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Architectural and physiological mechanisms of reduced size inequality in CO_2-enriched stands of common ragweed (*Ambrosia artemisiifolia*)

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Abstract

Testing whether and how subordinate individuals differ from dominants in the utilization of enriched CO_2 atmospheres is important for understanding future stand and community structure. We hypothesized that subordinate and dominant *Ambrosia artemisiifolia* L. (Asteraceae) (common ragweed) plants growing in dense stands would not equally acquire or utilize carbon gains from CO_2-enrichment, and that the resulting disproportionate growth gains to subordinates would reduce size inequalities in competing stands. We grew experimental stands of *A. artemisiifolia* in either ambient ($360\,\mu L\,L^{-1}$) or twice ambient ($720\,\mu L\,L^{-1}$) levels of atmospheric CO_2. We compared the relative growth, photosynthetic capacity, and architecture of subordinate and dominant plants in each treatment, and assessed size inequalities using the stand-level coefficient of variation (CV). In elevated CO_2, plants grew larger, but subordinate plants shifted more mass to upper stem allocation than dominants. Dominant plants demonstrated reduced leaf-level photosynthetic gains in elevated CO_2 compared with subordinate plants. Reduced CVs in plant size reflected smaller proportional growth gains by dominants over subordinates in elevated vs. ambient stands. We conclude that differences in the architectural and physiological responses of subordinate and dominant ragweed plants reduce competition and allow subordinate plants to catch up to dominants in elevated CO_2 conditions.

Keywords: Ambrosia artemisiifolia, CO_2, dominant, photosynthesis, plant architecture, ragweed, size inequality, subordinate

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Introduction

Elevated atmospheric CO_2 can alter the competitive performance of individuals in single- and mixed-species populations (Overdieck, 1993; Wayne *et al*., 1999; Navas *et al*., 2002; Poorter & Navas, 2003; Urban, 2003), resulting in potentially dramatic changes in future community structure (Jackson *et al*., 1994; LaDeau & Clark, 2001). Plant competition for light is usually considered asymmetric (Schwinning & Weiner, 1998; Soussana & Lafarge, 1998), in that dominant individuals preempt a disproportionate share of resources relative to their size (Weiner, 1990). The stimulation of photosynthesis and growth in dominant plants can reduce light availability and suppress the growth of subordinate plants in the lower canopy strata, thereby increasing size-inequalities among individuals in a stand (Hikosaka *et al*., 2003; Nagashima *et al*., 2003). However, CO_2 enrichment can also minimize size inequalities (Wayne & Bazzaz, 1995, 1997b; Wayne *et al*., 1999) presumably by suppressing the growth of light-saturated dominants, (Makino & Mae, 1999; Marek *et al*., 2002), stimulating growth of subordinates, or both (Naumburg *et al*., 2001). The physiological and morphological responses of individual plants to elevated CO_2 are well documented (Pritchard *et al*., 1999; Urban, 2003), but their mechanistic role in altering competitive interactions requires additional study. Testing whether dominants and subordinates respond differently to elevated CO_2 can better inform predictions about the

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effects of elevated CO_2 on future population and community structure.

In this study, we tested whether elevated CO_2 differentially alters physiological and architectural growth responses of subordinate and dominant plants in competing stands of the allergenic species *Ambrosia artemisiifolia* (common ragweed). *A. artemisiifolia* is a monoecious, herbaceous annual weed commonly found in disturbed habitats, old-fields, and roadsides throughout most of North America (Bassett & Crompton, 1975). An early-successional dominant, it forms dense monospecific stands during recolonization of old fields and other disturbed habitats (Abulfatih *et al*., 1979). *A. artemisiifolia* demonstrates enhanced growth and reproduction when grown at elevated CO_2 in monoculture and in mixed stands, including dramatically increased pollen production (Ziska & Caulfield, 2000; Wayne *et al*., 2002; Stinson & Bazzaz, 2006). As a recognized agricultural pest and primary source of aeroallergens in North America (Ziska & Caulfield, 2000), common ragweed has important ecological and human health impacts that especially warrant the study of this species' CO_2 responses in natural settings.

Our primary objective was to test whether subordinate and dominant plants differ in their physiological and developmental responses to elevated CO_2, and how this might affect stand development. Since CO_2-induced biomass gains by individually grown plants are usually greater at lower light levels (Gifford, 1977; Granados & Korner, 2002), we predicted that light-limited, subordinate plants would be more stimulated by elevated CO_2 conditions than light-saturated dominants, possibly due to photo-inhibition of dominants (Stitt & Krapp, 1999). Because the uppermost branches of dominant plants emerge from the canopy and receive the highest irradiance levels, we also predicted that subordinate plants would grow proportionally taller and allocate more biomass to upper crown architecture at elevated CO_2 than dominants. We, therefore, expected elevated CO_2 to reduce biomass and height disparities between dominant and subordinate plants through changes in physiology and branching architecture (Farnsworth *et al*., 1996), and to consequently result in more even stand structure (Wayne & Bazzaz, 1997a).

