

## Using growth analysis to interpret competition between a C<sub>3</sub> and a C<sub>4</sub> annual under ambient and elevated CO<sub>2</sub> \*

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**Summary.** Detailed growth analysis in conjunction with information on leaf display and nitrogen uptake was used to interpret competition between *Abutilon theophrasti*, a C<sub>3</sub> annual, and *Amaranthus retroflexus*, a C<sub>4</sub> annual, under ambient (350 µl l<sup>-1</sup>) and two levels of elevated (500 and 700 µl l<sup>-1</sup>) CO<sub>2</sub>. Plants were grown both individually and in competition with each other. Competition caused a reduction in growth in both species, but for different reasons. In *Abutilon*, decreases in leaf area ratio (LAR) were responsible, whereas decreased unit leaf rate (ULR) was involved in the case of *Amaranthus*. Mean canopy height was lower in *Amaranthus* than *Abutilon* which may explain the low ULR of *Amaranthus* in competition. The decrease in LAR of *Abutilon* was associated with an increase in root/shoot ratio implying that *Abutilon* was limited by competition for below ground resources. The root/shoot ratio of *Amaranthus* actually decreased with competition, and *Amaranthus* had a much higher rate of nitrogen uptake per unit of root than did *Abutilon*. These latter results suggest that *Amaranthus* was better able to compete for below ground resources than *Abutilon*. Although the growth of both species was reduced by competition, generally speaking, the growth of *Amaranthus* was reduced to a greater extent than that of *Abutilon*. Regression analysis suggests that the success of *Abutilon* in competition was due to its larger starting capital (seed size) which gave it an early advantage over *Amaranthus*. Elevated CO<sub>2</sub> had a positive effect upon biomass in *Amaranthus*, and to a lesser extent, *Abutilon*. These effects were limited to the early part of the experiment in the case of the individually grown plants, however. Only *Amaranthus* exhibited a significant increase in relative growth rate (RGR). In spite of the transitory effect of CO<sub>2</sub> upon size in individually grown plants, level of CO<sub>2</sub> did affect final biomass of competitively grown plants. *Abutilon* grown in competition with *Amaranthus* had a greater final biomass than *Amaranthus* at ambient CO<sub>2</sub> levels, but this

difference disappeared to a large extent at elevated CO<sub>2</sub>. The high RGR of *Amaranthus* at elevated CO<sub>2</sub> levels allowed it to overcome the difference in initial size between the two species.

**Key words:** Growth analysis – Competition – C<sub>3</sub>-C<sub>4</sub>-plants – CO<sub>2</sub> elevation

Research on the response of plant species to elevated levels of CO<sub>2</sub> has clearly shown large differences among them. Differences in response have been found to be significant among members of the same community (e.g. Carlson and Bazzaz 1980, 1982; Bazzaz and Garbutt 1988). Because of these differences we have postulated that with high CO<sub>2</sub> levels in the atmosphere competitive interactions may be significantly altered in these communities and that certain genotypes and species may become locally extinct after several generations of altered competition. Several recent studies have shown changes in competitive hierarchies under elevated CO<sub>2</sub> and that CO<sub>2</sub> interacts with other environmental factors, such as soil moisture (Bazzaz and Carlson 1984), and nutrients and light (Zangerl and Bazzaz 1984). Changes in competition should be particularly clear between C<sub>3</sub> and C<sub>4</sub> plants, because they are known to differ markedly in their photosynthetic growth responses to CO<sub>2</sub>. C<sub>3</sub> plants usually show substantial increases in photosynthesis and growth with elevated CO<sub>2</sub>, while C<sub>4</sub> plants usually do not, and both types increase their water-use efficiency (review in Björkman and Pearcy 1983).

Studies in which C<sub>3</sub> and C<sub>4</sub> plants have been grown in competition with each other have borne out this prediction. Bazzaz and Carlson (1984) and Zangerl and Bazzaz (1984) showed that the proportion of biomass of C<sub>4</sub> species relative to the biomass of several C<sub>3</sub> species declined at elevated CO<sub>2</sub> levels. The proportion of *Sorghum halepense*, a C<sub>4</sub> grass, decreased relative to *Festuca elatior*, a C<sub>3</sub> grass (Carter and Peterson 1983), and the performance of a C<sub>4</sub> weed (*Sorghum halepense* again) relative to a C<sub>3</sub> crop (*Glycine max-soybean*) also decreased with increasing CO<sub>2</sub> (Peterson et al. 1984). The latter study included some growth analysis that suggested that the competitive changes observed were caused by a greater increase in net assimilation rates (NAR, also called ULR, the change in plant weight per unit time divided by the average leaf area over the time period).

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One important goal of research on the ecological effects of elevated  $\text{CO}_2$  is to predict how  $\text{CO}_2$  will affect competitive interactions among plants. To progress toward this goal, we will have to learn much more about the mechanisms of competition and the ways in which  $\text{CO}_2$  affects these mechanisms. In order to get this kind of detailed view of competition, it is necessary to study the physiological responses of plants to  $\text{CO}_2$ , and to link this information with data about the outcome of competition. One way to link these two areas of research is with growth analysis (McGraw and Wulff 1983). Tolley and Strain (1984a, b, 1985) used this approach in a comparative study of *Pinus taeda* (Loblolly pine) and *Liquidambar styraciflua* (Sweetgum), making the prediction that elevated  $\text{CO}_2$  would give *L. styraciflua* competitive advantage over *P. taeda*, particularly in high-light, low-moisture situations, and that this would result from an increase in leaf-area production in the early seedling stage of *L. styraciflua*.

In this study we combine growth analysis with information on canopy display and nitrogen-content to develop a detailed, mechanistic description of the competitive interactions between *Abutilon theophrasti*, a  $\text{C}_3$  annual, and *Amaranthus retroflexus*, a  $\text{C}_4$  annual. Plants were grown both individually and in competition, and we compared data from the individual studies with data from the competitive studies to evaluate the practicality of predicting the outcome of competition using data on the performance of individuals.

## Materials and methods

### The species

*Amaranthus retroflexus* L. ( $\text{C}_4$ ) and *Abutilon theophrasti* Medic. ( $\text{C}_3$ ) are two annuals which are commonly found together on disturbed sites and as weeds of agricultural systems in the midwestern United States. Seeds of both species germinate easily and the plants grow quickly to reproductive maturity, producing fruits and seeds without needing external pollinators.

### Plant culture

Seeds were collected in the autumn from several individuals in an annual community in Illinois. The seed was put in cheesecloth bags, buried in sand, and placed outside for stratification from the beginning of November to the end of February. The seeds were then planted in 9 sand-filled flats, and each flat was placed in a separate glass-sided growth chamber with temperature and  $\text{CO}_2$  control (detailed description in Carlson and Bazzaz 1980, 1982). The chambers were randomly assigned to three  $\text{CO}_2$  levels (350, 500 and  $700 \mu\text{l l}^{-1}$ ). There were three chambers for each  $\text{CO}_2$  level. The chambers were located in a glasshouse and the natural light they received was supplemented by metal-arc lamps. Light levels on sunny days could be as high as  $2000 \mu\text{moles m}^{-2} \text{s}^{-1}$  photosynthetically active radiation (PAR 400–700 nanometers) and on overcast days no less than  $900 \mu\text{moles m}^{-2} \text{s}^{-1}$ . Daytime temperature was  $27 \pm 3^\circ \text{C}$ , nighttime temperature was  $23 \pm 2^\circ \text{C}$ , relative humidity was  $60\% \pm 5\%$  and day length was 16 hours.

After germination had taken place, individuals were transplanted to chambers with appropriate  $\text{CO}_2$  concentrations. Seedlings to be studied individually were planted in

$7.5 \times 7.5$  cm square pots containing a potting mixture of 3 sand to 1 soil to 1 perlite. Twenty-four pots of each species were placed in each chamber. In order to study the plants in competition, three individuals of each species were planted in  $10 \times 10$  cm square plastic pots containing the potting mixture described above. Individual plants were assigned at random to the various positions within the pots. Twelve competition pots were set up in each chamber.

Nutrients were supplied at a standard-strength application (50 ml per plant) of Miracle Gro (15:30:15 plus micronutrients) to the individuals and at a double-strength application (25 ml per plant) to the competitive pots every 5 days. This provided the same amount of nutrients per individual in both treatments.

### Measurements

Plants grew for ten days before the first harvest. Thereafter harvests were made every five days. At each harvest two individuals of each species and one competition pot, all chosen *a priori* at random, were taken from each chamber. The roots were carefully washed. The position and height of each leaf was noted and its area measured. Each plant was divided into root, stem, leaves, and reproductive parts, and dried to a constant weight at  $50^\circ \text{C}$  and weighed.

Plant parts from the entire experiment were separately ground using a Wiley Mill. Total nitrogen was determined by an ammonia distillation process using a semi-micro-Kjeldahl steam distillation unit (Bremner 1965), following aluminum block digestion (Gallaher et al. 1976).

