# Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated $CO_2^*$

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Summary. Seedlings of five tropical trees, Cecropia obtusifolia, Myriocarpa longipes, Piper auritum, Senna multijuga and Trichospermum mexicanum, were grown both as individuals, and in competition with each other at ambient (350) and two levels of elevated  $CO_2$  (525 and 700 µl l<sup>-1</sup>) for a period of 111 days. Growth, allocation, canopy architecture, mid-day leaf water potential and soil moisture content were assessed three times over this period for individually grown plants, and at the end of the experiment for competitively grown plants. In addition, leaf photosynthesis and conductance were assessed for the individually grown plants midway through the experiment, and light profile curves were determined for the competitive arrays at three stages of development. Elevated CO<sub>2</sub> did not affect photosynthesis or overall growth of the individually-grown plants but did affect canopy architecture; mean canopy height increased with CO<sub>2</sub> in Piper and Trichospermum and decreased in Senna. Stomatal conductance decreased slightly as CO2 increased from 350 to 525  $\mu$ l 1<sup>-1</sup> but this had no significant effect upon whole plant water use or leaf water potential. Soil moisture content for the individuals increased marginally as CO<sub>2</sub> increased, but this did not occur in the competitive arrays. There was a marked effect of CO<sub>2</sub> upon species composition of the competitive arrays; Senna decreased in importance as CO<sub>2</sub> increased while Cecropia, Trichospermum and Piper increased in importance. Stepwise regression analysis using competitive performance as the independent variable, and the various morphological and physiological parameters measured on the individually grown plants as independent variables, suggested that canopy height was the single most important variable determining competitive ability. Also significant were photosynthetic rate (particularly at low light levels) and allocation to roots early in the experiment. Light profiles in the canopy revealed that less than 15% of incident light penetrated to the level of mean canopy height. Results suggest that competition for light was the major factor determining community composition, and that CO<sub>2</sub> affected competitive outcome through its affect upon canopy architecture.

Key words: Competition – Seedlings – Tropical trees –  $CO_2$  elevation – Canopy architecture

Studies of plant competition have concentrated on examining the extent to which plants may reduce the growth of each other under various sets of conditions. Examples of this approach include DeWit type replacement series, relative yield-total studies, modeling with Lotka-Volterra equations, and most recently, neighborhood models (Firbank and Watkinson 1987; Weiner 1982; Pacala and Silanda 1985). It is difficult using this approach to extrapolate to different sets of conditions. The extent to which one plant may reduce the growth of another can vary markedly depending upon the availability of various resources and the presence or absence of other competitors (Bazzaz 1987).

Despite much progress in this area, relatively little attention has been given to understanding the mechanisms by which plants affect each others' growth. It is generally believed that competition by resource depletion (i.e. scramble competition) is the predominant mechanism (Whittaker 1975; Harper 1977). Although there is a large body of information on the physiological mechanisms which allow plants to efficiently utilize different levels of resources such as light, water, and nutrients, very few studies of competition actually try to assess how resource availability may be modified by the competitors (e.g. see Caldwell et al. 1987). A better understanding of plant competition would be achieved by considering: 1) to what extent plants affect their resource environment, and 2) how plants respond to these changes in resource availability. This approach would allow extrapolations to different sets of conditions. For example, if we know that species A predominates over species B in competition because it is more efficient at utilizing water at low levels of availability, we can predict how this relationship might shift as water availability is increased, or what might happen when species G, which tends to decrease water availability for the first two species, is added to the community.

Our overall objective in the present study is to determine to what extent competitive outcome among saplings of five tropical woody species grown at different carbon dioxide concentrations can be explained by the patterns of light and water uptake, and the efficiency by which the plants utilize these resources for growth. Previous work has shown competitive outcome in several simple temperate communities can change substantially with different CO<sub>2</sub> concentrations (Bazzaz et al. 1985). This study is an attempt to extend this survey to a simplified tropical community and to understand why these changes take place so that we may better predict how communities might change as  $CO_2$  levels increase. Emphasis was placed upon the uptake and use of

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light and water because  $CO_2$  is likely to interact with the availability of both of these resources (e.g. Bazzaz and Carlson 1984; Zangerl and Bazzaz 1984).

#### Materials and methods

#### The species

The five species chosen for this study were: Myriocarpa longipes, Trichospermum mexicanum, Senna multijuga, Piper auritum, and Cecropia obtusifolia. Seed was collected from the biological research station at Los Tuxtlas, Mexico. Los Tuxtlas is the principal research station of the Instituto de Biologia of the Universidad Nacional Autonoma de Mexico. The station is located at 95°04'W longitude, 18°34'N latitude on the eastern slopes of the Sierra de Los Tuxtlas, an area of rich soils of recent volcanic origin. The vegetation is high evergreen rainforest (Rzedowski 1978).