To test for differential physiological and/or developmental effects of CO_2 on dominant and subordinate plants, we grew stands of *A. artemisiifolia* at either ambient or twice-ambient levels of atmospheric CO_2 and assessed the growth, photosynthetic capacity, and branching architecture of individuals within each stand. Our experiment addressed the following specific questions: (1) How does elevated CO_2 affect the upper and lower stem architecture of competing individuals and does this response differ in subordinate vs. dominant plants? (2) How does elevated CO_2 alter the photosynthetic capacity of subordinate and dominant plants? (3) Do these physiological and morphological responses reduce competitive advantages of dominant individuals (i.e. do subordinates 'catch up' to dominants)? We show that subordinate plants catch up to dominants under elevated CO_2 conditions, via the combined effects of architectural differences, growth stimulation in subordinates, and photosynthetic suppression of dominants.

Materials and methods

Experimental design and analyses

In May 2002, we constructed 12 open-top chambers (1.5 m high × 1.5 m diameter) in a cleared plot at Harvard University's Concord Field Station, about 25 km east of Boston in Bedford, MA, USA (42°30′20″N, 71°18′9.5″W). This site was formerly a secondary-growth, mixed hardwood stand that was cleared of all trees and vegetation in 1999. Before construction of the chambers, vegetation was cleared and the field was leveled with a bulldozer, leaving a well-drained, sandy substrate with minimal organic topsoil. To provide an organic layer and homogenize soil conditions, we mechanically tilled to a depth of 30 cm and covered the area with 15 cm dry (~5 cm when watered), commercially produced loam. The chambers, built from PVC-tubing frames enclosed in 6-mil, greenhouse grade plastic sheeting (Hummert International, Earth City, MO, USA), were situated ~5 m apart and were numbered and randomly divided between treatments. Six chambers were maintained at elevated ($720\,\mu L\,L^{-1}$) CO_2 levels, day, and night. The control chambers were maintained at ambient levels ($360\,\mu L\,L^{-1}$) during the day and were allowed to fluctuate at regular ambient levels at night. We supplied CO_2 via injection from a liquid tank located on-site, beginning on 12 June and continuing until the final harvest in September. We used an IRGA (LI-800, LiCor, Lincoln, NE, USA) to sample air concentrations at a frequency of <5 min, which allowed us to maintain both ambient and elevated CO_2 levels within $\pm 50\,\mu L\,L^{-1}$ of the set point. Air temperature and air flow were regulated within 1.5 °C of ambient with electric fans.

A. artemisiifolia seeds were obtained from the second generation of our ambient CO_2-grown greenhouse stock at Harvard University (seeds derive from >100 individuals from three populations at the Phillips Tract, University of Illinois, USA originally collected in September 1999). We stratified seeds from the second generation of this stock in clean, moist sand for 16 weeks (February–May 2002) in a growth chamber set to 4/6 °C during an alternating 14 h dark/10 h light

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cycle. On 20 May 2002, we randomly sowed several hundred of these seeds into trays containing ~5 cm soil-less planting mixture (Pro-Mix 50, Premier Horticulture, Quebec, Canada). Trays were moved to an outdoor shelter providing 80% sunlight and ambient CO$_2$ levels. Germinants began emerging within 8 days and were maintained with an automatic mist irrigation system until approximately 75% germination was observed and most germinants were approximately 2.5 cm tall. At the time of peak germination (5 June), individual seedlings with 2–3 true leaves and less than 1 week old were randomly selected, tagged with metal bands, and transplanted into two replicate stands per chamber. Each stand was arranged within a ~0.60 m^2 area in identical hexagonal grids area consisting of 36 evenly spaced plants. This resulted in ~60 plants m^{-2}, a density typically observed for naturally occurring stands of *A. artemisiifolia* (Raynal & Bazzaz, 1975). We randomized the planting design using a random number generator to assign individual seedlings positions within each grid. 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. To minimize edge effects, plants on the outermost edge of each stand were excluded from observation and only the central 24 plants were measured. All nonexperimental plants were removed immediately by hand at least every 2–3 days.

In this design, each chamber was considered an independent replicate and the means for each pair of stands were pooled to produce chamber-level observations ($N = 6$). Thus, all analyses are based on simple ANOVA models using CO$_2$ level as the main effect. This approach is favorable to complicated nested analyses and preserves the independent replication necessary for appropriate hypothesis testing in single-factor analyses (Gotelli & Ellison, 2004). Where relationships between continuous variables were analyzed, Model II regressions were implemented and the slopes of significant correlations were subsequently compared with one-way ANCOVA using CO$_2$ as the main effect and the x variable of the regression as the covariate. Analyses for each set of variables are described in detail below.

