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Performance and allocation patterns of the perennial herb, *Plantago lanceolata*, in response to simulated herbivory and elevated CO_2 environments

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Summary. We tested the prediction that plants grown in elevated CO_2 environments are better able to compensate for biomass lost to herbivory than plants grown in ambient CO_2 environments. The herbaceous perennial *Plantago lanceolata* (Plantaginaceae) was grown in either near ambient (380 ppm) or enriched (700 ppm) CO_2 atmospheres, and then after 4 weeks, plants experienced either 1) no defoliation; 2) every fourth leaf removed by cutting; or 3) every other leaf removed by cutting. Plants were harvested at week 13 (9 weeks after simulated herbivory treatments). Vegetative and reproductive weights were compared, and seeds were counted, weighed, and germinated to assess viability.

Plants grown in enriched CO_2 environments had significantly greater shoot weights, leaf areas, and root weights, yet had significantly lower reproductive weights (i.e. stalks + spikes + seeds) and produced fewer seeds, than plants grown in ambient CO_2 environments. Relative biomass allocation patterns further illustrated differences in plant responses to enriched CO_2 atmospheres: enriched CO_2-grown plants only allocated 10% of their carbon resources to reproduction whereas ambient CO_2-grown plants allocated over 20%. Effects of simulated herbivory on plant performance were much less dramatic than those induced by enriched CO_2 atmospheres. Leaf area removal did not reduce shoot weights or reproductive weights of plants in either CO_2 treatment relative to control plants. However, plants from both CO_2 treatments experienced reductions in root weights with leaf area removal, indicating that plants compensated for lost above-ground tissues, and maintained comparable levels of reproductive output and seed viability, at the expense of root growth.

Key words: Allocation – Compensatory growth – Defoliation – Reproductive effort – Seed quality

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Studies investigating the effects of elevated carbon dioxide atmospheres on plant-insect herbivore interactions have focused on how these conditions alter the behavior and performace of insect herbivores (e.g. Lincoln et al. 1986; Fajer et al. 1989). Few studies, however, have explored how damage caused by herbivores will impact plant performace in enriched CO_2 atmospheres. Undamaged plants, especially those possessing the C_3 carbon-fixation pathway, increase their growth in elevated CO_2 atmospheres (Kramer 1981; Lemon 1983; Bazzaz 1990). However, if insect herbivore consumption levels also increase in elevated CO_2 environments (Lincoln et al. 1986; Fajer et al. 1989), enhanced vegetative growth (and the presumed concurrent rise in lifetime fitness; Harper 1977; Solbrig 1981), may be negated. Yet, if herbivory levels do not differ, damaged plants reared in enriched CO_2 environments may be better able to compensate for lost tissues and allocate a greater percentage of resources to reproduction, than would damaged plants reared in ambient CO_2 environments. This is because enriched CO_2 atmospheres provide both an augmented carbon resource base and a more favorable water balance, especially for C_3 plants (see Bazzaz 1990 for review), thereby creating abiotic conditions appropriate for successful compensation of tissues lost to herbivores (Belsky 1986; Chapin and McNaughton 1989; Maschinski and Whitham 1989).

To test whether elevated CO_2-grown plants can compensate for biomass loss resulting from herbivory, we grew *Plantago lanceolata* L. (Plantaginaceae) plants in either near ambient (380 ppm) or enriched (700 ppm) CO_2 atmospheres, while subjecting them to different levels of simulated herbivory. After 13 weeks, plants were harvested and their allocation to vegetative and reproductive structures were measured and compared. Seed quality was also compared by measuring both seed weight and seed viability. We anticipated that, in general, plants grown in elevated CO_2 conditions would have greater total shoot, root, and reproductive weights, and that damaged plants grown in elevated CO_2 environments would be better able to compensate for lost tissues

than would damaged plants grown in ambient CO_2 environments.