# Plant culture

Seeds of the five species were germinated in moist vermiculite. Based upon preliminary germination trials, planting of the seeds was staggered so that all five species emerged within one week of each other. When all species had at least two true leaves the seedlings were transplanted to either competitive arrays or individual pots. The competitive arrays were  $30 \times 25$  cm (8 l volume) flats and contained six individuals of each of the five species. Individual plants were randomly assigned to positions within the flats. The individually grown plants were grown in 12.5 cm pots (0.67 l). The growth medium consisted of a 1:1 mix of soil and turface<sup>®</sup>. Plants were grown in CO<sub>2</sub> controlled, glass enclosed chambers (Carlson and Bazzaz 1980, 1982) in a greenhouse at Harvard University in Cambridge, MA from April 25 to August 12, 1986. Plants received unsupplemented natural light. Maximum light levels were typically in the range of 1000 to 1200  $\mu$ moles m<sup>-2</sup> s<sup>-1</sup> on clear days. There were 12 chambers; four chambers at each of three CO<sub>2</sub> levels (350, 525, and  $700 \pm 30 \ \mu l \ l^{-1}$ ). Air temperature was maintained at  $30 \pm 3^{\circ}$  C (day) and  $27 \pm 3^{\circ}$  C (night). There were three competitive flats and three individually grown plants per species in each of the 12 chambers. The pots were watered to field capacity at 9:00 a.m. each day. The plants were fertilized on a monthly basis by watering with standard strength Peter's<sup>®</sup> soluble fertilizer (20-20-20).

# Measurements

#### Growth, allocation, and architecture

One individually grown plant per species from each of the 12 chambers (i.e. 4 replications of each  $CO_2 \times$  species combination) was harvested at 45, 67, and 111 days after transplanting. Plants in the competitive arrays were all harvested on day 111. At each harvest, the area and height (point of insertion on stem) of each leaf was measured, and individual plants were divided into leaves, stems and roots, then dried and weighed (in the case of the competitive plants only the aboveground parts were harvested).

To assess allocation patterns, the proportion of total biomass allocated to roots and to stems was calculated. Allocation to leaves was assessed by calculating leaf area ratio (leaf area per unit of total biomass,  $m^2 g^{-1}$ ), and specific leaf area (leaf area per unit of leaf biomass,  $m^2 g^{-1}$ ). The leaf area-height profile data were summarized prior to statistical analysis by calculating mean canopy height for each individual. The height of each leaf was weighted by the area of the leaf and the mean height for the entire plant calculated.

# Water relations

Whole plant water use of the individually grown plants was measured by gravimetrically determining daily water loss (i.e. transpiration plus evaporation from soil surface) for the individual pots reserved for the final harvest. Determinations were made at approximately weekly intervals and total water loss over the course of the experiment was estimated by fitting a polynomial curve to the water loss – time data and integrating under the curve. Total water use was then expressed in relation to final biomass to estimate the water requirement for growth. Soil moisture content of both the individual pots and competitive flats was determined gravimetrically at the final harvest. Mid-day leaf water potential was determined prior to each harvest using a PMS® model 650 pressure bomb. One recently expanded leaf was measured for each individually grown plant, and two randomly selected leaves per species per chamber were measured in the case of the competitive arrays.

#### Photosynthesis and conductance

Single leaf net photosynthesis and conductance were measured on the individually grown plants between days 80 and 103. There were four replications of each  $CO_2 \times$  species combination. Measurements were made at the  $CO_2$  level at which the plants were grown and at two levels of light (250 and 1400 µmoles m<sup>-2</sup> s<sup>-1</sup>). Measurements were made with a Bingham Interspace cuvette and controller in conjunction with a Binos IRGA (Bingham et al. 1980). The cuvette was maintained at a temperature of 30° C and a relative humidity of 75%.

# Light profiles

Light penetration in the canopy of the competitive arrays was assessed on days 40, 57, and 74. A linear array of six PPFD sensors spaced 5 cm apart was inserted at 10 cm intervals from 15 cm above ground surface to above the plant canopy. Instantaneous readings were taken at each height, using a Licor<sup>®</sup> model LI-1000 data logger. Readings from the six sensors at each height were averaged, and light penetration at various heights in the canopy was calculated as a percentage of that above the plant canopy.

#### Data analysis

Data were analyzed by Split-Plot analysis of variance with individual chambers as the main plots using the General Linear Models (GLM) procedure of the Statistical Analysis System (SAS). Treatment design was a  $5 \times 3$  factorial (five species crossed with three levels of CO<sub>2</sub>). The main effect of CO<sub>2</sub> was tested with the CO<sub>2</sub> × replication (i.e. chamber level replication) error term, and all other effects with the residual error term. Separate analyses were conducted for each harvest, and for the individual versus competitive data.

Table 1. Growth, allocation and architecture of individually grown plants at days 45 and 67. The designations C, M, P, S and T represent Cecropia, Myriocarpa, Piper, Senna and Trichospermum respectively. In most cases there was no significant effect of CO2 and so values presented here are averaged across CO2 levels. Values followed by the same letter are not significantly different from each other at the 0.05 level of probability 的复数复数 计正式分

