to roots and stems than to leaves, which may consequently enhance survival (Xu et al. 1994) or influence plant-plant competition (Wolfe et al. 1998). Furthermore, allocation may differ between annual and perennial plants. Perennials need to allocate at least some resources to roots or place carbohydrate in storage organs for future growth, yet annuals will allocate toward reproduction (Hardman and Brun 1971; Havelka et al. 1984a, b; Arp and Drake 1991). Thus, the consequences of photosynthetic adjustment at elevated CO_2 may differ depending on plant functional type and the associated pattern of resource allocation.

In a glasshouse study, the effects of elevated CO_2 on photosynthesis, biomass production and N allocation in three grass species representing different functional types (C_3 vs. C_4, annual vs. perennial) were measured. Results for the root growth and function for these species are presented elsewhere (Yoder et al. 2000). To reduce the confounding effect of phylogeny, three species within the Family Poaceae were selected. *Achnatherum hymenoides* (Roemer & Schultes) Barkworth and *Bromus madritensis* ssp. *rubens* (L.) Husnot are C_3 grasses. *Pleuraphis rigida* Thurber is a C_4 perennial and may have little or no increase in photosynthesis when exposed to elevated atmospheric CO_2. We hypothesized that a reduction in carboxylation efficiency would occur in the C_3 but not in the C_4 species, and we expected that allocation of N would differ between the annual and perennial C_3 species. *Achnatherum* is a perennial that has the potential to allocate biomass and N to storage in roots before the onset of senesence thereby optimizing future growth. Conversely, *Bromus* completes its life cycle in a single season and should preferentially allocate photosynthate derived from increased CO_2 toward reproduction (Hunt et al. 1991), thereby potentially increasing the fitness of individuals at elevated CO_2. All three species coexist in the Mojave Desert; therefore, the differential photosynthetic and developmental responses by individuals of each species may have important consequences on interactions among desert plants in the future with elevated CO_2.

Methods

Fifty-four pots were placed in each of two adjacent glasshouse rooms in the Fritz Went glasshouse facility at University of Nevada, Reno. The atmospheric CO_2 concentrations were maintained at ~360 μmol mol^{-1} (ambient) in one glasshouse and 1000 μmol mol^{-1} (elevated) in the other. Pots were constructed of 1 m tall PVC with 0.15 m diameter (volume = 17.6 L) and had a mesh bottom to allow drainage. Large pot size was selected to ensure that pot volume would not influence photosynthetic down-regulation (Thomas and Strain 1990; Arp 1991). A homogenous fill sand with approximately 2 μg g^{-1} NO_3 and 10 μg g^{-1} NH_4 was used as a potting substrate. In February 1997, treatments were assigned within each room: 3 species × 3 harvest dates × 6 replicates. Seeds of *Bromus*, *Achnatherum* and *Pleuraphis* were planted in monoculture, and seedlings were thinned to a density of 15 (*Bromus*), 8 (*Achnatherum*), and 5 (*Pleuraphis*) plants per pot one week after planting, which are similar to tiller densities found at the Nevada Desert FACE Facility (Jordan et al. 1999). All pots were watered twice a week to maintain soil water content near pot capacity. The three sampling dates corresponded to vegetative, anthesis and seed fill stages for *Achantherum* (45, 71 and 108 d, respectively) and *Bromus* (27, 55 and 85 d). *Pleuraphis* never flowered, thus sampling dates at 80, 122 and 161 d represent three vegetative stages.

