GLOBAL CHANGE ECOLOGY

K. A. Stinson · F. A. Bazzaz

CO$_2$ enrichment reduces reproductive dominance in competing stands of *Ambrosia artemisiifolia* (common ragweed)

Abstract Plants growing in dense stands may not equally acquire or utilize extra carbon gained in elevated CO$_2$. As a result, reproductive differences between dominant and subordinate plants may be altered under rising CO$_2$ conditions. We hypothesized that elevated CO$_2$ would enhance the reproductive allocation of shaded, subordinate *Ambrosia artemisiifolia* L. (Asteraceae) individuals more than that of light-saturated dominants. We grew stands of *A. artemisiifolia* at either 360 or 720 µL L^{-1} CO$_2$ levels and measured the growth and reproductive responses of competing individuals. To test whether elevated CO$_2$ altered size and reproductive inequalities within stands, we compared stand-level coefficients of variation (CV) in height growth and final shoot, root, and reproductive organ biomasses. Elevated CO$_2$ enhanced biomass and reduced the CV for all aspects of plant growth, especially reproductive biomass. Allocation to reproduction was higher in the elevated CO$_2$ than in the ambient treatment, and this difference was more pronounced in small, rather than large plant positive relationships between the CV and total stand productivity declined under elevated CO$_2$, indicating that growth enhancements to smaller plants diminished the relative biomass advantages of larger plants in increasingly crowded conditions. We conclude that elevated CO$_2$ stimulates stand-level reproduction while CO$_2$-induced growth gains of subordinate *A. artemisiifolia* plants minimize differences in the reproductive output of small and large plants. Thus, more individuals are likely to produce greater amounts of seeds and pollen in future populations of this allergenic weed.

Communicated by Rowan Sage

K. A. Stinson (✉) · F. A. Bazzaz
Organismic & Evolutionary Biology, Harvard University, Cambridge, MA, USA
E-mail: kstinson@oeb.harvard.edu
Tel.: +1-978-7243302
Fax: +1-978-7243595

K. A. Stinson
Harvard Forest, PO Box 68, Petersham, MA 01366, USA

Introduction

In natural plant populations, the growth advantages of large individuals over smaller ones can be either enhanced or reduced (Poorter et al. 2003; Wayne et al. 1999) by the extra carbon supply in elevated atmospheric CO$_2$. The resulting increase or decrease in size inequalities can in turn affect the relative reproductive output of dominant and subordinate plants (He et al. 2003; Wayne et al. 1999), potentially altering evolutionary and population dynamics (Thomas et al. 1993). Through changes in dominance hierarchies and future stand composition, growth and reproductive inequalities within mixed and single-species stands can also influence community structure, diversity, and ecosystem function (Huxman et al. 1999; Körner 2003).

Initial size differences due to variation in emergence time and early growth rates tend to become exacerbated by competition (Hartgerink et al. 1984). An increase in size inequalities is most often attributed to asymmetric competition for light, in which larger individuals preempt the light acquisition and suppress the growth of smaller ones (Weiner 1990). If CO$_2$-induced growth enhancements of larger individuals suppress smaller individuals, aboveground size inequality in the stand becomes more pronounced through time (Nagashima et al. 2003). However, since relative shoot growth of individually grown plants is often most responsive to elevated CO$_2$ at lower-light levels (Ehleringer et al. 1977; Granados et al. 2002), light-limited subordinate plants could become more stimulated by elevated CO$_2$ conditions than light-saturated dominants (Hattenschwiler 2001; Stitt et al. 1999). Release from carbon limitation in subordinates could then lead to reduced inequalities among individuals and create a more homogeneous stand structure (Wayne et al. 1997). Since competition for nutrients is generally less asymmetric than competition for light, CO$_2$

enrichment may not alter inequalities in root biomass as much as it does in shoot biomass (Berntson et al. 2000).

Ambrosia artemisiifolia L. (Asteraceae), or common ragweed, is a monecious annual herb found in old fields and other disturbed habitats throughout most of North America, where it forms dense monospecific stands (Abulfatih et al. 1979). Ragweed pollen is one of the most problematic aero-allergens throughout its range, and CO_2-induced enhancements to growth and reproduction in *A. artemisiifolia* have raised concerns about its future status as an allergenic and agricultural pest (Ziska et al. 2000). We hypothesized that under elevated CO_2, shaded ragweed subordinates would gain proportionally more biomass than light-saturated dominants, thereby minimizing size inequalities in populations. We also predicted that reduced inequalities in aboveground biomass would result in more homogenous reproductive success (i.e., decreased reproductive dominance) among subordinates and dominants. Carbon enrichment could enhance reproduction in subordinates by stimulating vegetative growth, and/or by increasing photosynthetic efficiency to afford greater reproduction per unit of growth (He et al. 2003). If carbon–nitrogen balance differs between subordinates and dominants, greater allocation to roots in nutrient-limited dominants than in subordinates might also reduce reproductive inequalities (Arp 1991; Stitt et al. 1999). Alternatively, intensified size inequalities resulting from size-biased growth advantages to large plants could magnify reproductive dominance within CO_2-enriched stands.

