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## ELEVATED CO<sub>2</sub> AND LEAF SHAPE: ARE DANDELIONS GETTING TOOTHIER?<sup>1</sup>

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Heteroblastic leaf development in *Taraxacum officinale* is compared between plants grown under ambient (350 ppm) vs. elevated (700 ppm) CO<sub>2</sub> levels. Leaves of elevated CO<sub>2</sub> plants exhibited more deeply incised leaf margins and relatively more slender leaf laminae than leaves of ambient CO<sub>2</sub> plants. These differences were found to be significant in allometric analyses that controlled for differences in leaf size, as well as analyses that controlled for leaf developmental order. The effects of elevated CO<sub>2</sub> on leaf shape were most pronounced when plants were grown individually, but detectable differences were also found in plants grown at high density. Although less dramatic than in *Taraxacum*, significant effects of elevated CO<sub>2</sub> on leaf shape were also found in two other weedy rosette species, *Plantago major* and *Rumex crispus*. These observations support the long-standing hypothesis that leaf carbohydrate level plays an important role in regulating heteroblastic leaf development, though elevated CO<sub>2</sub> may also affect leaf development through direct hormonal interactions or increased leaf water potential. In *Taraxacum*, pronounced modifications of leaf shape were found at CO<sub>2</sub> levels predicted to occur within the next century.

**Key words:** CO<sub>2</sub>, elevated; dandelion; leaf development, heteroblastic; *Plantago*; *Rumex*; *Taraxacum*.

Plants grown in elevated CO<sub>2</sub> atmospheres generally have increased rates of net photosynthetic carbon gain. Some direct consequences of this photosynthetic enhancement include increases in leaf carbohydrate concentrations, specific leaf weight, carbon:nitrogen ratios, and accelerated whole-plant growth (Bazzaz, 1990; Farrar and Williams, 1991; Poorter, 1993). Elevated CO<sub>2</sub> may also result in marked changes in plant morphogenesis. Attention to this aspect of CO<sub>2</sub> effects has focused largely on altered patterns of biomass allocation (e.g., Tissue and Oechel, 1987; Larigauderie, Hilbert, and Oechel, 1988; Baxter et al., 1994), with a few studies also documenting altered patterns of allometry and deployment (e.g., Sasek and Strain, 1988; Reekie and Bazzaz, 1989; Berntson and Woodward, 1992). Similarly, growth at elevated CO<sub>2</sub> might be expected to result in changes in the morphogenesis of individual leaves. A number of studies have noted modest increases in leaf size (Ford and Thorne, 1967; Ackerly et al., 1992), changes in stomatal density (e.g., Woodward and Bazzaz, 1988; Ferris and Taylor, 1994), and altered internal cellular anatomy (e.g., Madson, 1968). However, the few studies that have previously examined possible effects of elevated CO<sub>2</sub> on leaf shape have not reported any significant effect (Leadley, 1988; Sasek and Strain, 1989).

In spite of these previous negative results, it seems likely that elevated CO<sub>2</sub> levels may have substantial effects on leaf shape in certain plant species. Specifically, leaf carbohydrate levels have long been thought to be a critical determinant of leaf form in species that display

heteroblastic leaf development (Goebel, 1900; Lakon, 1918; Allsopp, 1965). The present study presents evidence for effects of elevated CO<sub>2</sub> on leaf shape, with a focus on *Taraxacum officinale* Weber. *Taraxacum* exhibits pronouncedly heteroblastic leaf development: the first few sets of leaves possess entire margins, while (under high-light conditions) subsequently produced leaves show a characteristic dentition pattern from which the plant's common name is derived (Dandelion: from M.F. dent de lion, or "lion's tooth"). The analyses presented are specifically aimed at distinguishing direct effects of elevated CO<sub>2</sub> on leaf shape from changes that may be correlated with altered leaf size or developmental order. Such allometric analyses are important in that elevated CO<sub>2</sub> may indirectly influence leaf shape through effects on leaf size and rates of leaf production.