### Data analysis

The experiment was designed as a split plot with three blocks (position of chambers within the glasshouse). The main effect of  $\text{CO}_2$  was tested with the Block  $\times$   $\text{CO}_2$  interaction mean square. The other experimental factors (species and competitive treatment) and their interactions were tested using the error mean square. The data from the different harvests were analyzed separately. The 0.05 level of probability was used for all tests of significance. Unless otherwise stated, all statements concerning "differences" among treatments are based upon this level of probability.

The leaf area versus height profile data were summarized prior to statistical analysis. Mean canopy height was determined by weighting the height of each leaf by the area of the leaf, and finding the overall mean height for individual plants. Allocation patterns were assessed by calculating: leaf area ratio (leaf area per unit total plant biomass,  $\text{m}^2 \text{g}^{-1}$ ), root/shoot ratio (root biomass per unit shoot biomass,  $\text{g g}^{-1}$ ), specific leaf area (leaf area per unit leaf biomass,  $\text{m}^2 \text{g}^{-1}$ ) and reproductive ratio (biomass of flowers and fruits per unit of total plant biomass,  $\text{g g}^{-1}$ ).

Estimates of the instantaneous rates of relative growth rate (growth per unit of plant biomass,  $\text{g g}^{-1} \text{d}^{-1}$ ), unit leaf rate (growth per unit of leaf area,  $\text{g m}^{-2} \text{d}^{-1}$ ) and unit root rate (nitrogen uptake per unit of root biomass,  $\text{g N g}^{-1} \text{d}^{-1}$ ) were calculated using the regression method of Hunt and Parsons (1974). Regression equations were fitted using the separate slopes model in the general linear model procedure (GLM) of the statistical analysis system (SAS) with chamber, competitive treatment, and species as categorical factors in the analysis. Cubic polynomial curves

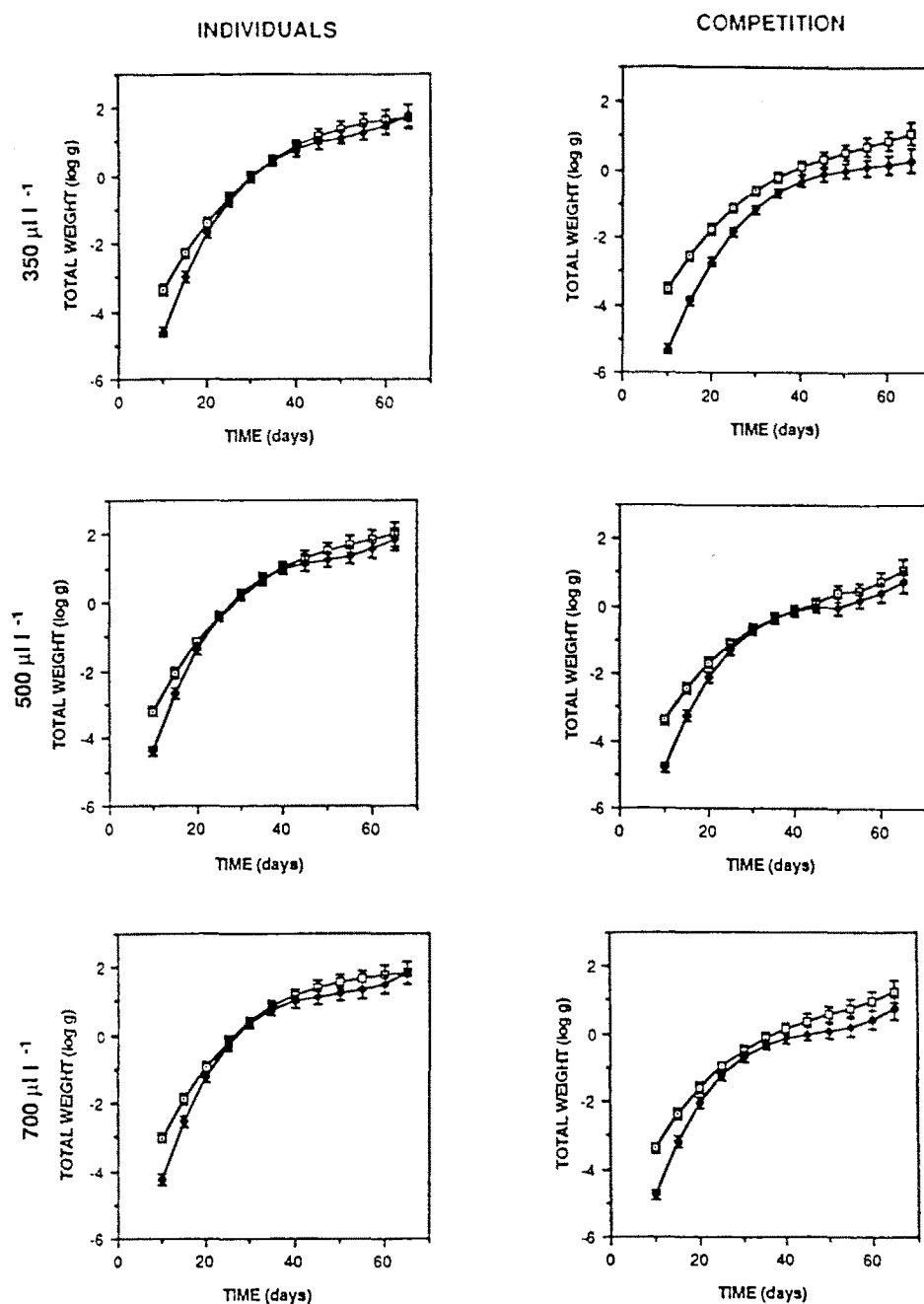


Fig. 1. Total biomass of *Abutilon theophrasti* (□) and *Amaranthus retroflexus* (■) grown either individually or in competition with each other at three levels of CO<sub>2</sub> (350, 500, and 700  $\mu\text{l l}^{-1}$ ). The error bars represent plus or minus 2 standard errors for a single treatment mean

were fitted uniformly across all treatment combinations and a common intercept was specified for each of the species. Data were transformed prior to the analysis by taking the natural logarithm of the original values. Differences among treatments in the derived variables were tested as described above with a split plot analysis of variance with chambers as the main plots. Analyses were done separately for each harvest.

For the purpose of data presentation, individual treatment means for all the variables considered are presented in figures 1 through 11. Statements made in this paper concerning differences among treatments, however, are based upon a factorial (2 species  $\times$  3 CO<sub>2</sub> levels  $\times$  2 levels of competition) analysis of variance and as such, may concern means averaged across one or more factors. As a result, when discussing main effects and one-way interactions between factors, the treatment means are known to be of

considerably more precision than indicated by the error bars in the figures. The figure error bars represent plus or minus two standard errors for a single treatment mean which is an average of 3 replications. Error bars for main effect means (see above concerning the main effect of CO<sub>2</sub>) and one-way interactions can be obtained by dividing the figure error bars by the number of levels over which the means have been calculated. For example, when comparing differences among species (i.e. species main effect) the error bars would be divided by 6 (3 levels of CO<sub>2</sub>  $\times$  2 levels of competition).

Stepwise multiple regression was used to examine which of the various physiological and architectural parameters of the two species may have contributed to their success in competition. The dependent variable was mean biomass per plant for the competitively grown plants at the final harvest for each of the two species in the nine chambers.