We tested (a) whether elevated CO_2 alters reproductive inequalities in dense stands of *A. artemisiifolia*; and (b) whether subordinate plants allocate more biomass to reproduction than dominant plants in elevated CO_2. We show that when subordinate plants are released from suppression by dominant plants in elevated CO_2, they also achieve higher reproductive payoffs than dominants per unit of vegetative growth.

Materials and methods

Experimental design

In May 2002, a total of twelve 1.5-m (in diameter) open-top chambers were constructed in a cleared plot at Harvard University's Concord Field Station, about 25 km east of the Boston urban area in Bedford (MA, USA). The site was formerly a secondary growth, mixed hardwood stand with typical haplothord soils, but all trees and topsoil were removed and the field was leveled with a bulldozer before starting the experiment. The remaining substrate is a well-drained, sandy deposit lacking organic topsoil. To provide an organic layer and homogenize soil conditions, the site was mechanically tilled to a depth of 30.0 cm and covered with 15.0-cm dry, commercially produced loam ($\sim$5 cm when watered) two weeks prior to the construction of the chambers.

The chambers were numbered and randomly divided between treatments. Six chambers were maintained at ambient (360 μL L^{-1}) and six were maintained at twice-ambient, or elevated (720 μL L^{-1}) CO_2 levels. CO_2 was supplied via injection from a liquid tank located on site, beginning on 22 June and continuing until the final harvest in September. A control system was implemented to monitor CO_2 levels within each chamber using an infrared gas analyzer (LI-800, LiCor, Lincoln, NE), which sampled air concentrations at a frequency of < 5 min. This controlled the CO_2 levels to within ± 50 μL L^{-1} of the set point. Air temperature was maintained within 1.5°C of ambient using electric fans to regulate airflow.

Seeds were collected in September 1999 from > 100 *A. artemisiifolia* individuals in three populations at the Phillips Tract, University of Illinois, USA to form the basis of our ambient CO_2-grown glasshouse stock at Harvard University. On 20 May 2002, seeds from the second generation of this stock were randomly sown into horticultural trays containing 5 cm of soilless planting mixture (Pro-Mix 50). Trays were placed outdoors beneath a shelter providing 80% sunlight. Germinants were maintained with an automatic mist irrigation system.

In mid-June, two stands were constructed within each open-top chamber using identical hexagonal arrays consisting of 36 evenly spaced, uniquely numbered positions. This resulted in a field density of 60 individuals m^{-2}, typical for naturally occurring stands of this species (Raynal et al. 1975). We used only seedlings in the most abundant developmental stage (2–3 true leaves, 2.0–2.5-cm tall) to ensure similar starting ontogeny and seedling size. The planting design was randomized to further reduce the possible effects of initial size. Individual seedlings were numbered and assigned to positions and treatments using a random number generator. To minimize transplant shock and ensure similar transplant recovery between treatments, we maintained all chambers at ambient CO_2 and misted seedlings with water twice daily for the first week. Thereafter, the CO_2 treatments were initiated and all chambers received natural rainfall. We provided equal amounts of supplemental water to all chambers during dry periods using an automated mist watering system suspended from the top of each chamber. Metal tags were affixed to each individual for identification at the time of harvest. To minimize edge effects, plants on the outermost edge of each stand were excluded from observation and only the central 24 plants were measured. To keep all chambers free of nonexperimental plants, weeds were removed immediately after their germination (at least every 2–3 days).

Plant growth

Height and number of leaves were measured nondestructively on all experimental plants on 01 July, 19 July, and 07 August (14, 33, and 52 days after the start of the

experiment). Survival within each stand was 99–100%, and did not differ between CO_2 treatments. The height of each plant was measured at the tip of the longest main stem. The upper stem crowns of one or two individuals per treatment overlapped somewhat late in the season, but were carefully separated at the time of harvest; the rest of the plants (98%) remained freestanding. As *A. artemisiifolia* is highly photoperiodic (Deen et al. 1998), all plants were harvested at a similar developmental stage during peak seed production and coinciding with the usual onset of senescence (early September). Root systems were extracted by digging a 35-cm trench around each stand, by watering to loosen the soil, and then by carefully hand-pulling individuals at the stem base. The high sand content of the field soils facilitated extraction of the major root system of each plant, allowing adjacent plants to be easily separated. Remaining soil was gently washed from roots in a small basin prior to drying. The loss of fine roots can lead to underestimates of root–shoot allocation but we are confident that fine root loss was similar in both treatments. Harvested plants were carefully sorted out into roots, shoots (stems and leaves), and reproductive structures (flower buds, flowers, and seeds), then oven-dried at 100°C to a constant mass and weighed.

Light availability within developing stands

Photosynthetically active radiation was measured as photon flux density (PPFD) with a gallium arsenide photo diode (GasP G1118, Hamamatsu Corp., Bridgewater, NJ, USA) on four representative sunny days during the growing season (12 July, 23 July, 31 July, and 07 August). In each stand, five target plants were chosen randomly, and measurements were made at 5-cm intervals along a vertical axis from the ground to the top of each target plant. The axis of measurement was located on the southern side of target plants at a distance from the main stem equal to one half of the canopy radius. Light data for all canopy depths in each stand were averaged over time to determine whether stand-level light conditions differed between treatments.