Methods

The System

Plantago lanceolata L. (Plantaginaceae) is a cosmopolitan, short-lived, perennial herb, which overwinters as a basal rosette (=shoots), and which produces spiked inflorescences at the end of fibrous stalks (= reproductive parts) under the appropriate conditions of day length (long days) and nutrient availability (Primack and Antonovics 1982). It is self-incompatible and wind-pollinated. When grown in enriched CO_2 atmospheres, *P. lanceolata* plants increase both their shoot and root weights (Fajer, unpublished data). In addition, under these conditions, the weights of individual seeds decline, but time to germination is shorter, and the percentage of seeds germinating and the subsequent size of these seedlings is greater (i.e. enhanced seed "quality"; Wulff and Alexander 1985).

The experiment

P. lanceolata seeds collected in Cambridge, MA, were germinated in vermiculite-filled flats and, after two weeks, transplanted individually into 10-cm round plastic pots containing a soil medium of 2:1:5 field soil, Turface® (montmorillonite clay), and sand. Plants were randomly assigned to either the ambient CO_2 (380 ppm $\pm$ 50 ppm) or the enriched CO_2 (700 ppm $\pm$ 35 ppm) treatment (initially 80 plants per treatment) and were placed into four environmentally-controlled growth chambers (see Fajer 1989), two chambers per CO_2 treatment. Once a week, plants were rotated between growth chambers to minimize chamber and pseudoreplication effects. Plants grew in all four chambers over the course of the experiment because CO_2 control could be reset within individual chambers to either the ambient or elevated CO_2 concentration.

Growing conditions were the following: the temperature regime was 27° C day: 25° C night, at 70% relative humidity, and light levels were 520 ± 30 µmol m^{-2} s^{-1}, with a photoperiod initially at 14 h. Although our experimental light levels were low compared to full sun exposure (1800–2000 µmol m^{-2} s^{-1}), plants may not have been severely light limited because of the long photoperiod and the presumed minimal water stress. Clearly, experimental results might have differed if plants were grown under higher light levels. Plants were watered daily for 7 weeks, then twice a day for the remaining 6 weeks of the experiment, and were individually fertilized once a week with 0.1 gram of Peters® 15:15:15 NPK water soluble fertilizer in 100 ml of water.

Three simulated herbivory treatments of different severities were performed on 4 week old plants before flowering had initiated: no leaves removed (control herbivory treatment), one out of every four leaves over 2 cm in length removed (intermediate herbivory treatment), and one out of every two leaves over 2 cm in length removed (high herbivory treatment). Leaf area from individual leaves was removed over a period of 3 days by clipping (with scissors) approximately 1/3 of the leaf area daily in order to approximate how a larva of a univoltine species (i.e. only one bout of herbivory during the plants' lifetimes) might remove foliar biomass over a number of days. This method only allows us to investigate how plants grown under different CO_2 concentrations respond to a controlled amount of leaf area loss; it does not purport to address other interactive effects which result when "real" herbivores eat plants. Plants had approximately 8–16 leaves of 2 cm or greater at the time of clipping, with 3–5 of these leaves fully extended. The mean dry weight of leaf material removed per plant was the following: ambient CO_2 plants: intermediate herbivory ($\bar{x}=0.24$ g, SE = 0.007, $n=22$), high herbivory ($\bar{x}=0.45$ g, SE = 0.024, $n=22$); enriched CO_2 plants: intermediate herbivory ($\bar{x}=0.41$ g, SE = 0.032, $n=22$), high herbivory ($\bar{x}=0.56$ g, SE = 0.020, $n=20$). This leaf material was not included in final shoot weight calculations.

At week 5, photoperiod was increased to 16 h to induce flowering (Primack and Antonovics 1982). By week 7, many plants still had not flowered, so photoperiod was increased to 18 h for 3 days, and then was returned to 16 h for the remainder of the experiment (6 weeks).