Leaf gas exchange

The change in net assimilation rate to incremental changes in intercellular CO_2 concentration (A-c_i response curve) was measured for each grass species at each sampling date. Leaf-level gas exchange measurements were conducted on the most recently-expanded leaf of a single plant in three of the total of six pots per treatment. A-c_i curves were generated using a programmable, open-flow gas exchange system (Li-6400, LI-COR, Lincoln, Nebraska, USA). Leaves from the elevated treatment were enclosed in a chamber, and net CO_2 assimilation rate (A_{net}) was measured as cuvette CO_2 concentration was changed incrementally from 1000 to 1500, 2000, 1000, 700, 550, 350, 225 and 100 μmol mol^{-1}. Similarly, A_{net} of leaves from the ambient room was measured at cuvette CO_2 concentrations 350, 225, 100, 350, 550, 700, 1000, 1500 and 2000 μmol mol^{-1}. Leaf temperature was maintained at 25°C for *Bromus* and *Achnatherum* and 30°C for *Pleuraphis*. Leaf-to-air vapor pressure deficit ranged between 1.8 to 2.0 during the early harvest and 2.4 to 2.8 during later harvests. Measurements were conducted under saturating photon flux densities (PPFD) greater than 1.0 mmol m^{-2} s^{-1} as determined from light response curves, and light was supplied using a quartz-halogen projection lamp. Intercellular CO_2 concentration (c_i) at each ambient CO_2 concentration (c_a) was calculated using the equations of von Caemmerer and Farquhar (1981). A paper image of the leaf was produced on photosensitive diazo paper and its area quantified in a leaf area meter (Li-3000A, LI-COR); this leaf area was used to recompute rates of gas exchange on an area basis. Maximum carboxylation efficiency of Rubisco (Vc_{max}) was estimated for each replicate as determined by Farquhar et al. (1980) and modified by Harley and Sharkey (1991) and Harley et al. (1992) using Photosynthesis Assistant (Dundee Scientific v. 1.1.2, Dundee, UK).

Plant mass, N and allocation

All plant tissues were removed from pots and sorted by tissue type (roots, leaves, culms, inflorescences and dead) at each harvest date. Tissues were dried in a convection oven at 45°C to a constant mass and subsequently weighed. N concentration (mg N g^{-1}) was determined with a Carbon-Hydrogen-Nitrogen analyzer (Perkin-Elmer 2400 Elemental Analyzer; Norwalk, Connecticut). Leaf area was determined on two individuals per pot using a Li-COR leaf area meter (Li-3000A, LI-COR). Specific leaf area (SLA, cm^2 g^{-1}) was calculated as the quotient between leaf area and dry mass; content of N per unit leaf area (NLA, mg N cm^{-2}) was calculated as the quotient between N concentration and SLA.

Statistical analyses

Leaf gas exchange responses, mass and N pools were analyzed for each species using SAS v. 6.10 (SAS, Institute, Inc., Cary, North Carolina). All responses except reproductive effort (RE) were analyzed with separate two-factor ANOVAs. CO_2 concentration and date were designated as fixed main effects. RE was analyzed separately for *Bromus* and *Achnatherum* in a single factor (CO_2) ANOVA at the final harvest. Residual mean square error was used as the F-test denominator in all tests for main and interaction effects. Violation of the equal variance assumption was examined in residual plots and using Levene's test. When necessary, data were transformed according to Box and Cox (1964). Violation of the normality assumption was examined in normality plots and tested according to D'Agostino (1971).

Results

Leaf gas exchange

Photosynthetic responses to elevated CO_2 derived from A-c_i relationships varied among the three Mojave Desert species (Figure 1). Net assimilation rate at growth CO_2 concentration (A_{net}) was greater at elevated CO_2 for *Bromus*, *Achnatherum* and *Pleuraphis* across all harvest dates at $P = 0.06$ (CO_2 effect). The maximum carboxylation efficiency of Rubisco (Vc_{max}) declined significantly for *Bromus* across all dates (CO_2 effect). For *Achnatherum*, the greatest decrease associated with elevated CO_2 occurred at the first harvest (CO_2 × date). In contrast, Vc_{max} for *Pleuraphis* declined only initially at elevated CO_2 (CO_2 × date), however significant CO_2-induced reductions for this species may have been obscured by large variation coupled with small sample size. Leaf N concentrations reflected the patterns in Vc_{max} with significant reductions in *Bromus* and *Achnatherum* at elevated CO_2, and no significant difference between CO_2 treatments for *Pleuraphis* (Table 1).