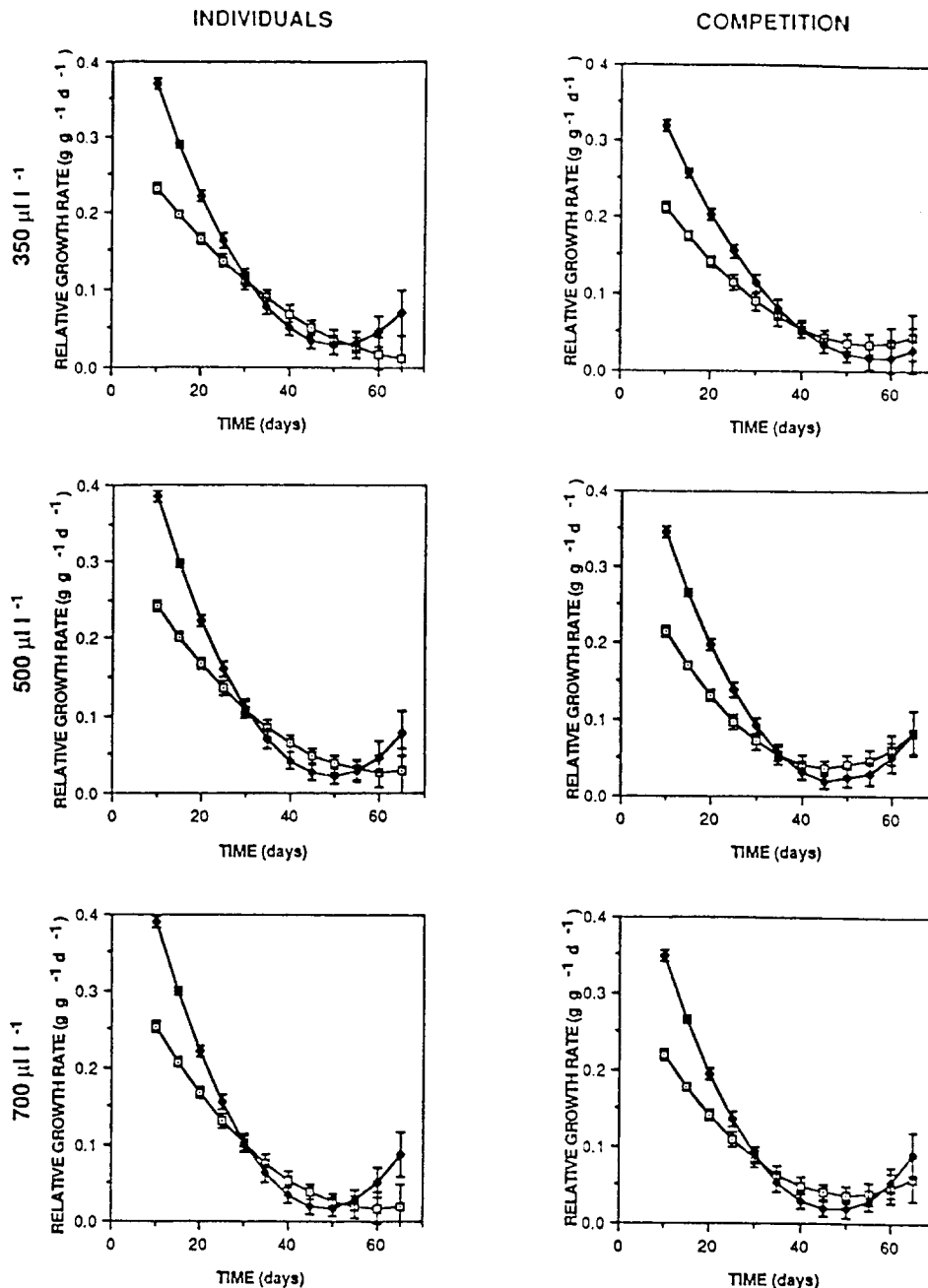
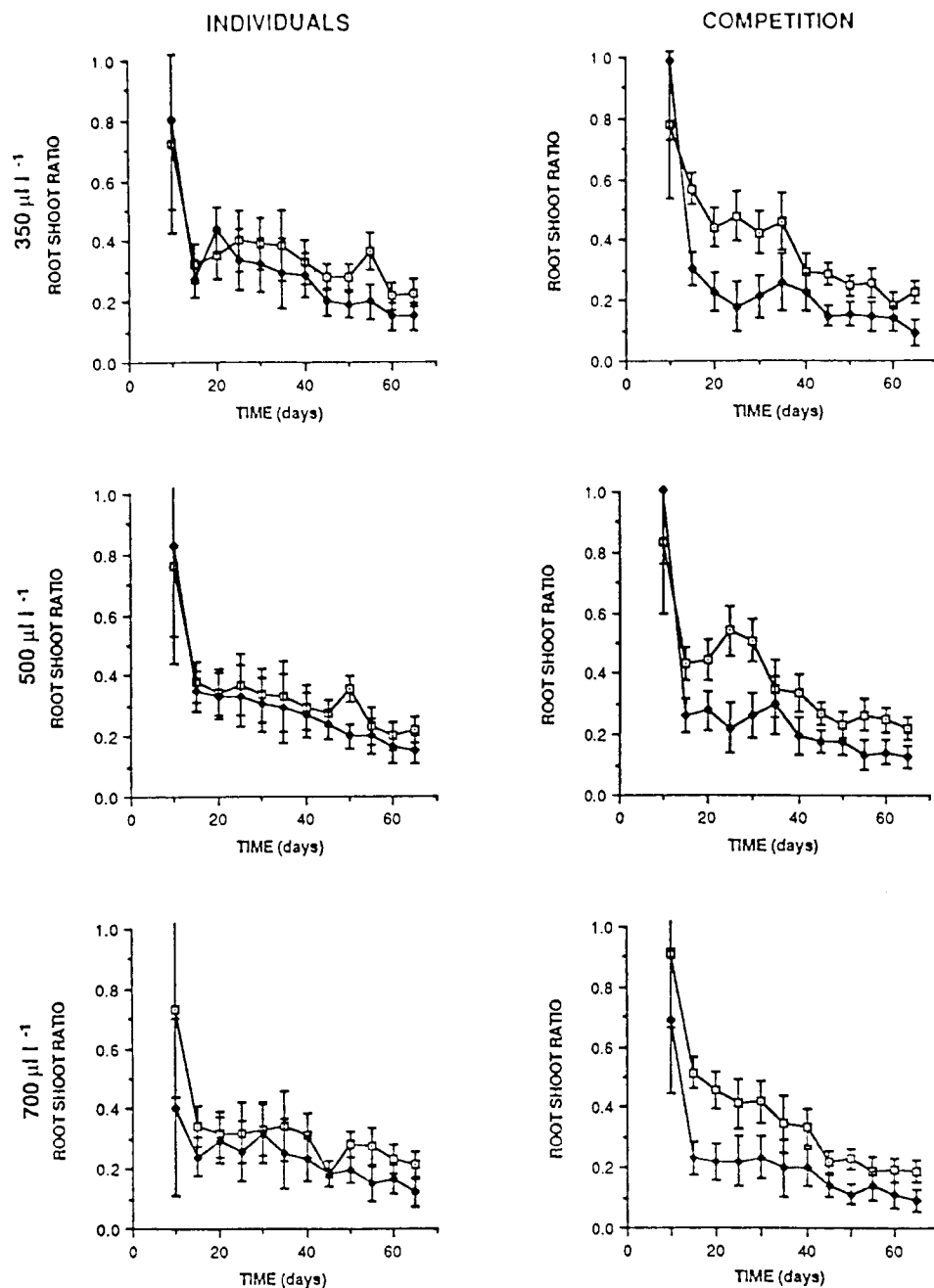


Fig. 2. Relative growth rate of *Abutilon theophrasti* (□) and *Amaranthus retroflexus* (■) grown either individually or in competition with each other at three levels of CO<sub>2</sub> (350, 500, and 700 µl l<sup>-1</sup>). The error bars represent plus or minus 2 standard errors for a single treatment mean

There were a total of 18 observations (2 species × 9 chambers). The "independent" variables consisted of: leaf area ratio, root shoot ratio, reproductive ratio, mean canopy height, unit leaf rate and unit root rate for the individually grown plants over the course of the experiment. In addition, cotyledon leaf area of the plants at the first harvest was included as a measure of the difference between species in starting capital.

When examining a large number of independent variables for predictive value in multiple regression, it is possible to include variables that do not have any real predictive value but are simply correlated with the dependent variable by chance. To minimize this possibility, principal component analysis (PCA) was employed to summarize the time course data for each of the above parameters into a smaller number of orthogonal variables before they were entered into the regression. Principal component analysis was ap-

plied to each parameter (eg. ULR) separately, such that the information from all 12 harvests was summarized into a smaller number of principal components. Only the minimum number of principal components necessary to account for >80% of the variation in a parameter across all harvests was retained by the PCA procedure. Typically, the first three components were retained for each of the various parameters. This procedure reduced the number of potential independent variables from 73 (6 different parameters measured at 12 different times plus cotyledon leaf area) to 22 with only a minimal loss in real information. These 22 independent variables were then entered into the stepwise regression procedure. Variables were entered one at a time into the model starting with the variable which accounted for the highest proportion of variation in the dependent variable. Variables were not entered into the model unless they were significant at the 0.05 level and at each step,



**Fig. 3.** Root/shoot ratio of *Abutilon theophrasti* (□) and *Amaranthus retroflexus* (■) grown either individually or in competition with each other at three levels of CO<sub>2</sub> (350, 500, and 700 µl l<sup>-1</sup>). The error bars represent plus or minus 2 standard errors for a single treatment mean.

any variable which was no longer significant at the 0.05 level was dropped from the model.