At week 13, mature seeds began to fall off the infructesences of some plants, so the experiment was terminated. Plants were harvested, and then separated into roots, shoots, and reproductive (stalks, spikes and seeds) parts. Roots were washed, and all plant parts were dried at 55° C, and weighed. Total shoot weight, percent shoot allocation, total root weight, percent root allocation, root/shoot ratio, total weight, total reproductive weight (i.e. stalk weight + spike weight + seed weight), percent reproductive allocation, and mature seed number were measured or calculated for each plant. Plants which did not flower were not included in the calculations of percent shoot allocation, percent root allocation and percent reproductive allocation. Leaf area (cm^2) was calculated by running freshly harvested leaves under a Li-Cor 3100 leaf area meter. Leaf specific weight per plant was also determined as leaf weight (g)/leaf area (cm^2).

For plants which flowered, 15–50 seeds per plant were randomly selected, and then weighed to determine mean individual seed weight per plant. To determine seed viability, these seeds were placed in a 10-cm petri dish on moistened filter paper under a thin layer of moistened vermiculite and allowed to germinate. Petri dishes were placed in a growth chamber under ambient CO_2 conditions, at 27° C day/20° night, 70% RH, and a 16 h photoperiod. Percent seed germination per plant and mean time to germinate for all seeds per plant were recorded.

For 2–3 days during week 5, plants in two chambers (one ambient CO_2 chamber and one enriched CO_2 chamber) experienced 24 h photoperiods. Therefore, plants which experienced the prolonged photoperiod were included in a separate block from those which did not. This block effect was included in a 3-way ANOVA (CO_2 X Simulated Herbivory × Block) after the appropriate log or arcsine transformations were performed on the data. The root weights of all plants (30) grown under ambient CO_2 X regular photoperiod block were lost after harvest; so, the effect of block on parameters which depended on root weight values (e.g. total plant weight) could not be evaluated for ambient CO_2-grown plants. Thus, for the remainder of the plants, parameters which depended upon root weight values were only analyzed with a Two-way ANOVA (CO_2 X Simulated Herbivory).

Results

Plants grown in enriched CO_2 atmospheres had significantly greater shoot weights (on average, 34% greater), which resulted from both increased total leaf areas per plant (on average, 17% greater), and from heavier leaves (i.e. greater leaf specific weights), than did plants grown in ambient CO_2 atmospheres (Tables 1, 2). In fact, average shoot weights from plants which grew in enriched CO_2 conditions were greater than those from plants which grew in ambient CO_2 conditions, regardless of herbivory level. Neither herbivory levels nor CO_2 X Herbivory interactions significantly affected total shoot weight, total leaf area, nor leaf specific weight (Tables 1, 2), meaning that plants from both CO_2 treatments compensated for lost photosynthetic tissue equally. Block effects were significant for total leaf area ($F=3.95$, df = 1,120. $P=0.049$) and leaf specific weight ($F=4.33$, df = 1,120. $P=0.040$), but not for total shoot weight

Table 1. Effect of CO_2 concentration and simulated herbivory on shoot and reproductive parameters for *Plantago lanceolata*