Data analysis

To test the effect of CO_2 on stand-level means for organ biomasses, we used a MANOVA model, which accounts for simultaneous variation among correlated characters (Sokal et al. 1995 p. 680). Raw data (shoot, root, and reproductive mass) were log-transformed as necessary to correct for nonnormality, prior to analysis. The effect of CO_2 was tested against the block (chamber) × CO_2 variance. Variance due to error was used as the F ratio denominator for all other terms. Variance due to stands within each chamber was pooled with the error term. Nondestructive measurements (height and number of leaves) were averaged separately by stand on each date

of observation, and the effects of CO_2 treatment and time were analyzed using repeated measures ANOVA. The effect of CO_2 was tested against the block (chamber) × CO_2 variance. The CO_2 × time interaction was tested against the block × CO_2 × time effect.

We quantified size inequalities using the coefficient of variation (CV), which is highly correlated with the Gini coefficient of size inequality (Weiner 1990; Weiner et al. 1984). CVs for shoot, root, reproductive, and total biomass, height, and number of leaves were calculated for each stand. Differences in CV between high and low CO_2 treatments were tested by MANOVA as above. We also quantified changes in size hierarchies by examining stand structure, as expressed by size-class frequency distributions for shoot, root, and reproductive biomass.

The effect of elevated CO_2 on biomass partitioning to different organs was examined after harvest by plotting allometric relationships between shoot and root biomasses and shoot and reproductive biomasses. Differences between treatments in the slopes of the resulting regression lines were tested with ANCOVA, using CO_2 treatment as a main effect and shoot biomass as the covariate. Significantly steeper slopes were interpreted as evidence for a CO_2 effect on the proportional allocation of biomass to different plant structures with respect to plant size.

Inferences about the intensity of light competition were made by relating total stand biomass to the CV for each trait using Model II regression. The slopes of these regressions provide a visual and statistical measure of the relative gains by large plants over smaller ones as stand size increases (Wayne et al. 1997). Differences between slopes of these regressions were tested with ANCOVA, using CO_2 treatment as a main effect and total stand biomass as a covariate.

Results

Biomass allocation and size inequalities

Elevated CO_2 significantly altered organ biomass and biomass partitioning in stands of *A. artemisiifolia* (MANOVA, $F = 0.843$, $P < 0.0001$). Stand-level biomass means for all plant structures (shoot, root, reproductive, and whole plant) were greater in high-CO_2 treatments (Table 1), indicating growth stimulation in all plant structures. Root to shoot allocation ratios increased only slightly in high CO_2 compared to ambient stands. The strongest biomass responses to CO_2 were observed in reproductive biomass and reproductive allocation ratio (repro to shoot), both of which nearly doubled in the elevated treatment. Stand-level coefficients of variation for organ biomasses and whole plant (total) biomass were lower in the CO_2-enriched treatments than in the ambient treatments (Table 1, MANOVA $F = 3.35$, $P = 0.02$). The CV_{repro} and $CV_{repro–shoot}$ were more reduced than the CVs for the other characters. Thus, elevated CO_2 increased reproductive biomass and

Table 1 Stand-level means ± 1 standard error and coefficients of variation (CV) for biomass and biomass allocation ratios (Main effects of CO_2 on plant characters significantly differ as tested by MANOVA (see text))

	Biomass (g plant^{-1})					
	Shoot	Root	Reproductive	Total	Root to shoot ratio	Repro to shoot ratio
Average stand-level means						
Ambient	1.38 ± 0.26	0.269 ± 0.06	1.33 ± 0.42	2.89 ± 0.69	0.182 ± 0.01	0.67 ± 0.35
Elevated	1.98 ± 0.26	0.395 ± 0.06	2.58 ± 0.37	4.92 ± 0.68	0.193 ± 0.00	1.20 ± 0.15
Stand-level coefficient of variation						
Ambient	79.34 ± 5.12	95.65 ± 9.74	112.75 ± 6.48	106.98 ± 39.10	33.12 ± 2.88	59.31 ± 3.65
Elevated	76.19 ± 7.04	84.85 ± 6.57	96.68 ± 7.60	83.06 ± 11.39	25.50 ± 1.61	29.91 ± 3.68

Average stand-level means for individual plant biomasses (g plant^{-1}) in *Ambrosia artemisiifolia* plants: shoot (stem + leaf), root, reproductive (flowers + fruits), total, root to shoot ratio, and repro to shoot ratio; Stand-level coefficient of variation (CV) for

A. artemisiifolia plants based on allocation to biomass–shoot (stem + leaf), root, reproductive (flowers + fruits), root to shoot ratio, and reproductive to shoot ratio. $N = 281$ individuals

reduced reproductive inequalities disproportionately to other organs.

Plants in the CO_2-enriched treatment allocated, on average, more reproductive biomass per gram shoot biomass than plants in ambient conditions (Fig. 1a). Slopes of regressions relating reproductive to shoot biomass were positive in both treatments ($P < 0.01$), but were significantly steeper in ambient versus elevated CO_2 (ANCOVA, $P < 0.001$ for the effects of CO_2 level, shoot mass, and CO_2 level $\times$ shoot mass on response variable = repro mass). As demonstrated by the convergence of the regression lines at greater plant sizes in Fig. 1a, smaller plants allocated more mass to reproduction per gram shoot mass relative to large plants in the elevated CO_2 treatment. Allometric relationships between shoot and root biomasses were positive in both treatments ($P < 0.01$) (Fig. 1b). Slopes of the regressions relating shoot to root mass did not differ between ambient and enriched-CO_2 conditions (ANCOVA, response variable = root mass: CO_2 level, $P = 0.151$; shoot mass, $P < 0.001$, CO_2 level $\times$ shoot mass, $P < 0.896$).