### MATERIALS AND METHODS

In a first experiment plants were grown in a glasshouse at Harvard University over a 4-mo period (September 1993–December 1993). The growth facility is temperature and CO<sub>2</sub> controlled. A total of six glasshouse modules were maintained at a constant temperature regime (26/18 C with a 14-hr day length), and two CO<sub>2</sub> levels, corresponding to ambient (350 ppm) and 2× ambient (700 ppm), giving three replicates per CO<sub>2</sub> treatment. Seeds were germinated in vermiculite within the growth modules, and after 1–2 wk seedlings were transplanted into two density treatments. Individually grown plants were grown in 15 cm internal diam × 20 cm deep pots. High-density plants were planted in a hexagonal array at density of 270 plant/m<sup>2</sup> in 38 × 48 cm × 20 cm deep plastic tubs. The high-density plants included a border region of 24 plants, and a "target" zone of 24 plants in the center of each tub: all measurements were made on the latter set. The initial experiment was a subset of a larger study examining CO<sub>2</sub> responses among nine species of herbaceous plants. Responses of leaf shape to elevated CO<sub>2</sub> also were quantified for two additional weedy rosette species: *Rumex crispus* L. and *Plantago major* L. Growth conditions for these species were identical to those for *Taraxacum*, though the timing of the experiments differed slightly.

In the first *Taraxacum* experiment the earliest produced leaves had

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TABLE 1. Growth responses to elevated CO<sub>2</sub> levels of individually grown *Taraxacum officinale*, *Plantago major*, and *Rumex crispus*. Plants were grown in native Massachusetts soil in 2-liter pots over a 5-mo growth period, with a sample size of 12 replicate plants in each of three chambers per CO<sub>2</sub> level (see Methods). Probability levels based on split-block ANOVA.

CO <sub>2</sub> level (ppm):	Species								
	<i>Taraxacum</i>			<i>Plantago</i>			<i>Rumex</i>		
	350	700	Ratio	350	700	Ratio	350	700	Ratio
Biomass (g)									
Total	8.85	12.36	1.40	3.46	3.50	1.01	10.31	12.04	1.17
Shoot	2.26	2.61	1.15	0.91	0.82	0.91	1.16	1.06	0.91
Root	6.60	9.75	1.48	2.64	2.76	1.04	9.15	11.63	1.27*
Root/shoot	2.81	3.86	1.37	10.85	17.10	1.58*	8.02	11.35	1.42*
SLW <sup>a</sup>	4.94	8.11	1.64*	5.85	6.28	1.07	3.70	4.21	1.14

<sup>a</sup> SLW = specific leaf weight.

\*  $P < 0.05$ .

senesced before plants were harvested, making it impossible to distinguish leaf developmental order. A second experiment was therefore conducted over a shorter time interval in order to investigate potential interactions between elevated CO<sub>2</sub> and developmental sequence in determining leaf shape. *Taraxacum* plants were grown individually under the same experimental conditions, except that a soil culture of pure vermiculite in 150-ml pots was used, fertilized on a weekly basis with 50 ml Peter's solution (20-20-20 NPK). For the second experiment there were initially eight plants per module; plants bearing at least nine leaves were harvested after a 42-d growth period.

In the first experiment leaves were measured on a subset of plants within each CO<sub>2</sub> and density treatment: all leaves from six individually grown plants and 18 high-density plants per CO<sub>2</sub> treatment were measured and digitized. Length and width of fresh leaves were measured to the nearest millimeter, and individual leaf area to the nearest 0.1 cm<sup>2</sup> (using a LI-COR 1600 leaf area meter: LI-COR, Lincoln, NE). Leaves were dried flat at 67 C for >2 d, and dry weights of individual leaves were determined to the nearest milligram. Leaf shape was further ana-

lyzed on the basis of digitized images of the dried leaves, using an automated image analysis program to quantify leaf area and perimeter (Image v. 1.4, W. Rasband, National Institutes of Health). In the second experiment a similar set of shape measurements were made on fresh leaves. For species other than *Taraxacum* leaf width, length, and petiole length (for *Rumex* and *Plantago*) were measured on fresh leaves to the nearest mm.

**Analysis**—Leaf shape was quantified in several ways. Our statistical analyses rely on bivariate allometric relationships between log-transformed leaf width, length, area, and perimeter. Possible differences between CO<sub>2</sub> treatments were detected using a modified analysis of covariance in which CO<sub>2</sub> level was treated as a fixed effect, and block and plant included as random effects (with plant nested within block). In using this approach, it is necessary to designate one measure as an independent (fixed effect) variable. Although slope estimates of allometric relationships may be better estimated by a model II regression technique (Harvey, 1982; Seim and Sæther, 1983), ANCOVA has customarily been used to detect treatment effects on allometric relationships (e.g., Weiner and Thomas, 1992). Reduced major axis regression was used to quantify allometric slopes where numerical values are of interest.