	Control (no herbivory)						Intermediate Herbivory						High Herbivory					
	Ambient CO_2			Enriched CO_2			Ambient CO_2			Enriched CO_2			Ambient CO_2			Enriched CO_2		
	$\bar{x}$	(se)	*n*	$\bar{x}$	(se)	*n*	$\bar{x}$	(se)	*n*	$\bar{x}$	(se)	*n*	$\bar{x}$	(se)	*n*	$\bar{x}$	(se)	*n*
Total shoot weight (g)	6.13	(0.28)	25	9.33	(0.42)	25	5.88	(0.36)	19	9.68	(0.56)	22	5.87	(0.44)	22	7.83	(0.41)	19
Total leaf area (cm^2)	436.5	(20.9)	25	552.6	(33.3)	25	434.0	(31.5)	19	540.2	(29.4)	22	445.8	(34.9)	22	484.3	(30.2)	19
Leaf specific weight (g/cm^2)	14.2	(0.4)	25	17.7	(0.8)	25	13.8	(0.47)	19	16.6	(0.42)	22	13.3	(0.35)	22	16.6	(0.59)	19
Total root weight (g)	6.52	(0.48)	14	9.79	(0.42)	25	6.49	(0.63)	9	9.05	(0.38)	22	5.76	(0.70)	11	7.74	(0.41)	19
Root: shoot ratio	1.11	(0.09)	14	1.08	(0.05)	25	1.09	(0.06)	9	0.98	(0.05)	22	1.20	(0.08)	11	1.01	(0.05)	19
Total weight (g)	15.7	(0.6)	14	20.9	(0.5)	25	16.5	(0.7)	9	20.6	(0.7)	22	13.8	(0.8)	11	17.8	(0.5)	19
Total reproductive weight (g)	3.14	(0.36)	25	1.77	(0.32)	25	3.68	(0.50)	19	1.86	(0.35)	22	3.02	(0.41)	22	2.23	(0.44)	19
Seed number (per plant)	707.9	(101.6)	25	529.4	(71.0)	25	626.1	(150.0)	19	426.1	(81.1)	22	666.9	(139.8)	22	512.5	(102.0)	19
Weight per seed (mg)	1.25	(0.07)	22	1.23	(0.08)	15	1.17	(0.08)	19	0.95	(0.08)	15	1.18	(0.06)	18	1.21	(0.06)	13
% Seeds germinating	95.9	(1.6)	22	95.6	(1.1)	15	91.2	(2.6)	19	90.8	(3.1)	15	93.8	(1.5)	18	93.5	(2.3)	13
Mean time to germinate (d)	4.33	(0.19)	22	4.43	(0.22)	15	4.66	(0.28)	19	5.20	(0.28)	15	4.36	(0.27)	18	4.48	(0.27)	13

(F = 2.01, df = 1,120. $P = 0.154$); and, for only total leaf area, the block X Herbivory interaction was significant (F = 3.33, df = 2,120. $P = 0.039$).

Both root weights and total weights (i.e. shoots + roots + reproductive structures) were affected by both CO_2 treatment and by simulated herbivory treatment. Plants grown in enriched CO_2 environments had greater root weights (on average, 29% greater), and also greater total weights (on average, 32% greater), than plants grown in ambient CO_2 environments (Tables 1, 2). As found for most plants (see Bazzaz 1990), *P. lanceolata* root: shoot ratios were significantly greater under enriched CO_2 conditions; however, root: shoot ratio was not significantly affected by either herbivory treatment or by CO_2 X Herbivory interaction (Tables 1, 2). Plants which experienced simulated herbivory had lower root weights and lower total weights than control plants (Tables 1, 2). For example, ambient CO_2-grown plants which experienced high simulated herbivory had, on average, 12% less root weight than ambient CO_2-grown controls, and enriched CO_2-grown plants which experienced high simulated herbivory had, on average, 21% less root weight than enriched CO_2-grown controls. However, root weights from enriched CO_2-grown plants which experienced high simulated herbivory still were, on average, about 16% greater than root weights from ambient CO_2-grown plants which were not defoliated (Table 1).

In contrast to vegetative characters, however, total reproductive weight and number of mature seeds were significantly lower in enriched CO_2 environments, by an average of 50% lower in some treatments (Tables 1, 2). Moreover, significantly more plants grown in enriched CO_2 atmospheres failed to flower compared to those plants grown in ambient CO_2 atmospheres (Ambient CO_2: 4/70 plants failed to flower; Enriched CO_2: 15/66 failed to flower; G = 8.59, $P < 0.005$). Again, neither herbivory levels, nor CO_2 X Herbivory interactions, significantly affected total reproductive weight and seed number (Tables 1, 2). Block effects also did not significantly affect these reproductive characters (for total reproductive weight: F = 0.18, df = 1,120. $P = 0.669$; for seed number: F = 2.69, df = 1,120. $P = 0.104$).