Competitive interactions and frequency of subordinates and dominants

Slopes of the regressions relating total stand biomass–biomass CVs were positive in ambient stands but not significant in elevated CO_2 stands (Fig. 2). In the ambient treatment, CVs for each organ mass increased ($P < 0.01$) as a function of total stand mass (Fig. 2a–c: CV_{shoot}, $R^2 = 0.55$; CVroot, $R^2 = .41$; and CV_{repro}, $R^2 = 0.32$). The effect of CO_2 level on CV_{repro} was significant ($P = 0.03$), but the $CO_2 \times$ total stand mass interaction term was not. ANCOVA tests for differences between slopes demonstrated no effects of CO_2 level or $CO_2 \times$ total standing biomass interaction terms on regressions relating total standing biomass to inequalities in shoot or root biomasses.

Plant biomass frequency distributions indicated proportionally greater growth stimulation of subordinate individuals in the elevated treatment than in the ambient

treatment (Fig. 3). Shoot, root, and reproductive size-classes were skewed toward a greater proportion of small versus large individuals in both treatments, but
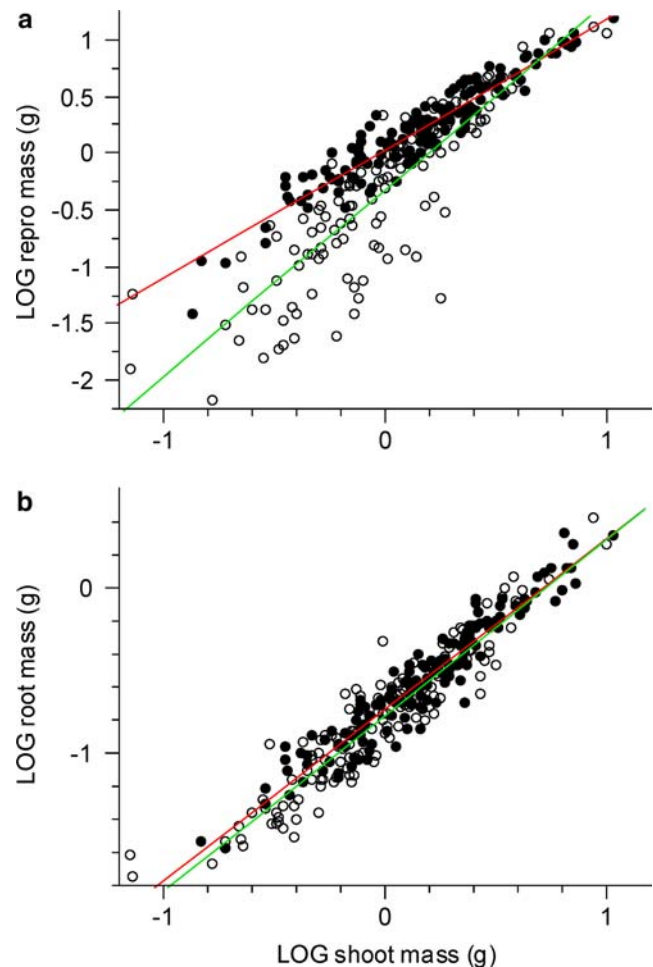

Fig. 1 Relationships between organ biomasses: **a** reproductive biomass (sum of masses for all buds, flowers, and seeds) as a function of shoot mass; **b** root biomass as a function of shoot mass. *Open* and *closed symbols* represent ambient (360 μL L^{-1}) and enriched (720 μL L^{-1}) CO_2 concentrations, respectively. **a** R^2 enriched = 0.91; R^2 ambient = 0.88; **b** R^2 enriched = 0.90; R^2 ambient = 0.75
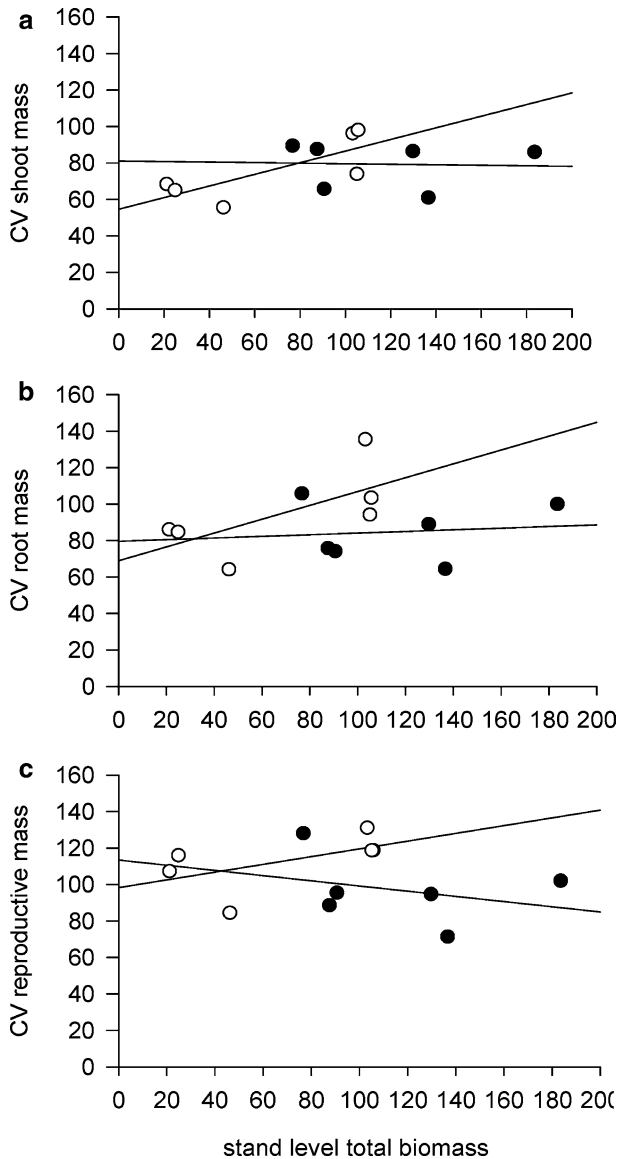
Fig. 2 Relationships between total stand biomass and CV for (**a**) shoot biomass, (**b**) root biomass, and (**c**) reproductive biomass. *Open* and *closed symbols* represent ambient (360 μL L^{-1}) and enriched (720 μL L^{-1}) CO_2 concentrations, respectively