## Results

### Overall growth

*Amaranthus* had a lower initial biomass than *Abutilon* (Fig. 1). In the individually grown plants, however, *Amaranthus* caught up to *Abutilon* by day 30. The effect of competition was to depress biomass production in both species particularly at later harvests and *Amaranthus* was less able to catch up to *Abutilon*. The effect of CO<sub>2</sub> was largely limited to early in the experiment; from day 15 to 40 biomass of *Amaranthus* increased as CO<sub>2</sub> increased, and from day 35 to 40 biomass of *Abutilon* increased with CO<sub>2</sub>. For

example, on day 35 the respective biomass values for 350, 500 and 700 µl l<sup>-1</sup> CO<sub>2</sub>, averaged across species and competitive treatment, were 1.01, 1.18 and 1.34 g ( $P < 0.0351$  for the main effect of CO<sub>2</sub>). The effect of CO<sub>2</sub> upon biomass disappeared after day 40 in the individually grown plants, but competitively grown *Amaranthus* continued to show some CO<sub>2</sub> enhancement late into the experiment. This effect can be seen in figure 1 as the tendency for the biomass of competitively grown *Amaranthus* to approach that of *Abutilon* as CO<sub>2</sub> increases.

The ability of *Amaranthus* to at least partially overcome the difference with *Abutilon* in initial size is reflected in their relative growth rates (RGR). Relative growth rate was initially higher in *Amaranthus* than in *Abutilon* (Fig. 2). It declined more rapidly in *Amaranthus*, however, so that by days 45 to 50, *Abutilon* had a higher rate (ex.  $P < 0.0001$  for the main effect of species on day 45). There was some

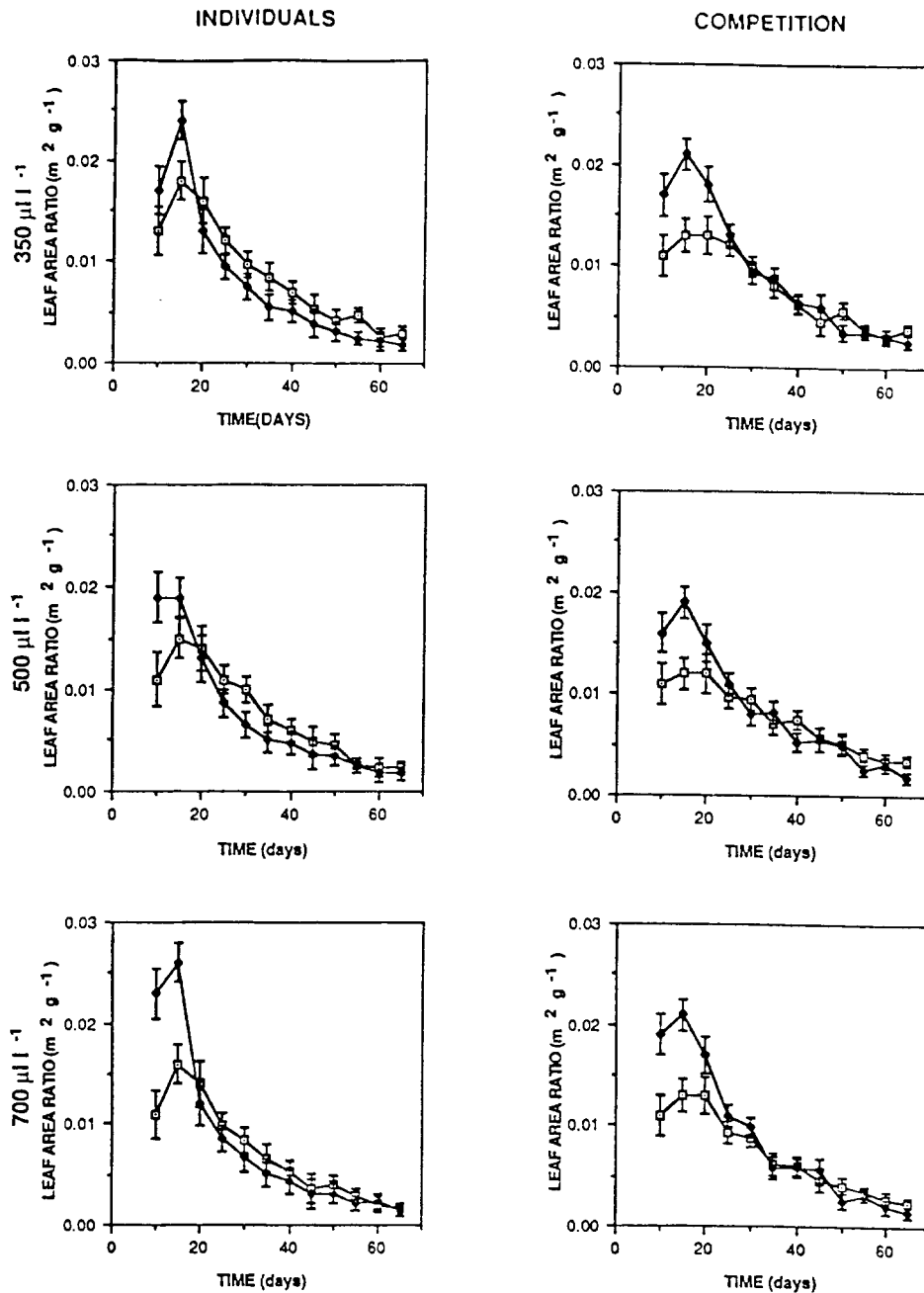


Fig. 4. Leaf area ratio of *Abutilon theophrasti* ( $\square$ ) and *Amaranthus retroflexus* ( $\blacksquare$ ) grown either individually or in competition with each other at three levels of  $\text{CO}_2$  (350, 500, and  $700 \mu\text{l l}^{-1}$ ). The error bars represent plus or minus 2 standard errors for a single treatment mean

tendency for RGR of individually grown *Amaranthus* to increase again at day 65 but this pattern was less evident in the competitive arrays. Competition decreased RGR in both species up to day 40, at which time RGR of both individual and competitive plants had declined to more or less the same rate. There was an initial increase in relative growth rate with  $\text{CO}_2$  in *Amaranthus* but there was no significant increase in *Abutilon*. On day 10, RGR of *Abutilon* averaged across competitive treatment was 0.222, 0.229 and 0.237, compared to 0.344, 0.366 and  $0.370 \text{ g g}^{-1}$  for *Amaranthus* at 350, 500 and  $700 \mu\text{l l}^{-1} \text{CO}_2$  ( $P < 0.0307$  for the  $\text{CO}_2 \times \text{species}$  interaction).

#### Allocation and architecture

With the exception of days 50 and 55 at  $350 \mu\text{l l}^{-1}$  and day 50 at  $500 \mu\text{l l}^{-1} \text{CO}_2$  there were no significant differences

in root/shoot ratio between *Amaranthus* and *Abutilon* plants grown as individuals (Fig. 3). Competition caused an increase in root/shoot ratio in *Abutilon* and a decrease in *Amaranthus* leading to significant differences in root/shoot ratio at most harvests.  $\text{CO}_2$  had no detectable effect upon root/shoot ratio.

Leaf area ratio (LAR) was higher in *Amaranthus* than in *Abutilon* at the first two harvests in all treatments, after this there were a scattering of harvests at which significant differences in LAR were found, in all cases LAR of *Amaranthus* was lower than that of *Abutilon* (Fig. 4). In all plants grown as individuals LAR peaked at day 15. In competition, peak LAR in *Abutilon* was still attained at day 15, but peak LAR in *Amaranthus* was delayed until day 20.  $\text{CO}_2$  had no significant effect upon LAR.

Specific leaf area (SLA) is the ratio of leaf area to leaf weight. Initially (days 10 and 15) *Amaranthus* had a higher