Seed quality parameters (i.e. weight per seed, percent seed germination, mean time to germinate) were not significantly affected by CO_2 treatment. In contrast, plants which experienced intermediate herbivory treatments appeared to have reduced individual seed weights (Tables 1, 2), although these differences in seed weight did not affect whether or when a seed germinated (i.e. no significant effect (i.e. $P < 0.05$) of herbivory treatment on either percent seeds germinating or on mean time to germinate, Table 2). Block effects were very significant for seed weight (F = 17.06, df = 1,90. $P < 0.001$), but did not affect percent seed germination (F = 0.99, df = 1,90. $P = 0.322$) nor mean time to germinate (F = 0.03, df = 1,90. $P = 0.867$). Seed weight was significantly affected by the interaction between CO_2 and block (F = 6.39, df = 1,90. $P = 0.013$).

These results can best be summarized by examining both patterns of relative carbon allocation (Fig. 1), and

Table 2. F-values and significance levels from Anovas of effects of CO_2 and herbivory on *Plantago lanceolata*. The other interaction terms not listed were all statistically insignificant [except for significant interactions between herbivory and block for leaf specific weight (df = 2, F = 3.33, $P = 0.039$) and between CO_2 and block for seed weight (df = 2, F = 6.39, $P = 0.013$)

	Source of variation								
	CO_2			Herbivory			CO_2 * Herbivory		
	F	(dF)	*P*	F	(df)	*P*	F	(df)	*P*
Total shoot weight	70.63	(1,120)	0.001	2.90	(2,120)	0.059	0.74	(2,120)	0.931
Total leaf area	10.29	(1,120)	0.002	0.93	(2,120)	0.396	0.28	(2,120)	0.760
Leaf specific weight	69.00	(1,120)	0.001	2.07	(2,120)	0.130	0.36	(2,120)	0.699
Total weight	69.50	(1, 94)	0.001	11.67	(2, 94)	0.001	0.51	(2, 94)	0.601
Total root weight	38.18	(1, 94)	0.001	4.35	(2, 94)	0.016	0.20	(2, 94)	0.823
Root: shoot ratio	3.93	(1, 94)	0.050	0.67	(2, 94)	0.516	0.68	(2, 94)	0.511
Total reproductive weight	14.03	(1,120)	0.001	0.30	(2,120)	0.744	0.35	(2,120)	0.704
Seed number	6.72	(1,120)	0.011	0.14	(2,120)	0.621	0.45	(2,120)	0.636
Weight per seed	0.54	(1, 90)	0.463	3.69	(2, 90)	0.029	2.22	(2, 90)	0.115
% Seeds germinating	0.16	(1, 90)	0.694	1.73	(2, 90)	0.182	0.17	(2, 90)	0.848
Mean day to germinate	1.98	(1, 90)	0.162	2.56	(2, 90)	0.083	0.31	(2, 90)	0.737

correlations between absolute (i.e. total) carbon allocation to different structures. Plants grown in enriched CO_2 environments generally allocated, on average, 45% of their carbon resources into shoots, 45% into roots, and 10% into reproductive structures, whereas plants grown in ambient CO_2 environments allocated, on average, approximately 37% of their carbon resources into shoots, 39% into roots, and 24% into reproductive structures (Fig. 1). Thus, plants grown in enriched CO_2 environments allocated significantly more, both in terms of absolute and relative amounts, to vegetative structures and significantly less, to reproductive structures than plants grown in ambient CO_2 environments. Simulated herbivory levels did not affect relative allocation patterns (for % shoot allocation: F = 0.83, df = 2,77, $P = 0.441$; for % root allocation: F = 0.53, df = 2,77, $P = 0.592$; for% reproductive allocation: F = 0.63, df = 2,77, $P = 0.535$), although plants which experienced herbivory tended to have a reduced percent allocation to roots compared to control plants. Moreover, absolute allocation to reproductive structures was negatively correlated with absolute allocation to vegetative structures in both CO_2 treatments, especially for enriched CO_2-grown plants (Ambient CO_2: log reproductive weight = 3.232 − 1.079 log shoot weight; n = 70, $r^2 = 0.291$, $P < 0.001$; Enriched CO_2: log reproductive weight = 5.085 − 0.907 log shoot weight − 1.018 log root weight, $n = 64$, $R^2 = 0.480$, $P < 0.001$).