more individuals remained in the smallest size classes in the ambient treatment than in the CO_2-enriched treatment. Conversely, more individuals entered the intermediate and large size-classes in enriched versus ambient-CO_2 conditions. An equal but small number of individuals reached the largest shoot size-class in both CO_2 treatments, but no plants in the ambient treatment were represented in the largest root or reproductive size-classes. Thus, more individuals reached intermediate size and reproductive classes in high CO_2 than in ambient conditions, but the frequency of large plants was not affected by this change in stand structure.

Light availability and plant growth

Plants grew taller and the number of leaves increased in high CO_2 compared to ambient conditions (Table 2). In both treatments, the average PPFD within stands was low early in the season due to small seedling stature, but thereafter the average amount of light in CO_2-enriched stands was reduced by ~200 μmol m^{-2} s^{-1} (Table 3). As a consequence of taller plant stature, elevated CO_2 stands received ~400 μmol m^{-2} s^{-1} less light in the upper portion of the vertical stand profile (>20 cm) than ambient stands. Below 10 cm, light levels were low in both treatments.

Discussion

Relative and size and reproductive success of dominants and subordinates

We found novel evidence that more uniform size structure results in more homogeneous reproductive success within *A. artemisiifolia* stands grown in elevated CO_2 compared to ambient conditions. In monospecific stands of other species, variation in shoot biomass has been shown to either decrease or increase in response to elevated CO_2 (Wayne et al. 1997). Low mortality in our experiment allowed us to compare biomass inequalities based on similar numbers of individuals in each stand, and reduced CVs in all plant organs can therefore be interpreted as evidence for diminished hierarchical structure among competing individuals (Weiner et al. 1984). Specifically, we interpret reduced inequality in height, number of leaves, and shoot mass as evidence for reduced asymmetric competition for light (Wayne et al. 1997), especially given that growth enhancements in lower-light conditions accompanied these findings. Reduced reproductive inequalities (CV_{repro} and $CV_{repro-shoot}$) can be further interpreted as a decline in reproductive dominance.

The positive relationship between total standing biomass and biomass inequality under ambient conditions further indicates that greater size or reproductive mass becomes more advantageous with increasing competitive intensity (Wayne et al. 1997). The decline in this relationship at elevated CO_2 demonstrates more homogeneous performance of dominants and subordinates across a range of plant densities, and thus provides direct evidence for the release of smaller plants from increasing competitive suppression. Our size-class data also confirmed that CO_2-induced growth stimulation was greater in smaller plants than in larger plants (Wayne et al. 1997). We conclude that in *A. artemisiifolia*, CO_2 influences stand-level dominance in reproductive output by reducing the effects of aboveground competition on the reproductive advantages of larger plants.