Plant growth and architecture

Plant height and total branch length (sum of the lengths of the extended main stem and any branching stems) of each experimental individual per stand were measured approximately every 21 days from June to August 2002. In early September, all stands were harvested and separated into root, reproductive, and shoot (stem and leaves) matter. To measure branching allocation, shoot matter was further subdivided into 10 cm vertical sections for each individual plant, beginning at the base of the plant above the root system and ending at the tip of the main stem (Fig. 1a). All subsections of biomass were oven-dried at 100 °C to a constant mass and weighed separately. Total shoot and total plant biomass measurements were obtained by summing the subsections. The stand-level means for each section and for total biomass were pooled for each pair of stands within a chamber to produce single observations for each chamber ($N = 6$). To visually assess differences between the treatments in canopy architecture, we plotted the mean total biomass produced at a given plant height for each CO$_2$ level. Model II Regressions of plant height against biomass were performed separately for each treatment, and an ANCOVA model (CO$_2$, plant height, and CO$_2$ × plant height as the main effects) was used to test for differences between CO$_2$ treatments in biomass and in the slope of the relationship between biomass and height.

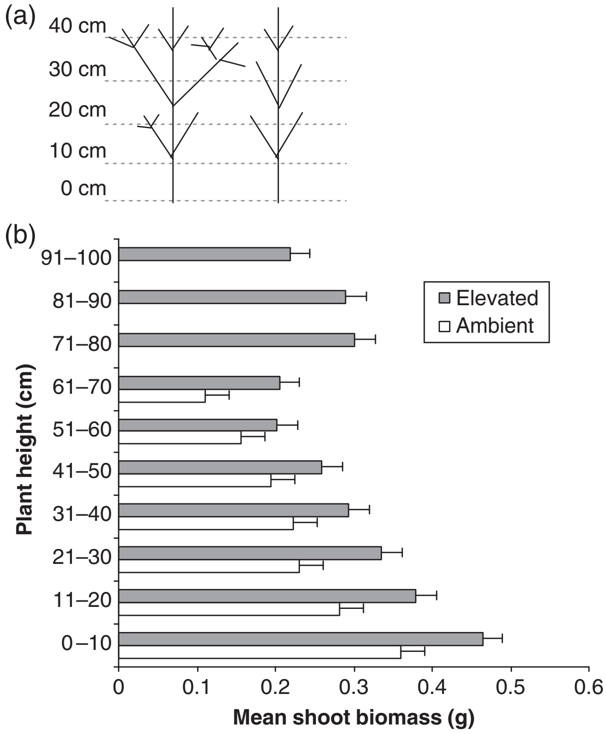

Fig. 1 (a) Schematic showing methods for quantifying plant architecture. Units were rounded to nearest whole number when dividing stem portions into upper and lower halves. (b) Average above ground biomass for vertical sections of ragweed plants grown in ambient (360 μL L^{-1}) and elevated (720 μL L^{-1}) CO$_2$ concentrations, represented by closed and open bars, respectively. Error bars represent ±1 standard error.

To determine whether subordinate and dominant plants demonstrated variation in vertical architecture, a two-way ANOVA model was constructed to test the effects of CO_2 concentration and size class (subordinate or dominant) on upper-to-lower stem allocation ratio. Plants within each stand were ranked by height and biomass and divided into two equal size classes: dominants (largest half) and subordinates (smallest half). The ratio of upper-to-lower stem biomass allocation was calculated separately for each plant by dividing the sum of the masses in the upper portion by the sum of those in the lower portion of all 10 cm vertical sections. The mid point of vertical height for each plant was rounded to the nearest base 10 to determine which sections comprised the upper and lower portions of the stem. The mean upper-to-lower biomass ratio for each size class was pooled for each chamber. This model included the main effects of CO_2 concentration, size class, and the interaction term. *Post hoc* analyses (Tukey's honest significant difference test (HSD)) were performed to compare mean upper with lower biomass allocation between subordinates and dominants in each CO_2 treatment.

To determine the effect of CO_2 on size inequality, the stand level coefficient of variation in biomass ($CV_{biomass}$) was calculated separately for each stand and these values were subsequently pooled for each chamber. The stand-level CV has been shown to be highly correlated with the Gini coefficient of size inequality (Weiner & Solbrig, 1984; Weiner, 1990) and was, therefore, used as a direct measure of inequality among individuals within a stand. The pooled chamber means for stand CVs were regressed against those for total biomass using Model II linear regression. The slopes of these regressions were calculated separately for each CO_2 level, providing a visual and statistical measure of the intensity of competition within each treatment (Wayne & Bazzaz, 1997a).

A repeated measures ANOVA model was used to determine the effects of CO_2 concentration on plant growth (total branch length) and size inequality ($CV_{total\ branch\ length}$) through time. As above, the stand-level means for total branch length and $CV_{total\ branch\ length}$ were pooled for each chamber to produce a single observation on each date.

Light availability in developing stands

Light levels were measured with a gallium arsenide photo diode (GasP G1118, Amamatsu Corp., Bridgewater, NJ, USA) on four representative sunny days during the growing season (12 July, 23 July, 31 July and 7 August). In each stand, five target plants were randomly chosen, 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 1/2 of the canopy radius. Light data for all canopy depths in each stand were averaged over time. Light levels were compared between the treatments using Model II linear regression of the vertical height increment against measured photosynthetically active radiation (PAR) level for each focal plant measured. Chamber level means were pooled for each vertical height increment at each CO_2 level, and separate regressions were calculated for each treatment. The slopes of the resulting regressions were compared with one-way ANCOVA, using CO_2 treatment as the main effect and vertical height increment as the covariate.