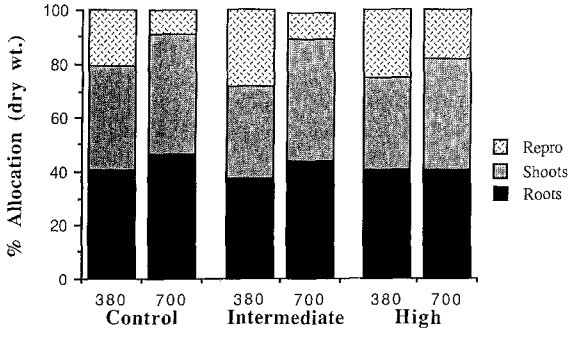

Fig. 1. Effects of CO_2 concentration and simulated herbivory on the percent allocation of biomass to vegetative and reproductive structures. CO_2 concentration significantly altered % shoot allocation (F = 22.4, df = 1,77, $P = 0.001$), % root allocation (F = 4.2, df = 1,77, $P = 0.043$), and % reproductive allocation (F = 22.4, df = 1,77, $P = 0.001$). However, neither simulated herbivory nor the interaction between CO_2 concentration and simulated herbivory significantly affected relative allocation patterns in *P. lanceolata*. 380 = 380 PPM (near ambient). 700 = 700 PPM (enriched). Control = no herbivory; Intermediate = every fourth leaf removed at week 4; High = every other leaf removed at week 4. Sample sizes are: Control: 14 ambient CO_2-grown plants, 25 enriched CO_2-grown plants; Intermediate herbivory: 9 ambient CO_2-grown plants, 21 enriched CO_2-grown plants; High herbivory: 11 ambient CO_2-grown plants, 19 enriched CO_2-grown plants

Discussion

Under elevated CO_2 conditions, *Plantago lanceolata* plants exhibited reduced absolute and relative allocation to reproductive structures (Tables 1, 2; Fig. 1). Reduced allocation to reproduction after 13 weeks may have resulted because enriched CO_2-grown plants experienced delayed flowering phenologies compared to ambient CO_2-grown plats. Although the uncontrolled 48-hour prolonged photoperiod found in two chambers (see Methods) may have also have affected the timing of *P. lanceolata* flower initiation, the interpretation that plants grown in enriched CO_2 environments have delayed flowering phenologies is consistent with results found using both perennial (Carter and Peterson 1983; Curtis et al. 1989) and annual graminoids (Garbutt et al. 1990). In contrast, studies using annual herbaceous plants have shown that those plants grown in enriched CO_2 environments usually flower and senesce earlier than those grown in ambient CO_2 environments (Paez et al. 1980; St. Omer and Horvath 1983; Garbutt and Bazzaz 1984; Garbutt et al. 1990; but see Bazzaz 1990 for review). Reduced absolute and relative reproductive weights for enriched CO_2-grown plants could also reflect an allocational shift in resources from reproductive to vegetative

stuctures in response to elevated CO_2 atmospheres, regardless of whether a change in flowering phenology occurred. Unfortunately, we did not collect the appropriate data to discern whether the lower levels of reproductive output observed for enriched CO_2-grown plants by week 13 resulted from a delayed initiation of flowering (i.e. change in phenology) and/or from a reduction in resources allocated to reproductive structures.