Fig. 3 Frequency distributions for (**a**) shoot (stem + leaf), (**b**) root, and (**c**) reproductive biomass size-classes. *Open* and *shaded bars* represent ambient (360 μL L^{-1}) and enriched (720 μL L^{-1}) CO$_2$ concentrations, respectively
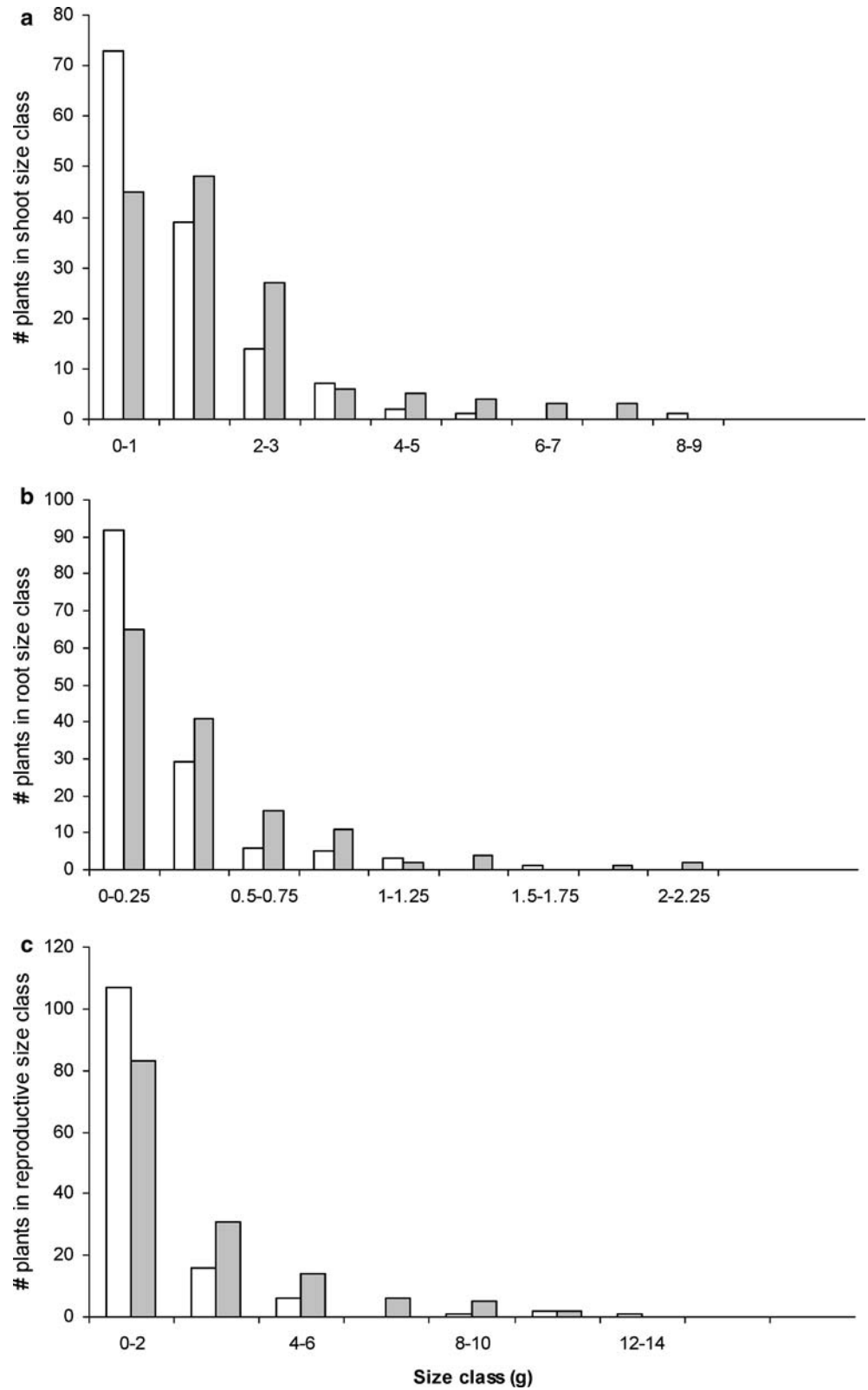
Reduced inequalities in the root mass and root–shoot allocation in our elevated CO$_2$ stands also suggest that reduced belowground asymmetric competition might have contributed to more uniform vegetative mass and reproductive success (Berntson et al. 2000). The few previous studies of density × CO$_2$ effects on more than one aspect of growth have shown enhancements to root and shoot mass (Berntson et al. 2000, 1997), or

Table 2 Repeated Measures ANOVA for effect of CO_2 and time on each trait ($N = 281$)

	df	F ratio	P value
Height (cm)			
CO_2	1	14.93	***
Time	3	2,875.10	***
Time $\times$ CO_2	3	5,135.05	***
No. Leaves			
CO_2	1	3.77	*
Time	3	1,262.87	***
Time $\times$ CO_2	3	2.93	*

vegetative and reproductive mass (Ackerly et al. 1995; He et al. 2003; Wayne et al. 1999), but we know of no other studies that address growth stimulation in all plant structures, or the reduction of whole-plant biomass inequalities within densely grown populations or communities.

Allometric shifts in reproductive allocation

We also tested whether elevated CO_2 would alter the relative allocation of biomass to different plant functions among densely grown *A. artemisiifolia* plants, and found that enhancements to reproductive output exceeded biomass gains in other plant organs. Increasing reproductive allocation is a common response of annual plants to increased availability of CO_2 and other resources (Farrar et al. 1991; Jablonski et al. 2002), but our study is among very few to show an allometric shift toward reproduction within populations of competing plants. In CO_2-enriched stands of multiple species, relationships between growth and reproduction can become more or less linear, or remain unchanged at increasing densities (Ackerly et al. 1995). Reproductive output in *Phytolacca americana* was sensitive to both density and CO_2 levels (He et al. 2003), whereas reproductive allocation of *Brassica kaber* increased in

elevated CO_2 but showed no apparent density dependence (Wayne et al. 1999). As indicated by the steeper allometric relationship between vegetative and reproductive mass in elevated CO_2 compared to ambient conditions, high CO_2 reduced the premium on light acquisition for the production of flowers and seeds in *A. artemisiifolia*. Since we observed little change in root–shoot allometric relationships in elevated CO_2, we did not find evidence for differential allocation to above- versus belowground growth. Thus, as a result of greater reproductive returns on both shoot and root growth, stand level reproduction is likely to increase in future populations of this allergenic weed.