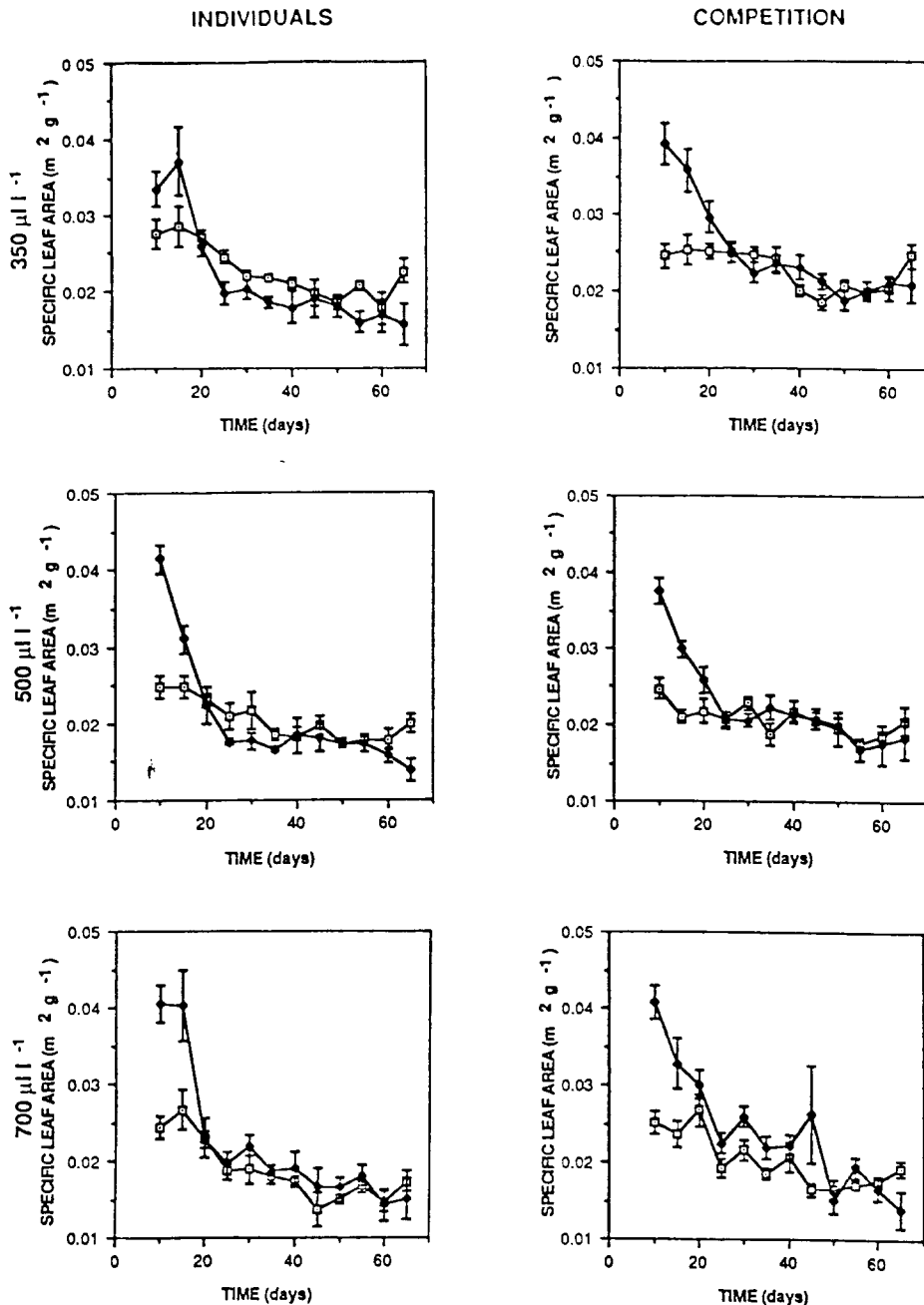


Fig. 5. Specific leaf area of *Abutilon theophrasti* ( $\square$ ) and *Amaranthus retroflexus* ( $\blacksquare$ ) grown either individually or in competition with each other at three levels of  $\text{CO}_2$  (350, 500, and  $700 \mu\text{l l}^{-1}$ ). The error bars represent plus or minus 2 standard errors for a single treatment mean

SLA than *Abutilon* (Fig. 5). After these harvests, while there were significant differences in particular treatments, there was no clear pattern. Competition tended to increase SLA in both species, particularly after day 15. Specific leaf area decreased with increasing  $\text{CO}_2$  concentration in *Abutilon*; SLA was significantly lower at  $700 \mu\text{l l}^{-1}$  than at  $350 \mu\text{l l}^{-1}$  at all harvest dates except days 10 and 15 in individually grown plants and days 10, 15, 20, 40, and 45 in competitively grown plants. *Amaranthus* showed much less response in SLA than did *Abutilon*. In individually grown *Amaranthus* the only significant difference was at day 10 when plants grown at  $350 \mu\text{l l}^{-1}$  had a lower SLA than those grown at  $700 \mu\text{l l}^{-1} \text{CO}_2$ . In *Amaranthus* grown in competition, plants at  $700 \mu\text{l l}^{-1}$  had lower SLA than plants grown at  $350 \mu\text{l l}^{-1} \text{CO}_2$  at days 30, 50, 60, and 65.

*Abutilon* generally displayed its leaf area at a greater height than *Amaranthus*, particularly later in the experiment

(Fig. 6). Competition tended to decrease mean canopy height with this effect being more pronounced in *Abutilon* than in *Amaranthus*. Carbon dioxide did appear to have some effect upon leaf display early in the experiment (ex.  $P < 0.0053$  for main effect of  $\text{CO}_2$  on day 20). Carbon dioxide tended to increase canopy height, particularly in *Amaranthus*, and in the individually grown plants; there were significant  $\text{CO}_2 \times \text{species}$  interactions on days 10, 20 and 35, and a significant  $\text{CO}_2 \times \text{level of competition}$  interaction on day 25.

*Amaranthus* flowered earlier and much more copiously than *Abutilon* (Fig. 7). Reproductive ratio was always lower in *Abutilon* than in *Amaranthus* although the very large errors associated with it sometimes precluded a significant test. Competition depressed both species and there was no species  $\times$  competitive treatment interaction. Carbon dioxide had no detectable effect upon reproductive ratio.

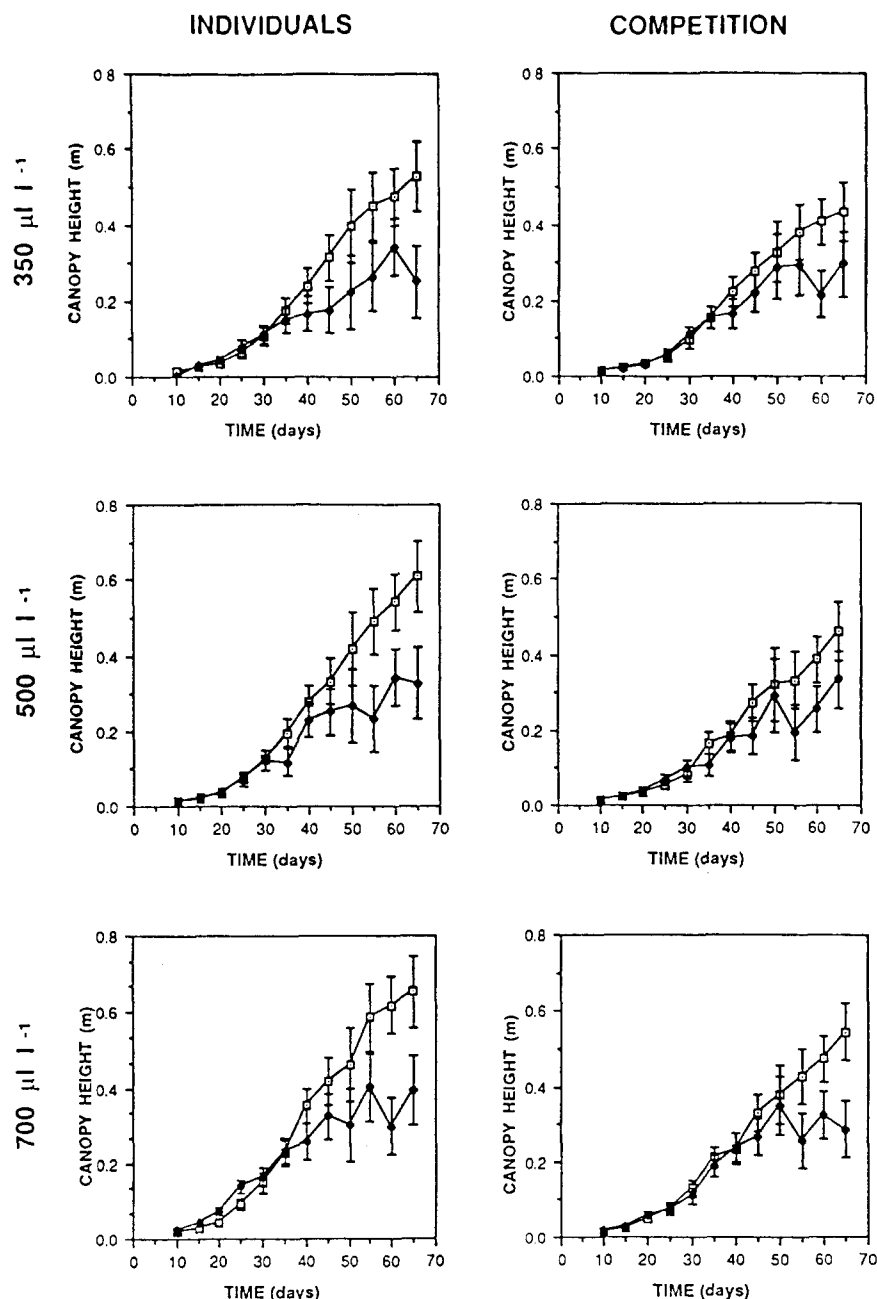


Fig. 6. Mean canopy height of *Abutilon theophrasti* (□) and *Amaranthus retroflexus* (■) grown either individually or in competition with each other at three levels of CO<sub>2</sub> (350, 500, and 700 µl l<sup>-1</sup>). The error bars represent plus or minus 2 standard errors for a single treatment mean

#### Rates of carbon and nitrogen uptake

*Amaranthus* had a higher unit leaf rate (ULR) than *Abutilon* both early (days 10 to 30) and late (days 60 to 65) in the experiment (Fig. 8). For example, averaged across competitive treatments and CO<sub>2</sub> levels, the ULR of *Amaranthus* on day 60 was 26.6 compared to 11.4 g m<sup>-2</sup> d<sup>-1</sup> for *Abutilon* ( $P < 0.0005$  for main effect of species). *Abutilon*, however, had a higher ULR from day 45 to 50 (ex.  $P < 0.0016$  on day 45). Competition generally depressed ULR up to day 45 after which there was no difference between individually and competitively grown plants. The effect of competition upon ULR was greater in *Amaranthus* than in *Abutilon*. There was no main effect of CO<sub>2</sub>, but there was a CO<sub>2</sub> × species interaction on days 15 to 30; the ULR of *Abutilon* increased from 350 to 700 µl l<sup>-1</sup> while that of *Amaranthus* remained constant or decreased slightly as CO<sub>2</sub> increased.