Species	Total biomass (g)	Root (%)	Stem 1 (%) (	Leaf area m²)	Leaf area ratio $(m^2 g^{-1})$	Specific leaf area $(m^2 g^{-1})$	Mean canopy height
Day 45							a contract
С	1.50b	23b	16b	).035a	0.024c	0.038c	0.11b
М	0.53d	19c	7d 0	0.017Ъ	0.033a	0.045b	0.03c
$\mathbf{P}^{(n_1,n_2,\dots,n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n-1},n_{n_{n-1},n_{n-1},n_{n-1},n_{n_{n-1},n_{n-$	1.21 bc	26 a	9c 0	).033a	0.028b	0.044Ъ	0.03c
$S \in \mathbb{C}^{n} \to \mathbb{C} \setminus \{1, \dots, n\}$	2.41 a	27a	20a 0	).037a	0.016d	0.030d	0.20 a
$T: \mathbb{C}^{n \times n} \to \mathbb{C}^{n \times n} \to \mathbb{C}^{n \times n}$	0.99 cd	24ab	15b 0	).030a	0.031 ab	0.051 as a store store of a	
Day 67	a da entre entre de la composition de l Portes de la composition de la compositi	and or wale f	, <sup>a</sup> nteran Ma Homen	an order	an an an thair. Tha an thair an thair	sve dense og fær verse se here ser	ประสารสุดประวัติ 25 (1995) เป็นประวัติ
С	9.05a	20b	31a (	).100 a	0.011d	0.022c	0.28b
Μ	3.27c	19b	15b (	).089a	0.029 a	0.045a	0.10c
Р	5.65b	31a	18b C	).085a	0.016c	0.031b	0.09c
S	6.13b	20b	35a C	).075a	0.013cd	0.028 bc	0.35,a
T	5.22b	23b	31 a C	).093a	0.019b	0.041 a	0.30b

(a) and (b) and (b) and (b) are setting to be a set of the set

For the photosynthesis and conductance data the above design was modified to include light level as a repeated measure. The biomass and total leaf area data from the competitive arrays were transformed prior to analysis by taking the logarithms of the original values. The arc sin transformation was used for all proportional data. The 0.05 level of probability was used for all tests of significance. In cases where there was a significant F-test for a factor, the significance of differences among treatment means was determined by paired-t tests. All "differences" among means referred to in the text are significant at the 0.05 level unless otherwise stated.

To determine which of the various morphological and physiological traits of these species may have contributed to their success in the competitive arrays, stepwise regression analysis was used. As a measure of competitive success, the average biomass of each species in the competitive arrays in each of the twelve chambers was used as the dependent variable. The independent variables consisted of all the morphological and physiological traits measured on the individually grown plants (see Table 3) for each species at the three harvests. Size-related characters such as total weight or leaf area were not included. A forward stepwise procedure was followed such that variables were added one by one to the model. The F statistic for a variable to be added had to be significant at the 0.05 level, and, after a variable was added, any variables already in the model that were no longer significant at the 0.05 level were deleted.

In assessing a large number of independent variables as predictors in regression analysis it is possible for one or more of the independent variables to be related to the dependent variable by chance alone. To examine this possibility, but at the same time minimize the loss of information resulting from reducing the number of possible predictors, principal component analysis was used to summarize the information in the 24 original independent variables into a fewer number of orthogonal (non-correlated variables). These new orthogonal variables (the principal components) were then used as independent variables in regression analysis as described above. There is a provide set of the description of the

# Results Individually grown plants

Growth, allocation, and architecture. Carbon dioxide had relatively little effect on the individually grown plants, particularly at the first two harvests. Therefore, data for the first two harvests were averaged across CO<sub>2</sub> levels and are presented in Table 1. For those few cases where CO2 did have a significant effect, the relevant data are presented in the text (see below). The full data set for the final harvest is presented in Figs. 1 and 2. There was no effect of CO<sub>2</sub> on total biomass at either of the first two harvests, but at the final harvest biomass of *Cecropia* decreased slightly at 525  $\mu$ l l<sup>-1</sup> while that of Trichospermum increased at 525 µl  $1^{-1}$  (Fig. 1, P < 0.0022for the  $CO_2 \times$  species interaction). Species differed in the amount of biomass produced. In general Cecropia, Trichospermum, and Senna produced more biomass than Piper and Myriocarpa, particularly in the latter part of the experiment. The rankings varied somewhat depending upon harvest. Senna was larger than Cecropia and Trichospermum early in the experiment (Table 1, day 45) but by the final harvest was smaller than Cecropia and similar to Trichospermum (Fig. 1). Myriocarpa was initially smaller than Piper but this difference disappeared by the final harvest. Piper was similar in size to Cecropia, Trichospermum and Senna early in the experiment, but was smaller by the final harvest.

Differences among species in total leaf area varied depending upon harvest (Table 1, Fig. 1). At the first harvest, Myriocarpa had a lower leaf area than any of the other species. There were no differences among species at the second harvest, and at the final harvest, Trichospermum, Myriocarpa, and Cecropia had a greater leaf area than Senna or Piper. There was no effect of  $CO_2$  upon leaf area. There was no effect of CO<sub>2</sub> upon allocation patterns, except for the earliest harvest with regard to stems where there was a significant  $CO_2 \times species$  interaction (P< 0.0211). Allocation to stems tended to increase with CO<sub>2</sub> in all species except Myriocarpa. The proportion of biomass allocated to stems at 350, 525 and 700  $\mu$ l l<sup>-1</sup> CO<sub>2</sub> for the



Fig. 1A–D. Total biomass (A), leaf area (B), leaf area ratio (C), and specific leaf area (D) of individually grown plants at day 111. The designations C, M, P, S, and T represent Cecropia, Myriocarpa, Piper, Senna, and Trichospermum respectively. Within each species the three bars from left to right represent 350, 525, and 700  $\mu$ l 1<sup>-1</sup> CO<sub>2</sub>. In A, the different shadings within each bar from bottom to top represent roots, stems, and leaves. Error bars represent two standard errors of a single treatment mean. The error bars in A are for total biomass

five species were: 14, 16 and 17% (Cecropia); 8, 7 and 7% (Myriocarpa); 8, 8 and 11% (Piper); 19, 22 and 19% (Senna); 13, 17 and 16% (Trichospermum). The species differed in their allocation patterns. Most notably, Myriocarpa allocated relatively little biomass to roots and stems (see below concerning LAR), and *Piper* allocated a relatively large proportion of its biomass to roots, primarily at the expense of stem allocation (Table 1, Fig. 1). The differences between Myriocarpa and the other species were most marked at day 45, while the difference between Piper and the other species was clearest at day 67. Cecropia, Trichospermum and Senna had similar allocation patterns. There were differences among these three species only at day 45 where Senna allocated more of its biomass to roots and stems than did Cecropia, and had a higher stem allocation than did Trichospermum or Cecropia.