Physiological aspects of reduced reproductive dominance

Subordinate plants probably achieved enhanced reproductive status in CO_2-elevated stands by shifting proportionally more photoassimilates toward reproductive biomass than in ambient stands (Jablonski et al. 2002). As demonstrated by the convergence of slopes in Fig. 1a, the CO_2-induced allometric shift toward reproduction was most pronounced in subordinate plants (i.e., smaller plants gained proportionally more reproductive biomass per gram of stem mass in response to elevated CO_2 than larger plants). Many plants exhibit greater CO_2-induced growth enhancements at lower-light levels (Ehleringer et al. 1977), and low-light compensation under elevated CO_2 can benefit smaller individuals growing in the shade while inhibiting photosynthesis in dominant plants (Osborne et al. 1997). Since photosynthetic enhancement under elevated CO_2 is often downregulated over time by increasing nutrient limitation (Arp 1991), nutrient-limited dominants can also become suppressed during later stages of shoot growth (e.g., Nagashima et al. 2003). We did not observe direct suppression of growth in dominants, but instead found that, as CO_2 stimulated growth in all individuals, subordinate plants profited more in terms of

Table 3 Stand-level means ± standard errors for within-canopy photon flux density (PPFD), plant height, and number of leaves in elevated-CO_2 and ambient stands of *A. artemisiifolia*

	M ± SE 12 July	M ± SE 23 July	M ± SE 31 July	M ± SE 07 August
Mean canopy PPFD (μmol m^{-2} s^{-1})				
Ambient	769.35 ± 52.75	962.45 ± 64.73	$1,201.71 \pm 61.27$	$1,074.57 \pm 60.35$
Elevated	772.89 ± 47.04	$1,002.86 \pm 51.86$	950.29 ± 54.49	982.40 ± 46.82

	M ± SE 01 July	M ± SE 08 July	M ± SE 19 July	M ± SE 31 July	M ± SE 07 August
Height (cm)					
Ambient	2.45 ± 0.07	5.04 ± 0.17	7.60 ± 0.28	11.94 ± 0.48	19.27 ± 0.72
Elevated	2.54 ± 0.09	5.07 ± 0.19	9.18 ± 0.35	16.83 ± 0.79	25.93 ± 1.12
No. Leaves					
Ambient	5.50 ± 0.11	8.15 ± 0.15	12.02 ± 0.38	13.86 ± 0.52	13.35 ± 0.28
Elevated	5.53 ± 0.12	8.65 ± 0.16	12.73 ± 0.35	15.30 ± 0.52	14.45 ± 0.37

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$

growth and reproductive output than dominants in elevated CO_2.

Variation in early seedling growth and adult maturation rates in enriched CO_2 compared to ambient conditions may also have contributed to reduced biomass inequalities in our high CO_2 stands (Farnsworth et al. 1996). Our stands were assembled at the seedling stage, so we did not consider potential effects of variation in seed germination and seedling establishment on stand development (Weiner 1990). However, as indicated by the growth profiles shown in Table 3, early stages of growth did not appear to be affected by elevated CO_2. During later stages of growth, changes in leaf area indices could have altered light quality as well as quantity in elevated CO_2 stands (Hirose et al. 1997). Effects of altered red to far-red ratios on stem elongation and other aspects of physiology and development could therefore have influenced the relative performance of subordinates and dominants (Arnone et al. 1993; Hirose et al. 1997; Makino et al. 1999). Ragweed's high photoperiodicity resulted in similar reproductive phenology and senescence in both treatments, indicating that growth and size inequalities had leveled off by the time of harvest. We, therefore, attribute reduced reproductive dominance within elevated CO_2 stands primarily to a shift in overall biomass allocation, rather than differences in developmental rates between high CO_2 and ambient-grown plants.

Implications

Ambrosia artemisiifolia is one of the most common pioneer species in North America, forming monospecific stands that are major vegetative components of disturbed sites throughout North America (Abulfatih et al. 1979). Increased stand-level reproduction and higher reproductive allocation of subordinates at elevated CO_2 could amplify the stimulation of allergenic pollen production observed in singly grown ragweed plants (Wayne et al. 2002; Ziska et al. 2000). More homogeneous reproduction between subordinates and dominants also implies that a larger number of individuals will contribute propagules to future generations. Through changes in genetic structure, gene flow and/or increased population size, reduced reproductive dominance could in turn affect evolutionary and population dynamics of ragweed in future environments (Ackerly et al. 1995; Hartgerink et al. 1984; Thomas et al. 1999). As a direct result of increased stand-level seed production, *A. artemisiifolia* could also become more abundant in the field, thereby increasing in its agricultural presence and potentially altering successional and ecosystem dynamics in old-field communities (Huxman et al. 1999; Raynal et al. 1975).