This interaction can be seen in Fig. 10 as the tendency for the ULR curves of the two species to approach each other as the level of CO<sub>2</sub> increases. This pattern is clearest in the case of the individually grown plants but can also be observed in the competitively grown plants. The ULR at day 20, and at 350 µl l<sup>-1</sup>, was 11.5 and 15.4 g m<sup>-2</sup> d<sup>-1</sup> for *Abutilon* and *Amaranthus* respectively when arranged across individually and competitively-grown plants, compared to 13.5 and 15.5 at 700 µl l<sup>-1</sup> ( $P < 0.0148$  for the CO<sub>2</sub> × species interaction).

Except for a brief interval from day 45 to 50, *Amaranthus* always had a higher unit root rate (rate of nitrogen uptake per unit of root biomass) than *Abutilon* (Fig. 9). Competition depressed URR early in the experiment but this effect disappeared by day 35; this effect was more pronounced in *Abutilon* than in *Amaranthus*. Unit root rate (URR) was one of the few parameters in which there was



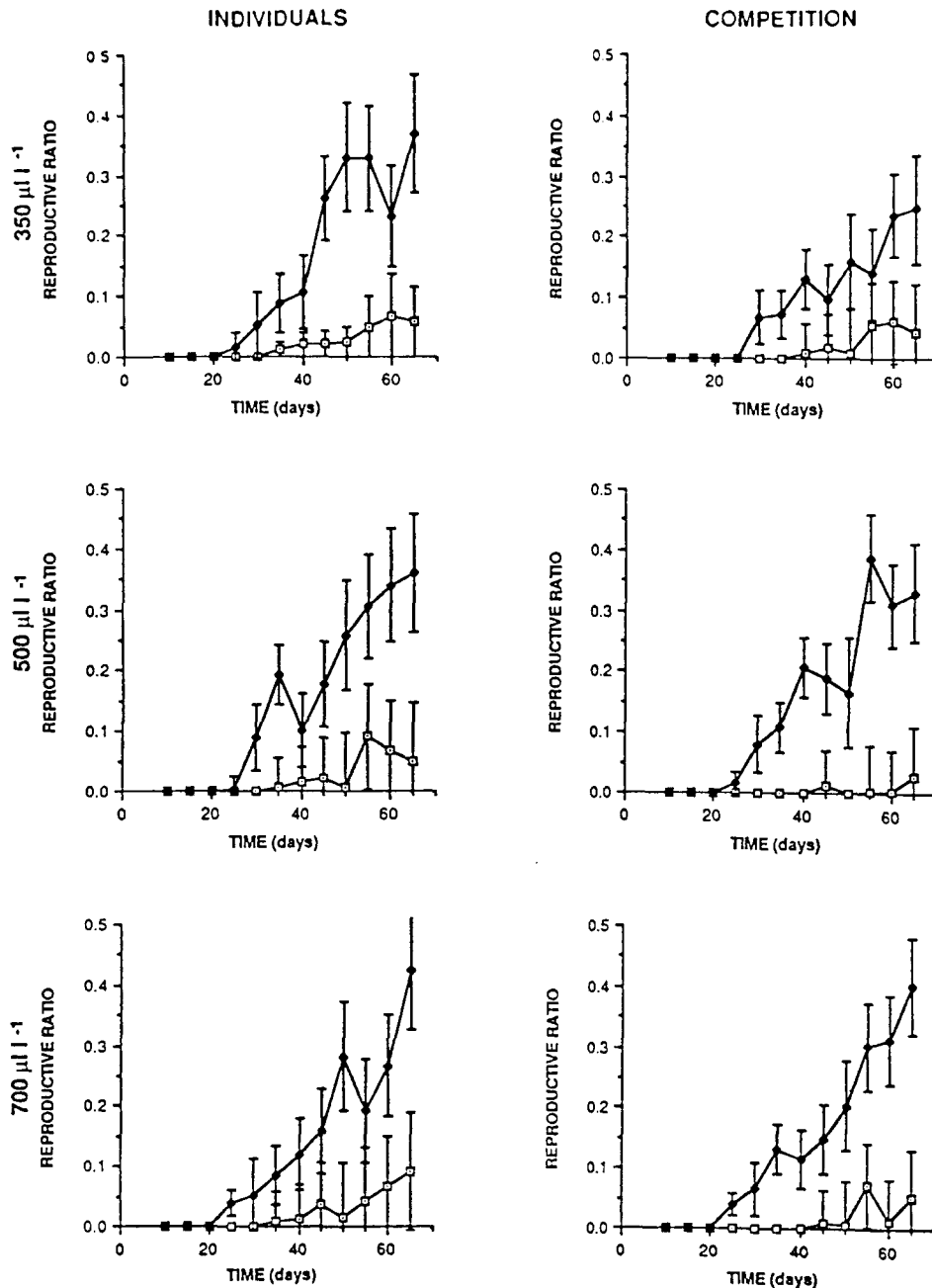


Fig. 7. Reproductive ratio of *Abutilon theophrasti* (□) and *Amaranthus retroflexus* (■) grown either individually or in competition with each other at three levels of  $\text{CO}_2$  (350, 500, and  $700 \mu\text{l l}^{-1}$ ). The error bars represent plus or minus 2 standard errors for a single treatment mean.

a main effect of  $\text{CO}_2$ . Carbon dioxide increased URR in both species from days 60 to 65 but this effect was greatest in *Amaranthus*. There were also  $\text{CO}_2 \times$  species interactions on days 30 to 40 (the difference between species was greatest at  $350 \mu\text{l l}^{-1}$ ) and on days 10 to 15 (the difference between species was greatest at  $700 \mu\text{l l}^{-1}$ ). Unit root rate was less affected by competition at low  $\text{CO}_2$  than at high  $\text{CO}_2$  (days 10 to 20); this effect was more pronounced in *Amaranthus* than in *Abutilon*.

#### Stepwise multiple regression

The stepwise regression procedure retained only one variable as a predictor of final biomass in the competitively-grown plants. Initial size as measured by cotyledon leaf area was positively correlated with final biomass and, by itself, was able to explain almost half (48.5%) of the total

variation. Although there were no differences among  $\text{CO}_2$  treatments in cotyledon leaf area, there were strong species differences. The cotyledon leaf area for *Amaranthus* was much smaller than that of *Abutilon* and this was associated with poor competitive performance (Fig. 10).

#### Discussion

##### Differences between species

The large initial differences in biomass between species (Fig. 1) were due to the different seed sizes of the two species. The ability of the individually grown *Amaranthus* to rapidly increase in size relative to *Abutilon*, overcoming the difference in starting capital, was due to a combination of factors. Early in the experiment *Amaranthus* had both