Physiological measurements

To determine how photosynthetic capacity differed between subordinate and dominant plants in elevated CO_2 environments, maximum leaf-level net photosynthetic rates (P_{max}) were measured on a single, overcast day in mid summer (22 July), using a LICOR 6400 gas exchange system. CO_2 concentration, humidity, air temperature and light were maintained at constant levels ($360\ \mu L\ L^{-1}$ 60%, 28 °C, and $1500\ \mu moL\ m^{-2}\ s^{-1}$, respectively) during the gas exchange measurements. P_{max} values were obtained from the topmost and bottommost fully expanded leaves of all plants in three randomly selected stands per treatment.

The physiological responses of subordinates and dominants were assed using Model II Regression of P_{max} as a function of plant size (total branch length). Regressions were run separately for each treatment and each architectural category (upper or lower branches). To determine whether subordinate and dominant individuals differed in their physiological responses to elevated CO_2, differences between the slopes of significant regression results were tested with ANCOVA, using CO_2 treatment as the main effect and total branch length as a covariate.

Results

Effects of CO_2 on plant growth and architecture

The regression of plant biomass against vertical height was negative and highly significant in both CO_2 treatments (Table 1a), indicating that biomass allocation decreased with increasing vertical stem heights in both treatments. However, plants grown at elevated CO_2 grew taller and allocated more mass to upper stem architecture than those grown at ambient levels, as

Table 1 Results of linear regressions of (a) biomass against plant height; (b) PAR against plant height; (c) $CV_{biomass}$ against total stand mass for each CO_2 treatment; and (d) *P*-max against plant size

	Treatment	Model	R^2	df; Mod ∣ err	MS; Mod ∣ err	*F*	*P*
(a)	Elevated	Mass = 0.352–0.002ht	0.41	1 ∣ 18	0.064 ∣ 0.005	12.54	0.002
	Ambient	Mass = 0.314–0.003ht	0.63	1 ∣ 12	0.053 ∣ 0.003	18.54	0.001
(b)	Elevated	PAR = 659.272 + 84.99ht	0.91	1 ∣ 8	59 542 ∣ 7045	84.89	<0.0001
	Ambient	PAR = 612.45 + 130.50ht	0.95	1 ∣ 8	1 021 829 ∣ 8251	123.84	<0.0001
(c)	Elevated	CV = 82.69–0.04mass	0.01	1 ∣ 4	9.62 ∣ 262.75	0.04	0.860
	Ambient	CV = 59. 75 + 0.45mass	0.74	1 ∣ 4	845.08 ∣ 76.24	11.09	<0.05
(d)	Upper leaves						
	Elevated	$P_{max} = 1.05 + 0.12$tbl	0.39	1 ∣ 71	162.91 ∣ 3.61	45.18	<0.0001
	Ambient	$P_{max} = -0.76 + 0.344$tbl	0.45	1 ∣ 70	258.64 ∣ 4.95	52.33	<0.0001
	Lower leaves						
	Elevated	$P_{max} = 0.71 + 0.028$tbl	0.08	1 ∣ 71	5.70 ∣ 1.57	3.62	0.070
	Ambient	$P_{max} = 0.61 + 0.023$tbl	0.02	1 ∣ 70	0.74 ∣ 0.93	0.80	0.370

Treatment-level comparisons of significant slopes (ANCOVA) are reported in text.
PAR, photosynthetically active radiation; CV, coefficient of variation.

Table 2 Two-way ANOVA for effect of CO_2 treatment and size class (subordinate or dominant) on the upper : lower biomass ratio

Source	df	SS	*F*	*P*
$[CO_2]$	1	0.24	4.92	0.03
size class (sub or dom)	1	0.00	0.04	0.85
$[CO_2] \times$ size class	1	0.20	4.27	0.04

The upper : lower biomass ratio is calculated as the proportion of biomass allocated to the upper and lower half of each stem, as calculated in cm of height.