We also quantified leaf shape using a "dissection index" (DI), calculated as the ratio of leaf perimeter to the square root of leaf area, standardized so that a circular leaf would have a value of 1.0 or  $DI = (P/2A) \cdot (A/\pi)^{1/2}$ ; where  $P$  is leaf perimeter, and  $A$  is leaf area (Kincaid and Schneider, 1983; McLellan, 1993). Some previous experiments with *Taraxacum* have calculated a "leaf shape index" as the proportion of leaf lamina area "removed" as a consequence of leaf lobing (Sanchez, 1967, 1971; Sanchez and Cogliatti, 1975). We found that such an index could not be reliably calculated for highly lobed leaves, because *Taraxacum* leaves often develop a wide range of teeth sizes along the lamina, thus making it necessary to arbitrarily distinguish major and minor teeth to calculate the area for a hypothetical entire leaf corresponding to a given lobed leaf. The perimeter-based analysis used avoids this difficulty. Other statistical analyses follow Sokal and Rohlf (1981) and Rice (1989).

## RESULTS

The species under consideration showed relatively modest growth responses to elevated CO<sub>2</sub> at final harvest (Table 1), with biomass response ratios (700/350) ranging from 1.01 to 1.40. Similarly small effects were observed on total leaf number, leaf area, and leaf size at final harvest (data not shown). In contrast, all three species showed larger effects of elevated CO<sub>2</sub> on root:shoot biomass ratios, with response ratios ranging from 1.37 to

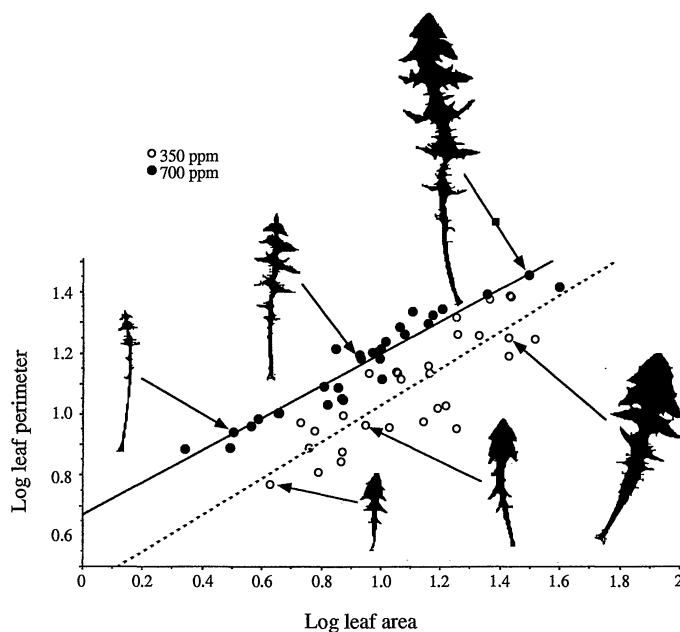


Fig. 1. Allometric relationships between leaf area and leaf perimeter for individually grown *Taraxacum officinale* at ambient and elevated CO<sub>2</sub> levels. Reduced major axis lines are shown. Leaf profiles of small, medium, and large leaves falling close to the fitted curves for each CO<sub>2</sub> level are illustrated.

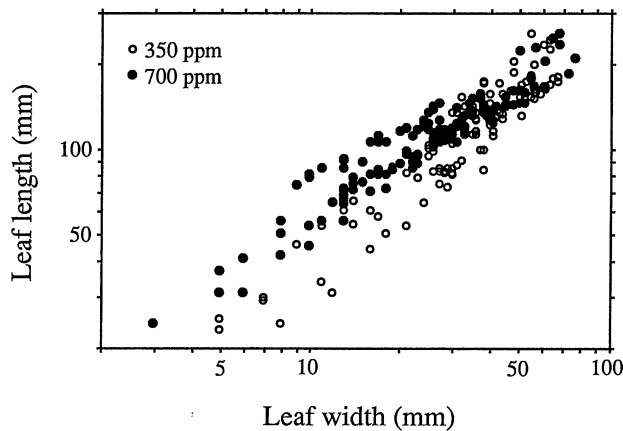


Fig. 2. Allometric relationships between leaf length and leaf width for individually grown *Taraxacum officinale* at ambient and elevated  $\text{CO}_2$  levels. The allometric slope value is significantly lower at elevated  $\text{CO}_2$  (see Table 2).