Plant mass, N and allocation

Elevated CO_2 altered plant mass, but not plant N, with the most dramatic responses for the C_3 species. Plant mass increased for *Bromus* and for *Achnatherum* at elevated compared with ambient CO_2 across all harvest dates, but mass of *Pleuraphis* plants was not statistically different between CO_2 treatments (Fig. 2). Total plant N was not statistically different between CO_2 treatments for all species, indicating no enhanced uptake of N under elevated CO_2 (Fig. 2). This lack of a CO_2 effect does not appear to reflect a deficiency in the initial N availability as no evidence of nutrient deficiencies was observed during the study. N per unit leaf area (NLA) decreased in *Bromus* but leaf area expressed per unit mass (SLA) was not statistically different between CO_2 treatments (Table 1). A significant decrease in NLA for *Achnatherum* was accompanied by a decrease in SLA (Table 1). Neither NLA nor SLA was statistically different between CO_2 treatments for *Pleuraphis*.

Allocation patterns for plant mass and N within whole plants varied among species at elevated CO_2. Root : shoot ratios did not differ significantly between CO_2 treatments for either *Bromus* or *Pleuraphis* but declined in *Achnatherum* (Fig. 3) due to greater proportional increases in shoots compared to increases in root biomass at elevated CO_2. In addition, both *Bromus* and *Achnatherum* significantly increased reproductive effort (RE) at elevated CO_2, measured as the ratio of the mass of inflorescences to total plant mass. *Pleuraphis* did not initiate flowering during this experiment, and so RE was not tested for this species.

Discussion

Adjustment of photosynthetic capacity in response to elevated CO_2 was demonstrated for the two C_3 species, *Bromus* and *Achnatherum,* and allocation of N within the plant differed with functional type. However, photosynthetic capacity was not lower and patterns of N distribution did not change at elevated CO_2 for the C_4 grass *Pleuraphis*, even though net CO_2 assimilation rates were greater. While enhanced photosynthesis in C_4 grasses is typically attributed to indirect CO_2 effects on improved water relations (Rogers et al. 1983; Knapp et al. 1993; Owensby et al. 1993), pre-dawn water potentials were not statistically different between CO_2 treatments for *Pleuraphis* during this study (see Yoder et al. 2000). Thus, other factors related to the type of decarboxylating enzyme in the bundle sheath cells (LeCain and Morgan 1998) or taxonomic origin (Kellogg et al. 1999) may distinguish which C_4 grasses will respond to elevated CO_2.

Patterns of A-c_i response, carbon acquisition and whole plant N allocation of C_3 species in this study support the hypothesis that when the amount of photosynthetic enzymes is reduced as a result of acclimation to elevated CO_2, "the resource-use efficiency of photosynthesis is enhanced and the pool of resources available for investment into limiting processes is greater over the life of the plant" (Sage 1994). The total increase in whole plant biomass for *Bromus* and *Achnatherum* under elevated CO_2 suggests that efficiency of N use in the leaf is increased by maintaining similar (*Achnatherum*) or higher (*Bromus*) rates of A_{net}, and a repartitioning of N away from Rubisco to other N pools within the plant (Xu et al. 1994). Elevated CO_2 appears to redirect the investment of resources from leaves to reproductive tissues in *Bromus*, a short-lived species whose life history strategy is defined by the production of many offspring at the expense of belowground allocation. However, under elevated CO_2, the associated investment of photosynthate into reproduction may result in reduced seed quality or seedling performance (Huxman et al. 1998b, 1999, 2001). Therefore, *Bromus* will benefit from the down-regulation response if the more abundant seed production under elevated CO_2 is great enough to outweigh the reduced seed quality and seedling performance.