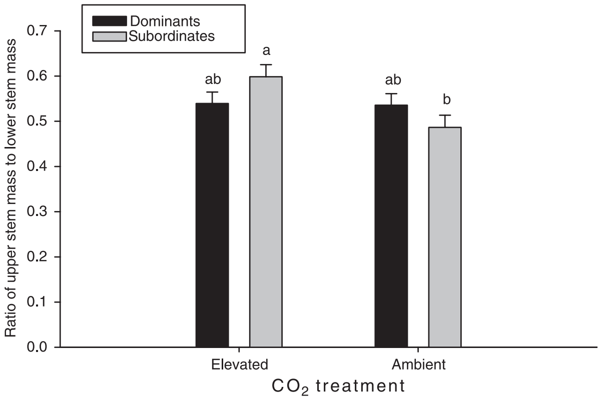

Fig. 2 Ratio of biomass allocated to upper vs. lower half of shoots in subordinate and dominant ragweed plants grown at ambient (360 μL L^{-1}) and elevated (720 μL L^{-1}) CO_2. Different lettering indicates significant differences between groups as indicated by Tukey's HSD *post hoc* tests ($P < 0.05$).

shown by the mean biomasses produced by each vertical section of stem (Fig. 1b). Analysis of covariance further demonstrated that plants attained significantly higher biomass and in the elevated treatment, and that biomass accumulation per cm of height was proportionally greater in elevated compared with ambient conditions (ANCOVA $F_{CO_2,1df} = 37.16$, $P < 0.0001$; $F_{ht,1df} = 80.57$, $P < 0.0001$; $F_{CO_2 \times ht,1df} = 6.77$, $P = 0.02$). Thus, plants in elevated CO_2 were generally larger and produced more crown architecture than those in ambient CO_2.

There were significant effects of CO_2 level and $CO_2 \times$ size class on the ratio of upper-to-lower stem biomass (Table 2), indicating that the relative biomass allocation to upper stem architecture differed between treatments and between subordinates and dominants. Subordinate plants grown in elevated CO_2 stands allocated the most biomass to upper stem branches compared with all other groups (Fig. 2). Different lettering of the bars in Fig. 2 indicate the results of Tukey's HSD post-hoc tests between groups, which demonstrated significant CO_2-enhancement of upper-to-lower stem biomass ratios in subordinate plants ($P < 0.05$), but not in that of dominant plants.

Plant growth rates did not differ between CO_2 treatments. Repeated measures ANOVA demonstrated significant increases in total branch length through time, but showed no effect of elevated CO_2 level or the $CO_2 \times$ time interaction term on total branch length ($F_{CO_2,1df} = 1.37$, $P = 0.31$; $F_{time,\,3df} = 21.99$, $P = 0.04$; $F_{CO_2 \times time,\,3df} = 0.33$, $P = 0.81$). Mortality was less than 4.0% in all stands and did not differ between treatments.

Light availability

The linear regression of PAR level against vertical plant height was positive and highly significant in both CO_2 treatments (Table 1b), indicating that light increased as

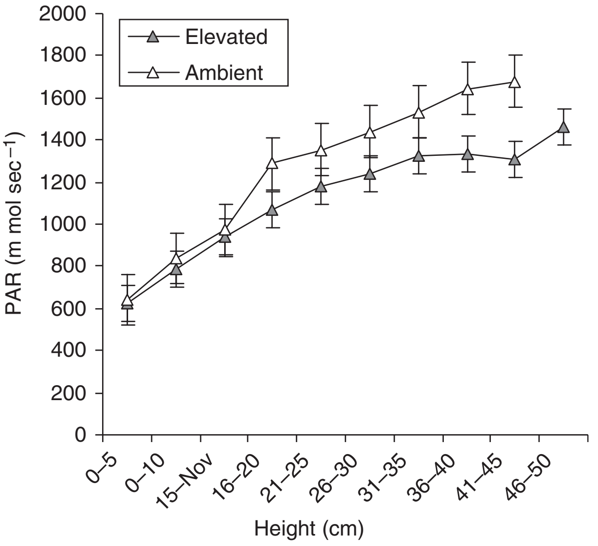

Fig. 3 Light levels through the vertical profile of competing ragweed stands. Open and closed symbols represent ambient (360 μL L^{-1}) and elevated (720 μL L^{-1}) CO_2 concentrations, respectively. Data points symbolize mean photosynthetically active radiation (PAR) values for each treatment for three dates on which measurements were taken. Error bars represent ±1 standard error.

a function of plant height in both ambient and elevated CO_2 treatments (Fig. 3). The average available PAR at heights below 20 cm was similar in both treatments. Above 20 cm, PAR was ~200 μmoL m^2 s^{-1} higher on average in the ambient stands compared with elevated CO_2 stands and was highest at 80 cm and above. Analysis of covariance confirmed that the relationship between plant height and PAR was steeper and more positive in elevated compared with ambient conditions ($F_{CO_2,1df} = 22.92$, $P < 0.001$; $F_{ht,1df} = 212.02$, $P < 0.0001$; $F_{CO_2 \times ht,1df} = 9.46$, $P < 0.01$). Thus, the observed increase in plant growth and upper stem allocation in the elevated treatment resulted in reduced light availability (i.e. shading) in the upper canopy sections of elevated CO_2-grown stands.