1.58. Specific leaf weight (SLW) was higher at elevated  $\text{CO}_2$  in all three species, with the effect being particularly pronounced for *Taraxacum*.

*Taraxacum* showed the most dramatic effects of elevated  $\text{CO}_2$  on leaf shape, particularly as evidenced by altered allometric relationships between leaf area and leaf perimeter (Fig. 1). In the analysis of covariance for this relationship, differences between intercept values were highly significant ( $P < 0.0001$ ), but no difference in slope was detected ( $P > 0.05$ ). Differences in area-perimeter relationships were primarily due to more pronounced dentation along the lamina margin at elevated  $\text{CO}_2$  (Fig. 1). However, elevated  $\text{CO}_2$  also had some effect on leaf elongation, as reflected by altered leaf length-leaf width allometries (Fig. 2; ANCOVA results: slopes different at  $P < 0.0001$ ). This elongation effect also contributes to the observed change in area-perimeter allometries. Differences in area-perimeter and length-width relationships were also detected in *Taraxacum* plants grown at high density (Fig. 3; Table 2). The same pattern of allometric differences between elevated and ambient  $\text{CO}_2$  was observed; however, the magnitude of these differences was less than that found for individually grown plants.

In the allometric relationships illustrated in Fig. 1, estimated slopes for leaf perimeter-leaf area relationships were not significantly different from 0.5 (model I regression slopes are 0.601 and 0.527 and reduced major axis slopes are 0.728 and 0.552, respectively, for ambient and elevated  $\text{CO}_2$  plants). Therefore the slope of the relationship between leaf perimeter and the square root of leaf is approximately equal to 1. This pattern supports the use of the ratio-based dissection index to describe the effects of elevated  $\text{CO}_2$  on leaf form, since under these (and only these) conditions is DI independent of leaf size. Values of DI for ambient and elevated  $\text{CO}_2$  leaves were 3.26 ( $\pm 0.14$ ) and 4.65 ( $\pm 0.09$ ), respectively.

In several previous studies, plants grown at elevated  $\text{CO}_2$  have been found to produce a greater number of leaves per unit time than plants grown at ambient  $\text{CO}_2$  (e.g., Rogers et al., 1984; Sasek and Strain, 1991; Ackery et al., 1992). We therefore also investigated the pos-

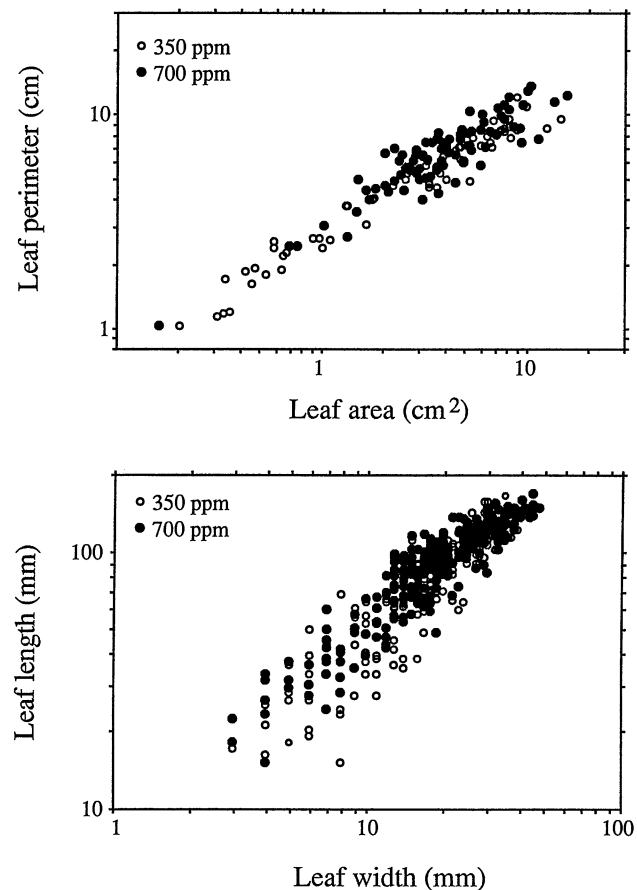


Fig. 3. Allometric relationships between leaf area and leaf perimeter (top panel), and leaf length and leaf width (bottom panel) for *Taraxacum officinale* grown in high density monocultures at ambient vs. elevated  $\text{CO}_2$  levels. (See Table 2 for statistical analyses.)