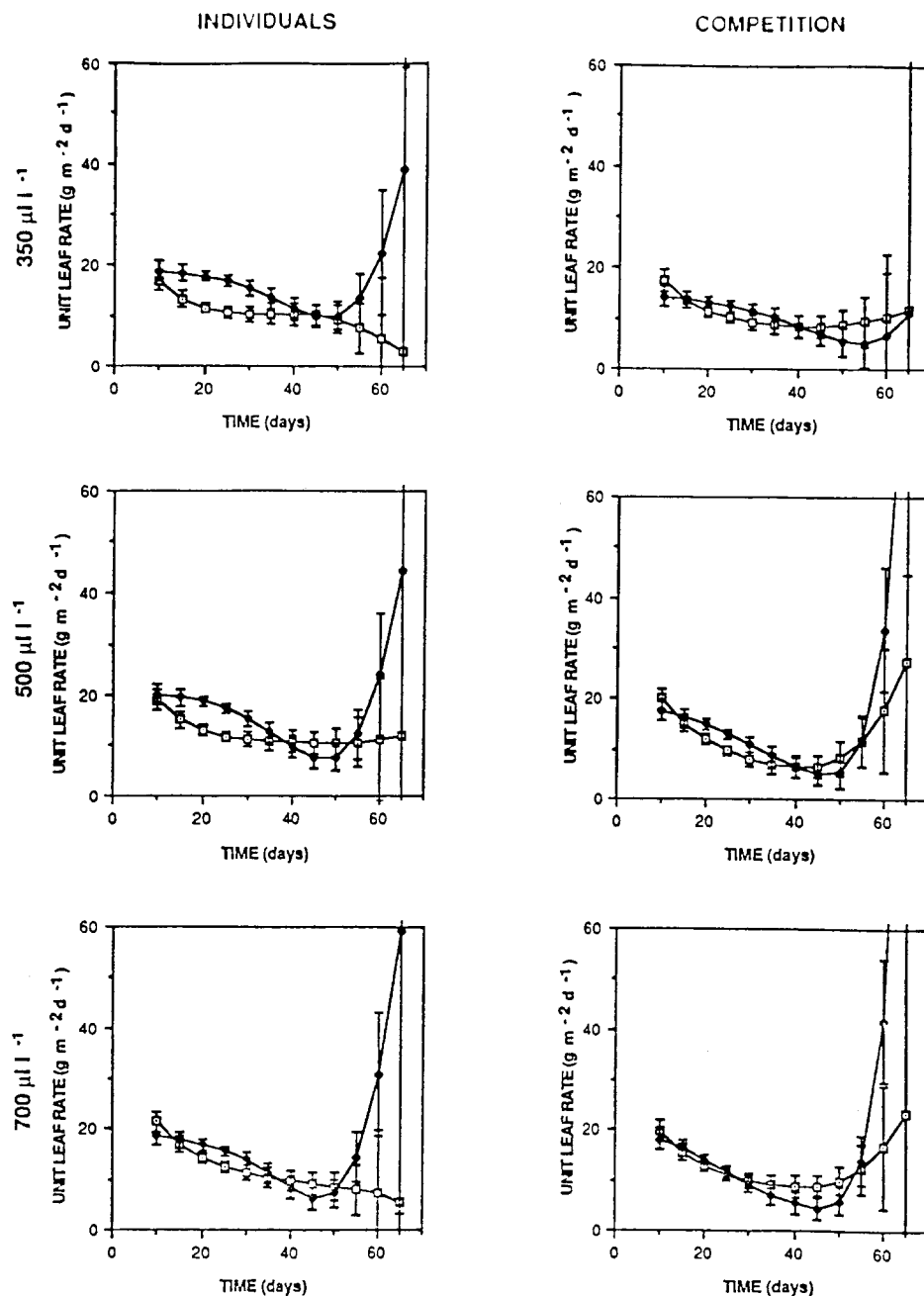


Fig. 8. Unit leaf rate of *Abutilon theophrasti* ( $\square$ ) and *Amaranthus retroflexus* ( $\blacksquare$ ) grown either individually or in competition with each other at three levels of CO<sub>2</sub> (350, 500, and 700  $\mu\text{l l}^{-1}$ ). The error bars represent plus or minus 2 standard errors for a single treatment mean.

a higher unit leaf rate (Fig. 8) and leaf area ratio (Fig. 4) than *Abutilon*. These two factors combined account for the high initial relative growth rate of *Amaranthus* (Fig. 2). The high unit leaf rate of *Amaranthus* is probably a reflection of the generally high maximum photosynthetic rates exhibited by C<sub>4</sub> plants. The large initial LAR of *Amaranthus* was primarily a function of its specific leaf area (Fig. 5), allocation to parts other than leaves being similar to that of *Abutilon*. Since the root/shoot ratio of *Amaranthus* was similar to that of *Abutilon* (Fig. 3) and its rate of nitrogen uptake was actually superior (Fig. 9). This would have allowed *Amaranthus* to obtain the nitrogen necessary to maintain a high photosynthetic rate.

The reason why the growth of *Amaranthus* started to slow down relative to *Abutilon* around day 30 (Fig. 2) seems to be related to its early reproduction (Fig. 7). At the same time reproduction was initiated LAR declined markedly

to a level below that of *Abutilon* (Fig. 4). This decline was due to both the increase in the proportion of reproductive structures and associated stems relative to leaf area, as well as to a decline in SLA. The decrease in SLA is probably a reflection of the generally smaller leaves produced by *Amaranthus* once it flowers. The smaller leaves would have a lower ratio of leaf area to weight than larger leaves. Later in the experiment (i.e. days 40–50) reductions in unit leaf rate helped contribute to the generally reduced performance of *Amaranthus* (Fig. 8). The decrease in ULR is probably due to translocation of nutrients out of the leaves in order to supply the maturing reproductive structures. Data for *Amaranthus* exhibited a sharp (but usually non-significant) increase in ULR after day 50. This is an artifact resulting from the fact that most of the leaves had dropped by this time while the stem and reproductive structures were still green and, therefore, probably still photosynthesizing.

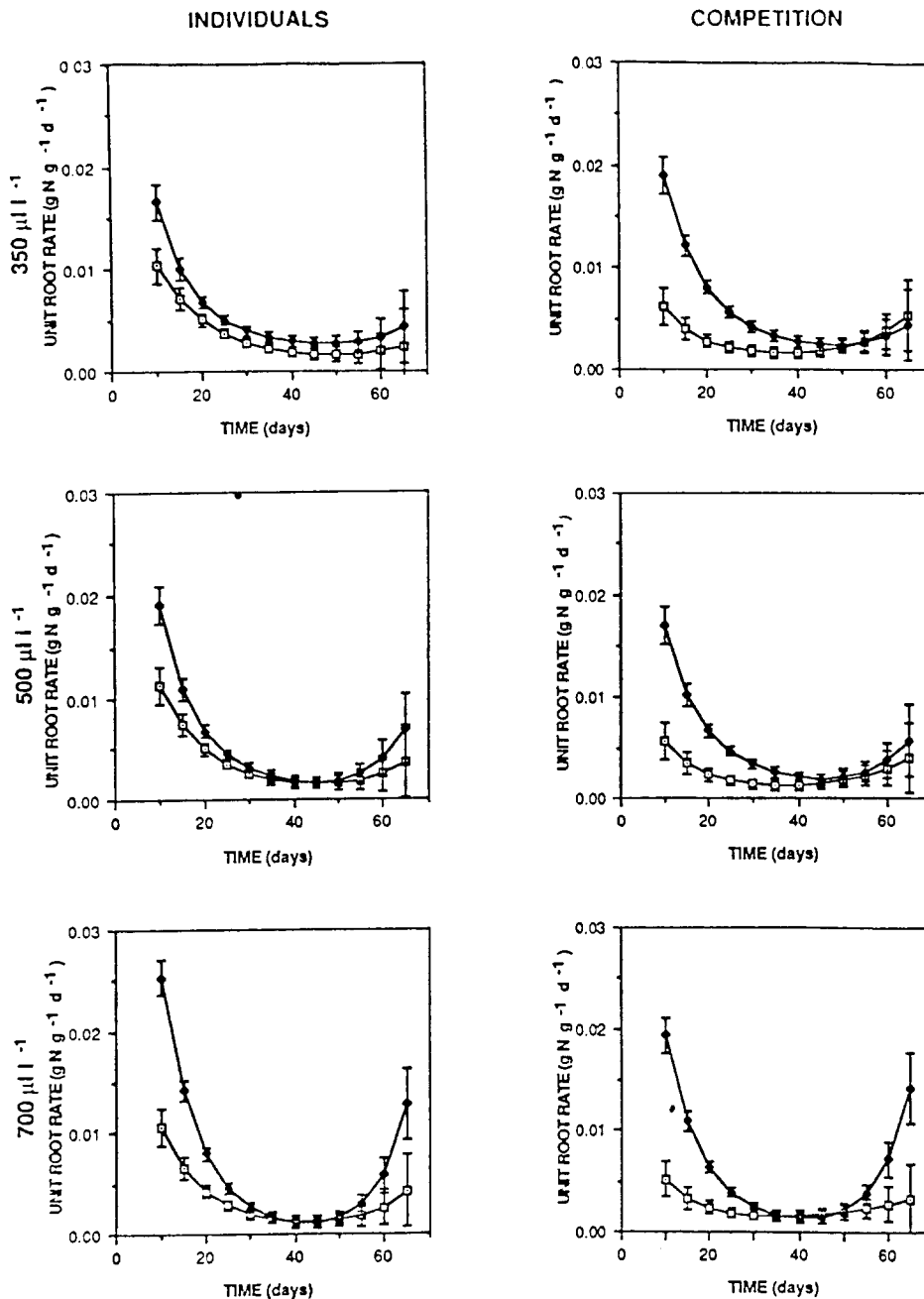


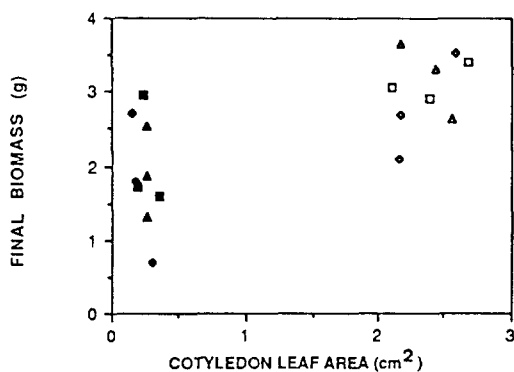
Fig. 9. Unit root rate of *Abutilon theophrasti* (□) and *Amaranthus retroflexus* (■) grown either individually or in competition with each other at three levels of CO<sub>2</sub> (350, 500, and 700 µl l<sup>-1</sup>). The error bars represent plus or minus 2 standard errors for a single treatment mean