For an annual plants species, reduced seed production and a delayed initiation of flowering could signify a fitness decline and thus, a reduced presence in future plant communities (e.g. Garbutt and Bazzaz 1984, Zangerl and Bazzaz 1984). However, because *P. lanceolata* can reproduce over a number of growing seasons, equating its lifetime fitness with the reproductive output of a single shortened growing season is inappropriate. Increased vegetative growth (at the expense of reproductive output) during one season could lead to increased overwinter survivorship and then larger rosettes at the beginning of the second growing season. This, in turn, could result in superior competitive ability, and presumably an enhanced reproductive output, during the second growing season (see review by Antonovics 1980). However, if overwinter survivorship and subsequent reproductive effort is not enhanced for plants grown under enriched CO_2 environments, individuals which allocate resources earlier and to a greater extent to sexual reproduction may succeed at the expense of those which preferentially allocate to vegetative structures.

The ability of a plant to compensate for leaf area lost to herbivores may depend upon, among other factors, the availability of resources within reach of the individual (e.g. nutrients, water and light) necessary for plant growth and reproduction (Belsky 1986; Chapin and McNaughton 1989; Maschinski and Whitham 1989). We therefore anticipated that *P. lanceolata* plants which grew in enriched CO_2 environments, a high carbon resource environment with potentially more favorable water relations, would be more able to compensate for photosynthetic tissues lost to simulated herbivory than would plants which grew in ambient CO_2 environments. Instead, under our experimental conditions, *P. lanceolata* plants responded to simulated herbivory treatments in fundamentally the same manner regardless of their CO_2 environment: plants which experienced herbivory compensated for lost leaves (shoots) and maintained similar reproductive output and seed viability, at the expense of root growth.

Enriched CO_2-grown plants which experienced simulated herbivory lost a greater percentage of final root biomass relative to controls than did ambient CO_2-grown plants (Table 1, Fig. 1), although root weights for enriched CO_2-grown plants were greater than for ambient CO_2-grown plants, regardless of herbivory regime (Table 1). Thus, resource rich, elevated CO_2 environments were not more conducive to successful compensation for tissues lost to herbivores. Instead, the impact of herbivory on plants growing in favorable environments is potentially greater because the loss of potential growth between defoliated and non-defoliated plants is greater (e.g. Mihaliak and Lincoln 1989).

To conclude, *P. lanceolata* plants which allocate more resources to vegetative rather than reproductive structures under elevated CO_2 conditions may not become less important components of their plant communities. Instead, increased allocation to vegetative structures in a plant's first year may enhance survivorship, ultimately leading to similar or enhanced lifetime reproductive success. This potential benefit of increased allocation to vegetative structures may be augmented in future high CO_2 atmospheres, because, under these conditions, the interactions among individual plants are likely to intensify as a result of increased plant growth (the "CO_2 fertilization effect"; see review by Bazzaz 1990). Those plants which initially allocate to reproduction at the expense of vegetative growth (note the trade-off between reproductive and vegetative characters) may become less competitive than their larger "CO_2 fertilized" neighbors and therefore jeopardize both future survivorship over the winter, as well as reproduction.

The effects of herbivore damage may also be more dramatic in a high CO_2 world. In this experiment with *P. lanceolata* plants, a given level of herbivory under elevated CO_2 conditions resulted in a greater proportional reduction in root growth than under ambient CO_2 conditions. Because undamaged plants generally produce larger root systems when grown under elevated CO_2 atmospheres (Bazzaz 1990; Table 1), the difference in the root system development between damaged and undamaged plants in elevated CO_2 environments may be greater than that found in ambient CO_2 environments. Damaged plants grown in a high CO_2 world may therefore experience a greater competitive disadvantage for underground resources compared to damaged plants grown in an ambient CO_2 world.

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