The most pronounced difference among treatments in leaf area ratio (LAR) was the high ratio value for *Myriocarpa* relative to the other species (Fig. 1). Following *Myriocarpa* in the amount of leaf area per unit of biomass were *Piper* and *Trichospermum*, which were in turn followed by *Senna* and *Cecropia*. Although there were some minor dif-

Fig. 2. Leaf area profile of individually grown plants at day 111. Each division on the horizontal axis represents  $0.01 \text{ m}^2$ . Leaf area was summed over 0.1 m intervals for presentation. The designations C, M, P, S, and T represent Cecropia, Myriocarpa, Piper, Senna and Trichospermum respectively. The numbers given above each species represents the mean canopy height (m) for that treatment





**Fig. 3.** Single leaf net photosynthesis and conductance of individually grown plants at low (250) and high (1400  $\mu$ mole m<sup>-2</sup> s<sup>-1</sup>) light. The designations *C*, *M*, *P*, *S*, and *T* represent *Cecropia*, *Myriocarpa*, *Piper*, *Senna* and *Trichospermum* respectively. Within each species the three bars from left to right represent 350, 525, and 700  $\mu$ l l<sup>-1</sup> CO<sub>2</sub>. Error bars represent two standard errors of a single treatment mean

ferences in the rankings of the species in the earlier harvests, the same general trends were evident (Table 1). There was no effect of  $CO_2$  on LAR.

Specific leaf area (SLA) was one of the few variables on which  $CO_2$  had a consistent effect across all species; specific leaf area declined with  $CO_2$  (Fig. 1). This effect was only apparent at the final harvest, however (P < 0.0485for the main effect of  $CO_2$ );  $CO_2$  had no effect early in the experiment. Differences among species in specific leaf area were marked early in the experiment (Table 1), but these differences were much less pronounced by the end of the experiment (Fig. 1). In general, *Trichospermum*, *Myriocarpa* and to a lesser extent, *Piper*, tended to have a relatively high SLA compared to *Senna* and *Cecropia*. The exact rankings, however, did vary slightly among harvests.

There were marked differences among both species and  $CO_2$  treatments in where leaves were displayed (Table 1, Fig. 2). The mean canopy height (i.e. the average height of individual leaves weighted by the area of the leaves) tended to be highest in *Senna*, followed by *Trichospermum* and *Cecropia*, which were in turn higher than *Piper* and *Myriocarpa*. The difference between *Senna* and *Cecropia*-*Trichospermum* was only significant early in the experiment (days 45 and 67). *Piper* and *Myriocarpa* on the other hand had similar heights early in the experiment (Table 1) but by the final harvest *Piper* (mean canopy height=0.25 m) was taller than *Myriocarpa* (0.15 m). The effect of  $CO_2$  upon leaf display was only significant at the final harvest (P < 0.0411 for the  $CO_2 \times$  species interaction); mean canopy

height increased with  $CO_2$  in *Piper* and *Trichospermum* and decreased in *Senna* (Fig. 2).

Photosynthesis and conductance. There were differences, both among species (P < 0.002) and between light levels (P < 0.0002) in photosynthetic rates (Fig. 3). Senna had the highest rate (9.9  $\mu$ moles m<sup>-2</sup> s<sup>-1</sup>) and was followed by Trichospermum (7.6), Piper (7.4), and Cecropia (6.7), all three of which had rates greater than that of Mvriocarpa (4.9). Photosynthesis measured at high light (7.8 µmoles  $m^{-2} s^{-1}$ ) was only slightly greater than that at low light (6.8). Although  $CO_2$  had no effect on photosynthesis, there was an effect of  $CO_2$  upon conductance (P<0.0083). Conductance declined from 0.663 to 0.503 cm s<sup>-1</sup> as  $CO_2$  increased from 350 to 525  $\mu$ l 1<sup>-1</sup> (Fig. 3). Increasing CO<sub>2</sub> from 525 to 700 µl l<sup>-1</sup>, however, had no significant effect. The decline in conductance with elevated CO<sub>2</sub> cannot account for the lack of response in photosynthesis to  $CO_2$ . Calculation of CO<sub>2</sub> concentration within the leaves (von Caemmerer and Farquhar 1981) indicated that internal  $CO_2$  was not markedly depleted by the partial stomatal closure. Internal CO2 concentrations, averaged across light levels and species were 301, 407 and 573  $\mu$ l l<sup>-1</sup> at 350, 525 and 700  $\mu$ l l<sup>-1</sup> external CO<sub>2</sub> (P<0.0005 for the main effect of CO<sub>2</sub>). There were also differences among species (P < 0.0097) and between light levels (P < 0.0001) in conductance. Trichospermum (0.772 cm  $s^{-1}$ ) had a higher conductance than Cecropia (0.490) and Piper (0.430), and both Trichospermum and Senna (0.626) had a higher rate than