sibility that the observed changes in leaf shape were due to differences in developmental order. In the second experiment, dissection index (DI) values for leaves were compared on the basis of developmental order. For leaf numbers 3–9, there was a consistent trend toward higher DI values at elevated  $\text{CO}_2$  (Fig. 4). The relationship between leaf number and DI was approximately linear over this range. We therefore statistically tested effects of elevated  $\text{CO}_2$  on heteroblastic development on the basis of a difference in the slopes of these two relationships. Using a modified ANCOVA in which block and plant individual are included as random factors, the  $\text{CO}_2 \times$  leaf number interaction term was significant ( $P < 0.0001$ ).

Effects of elevated  $\text{CO}_2$  on leaf shape were also detected in parallel experiments conducted with *Plantago major* and *Rumex crispus* (Table 2). In the case of *Plantago*, leaf laminae were slightly narrower at elevated  $\text{CO}_2$ . This effect was detected as a small but (at least at high density) statistically significant change in the allometric relationship between leaf length and width. Concomitant effects were also found on leaf length-area and width-area relationships (though these are only marginally significant). In *Rumex* no significant effects on the allometry of leaf laminae were detected. However, the petiole of small leaves was relatively greater at elevated  $\text{CO}_2$  (Fig.

TABLE 2. Summary of statistical tests for effects of elevated CO<sub>2</sub> on leaf allometry in *Taraxacum officinale*, *Plantago major* and *Rumex crispus*. The following abbreviations are used for leaf size metrics: Pm = perimeter of leaf lamina; L = length of leaf lamina; W = width of leaf lamina at widest point perpendicular to midrib; A = total area of leaf (lamina + petiole); Pt = length of petiole. Probability values are listed for modified ANCOVAs for each bivariate relationship. In cases where a significant heterogeneity of allometric slopes was found, results for intercept differences are not given. Probability values listed in boldface are significant in a tablewide analysis using a sequential Bonferroni correction.

Species	Individually grown			High density		
	Allometric relationship	Slope test	Intercept test	Allometric relationship	Slope test	Intercept test
<i>Taraxacum officinale</i>	Pm-A	ns	<b><i>P</i> &lt; 0.0001</b>	Pm-A	ns	<b><i>P</i> &lt; 0.0001</b>
	L-A	<b><i>P</i> &lt; 0.0001</b>	—	L-A	ns	<b><i>P</i> &lt; 0.0001</b>
	W-A	ns	<b><i>P</i> &lt; 0.0001</b>	W-A	<b><i>P</i> &lt; 0.0001</b>	—
	Pm-L	ns	<b><i>P</i> &lt; 0.0001</b>	Pm-L	<b><i>P</i> &lt; 0.0001</b>	—
	W-L	<b><i>P</i> &lt; 0.0001</b>	—	W-L	ns	<b><i>P</i> &lt; 0.0001</b>
	Pm-W	ns	<b><i>P</i> &lt; 0.0001</b>	Pm-W	<i>P</i> = 0.0148	—
<i>Plantago major</i>	L-A	<i>P</i> = 0.0241	—	L-A	ns	<i>P</i> = 0.0318
	W-A	ns	ns	W-A	<i>P</i> = 0.0298	—
	Pt-A	ns	ns	Pt-A	ns	ns
	W-L	ns	<i>P</i> = 0.0471	W-L	ns	<b><i>P</i> &lt; 0.0001</b>
	Pt-L	ns	ns	Pt-L	ns	ns
	Pt-W	ns	ns	Pt-W	ns	ns
<i>Rumex crispus</i>	L-A	ns	ns	L-A	ns	ns
	W-A	ns	ns	W-A	ns	ns
	Pt-A	<i>P</i> = 0.0201	—	Pt-A	ns	<b><i>P</i> &lt; 0.0001</b>
	W-L	ns	ns	W-L	ns	ns
	Pt-L	ns	<b><i>P</i> = 0.0010</b>	Pt-L	ns	<b><i>P</i> &lt; 0.0001</b>
	Pt-W	<b><i>P</i> = 0.0040</b>	—	Pt-W	ns	<b><i>P</i> &lt; 0.0001</b>

5), as evidenced by highly significant allometric slope or intercept differences for relationships between petiole length and leaf width, length, and area (Table 2).

