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Responses of communities of tropical tree species to elevated CO_2 in a forest clearing

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Abstract Communities of ten species of tropical forest tree seedlings from three successional classes were grown at ambient and elevated CO_2 in large open-top chambers on the edge of a forest in Panamá. Communities grew from 20 cm to approximately 2 m in height in 6 months. No enhancements in plant biomass accumulation occurred under elevated CO_2 either in the whole communities or in growth of individual species. Reductions in leaf area index under elevated CO_2 were observed, as were decreases in leaf nitrogen concentrations and increases in the C:N ratio of leaf tissue. Species tended to respond individualistically to elevated CO_2, but some generalizations of how successional groupings responded could be made. Early and mid-successional species generally showed greater responses to elevated CO_2 than late-successional species, particularly with respect to increases in photosynthetic rates and leaf starch concentrations, and reductions in leaf area ratio. Late-successional species showed greater increases in C:N ratios in response to elevated CO_2 than did other species. Our results indicate that there may not be an increase in the growth of regenerating tropical forest under elevated CO_2, but that there could be changes in soil nutrient availability because of reductions in leaf tissue quality, particularly in late-successional species.

Key words Elevated CO_2 · Biomass allocation · Successional status · Leaf chemistry · Tropical forest tree species

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Introduction

The atmospheric CO_2 concentration has been increasing rapidly since the industrial revolution in the last century. Its concentration is predicted to approximately double within the next century, profoundly affecting the biosphere (Tans et al. 1990; Schlesinger 1991; Gates 1993). Because CO_2 is the substrate for photosynthetic carbon fixation in plants, it was proposed that elevated levels of atmospheric CO_2 would increase photosynthesis. This in turn would lead to enhanced plant growth and carbon sequestration of some of the "extra" CO_2 in the atmosphere into forests and their soils (reviewed in Bazzaz 1990). To evaluate this prediction, global carbon budgets have been calculated and estimates made of the importance of forests in regulating CO_2 concentrations in the atmosphere (e.g., Brown and Lugo 1982; Polglase and Wang 1992; Dixon et al. 1994).

Tropical forests store approximately 40% of the earth's biomass (Dixon et al. 1994). Because of high rates of deforestation in tropical forests they have been estimated to be a net source of CO_2 to the atmosphere (Dixon et al. 1994), although there is evidence that intact tropical forests are net CO_2 absorbers (Grace et al. 1995). Whether tropical forests have the potential to be sinks for atmospheric CO_2 is undecided (Dixon et al. 1994; Grace et al. 1995; Lloyd and Farquhar 1996). If elevated CO_2 does increase growth of tropical forest plants in existing and/or regenerating forests, tropical forests could, at least in the short term, sequester atmospheric CO_2. If tropical forest growth is not stimulated by elevated CO_2, and extra carbon is incorporated into fast-cycling belowground carbon pools (Hungate et al. 1997), then there could be enhanced rates of forest turnover (Phillips and Gentry 1994), possibly because of reduced soil nutrient availability due to feedback from soil microbial processes (Comins and McMurtrie 1993; Diaz et al. 1993; McGuire et al. 1995; Berntson and Bazzaz 1996). Experiments assessing the influence of elevated CO_2 on the productivity of plant species from tropical ecosystems have

shown conflicting results. Plants grown individually in pots have shown increases in biomass accumulation when kept under elevated CO_2 (Oberbauer et al. 1985; Ziska et al. 1991; Winter and Lovelock, in press), while those in experiments where plants have been grown in competing arrays (Reekie and Bazzaz 1989), or in glasshouse-maintained micro-ecosystems (Körner and Arnone 1992; Arnone and Körner 1995) have shown very little increase in biomass accumulation.

Elevated atmospheric CO_2 may also affect tropical forest species diversity (Bazzaz 1990; Körner 1996). This is because species may have differential sensitivities to elevated CO_2 which might alter their competitive abilities (Oberbauer et al. 1985; Reekie and Bazzaz 1989; Ziska et al. 1991; Ceulemans and Mousseau 1994). Because of the enormity of the task of assessing individual species responses to elevated CO_2, especially in natural ecosystems, it has been suggested that research focus on understanding the response of representative species of functional groupings of plants to elevated CO_2. Such studies have shown that elevated CO_2 favors fast-growing species at the expense of slower-growing species (Poorter 1993; Roumet and Roy 1996). In contrast, other investigators have asserted that all species are likely to respond similarly to elevated CO_2 (Loehle 1995; Lloyd and Farquhar 1996; Winter and Lovelock, in press).