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Fig. 4A–C. The water requirement for growth (A), soil water content (B), and leaf water potential (C) for individually grown plants at day 111. The designations C, M, P, S, and T represent *Cecropia*, *Myriocarpa*, *Piper*, *Senna*, and *Trichospermum* respectively. Within each species the three bars from left to right represent 350, 525, and 700 µl l<sup>-1</sup> CO<sub>2</sub>. Error bars represent two standard errors of a single treatment mean

*Myriocarpa* (0.306). Conductance increased from 0.430 to 0.619 cm s<sup>-1</sup> as light level increased; the most noticeable light effect was exhibited by *Piper* (P < 0.0019 for the light × species interaction).

Water relations. The water requirement for growth of the individual plants showed consistent but nonsignificant decreases as the level of  $CO_2$  increased (Fig. 4). There were significant differences among species, however (P < 0.0006). Cecropia and had a lower water requirement than the other species.



**Fig. 5A, B.** Aboveground biomass (A) and percent community composition (B) for competitively grown plants at day 111. In A, the designations C, M, P, S, and T represent *Cecropia, Myriocarpa, Piper, Senna,* and *Trichospermum* respectively. Within each species the three bars from left to right represent 350, 525, and 700  $\mu$ l l<sup>-1</sup> CO<sub>2</sub>. Error bars represent two standard errors of a single treatment mean.  $\blacksquare$  *Cecropia;*  $\square$  *Myriocarpa;*  $\blacksquare$  *Piper;*  $\boxtimes$  *Senna;*  $\boxtimes$  *Trichospermum* 

Mid-day soil moisture content of the individual pots increased as  $CO_2$  increased (P < 0.0182 for the main effect of  $CO_2$ , Fig. 4). *Trichospermum* pots had a lower moisture content than any of the other species while *Senna* pots were lower than *Myriocarpa* (P < 0.0001 for the main effect of species).

There were dramatic differences among species in leaf water potential (Fig. 4). In *Cecropia, Myriocarpa*, and *Piper*, water potential remained close to zero regardless of date or  $CO_2$  treatment. In *Senna* and *Trichospermum* water potential was much less and tended to become more negative as the experiment progressed (data from earlier harvests not presented). *Senna* had a slightly more negative potential than *Trichospermum*. There was no effect of  $CO_2$  on plant water potential.

# Competitively grown plants

Growth, allocation, and architecture. Senna had the largest biomass followed by Cecropia and Trichospermum, which were larger than Piper, which in turn was larger then Myriocarpa (Fig. 5A). In contrast to the individually grown plants,  $CO_2$  had a major effect upon the biomass of plants

in the competitive arrays (P < 0.0015). The effect differed between species, however (P < 0.0001 for the CO<sub>2</sub> × species interaction). Aboveground biomass increased with CO<sub>2</sub> in *Cecropia, Myriocarpa, Piper,* and *Trichospermum,* and decreased in *Senna*. The differences between CO<sub>2</sub> levels and species in biomass can be graphed as percent composition of these communities (Fig. 5B). At 350 µl l<sup>-1</sup>, the community was heavily dominated by *Senna* which composed almost 50% of total community biomass. *Cecropia, Trichospermum,* and *Piper* made up most of the remaining community biomass. *Myriocarpa* only made up about 3% of community biomass. As the level of CO<sub>2</sub> increased the importance of *Senna* decreased substantially being replaced primarily by *Trichospermum* and *Piper* at 525 µl l<sup>-1</sup> and by *Cecropia, Trichospermum,* and *Piper* at 700 µl l<sup>-1</sup>.

Total leaf area of the various species and treatments displayed essentially the same patters as aboveground biomass (Fig. 6A). Senna and Trichospermum had the highest leaf areas followed by Cecropia and Piper. Myriocarpa had a smaller total leaf area than any of the other species. Elevated  $CO_2$  decreased leaf area in Senna and increased it in Trichospermum.

The species differed in the proportion of aboveground biomass allocated to stems versus leaves (P < 0.0001, data not presented). The ranking of species with regard to allocation of biomass to stems was essentially identical to the ranking of species with regard to aboveground biomass (Senna > Trichospermum = Cecropia > Piper > Myriocarpa).Leaf area ratio declined with  $CO_2$  (P<0.0329 for main effect of  $CO_2$ ), except in the case of Senna, which showed a slight increase (P < 0.002 for  $CO_2 \times$  species interaction, Fig. 6B). Myriocarpa had the highest leaf area ratio, followed by Piper and Trichospermum, which were not significantly different from each other, and then Cecropia and finally Senna. Specific leaf area (Fig. 6C) showed much the same pattern as leaf area ratio; there was a more or less general decline in specific leaf area with CO<sub>2</sub> with the exception of Senna. Myriocarpa and Trichospermum had the highest specific leaf area followed by Cecropia and Piper and finally Senna with the lowest specific leaf area.

The relative positions at which the leaf area of the various species was displayed in the competitive arrays (Fig. 7) showed similar pattern to the display of leaves in the individually grown plants. Mean canopy height was highest in *Senna*, followed closely by *Trichospermum* and then *Cecropia*. *Piper* was substantially shorter than either of these three species and taller than *Myriocarpa*. Elevated CO<sub>2</sub> increased mean canopy height in *Cecropia*, *Piper*, and *Trichospermum*, and decreased it in *Senna* (P < 0.0002 for the CO<sub>2</sub> × species interaction).