## DISCUSSION

Our results indicate that growth at elevated CO<sub>2</sub> accelerates the development of "mature" or "high light" type leaves in *Taraxacum*. This observation recalls a substantial body of early work examining environmental effects on heteroblastic leaf development (cf. Allsopp, 1965, 1967). For example, production of adult leaf forms is often favored by high light levels and root removal or restriction, while shading, nutrient additions, and removal of actively photosynthesizing tissue favor production of juvenile leaves (cf. Lakon, 1918). These observations are consistent with the hypothesis that changes in the relative concentrations of leaf carbohydrates vs. mineral nutrients strongly affect the patterns of cell proliferation and expansion that determine leaf shape. Although we did not directly assay leaf carbohydrates, previous studies have consistently found increases in leaf carbohydrates under elevated CO<sub>2</sub> in herbaceous plants (e.g., Madsen, 1968; Sasek and Strain, 1989; Farrar and Williams, 1991). As in the case of effects of leaf C:N ratios on herbivore defense (Fajer, Bowers, and Bazzaz, 1992), elevated CO<sub>2</sub> growth studies provide one of the most direct experimental approaches to manipulating leaf carbohydrate levels.

The present experiment is thus consistent with the hypothesis that CO<sub>2</sub> enhances leaf carbohydrate levels, and that one or another carbohydrate (perhaps sucrose: cf. Farrar, 1990) are directly involved in a signal transduction pathway that ultimately results in altered patterns of cell proliferation and expansion. However, two alternative physiological explanations for the effect also should

be considered. First, most plants reduce stomatal aperture in response to elevated CO<sub>2</sub>, which commonly results in increases in leaf turgor pressure (cf. Sasek and Strain, 1989). Expansion of developing leaf cells is turgor dependent. Such changes in leaf water status may thus affect heteroblastic development. This might account for the petiole elongation response seen in *Rumex*; however, changes in leaf dentition, as seen in *Taraxacum*, seem unlikely to be in any way a direct result of increased leaf turgor. A second alternative hypothesis is that CO<sub>2</sub> interacts directly with plant hormones or hormone receptors that mediate heteroblastic development. For example, CO<sub>2</sub> regulates the synthesis of ethylene, and a doubling in CO<sub>2</sub> concentration results in pronounced changes in ethylene production in some plant species (e.g., Lu and Kirkham, 1992). Another possible direct hormonal interaction is with phytochrome, which almost certainly is involved in developmental responses of *Taraxacum* leaf shape to increased light (Sanchez, 1971). This scenario is particularly plausible in light of recent work on the effects of elevated CO<sub>2</sub> on flowering phenology (cf. Reekie, Hicklenton, and Reekie, 1994). Further work on the physiological mechanisms underlying these patterns is clearly of great interest. Heteroblastic leaf development in species such as *Taraxacum* may be a particularly useful model system in which to examine possible interactions between CO<sub>2</sub> and hormonal regulation of plant development.

How general are effects of CO<sub>2</sub> on leaf shape? Leadley and Reynolds (1989) found no effect of elevated CO<sub>2</sub> on allometric relationships among the length, width, and area of soybean (*Glycine max*) leaflets at various stages of development. Several other studies have derived allometric equations to predict leaf area as a function of length, but have not noted any differences between CO<sub>2</sub>