Greater allocation belowground at elevated CO_2 should ensure future growth and survivorship for *Achnatherum* in arid environments where the availability of water and nutrients in the rhizosphere is ephemeral and heterogeneously distributed. *Achnatherum* had similar net assimilation rates between CO_2 treatments and, as inferred from A-c_i relationships, reduced the rate of maximum carboxylation by Rubisco while increasing tissue biomass under elevated CO_2. N that is conserved and allocated away from photosynthesis could be invested in processes belowground, which in turn may help capture limiting resources and enhance growth and survival. Fine root production enhances resource acquisition but at the potential cost of greater root turnover rates (Persson 1982). As reported for this experiment in a companion paper, *Achnatherum* increased total root mass under elevated CO_2, but neither root surface area nor root respiration measurements were significantly affected by CO_2 treatment (Yoder et al. 2000). However, N uptake on a whole root-system basis ($NO_3 + NH_4$ uptake capacity × root biomass) was positively influenced by elevated CO_2 for *Achnatherum* after anthesis. The investment of proportionately greater root biomass under an elevated CO_2 environment, resulting in greater uptake of N by the whole root system, could place *Achnatherum* at a competitive advantage compared with species that do not increase root-system N uptake capacity in the Mojave Desert.

Plants grown at elevated CO_2 that down-regulate photosynthesis may allocate N away from photosynthetic enzymes such as Rubisco toward more limited processes within the plant (Xu et al. 1994). However, we recognize that changes in N status within the leaf should be interpreted cautiously with regard to changes in specific leaf area (SLA). Leaves of *Bromus* had lower leaf N concentrations and reduced Vc_{max} under elevated CO_2. SLA was unchanged, but NLA (N per unit leaf area) was lower under elevated CO_2. Thus, *Bromus* shifted N away from leaves, and in the case of this short-lived annual species, allocated N toward reproduction. *Achnatherum* also demonstrated both lower leaf N concentration and Vc_{max} under elevated CO_2. However, SLA for *Achnatherum* was decreased in plants grown at elevated CO_2 so we cannot discount that lower Vc_{max} arose due to carbohydrate accumulation (Bazzaz 1990; Wong 1990, Kuehny et al. 1991; Rogers et al. 1996; den Hertog et al. 1998) or changes in leaf thickness and number of cell layers in the leaf (Thomas and Harvey 1983).

Down-regulation of photosynthesis in C_3 species grown at elevated CO_2 may also reflect N deficiency (Drake et al. 1997), accelerated plant age (Coleman et al. 1993), or reduced uptake capacity of N (BassiriRad et al. 1997). As stated previously, no visible symptoms of N deficiency were detected. Plant age also does not fully explain lower N concentration at elevated CO_2 because leaf N expressed on a leaf area basis (NLA) did not show a significant interaction between CO_2 treatment and sampling date for any of the species examined. In this study, the ability of roots to take up N was unaffected by elevated CO_2 for both C_3 species at anthesis; uptake of NO_3 in *Achnatherum* and NH_4 in *Bromus* at elevated CO_2 was reduced during the seed fill stage only (Yoder et al. 2000).

Reduced uptake of N does not fully explain why leaves had lower N at earlier sampling dates. Therefore, N deficiency, early onset of senescence and reduced N uptake at elevated CO_2 did not appear to play a major role in down-regulation of photosynthesis for *Bromus* and *Achnatherum*. Thus, the reallocation of N away from photosynthesis best explains the down-regulation response to elevated CO_2, at least for *Bromus,* in this study.