# Light profiles

Carbon dioxide had little effect upon light profiles within the competitive canopies (Fig. 8). There was no effect of  $CO_2$  upon percent light penetration on either day 40 or day 74. Light level at mid-canopy, however, was depressed at 525, relative to both 350 and 700 µl  $1^{-1}$  CO<sub>2</sub> on day 57 (data not presented).

#### Water relations

Water potential of the competitive plants (data not presented) was essentially identical to that of the individual



Fig. 6A–C. Leaf area (A), leaf area ratio (B), and specific leaf area (C) of competitively grown plants at day 111. The designations C, M, P, S, and T represent Cecropia, Myriocarpa, Piper, Senna, and Trichospermum respectively. Within each species the three bars from left to right represent 350, 525, and 700  $\mu$ l l<sup>-1</sup> CO<sub>2</sub>. Error bars represent two standard errors of a single treatment mean

plants at final harvest (Fig. 4C). Water potential of *Cecropia*, *Myriocarpa* and *Piper* approached zero while that of *Senna* was in the range of -1.2 to -1.6 MPa and that of *Trichospermum* was slightly higher. Again, there was no effect of CO<sub>2</sub>. Water content of the soil in the competitive arrays averaged 38.5% and did not vary with CO<sub>2</sub>.



**Fig. 7.** Leaf area profile of competitively grown plants at day 111. Each division on the horizontal axis represents  $0.001 \text{ m}^2$ . Leaf area was summed over 0.1 m intervals for presentation. The designations *C*, *M*, *P*, *S*, and *T* represent *Cecropia*, *Myriocarpa*, *Piper*, *Senna*, and *Trichospermum* respectively. The numbers given above each species represents the mean canopy height (m) for that treatment

# Regression analysis

Stepwise regression of the biomass of plants in the competitive arrays on physiological and morphological parameters of the individually grown plants revealed that over 92% of the total variation in competitive performance can be correlated with only six variables (Table 2). These variables included mean canopy height at the last harvest, leaf area ratio both early and late in the experiment, net photosynthesis at low, and to a lesser extent, at high light, and allocation to roots early in the experiment. Leaf area ratio and net photosynthesis at high light were negatively correlated with performance while all other variables were positively correlated with performance. Mean canopy height was the first variable entered into the regression and accounted for over 60% of total variation in performance. The remaining five variables accounted for progressively smaller proportions of the remaining 32% of variation accounted for by the model.

Principal component analysis of the independent variables used in the above regression analysis indicated that over 95% of the variation in the original 24 variables could be summarized by the first 11 principal components. Stepwise regression of competitive performance on these 11 new orthogonal (non-correlated) variables revealed that over 85% of variation in performance can be accounted for by



Fig. 8. Light profile in competitive arrays at day 74. Maximum light levels above the canopy were in the range of  $1000-1200 \mu$  moles m<sup>-2</sup> s<sup>-1</sup>. Lines represent exponential curves fitted to the transformed data by linear least squares regression.  $\blacklozenge$  350;  $\Box$  525; + 700

**Table 2.** Summary of stepwise regression analysis using the mean biomass per species per chamber as the dependent variable, and the physiological and morphological characters measured on the individually grown plants as the independent variables. Only those variables significant at the 0.05 level were added to the regression model. The overall  $R^2$  for the model was 0.922 (error df=31, P < 0.0001)

Variable	Partial R <sup>2 a</sup>	Relationship to the dependent variable	Level of significance
Mean canopy height at day 111	0.603	+	0.0005
Leaf area ratio at day 45	0.138		0.0005
Net photosynthesis at low light	0.073	+	0.0001
Proportion of biomasss allocated to roots at day 45	0.054	+	0.0001
Leaf area ratio at day 111	0.037		0.0006
Net photosynthesis at high light	0.016		0.0017

<sup>a</sup> The incremental increase in the proportion of total variance explained by the model in the order in which the variables were added to the model by the selection procedure

2 factors: the first and third principal components. The first principal component which accounted for almost 77% of variation in competitive performance was primarily a measure of height. The variables which contributed most to this factor were mean canopy height and allocation of biomass to stems at the various harvests (Table 3). The third principal component which accounted for 9% of variation in competitive performance was also closely related to allocation patterns; it was negatively related to root allocation and positively related to leaf area ratio. Since the relation-

**Table 3.** Factor patterns for principal components 1 and 3 of the original independent variables used in the regression analysis. Principal components 1 and 3 accounted for 38.4 and 10.0% of the variation in the original variables, respectively

Original variables <sup>a</sup>	Principal Component 1	Principal Component 3
Conductance H	0.225	-0.151
Conductance L	0.432	0.041
Leaf area ratio 1	-0.691	0.421
Leaf area ratio 2	-0.628	0.453
Leaf area ratio 3	-0.732	0.271
Net photosynthesis H	0.474	-0.365
Net photosynthesis L	0.493	-0.217
Allocation to roots 1	0.311	-0.582
Allocation to roots 2	-0.243	-0.545
Allocation to roots 3	-0.180	-0.588
Allocation to stems 1	0.879	0.128
Allocation to stems 2	0.841	0.251
Allocation to stems 3	0.817	0.257
Specific leaf area 1	-0.385	0.349
Specific leaf area 2	-0.450	0.349
Specific leaf area 3	-0.306	0.180
Water potential 1	0.753	0.059
Water potential 2	0.783	0.099
Water potential 3	0.782	0.056
Water requirement for growth	-0.116	-0.387
Water content of soil 3	-0.441	-0.135
Mean canopy height 1	0.878	0.162
Mean canopy height 2	0.877	0.326
Mean canopy height 3	0.887	0.143

<sup>a</sup> The designations H and L represent measurements made at either high or low light irradiance, while the designations 1, 2, and 3 represent harvests at days 45, 67, and 111 respectively

ship between the third principal component and competitive performance was negative, allocation to roots was positively correlated to performance.