Size inequalities and size-asymmetric interactions

The linear regression of $CV_{biomass}$ against total stand mass was highly significant in ambient, but not elevated CO_2 (Fig. 4; Table 1c). In the ambient treatment, the $CV_{biomass}$ increased as a function of total stand mass. When mortality is similar across treatments, reduced coefficients of variation in size, by definition, indicate a smaller proportional difference between dominants over subordinates (Weiner & Solbrig, 1984). Thus, the positive relationship between the stand-level $CV_{biomass}$ and total stand biomass in ambient CO_2 indicates disproportionate size advantages of dominant ragweed plants over subordinates under increasingly crowded conditions. The nonsignificant relationship between $CV_{biomass}$ and total stand mass further indicates that elevated CO_2 eliminates the relative advantage of dominant plants over subordinate plants at increasing levels of competition in the stand.

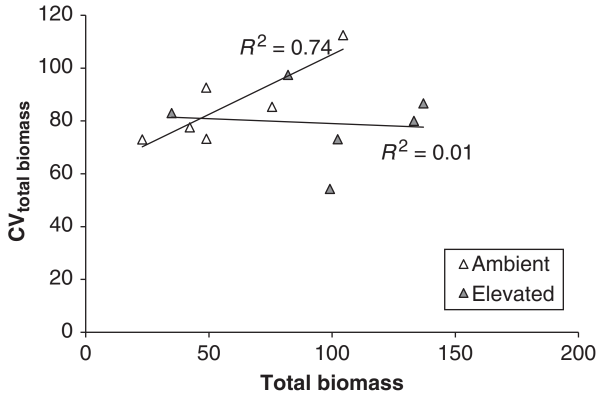

Fig. 4 Relationship between total stand biomass and the stand-level coefficient of variation (CV) for total plant biomass in competing ragweed stands. Open and closed symbols represent ambient (360 μL L^{-1}) and elevated (720 μL L^{-1}) CO_2 concentrations, respectively.

Repeated measures ANOVA demonstrated a significant effect of CO_2 on the $CV_{total\ branch\ length}$, but there were no effects of time or $CO_2 \times$ time on $CV_{total\ branch\ length}$ ($F_{CO_2,\ 1df} = 8.29$, $P = 0.05$; $F_{time,\ 3df} = 8.52$, $P = 0.11$; $F_{CO_2 \times time,\ 3df} = 3.05$, $P = 0.26$). The chamber-level mean $CV_{total\ branch\ length}$ declined through time in the elevated treatment; in contrast the $CV_{total\ branch\ length}$ in the ambient treatment increased with time (Fig. 5). Thus, inequalities in plant size were diminished by CO_2-enrichment as the stands matured.

Physiological gains by subordinates in elevated CO_2

Linear regressions of maximum leaf level photosynthetic rate (P_{max}) against total branch length were positive and highly significant in upper canopy leaves in both treatments but were non-significant in lower canopy leaves (Fig. 6, Table 1d). Photosynthetic rates in upper canopy leaves were significantly greater in the ambient treatment and increased more as a function of size compared with those in the elevated treatment (Fig. 6a). P_{max} did not differ between treatments in the lower canopy leaves (Fig. 6b). ANCOVA indicated significant effects of CO_2 treatment ($F_{CO_2,\ 1df} = 25.52$, $P < 0.001$), total branch length ($F_{tbl,1df} = 61.68$, $P < 0.001$), and $CO_2 \times$ total branch length ($F_{CO_2 \times tbl,\ 1df} = 15.16$, $P < 0.001$) on P_{max} in upper canopy leaves. Since P_{max} increased significantly with size, dominant plants demonstrated higher photosynthetic activity in their upper leaves

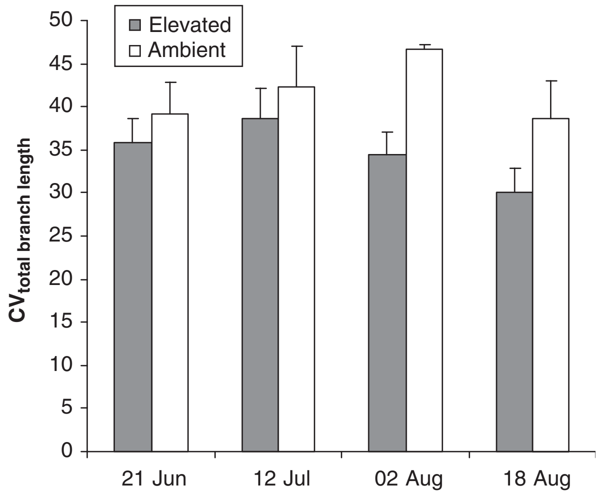

Fig. 5 Average stand-level coefficient of variation (CV) in total branch length within competing ragweed stands. Open and closed bars represent elevated ($720\,\mu L\,L^{-1}$) and ambient ($360\,\mu L\,L^{-1}$) CO_2 concentrations, respectively. Error bars represent ±1 standard error.

than subordinate plants in both treatments. However, the declining slope in the relationship between P_{max} and total branch length in the elevated CO_2 treatment indicates that physiological gains by dominant plants were diminished by CO_2-enrichment.