Our results suggest that photosynthetic down-regulation in a world with greater atmospheric CO_2 concentrations influences species differentially based on their pattern of internal resource partitioning. For example, our results are consistent with predictions that downward adjustment of Rubisco and N investment for photosynthesis in the two Mojave Desert C_3 grass species will increase whole plant performance in an elevated CO_2 environment, whereas Rubisco, N investment, and hence plant growth of C_4 perennial species is expected to change little as atmospheric CO_2 continues to rise. Differences among functional types in the use and internal adjustment of resources such as N will potentially influence fecundity and survival among individual plants. In turn, these differences may have major implications for species interactions, community assembly and ecosystem processes in the future as atmospheric CO_2 concentrations continue to rise.

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Table 1. *P*-values and means (n=6, ± SE) of leaf N concentration ([N], mg N g^{-1} DW), N per unit leaf area (NLA, mmol N m^{-2}), and specific leaf area (SLA, cm^2 g^{-1}) for plants grown at ambient (360 µmol mol^{-1}) and elevated (1000 µmol mol^{-1}) atmospheric CO$_2$ concentrations.

		Bromus		*Achnatherum*		*Pleuraphis*	
	Date	***Ambient***	***Elevated***	***Ambient***	***Elevated***	***Ambient***	***Elevated***
[N]	1	19.0 (1.4)	12.7 (0.4)	22.5 (1.2)	16.3 (0.5)	19.1 (2.0)	15.6 (1.7)
	2	7.9 (0.3)	4.7 (0.2)	10.5 (0.1)	7.4 (0.4)	10.6 (1.4)	10.6 (1.3)
	3	6.4 (0.9)	5.2 (0.8)	7.5 (0.8)	5.3 (0.7)	7.4 (0.8)	9.3 (1.4)
	CO$_2$	< 0.01		< 0.01		0.65	
	Date	< 0.01		< 0.01		<0.01	
	CO$_2$ × date	0.02		0.07		0.20	
NLA	1	53 (6)	42 (4)	193 (12)	157 (4)	140 (17)	130 (22)
	2	29 (1)	15 (1)	136 (19)	98 (6)	97 (18)	106 (21)
	3	24 (5)	20 (5)	114 (11)	87 (9)	76 (17)	54 (6)
	CO$_2$	< 0.01		< 0.01		0.59	
	Date	< 0.01		< 0.01		< 0.01	
	CO$_2$ × date	0.54		0.88		0.67	
SLA	1	260 (15)	220 (16)	84 (3)	74 (3)	99 (3)	91 (11)
	2	198 (14)	218 (3)	56 (2)	55 (3)	81 (5)	78 (14)
	3	199 (14)	98 (45)	46 (2)	43 (2)	75 (10)	125 (14)
	CO$_2$	0.62		0.03		0.15	
	Date	0.02		< 0.01		0.15	
	CO$_2$ × date	0.11		0.25		0.02	