References

Abulfatih HA, Bazzaz FA, Hunt R (1979) Biology of *Ambrosia trifida* l.: Growth and biomass allocation. New Phytol 83:829–838

Ackerly DD, Bazzaz FA (1995) Plant growth and reproduction along CO_2 gradients - nonlinear responses and implications for community change. Glob Change Biol 1:199–207

Arnone JA, Korner C (1993) Influence of elevated CO_2 on canopy development and red:far-red ratios in two storied stands of *Ricinus communis*. Oecologia 94:510–515

Arp WJ (1991) Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. Plant Cell Environ 14:869–875

Berntson GM, Wayne PM (2000) Characterizing the size dependence of resource acquisition within crowded plant populations. Ecology 81:1072–1085

Berntson GM, Wayne PM, Bazzaz FA (1997) Below-ground architectural and mycorrhizal responses to elevated CO_2 in *Betula alleghaniensis* populations. Funct Ecol 11:684–695

Deen W, Hunt T, Swanton CJ (1998) Influence of temperature, photoperiod, and irradiance on the phenological development of common ragweed (*Ambrosia artemisiifolia*). Weed Sci 46:555–560

Ehleringer J, Bjorkman O (1977) Quantum yields for CO_2 uptake in C-3 and C-4 plants - dependence on temperature, CO_2, and O_2 concentration. Plant Physiol 59:86–90

Farnsworth EJ, Ellison AM, Gong WK (1996) Elevated CO_2 alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L). Oecologia 108:599–609

Farrar JF, Williams ML (1991) The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant Cell Environ 14:819–830

Granados J, Korner C (2002) In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. Glob Change Biol 8:1109–1117

Hartgerink AP, Bazzaz FA (1984) Seedling-scale environmental heterogeneity influences individual fitness and population structure. Ecology 65:198–206

Hattenschwiler S (2001) Tree seedling growth in natural deep shade: functional traits related to interspecific variation in response to elevated CO_2. Oecologia 129:31–42

He JS, Bazzaz FA (2003) Density-dependent responses of reproductive allocation to elevated atmospheric CO_2 in *Phytolacca americana*. New Phytol 157:229–239

Hirose T, Ackerly DD, Traw MB, Ramseier D, Bazzaz FA (1997) CO_2 elevation, canopy photosynthesis, and optimal leaf area index. Ecology 78:2339–2350

Huxman TE, Hamerlynck EP, Smith SD (1999) Reproductive allocation and seed production in *Bromus madritensis ssp rubens* at elevated atmospheric CO_2. Funct Ecol 13:769–777

Jablonski LM, Wang XZ, Curtis PS (2002) Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. New Phytol 156:9–26

Körner C (2003) Ecological impacts of atmospheric CO_2 enrichment on terrestrial ecosystems. Philos Trans R Soc Lond A Math Phys Eng Sci 361:2023–2041

Makino A, Mae T (1999) Photosynthesis and plant growth at elevated levels of CO_2. Plant Cell Physiol 40:999–1006

Nagashima H, Yamano T, Hikosaka K, Hirose T (2003) Effects of elevated CO_2 on the size structure in even-aged monospecific stands of *Chenopodium album*. Glob Change Biol 9:619–629

Osborne CP, Drake BG, LaRoche J, Long SP (1997) Does long-term elevation of CO_2 concentration increase photosynthesis in forest floor vegetation? Indiana strawberry in a Maryland forest. Plant Physiol 114:337–344

Poorter H, Navas ML (2003) Plant growth and competition at elevated CO_2: On winners, losers and functional groups. New Phytol 157:175–198

Raynal DJ, Bazzaz FA (1975) Interference of winter annuals with A mbrosia artemisiifolia in early successional fields. Ecology 56:35–49

Sokal RR, Rohlf FJ (1995) Biometry: The principles and practice of statistics in biological research. WH Freeman and Company, New York

Stitt M, Krapp A (1999) The interaction between elevated carbon dioxide and nitrogen nutrition: The physiological and molecular background. Plant Cell Environ 22:583–621

Thomas SC, Bazzaz FA (1993) The genetic component in plant size hierarchies - norms of reaction to density in a Polygonum species. Ecol Monogr 63:231–249

Thomas SC, Jasienski M, Bazzaz FA (1999) Early vs. Asymptotic growth responses of herbaceous plants to elevated CO_2. Ecology 80:1552–1567

Wayne P, Bazzaz FA (1997) Light acquisition and growth by competing individuals in CO_2-enriched atmospheres: Consequences for size structure in regenerating birch stands. J Ecol 85:29–42

Wayne P, Foster S, Connolly J, Bazzaz F, Epstein P (2002) Production of allergenic pollen by ragweed (Ambrosia artemisiifolia L.) is increased in CO_2-enriched atmospheres. Ann Allergy Asthma Immunol 88:279–282

Wayne PM, Carnelli AL, Connolly J, Bazzaz FA (1999) The density dependence of plant responses to elevated CO_2. J Ecol 87:183–192

Weiner J (1990) Asymmetric competition in plant-populations. Trends Ecol Evol 5:360–364

Weiner J, Solbrig OT (1984) The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334–336

Ziska LH, Caulfield FA (2000) Rising CO_2 and pollen production of common ragweed (Ambrosia artemisiifolia), a known allergy-inducing species: Implications for public health. Aust J Plant Physiol 27:893–898