Discussion

Reduced size inequality at elevated CO_2

We found evidence that changes in morphology and physiology both contributed to reduced size inequality within competing stands of *A. artemisiifolia*. We conclude first that elevated CO_2 minimizes the proportional differences between dominants and subordinates from the observed reduction in the coefficients of variation in plant size (Weiner & Solbrig, 1984). The decline in $CV_{total\ branch\ length}$ through time in the elevated treatment demonstrates that subordinates effectively ‘catch up’ to dominants in high CO_2 conditions. Moreover, elevated CO_2 mitigates competitive intensity as stand biomass increases, as indicated by the evening out of stand-level $CV_{biomass}$ as a function of total stand mass (Weiner & Solbrig, 1984). In contrast, size inequalities are exacerbated over time and in increasingly crowded conditions in ambient conditions. Elsewhere, elevated CO_2 appears to equalize intraspecific size variation in both woody and herbaceous plant species, but this is not consistently found across all taxa (Navas, 1998; Poorter & Navas, 2003). In monospecific stands of woody plants, size differences between subordinates and dominants have been shown to decrease (Wayne & Bazzaz, 1997a) or increase (Nagashima *et al*., 2003) in response to elevated CO_2. Here and elsewhere, size-related performance advantages in stands of herbaceous plants were also diminished by CO_2 (Wayne *et al*., 1999, Stinson & Bazzaz, 2006). In other weedy species, CO_2 may influence meristem changes in both dominants and subordinates without altering competitive dominance. For example, elevated CO_2 altered branching patterns in the herbaceous annual plant *Impatiens pallida*, but did not affect size structure within developing stands (Berntson & Weiner, 1991). In another study, the growth and physiology of individually grown tree seedlings were unresponsive to elevated CO_2, but alterations to the canopy structure of individual plants altered species composition in mixed stands (Reekie & Bazzaz, 1989). Thus, our findings support recent research demonstrating that CO_2 reduces intraspecific competition in this species (Stinson & Bazzaz, 2006), but may not apply when *A. artemisiifolia* is grown with other taxa.

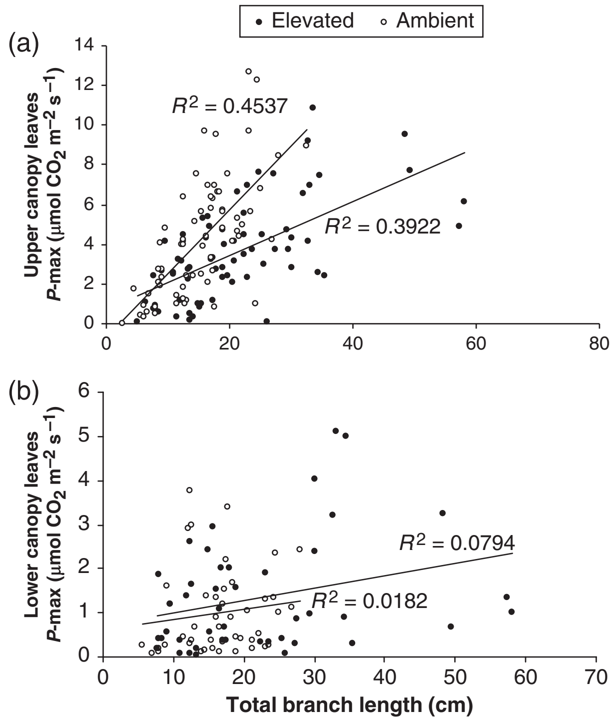

Fig. 6 P_{max} measurements for (a) upper canopy leaves (ANCOVA, $P<0.01$) and (b) lower canopy leaves of ragweed plants as a function of total branch length (ANCOVA ns). Open and closed symbols represent measurements for individual plants under ambient ($360\,\mu L\,L^{-1}$) and elevated ($360\,\mu L\,L^{-1}$) CO_2 concentrations, respectively.

Because our stands were assembled at the seedling stage, we did not consider potential effects of variation in seed germination and early seedling establishment, which may play a key role in size variation (Pickett &

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Baskin, 1973; Morse & Bazzaz, 1994; Weiner *et al*., 1997). However, as indicated by Fig. 5, the effect of CO_2 on size inequalities was most important during later stages of growth in this study. Since both treatments had similar growth rates and were harvested at the onset of senescence, the final CV measurements reflected size variation within mature stands (i.e. there was no evidence that the ambient treatment stands would show further reduction in CV over time). Other natural abiotic and biotic variation could alter the relative performance of individuals growing together in natural settings (Crawley & Weiner, 1991; Ceulemans & Mousseau, 1994; Berntson *et al*., 1997; Thomas *et al*., 1999). For instance, although we kept soil conditions constant in this study, nitrogen limitation may further contribute to the suppression of dominant plants in the field. Environmentally determined and species-specific changes in root architecture can also alter nitrogen uptake of competing plants (Berntson *et al*., 1997), thereby influencing stand development.