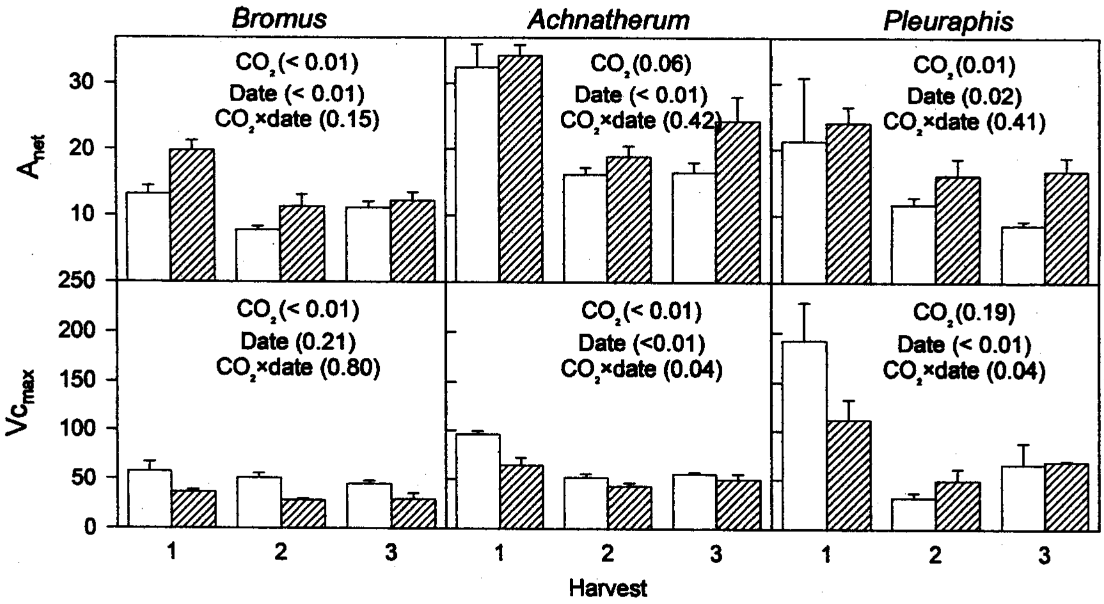
Figure legends

Fig. 1. Mean (± SE, n=3) net CO_2 assimilation rate at growth CO_2 concentration (A_{net}) and maximum rate of carboxylation efficiency of Rubisco (Vc_{max}) for three grasses exposed to 360 (clear bars) and 1000 μmol mol^{-1} CO_2 (hatched bars). P values from 2-factor ANOVAs are shown in parentheses.

Fig. 2. Mean (n=6, ± SE) plant mass (g ind^{-1}) and total tissue N (mg N ind^{-1}) for three grass species grown at 360 and 1000 μmol mol-^{1} CO_2 (note different ordinate scales among species). P values from 2-factor ANOVAs are shown in parantheses.

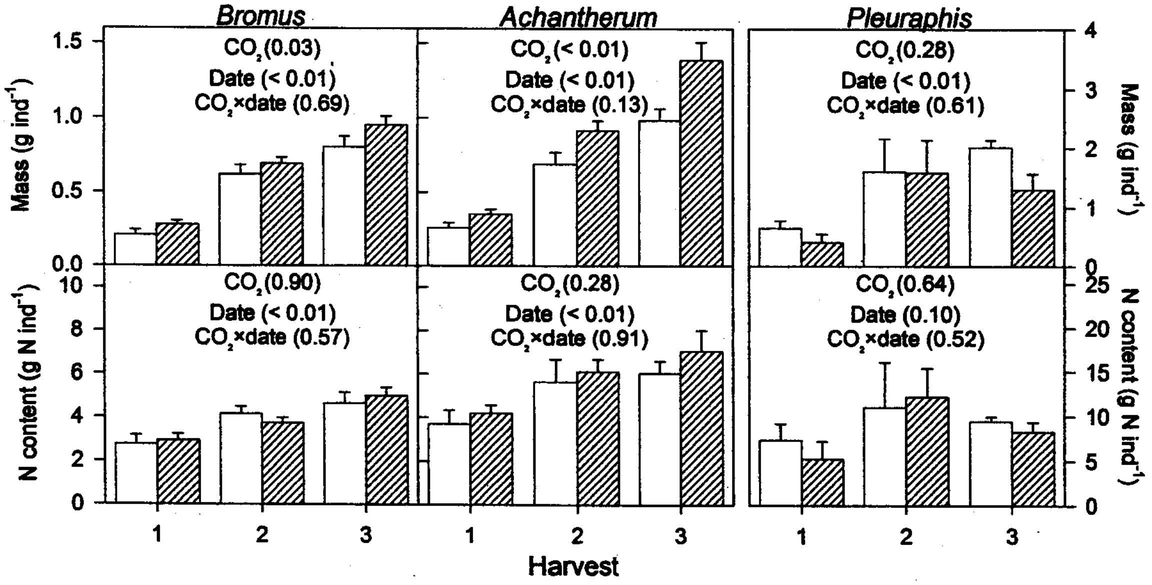
Fig. 3. Mean (± SE, n = 6) root:shoot ratio and reproductive effort at final harvest (RE) for *Bromus* (a.), *Achnatherum* (b.) and *Pleuraphis* (c.) exposed to 360 (clear bars) and 1000 μmol mol^{-1} CO_2 (hatched bars). Note different ordinate scales between C_3 species and *Pleuraphis*. *Pleuraphis* did not produce flowers, and thus RE is not analyzed. *P*-values from 2-factor ANOVAs are shown in parentheses.