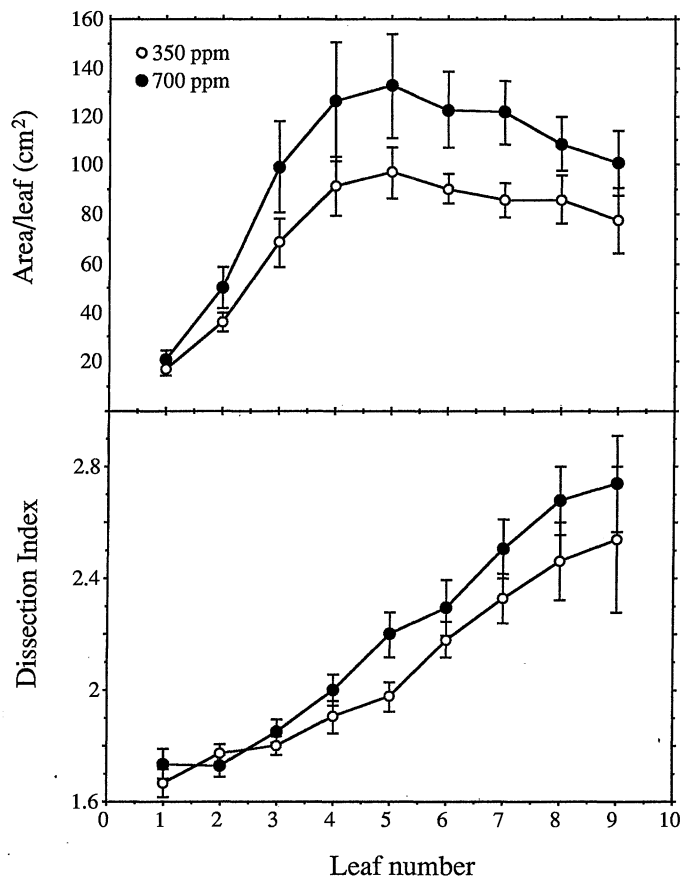


Fig. 4. Individual leaf area and dissection index (DI) in relation to leaf number for individually grown *Taraxacum officinale* at ambient and elevated CO<sub>2</sub> levels. DI is calculated as the ratio of leaf perimeter to the square root of leaf area, standardized so that DI = 1 for a circular leaf (see Methods). All values are plotted  $\pm 1$  SE.

treatments. For example, CO<sub>2</sub> apparently also had little effect on leaf shape in kudzu (*Pueraria lobata*: Sasek and Strain, 1989) and velvetleaf (*Abutilon theophrasti*: Ackery et al., 1992). In contrast, all three of the species included in the present study displayed some detectable effect of CO<sub>2</sub> on leaf shape. All three species also have in common a rosette growth form with leaves borne directly at the soil surface. CO<sub>2</sub> concentrations at ground level may commonly exceed 1,000 ppm, depending on soil respiration and wind movement (e.g., Schwartz and Bazzaz, 1973). One might therefore speculate that elevated CO<sub>2</sub> is not an evolutionarily novel environment for such plants, and that many prostrate species may therefore exhibit evolved developmental responses to CO<sub>2</sub> levels in the 300–1,000 ppm range. Specifically, petiole elongation in response to CO<sub>2</sub> may ensure that leaf laminae are displayed above the soil surface.

How important are effects of CO<sub>2</sub> on leaf shape? In comparison to recent studies aimed at predicting the future carbon balance of global vegetation, toothier dandelions may seem a rather esoteric outcome of anthropogenic changes in atmospheric composition. However, it should be noted that small changes in leaf morphology and display can have quite large effects on whole-plant carbon balance. For examples, in studies of sun-shade

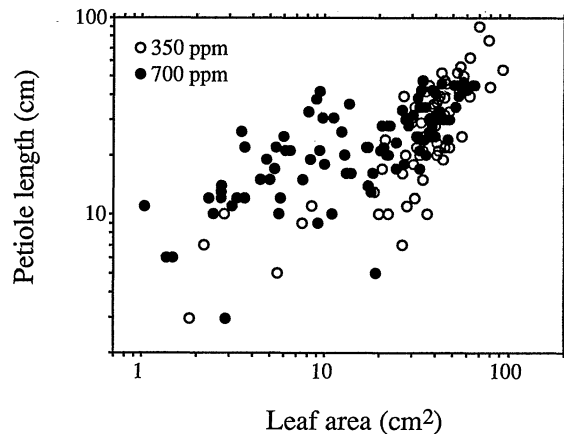


Fig. 5. Allometric relationships between petiole length and leaf area for individually grown *Rumex crispus* at ambient and elevated CO<sub>2</sub> levels. Slopes differ at  $P < 0.05$  (see Table 2).

acclimation these effects have occasionally been shown to be of substantially greater functional significance than changes in leaf-level photosynthesis (e.g., Niklas, 1989; Niklas and Owens, 1989). Systematic changes in leaf morphology also could have pronounced effects on canopy roughness, boundary layer conductance, and canopy-level optical properties. More broadly, the prospect that globally increasing CO<sub>2</sub> levels may have substantial and unexpected consequences to plant developmental processes should be taken seriously.

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