### Discussion

#### Growth and photosynthesis

The general lack of response to  $CO_2$  in overall growth and photosynthesis in the individually grown plants was somewhat surprising (Figs. 1 and 3). Fast-growing temperate  $C_3$ plants commonly exhibit a substantial increase in growth with a doubling of  $CO_2$  concentration (Carlson and Bazzaz 1980; Cure 1985). In the only other study in which tropical tree seedlings were grown under controlled  $CO_2$  conditions (Oeberbauer et al. 1985) both species involved, (*Ochroma lagopus* and *Pentaclethra macroloba*), showed a slight decrease in photosynthesis when grown at 675 versus 350 µl  $1^{-1}$  CO<sub>2</sub>. In contrast to the present study, however, these authors did find enhanced growth at the higher CO<sub>2</sub> level, which they attributed to enhancement of photosynthesis by CO<sub>2</sub> early in the experiment (they measured photosynthesis at the end of the experiment only).

Short-term experiments with both temperate and tropical species in which leaves formed at ambient  $CO_2$  levels are subjected to elevated  $CO_2$  levels invariably show marked enhancement of photosynthesis with  $CO_2$  (Oechel and Strain 1985). However, plants grown under elevated  $CO_2$  concentrations usually show a less marked effect of  $CO_2$  upon photosynthesis. The reasons for the reduction in photosynthetic potential after long periods of exposure to elevated  $CO_2$  are not understood but may be related to end-product inhibition and the subsequent physiological changes in leaves in response to the surplus of fixed carbon (Sasek et al. 1985). It has been suggested that differences among plants in their long-term response to  $CO_2$  may depend at least in part upon the ability of the plants to use an increased supply of photosynthates (Oechel and Strain 1985). The decrease in specific leaf area with  $CO_2$  in our study (Figs. 1 and 6) suggests that carbohydrate may have been accumulating in the leaves and that these species were not particularly efficient in translocating and utilizing the extra carbohydrate.

Another factor which may help explain the general lack of response to elevated  $CO_2$  is limitation by other resources. As discussed below, the availability of both light and mineral nutrients appear to have been important factors in determining competitive outcome. It seems likely that the availability of these resources also limited growth of the individually-grown plants (albeit to a lesser degree). Limitation by both light and nutrient availability have been shown to affect response to elevated  $CO_2$  (Zangerl and Bazzaz 1984).

The two situations where  $CO_2$  did have an effect upon growth of individuals in this experiment, the depressed growth of Cecropia and the enhanced growth of Trichospermum at 525  $\mu$ l l<sup>-1</sup> (Fig. 1), cannot be explained at the present time. A number of other studies have documented similar patterns in which response to ca. 500  $\mu$ l l<sup>-1</sup> CO<sub>2</sub> is markedly different from the response to either 350 or 700 µl  $1^{-1}$  CO<sub>2</sub> (Bazzaz and Garbutt 1988). In the past such responses have usually been attributed to chamber effects. In many of these studies there was only one chamber per  $CO_2$  level, which meant that random differences between chambers not related to CO<sub>2</sub> concentration could have a marked effect upon the results. The relatively large number of chambers per  $CO_2$  level (4) used in the present study, however, argues against this explanation. More detailed analyses of the physiological changes which take place in plants grown at different  $CO_2$  levels will be required to explain this effect.

# Allocation and architecture

Elevated  $CO_2$  concentrations often result in a greater allocation of resources to non-photosynthetic structure (eg. stems and roots), which in turn results in a lowered leaf area ratio even though total leaf area per plant may increase (Oechel and Strain 1985). Although there was a tendency for these changes in allocation to occur in the present experiment, the effects were not large and were often transitory (Table 1, Figs. 1 and 6).

Much more marked than changes in allocation with  $CO_2$ , were changes in shoot architecture (Figs. 2 and 7). Interestingly, the effect of  $CO_2$  was different depending upon the species; increasing canopy height in *Piper, Trichospermum*, and to a lesser extent in *Cecropia*, and decreasing it in *Senna*. As changes in allocation of biomass to stems in these species with  $CO_2$  were small, these differences seem to be due, at least in part, to changes in cambial versus apical growth, and to changes in branching patterns. Previous studies have not examined the effect of  $CO_2$  upon shoot architecture in the same detail as we have, but increases in plant height with  $CO_2$  have been reported by

a number of studies (Sionit et al. 1985; Paez et al. 1984). No one seems to have reported decreases in height with increased  $CO_2$ .