Figure 1



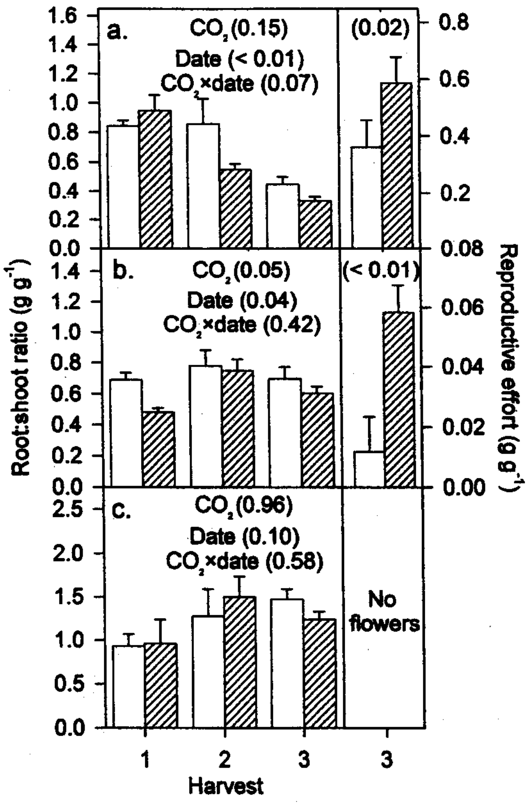
Bromus
Achnatherum
Pleuraphis
A_{net}
Vc_{max}
30
20
10
250
200
150
100
50
0
CO_2(< 0.01)
Date (< 0.01)
CO_2×date (0.15)
CO_2(0.06)
Date (< 0.01)
CO_2×date (0.42)
CO_2(0.01)
Date (0.02)
CO_2×date (0.41)
CO_2(< 0.01)
Date (0.21)
CO_2×date (0.80)
CO_2(< 0.01)
Date (<0.01)
CO_2×date (0.04)
CO_2(0.19)
Date (< 0.01)
CO_2×date (0.04)
1
2
3
1
2
3
1
2
3
Harvest

Figure 2



Bromus
Achantherum
Pleuraphis
CO_2(0.03)
Date (< 0.01)
CO_2×date (0.69)
CO_2(< 0.01)
Date (< 0.01)
CO_2×date (0.13)
CO_2(0.28)
Date (< 0.01)
CO_2×date (0.61)
CO_2(0.90)
Date (< 0.01)
CO_2×date (0.57)
CO_2(0.28)
Date (< 0.01)
CO_2×date (0.91)
CO_2(0.64)
Date (0.10)
CO_2×date (0.52)
Mass (g ind^{-1})
N content (g N ind^{-1})
0.0
0.5
1.0
1.5
0
2
4
6
8
10
0
1
2
3
4
0
5
10
15
20
25
1
2
3
Harvest

Figure 3


a.
CO₂ (0.15)
Date (< 0.01)
CO₂×date (0.07)
(0.02)
b.
CO₂ (0.05)
Date (0.04)
CO₂×date (0.42)
(< 0.01)
c.
CO₂ (0.96)
Date (0.10)
CO₂×date (0.58)
No flowers
Root:shoot ratio (g g-1)
Reproductive effort (g g-1)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
2.5
2.0
1.5
1.0
0.5
0.0
0.8
0.6
0.4
0.2
0.08
0.06
0.04
0.02
0.00
1
2
3
3
Harvest