#### Individual versus competitively grown plants

Competition (both inter- and intra-specific) caused a reduction in the growth of both species, but the growth of *Amaranthus* was generally depressed more than that of *Abutilon*. The major reason for this appears to be differences in amount of starting capital between the two species (Fig. 10). *Amaranthus* with its much smaller seeds was at a disadvantage in competing against *Abutilon*. The reasons for the decrease in growth with competition differed between species. In *Amaranthus*, the major cause for reduced performance was a general decrease in ULR (Fig. 8). In contrast, *Abutilon* showed little, if any reduction in ULR. The reduced ULR of *Amaranthus* was probably the result of shading, both by other *Amaranthus* individuals as well as by *Abutilon*. There was substantial leaf overlap among neighboring plants within the competitive pots. Plants with the

C<sub>4</sub> pathway have a lower initial slope in their photosynthetic light response curve than C<sub>3</sub> plants (Björkman and Pearcy 1983) which would explain why the ULR of *Abutilon* was not affected to the same degree as *Amaranthus*. Also, the greater height at which leaf area was displayed in *Abutilon* than in *Amaranthus* would tend to enhance the ability of *Abutilon* to compete with *Amaranthus* for light (Fig. 6).

The major reason for the reduced performance of *Abutilon* in competition appears to be an initial decrease in LAR (Fig. 4, days 10 to 20). This decrease was linked with a pronounced increase in root/shoot ratio (Fig. 3) suggesting that it was competition for below ground resources which was the primary driving force behind the reduction in LAR and its consequent effect on overall growth. The root/shoot ratio of *Amaranthus* actually decreased slightly with competition indicating that it was better able to compete for below



**Fig. 10.** Correlation between competitive outcome and starting capital ( $r^2=0.485$ ). Final biomass is used as an indicator of competitive success and cotyledon leaf area as a measure of starting capital (seed size). The different symbols represent the various species and  $\text{CO}_2$  treatment combinations.  $\diamond$  Abutilon 350;  $\square$  Abutilon 500;  $\triangle$  Abutilon 700;  $\diamond$  Amaranthus 350;  $\square$  Amaranthus 500;  $\triangle$  Amaranthus 700

ground resources than *Abutilon*. This ability was reflected in its high URR (Fig. 9).

#### Effect of $\text{CO}_2$ upon individually grown plants

Although  $\text{CO}_2$  increased the initial growth of both *Abutilon* and *Amaranthus* when grown as individuals (Fig. 1, days 10–40) the reason for this increase differed between the two species. In *Abutilon*, the increased growth resulted from an increase in unit leaf rate (Fig. 8). In *Amaranthus* on the other hand, there was no significant increase in either LAR or ULR. Since RGR is a linear combination of LAR and ULR, it appears that the significant increase in RGR was due to nonsignificant increases in either LAR or ULR, or to a combination of both. Inspection of the LAR and ULR values suggest that increases in LAR were probably more important than increases in ULR. Unit leaf rate in *Amaranthus* in some cases actually decreased slightly with increased  $\text{CO}_2$ .

The difference between the two species in the response of ULR to  $\text{CO}_2$  are in accord with theoretical predictions of the effect of  $\text{CO}_2$  on photosynthesis of  $\text{C}_3$  and  $\text{C}_4$  species, and with actual measurements of the effect of  $\text{CO}_2$  upon single leaf photosynthetic rates. Our study, however, shows that in spite of the lack of any major effect of  $\text{CO}_2$  upon photosynthesis, the growth of  $\text{C}_4$  species can increase to the same extent as that of  $\text{C}_3$  species in response to  $\text{CO}_2$ . In *Amaranthus*, this ability appears to be related, in part, to a decrease in biomass allocation to roots with  $\text{CO}_2$ , resulting in a higher LAR (neither of these effects were significant at the 0.05 level). This presumed decrease in allocation to roots may be related to a decrease in stomatal aperture with  $\text{CO}_2$  (Björkman and Pearcy 1983). With stomatal closure, transpiration would be reduced, enhancing the water status of the plant which might allow less resources to be allocated to root growth. In *Amaranthus* unit root rate was high and increased with  $\text{CO}_2$ , suggesting that even though allocation to roots may decrease with  $\text{CO}_2$ , this would not have a major impact on nutrient absorption.

The point at which the  $\text{CO}_2$  effect upon growth in *Abutilon* disappears (day 40) is closely preceded by the point at which SLA is first affected by  $\text{CO}_2$  (Fig. 5);  $\text{CO}_2$  decreases the amount of area per unit of leaf weight. This decline

in SLA did not affect the LAR of the plants, but the effect of  $\text{CO}_2$  upon ULR declines in concert with SLA. The decline in SLA suggests that the products of photosynthesis may have been accumulating in the leaves rather than being translocated to other plant parts. It has been suggested that end product inhibition resulting from such an accumulation may be responsible for differences among plants in the response of photosynthesis to elevated  $\text{CO}_2$  (Sasek et al. 1985). However, this cannot explain the decline of the  $\text{CO}_2$  effect in *Amaranthus* as neither ULR nor SLA showed any marked response to  $\text{CO}_2$ . The reason for the decline of the  $\text{CO}_2$  effect in *Amaranthus* as the plants grow is unclear, but may be related to constraints placed upon allocation patterns when plants flower. Such constraints may prevent increased allocation to leaves which apparently was one of the causes of the  $\text{CO}_2$  effect in *Amaranthus*.

#### Effect of $\text{CO}_2$ upon competition

*Amaranthus* responded to  $\text{CO}_2$  earlier, and to a greater extent, than did *Abutilon*. As a result, the competitive balance shifted depending upon level of  $\text{CO}_2$  (Fig. 1). At  $350 \mu\text{l l}^{-1} \text{CO}_2$ , *Amaranthus* was not able to overcome the initial difference in starting capital (seed size) between the two species and was never able to catch up to *Abutilon*. At higher levels of  $\text{CO}_2$ , however, the higher initial RGR of *Amaranthus* allowed it to rapidly catch up to *Abutilon* and there was no difference in the final biomass of the two species. Competitive balance therefore shifted in favour of the  $\text{C}_4$  species as the level of  $\text{CO}_2$  increased in spite of the fact that the ULR of the  $\text{C}_3$  species was more favorably enhanced by  $\text{CO}_2$  than that of the  $\text{C}_4$  species.

#### Conclusion

The results of this experiment show three things. First, response to  $\text{CO}_2$  is primarily limited to early growth stages. Changes in patterns of growth with age, accumulation of carbohydrate leading to end product inhibition and/or limitation of other resources apparently prevent older (larger) plants from responding to elevated  $\text{CO}_2$ . This finding has important consequences because many of the previous studies that showed marked increases in growth with elevated  $\text{CO}_2$  were relatively short-term studies. Current predictions of substantially increased plant growth with  $\text{CO}_2$  may not materialize in the long run. However, this does not necessarily mean that  $\text{CO}_2$  will not be an important factor in determining community composition. As shown here, differences among species in their initial response to  $\text{CO}_2$  can influence final competitive outcome.

Secondly, even though  $\text{C}_4$  plants may exhibit little increase in photosynthesis with increase in  $\text{CO}_2$ , this does not necessarily mean they will lose out in competition with  $\text{C}_3$  plants at elevated  $\text{CO}_2$  levels. In the present case, *Amaranthus*, a  $\text{C}_4$  plant, actually became more competitive with regard to *Abutilon*, a  $\text{C}_3$  species, at high  $\text{CO}_2$ . The reason for this is not entirely clear but appears to be related to a combination of marginal increases in ULR and to changes in allocation patterns leading to increases in LAR.

Finally, this experiment illustrates that growth analysis, a tool which has long been used in understanding the growth of single species, can be also used as an effective means of interpreting the results of competition. Growth analysis by itself, however, may have its limitations. For

example, the reason why *Amaranthus* responded so positively to CO<sub>2</sub> when grown in competition is not clear from the growth analysis results. We suspect this response is due to changes in allocation patterns resulting from increased availability of water. It is likely that the utility of growth analysis in interpreting the results of competition would be greatly enhanced if combined with a knowledge of resource availability. In understanding competition it is important to not only examine the ability of plants to take up resources from the environment, but to assess the relative availability of these resources in the environment, as this is the ultimate level at which plants interact.

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