# Water relations

The decrease in stomatal conductance with increased  $CO_2$  that was observed in this experiment (Fig. 3) is in accord with the data on temperate species (reviews in Oechel and Strain 1985) and with that of Oberbauer et al. (1985) for *Ochroma lagopus* and *Pentaclethra macroloba*. Stomatal conductance of *Piper hispidum* grown at ambient  $CO_2$  is insensitive to short-term fluctuations in  $CO_2$  (Mooney et al. 1983) but these results are not comparable to our study where plants were grown at the  $CO_2$  level at which conductance was measured. Plants grown at elevated  $CO_2$  concentrations often develop leaves with fewer stomata (Woodward 1987) which will affect stomatal conductance quite apart from any direct effect of  $CO_2$  on stomatal aperature.

The decrease in stomatal conductance that was observed (Fig. 3) tended to decrease the water requirement for plant growth (Fig. 4A) and resulted in a higher soil water content for individual plants grown at elevated CO<sub>2</sub> concentrations (Fig. 4B). The differences in water content were small, however, and had no effect on plant water potential (Fig. 4C). Overall, in spite of the tendency for CO<sub>2</sub> to decrease stomatal conductance, CO<sub>2</sub> had little effect upon plant water relations under the relatively well-watered conditions of this experiment. Similar patterns were also found for the competitive arrays where CO<sub>2</sub> had no effect on either soil moisture content or plant water potential.

#### Competitive outcome

The overall performance of individuals was not a good predictor by itself of performance in the competitive arrays (i.e. compare Figs. 1A and 5A). The regression analyses, however, suggest that competitive performance was highly correlated with a small number of morphological and physiological traits (Tables 2 and 3). Most important of these traits were canopy height, together with the correlated trait of biomass allocation to stems. There were major differences among both species and  $CO_2$  levels in these traits suggesting that they helped explain both species and  $CO_2$ effects on competitive performance. Two other traits which were positively correlated with competitive performance were photosynthesis at low light and increased allocation to roots. There were differences among species, but not among  $CO_2$  treatments in these traits.

The fact that height of leaf display as well as photosynthesis at low light were important factors in determining competitive performance suggests that competition for light was important in this system. This suggestion is supported by the light profiles in the arrays which indicate that a substantial portion of the leaf area in the communities received only low light. Canopy height, averaged across species, was 0.37 m in the competitive arrays. Reference to figure 7 indicates that less than 15% of incident light penetrated the canopy to this level. Maximum light levels above the canopy were approximately 1000–1200 µmoles m<sup>-2</sup> s<sup>-1</sup>. The general lack of any major response to photosynthesis to increased light (Fig. 3) also implies that the plants were producing "shade" leaves which can better take advantage of the low light levels. The importance of root allocation in determining competitive success implies that competition for either water or nutrients may also have been of some importance early in the experiment. As none of the water relations parameters were correlated with competitive performance, it seems likely that it was competition for nutrients rather than water which was more crucial.

The various analyses and results discussed above can be summarized with regard to competitive interactions by the following postulated scenario. Early in the experiment the major interaction among species was competition for nutrients; this allowed Piper, with its high proportion of biomass allocated to roots to gain an early competitive edge (this is also true to a lesser extent for Senna and Trichospermum). Very rapidly, however, the canopy closed in and competition for light became the overiding factor determining competitive success. Senna, Trichospermum and Cecro*pia* with their greater biomass allocation to stems were able to overshadow the other species and came to predominate. Senna, in particular, because of its high photosynthetic rate relative to the other species, and its shoot architecture was very successful. Myriocarpa and Piper both displayed their leaves at the same height (at 350  $\mu$ l l<sup>-1</sup> CO<sub>2</sub>), but Myriocarpa was more affected by competition than Piper probably because of the early advantage of Piper in nutrient competition. The effect of enhanced CO<sub>2</sub> on competition was through its effect on canopy architecture. Elevated CO<sub>2</sub> decreased canopy height in Senna and increased it in Cecropia, Piper and Trichospermum increasing the competitive ability of these species relative to Senna. Carbon dioxide also had an effect on water use but under the well-watered conditions of this experiment this did not affect competitive outcome. Under conditions of water stress elevated CO<sub>2</sub> would likely have favoured the growth of those species with a higher water requirement for growth (Fig. 4).

#### Conclusion

Our objective was to answer the question: can competitive outcome be predicted from a knowledge of resource availability and the physiological attributes of the individual species? We have shown that in the present case it is possible to interpret the results of competition in terms of resource availability and various attributes of the species which influence their ability to capture and utilize resources. We have also demonstrated that simple regression models using morphological and physiological attributes of the species as the independent variables can explain a large proportion of the total variance in competitive success. These regression models are predictive only in a limited sense, however. As conditions under which the study is conducted are changed (e.g. level of water availability), the predictions of the model would very likely no longer hold. Nevertheless, we feel this approach can form the basis for models that are able to predict competitive outcome over a wider range of conditions. Information on the physiological attributes of the individual species together with their patterns of resource uptake can be combined in a mechanistic physiological model of competition. Models of this type for single species already exist in the form of crop growth models (e.g. see Reynolds and Acok 1985). What is needed is to combine simplified growth models for different species in the context of the overall level of resource availability, and the extent to which each of the competitors affects the common resource environment. Mechanistic models such as the one described have the potential to be more widely applicable than current empirical models. Rather than considering species-specific effects which are no longer relevant as the species composition, or the environment of the community is changed, a mechanistic model considers the specific traits that make a species a good competitor under various conditions and, therefore, is more easily adapted to different situations.

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