Architectural shifts in high CO_2 stands

In general, *A. artemisiifolia* plants produced fuller crowns in elevated CO_2 compared with ambient conditions by allocating more biomass to middle and upper branches than those grown in ambient stands, supporting the prediction that reduced apical dominance would accompany CO_2-induced growth enhancements (Pritchard *et al*., 1999). In some studies, CO_2-induced growth enhancements have occurred without architectural changes (VanderKooij & DeKok, 1996). Elevated CO_2 has been shown to alter leaf anatomy and plant morphology in other densely growing plant populations (Farnsworth *et al*., 1996; Naumburg *et al*., 2001) but the effect on stand structure is unknown. Elsewhere, altered branching and crown orientation in elevated CO_2 conditions have reduced light availability to surrounding individuals, thereby suppressing performance of subordinate plants (Ackerly & Bazzaz, 1995; Naumburg *et al*., 2001). Here, our analysis of upper-to-lower stem biomass ratios demonstrates that elevated CO_2 altered plant architecture primarily in subordinate, not dominant *A. artemisiifolia* plants (Fig. 2). Thus, subordinate plants grew proportionally taller, and produced proportionally more upper crown structure in elevated CO_2 than those in the ambient treatment. We, therefore, attribute the architectural effects of elevated CO_2 to reduced biomass differences in the mid to upper portions of the canopy, rather than pronounced overtopping of subordinate individuals by dominants, and provide novel evidence for a developmental mechanism by which subordinates catch up to dominants in developing plant canopies.

Since gender allocation and reproductive success in *A. artemisiifolia* are dependent on relative size dominance over neighbors (Traveset, 1992; Lundholm & Aarssen, 1994), branching patterns (Traveset, 1992), and plant biomass (Ackerly & Jasienski, 1990), the observed architectural responses of subordinates in this study could have additional implications for CO_2 effects on pollen and seed production (Ziska & Caulfield, 2000; Wayne *et al*., 2002).

Photosynthetic suppression of dominants in high CO_2

The relationship between size and photosynthetic rate was more positive in upper than in lower leaves, suggesting that carbon assimilation increases more with size near the top of the canopy than in deeply-shaded, lower branches. However, the treatment-level differences in the relationship between $P_{\max}$ and total branch length also indicated that photosynthetic activity was less size-dependent in elevated than in ambient CO_2. As reported in other studies, we observed CO_2-induced growth enhancements in reduced light conditions (Wheeler *et al*., 1991; Bazzaz & Miao, 1993), suggesting that surplus carbon in a CO_2-enriched environment allows compensatory growth responses in spite of the shading effect of overall growth stimulation in the stand. We also observed reduced $P_{\max}$ in dominant plants at elevated CO_2, indicating that photosynthetic activity is greatest in the mid canopy where light levels were intermediate and suppressed at the highest light levels.

The reduced photosynthetic rates of dominant individuals at elevated CO_2 suggest inhibitory effects of light-saturation on growth in high light environments (e.g. Wheeler *et al*., 1991; Bazzaz & Miao, 1993). Relatively higher growth enhancements are generally observed under low irradiance due to an increase in the quantum yield efficiency of C3 species grown in elevated CO_2 (Ehleringer & Bjorkman, 1977; Long & Drake, 1991; Marek *et al*., 2002). Evidence from other species indicates that the build up of photo-assimilates in high light/high CO_2 environments can exceed the capacity of plants to either transport, store, or utilize sugars (Sasek *et al*., 1985; Stitt, 1991), leading to stronger end-product inhibition of photosynthetic response to CO_2 in larger plants exposed to high light (Stitt & Krapp, 1999). In addition, photosynthetic enhancement at elevated CO_2 is often down-regulated over time due to increasing nutrient limitation (Arp *et al*., 1998), so nutrient-limited dominants may have become suppressed during later stages of shoot growth in our study (e.g. Nagashima *et al*., 2003). Leaf ontogeny and developmental variation could also influence our findings (Kelly *et al*., 1991) but were not measured in detail here.

In another study, subordinate plants with more prostrate shoots were able to retain longer photosynthetic activities than erect, dominant plants receiving higher photosynthetic photon flux density (Cui *et al*., 2003). In *A. artemisiifolia*, allocation to upper stem biomass resulted in a higher photosynthetic payoff to partially shaded, subordinate plants than to canopy-emergent dominants. Since the size advantages of dominant ragweed plants over subordinate ones diminished under elevated CO$_2$ (Figs 4 and 5) we conclude that light-suppression in dominants reduced asymmetric competition for light (Wayne & Bazzaz, 1997a).

We, therefore, attribute reduced within-stand size inequality in elevated CO$_2$ conditions to the physiological suppression of dominant plants, as well as architectural changes that favored greater photosynthetic activity in the more shaded upper branches of subordinates. Because the release of subordinate individuals undergoing disproportionate growth and photosynthetic gains is likely to enhance the total reproductive success within a stand (Stinson & Bazzaz, 2006) and may therefore lead to larger future population sizes (Berntson & Weiner, 1991) or increased community-level dominance (Jackson *et al*., 1994), our findings provide evidence for physiological and morphological mechanisms by which elevated CO$_2$ could enhance *A. artemisiifolia*'s status as an agricultural pest and allergenic weed.

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