In tropical forests, tree species have a wide range of growth rates that are correlated with their successional status (Bazzaz and Pickett 1980; Kitajima 1994; Condit et al. 1996). Species that are fast growing are early successional and inhabit large gaps in the forest or forest edges. Those that are shade tolerant and slow growing are late successional, their seedlings often persisting in the understory for years. An intermediate grouping of building-phase or mid-successional species can also be recognized. If elevated CO_2 affects species from some successional groupings more than others, then this could facilitate predictions as to the nature of changes in forest diversity and functioning under elevated CO_2.

In this paper we describe work where we tested whether elevated CO_2 increases biomass accumulation of tropical plant communities growing under natural conditions in a regenerating tropical forest landscape. We installed eight large open-top chambers on the edge of a tropical forest in Panamá. Within the chambers we grew a mixture of ten tropical species with a range of successional status in natural soil under either ambient-or elevated-CO_2 conditions for about 6 months. We monitored growth and plant biomass accumulation of the whole community and of individual species. By growing tropical tree species with different successional status we also aimed to test whether elevated CO_2 influences the growth of species of similar successional status in a predictable way.

Materials and methods

Plant communities were grown in eight octagonally shaped 1.9-m-diameter, 2.5-m-tall open-top chambers on vacant grassland adjoining forest of Parque Natural Metropolitano, Panamá, from February to August 1996. At the start of the experiment (February–April), which was in the second half of the dry season, plants were watered daily. Soils at the site are poor, having on average 2.25% organic matter, pH 5.9, total nitrogen (N) 0.144%, total phosphorus (P) 0.013%, total carbon (C) 1.42%, and a C:N ratio of approximately 10. The open-top chambers were made of aluminum frame covered with clear plastic film and ventilated with fans (model 4C 054 A, capacity 26 m^3 min^{-1}, Dayton, Niles, Ill.). The chambers were arranged in pairs with one fan ventilating each pair of chambers. The target CO_2 concentration was twice ambient (approximately 700 ppm). To achieve this, CO_2 was delivered for 24 h per day to one of each pair of chambers by injection of pure CO_2 at a constant flow rate. CO_2 concentrations within the chambers were measured every 10 s for periods of 30 min in the morning, midday, and evening on days at both the beginning and end of the experiment. Additional measures were made throughout the experiment to confirm the CO_2 concentrations were about twice ambient in the elevated-CO_2 chambers. CO_2 was bubbled through a saturated solution of potassium permanganate to remove any ethylene impurities before it was delivered to the chambers. For the first 2 months of the experiment, only the lower 1.2 m of the chambers were covered with plastic film. The air inside the chambers was exchanged twice every minute. The flow rate of pure CO_2 into the ventilation stream at this time was 5 l min^{-1}, giving a mean CO_2 concentration within the chambers of 628 (SD ± 59) ppm. The CO_2 concentration ranged between 440 and 780 ppm, but for 90% of the time was between 540 and 700 ppm. After the first 2 months, the chamber walls were completely covered with plastic film. The air within the chambers was exchanged once per minute, which was sufficient to maintain close to ambient air temperatures within the chambers (Fig. 1). The flow rate of pure CO_2 into the ventilation stream was 4 l min^{-1}, giving a mean CO_2 concentration within the chambers of 700 (SD ± 84) ppm. The CO_2 concentration ranged between 440 and 900 ppm, but for 80% of the time was between 540 and 740 ppm. Ambient CO_2 concentrations varied diurnally between 350 and 400 ppm, the higher values being recorded at night. Temperature and humidity inside and outside the chambers were measured with an Assman psychrometer (Oaklon 37210 series, Cole Palmer, Ill.). Temperatures within the chambers varied between 21 and 33°C, exceeding air temperatures outside the chambers by a maximum of 2°C (Fig. 1). Relative humidity declined during the day from 100 to approximately 60% and was similar inside and outside the chambers (Fig. 1). Photon flux densities (PFD) reached up to 2200 μmol m^{-2} s^{-1} and were similar inside and outside the chambers (Fig. 1). By the end of the experiment, PFD at ground level in the chambers was approximately 10% of the PFD incident at the top of the chamber (Fig. 1).

Ten species of trees were grown within each chamber for 6 months. The experiment was terminated at this time because two of the species were approximately 2 m tall. The nine local species were each allocated to spaces approximately 30 × 30 cm in size within a 3 × 3 matrix, and then surrounded with a border of a tenth species exotic to Panamá, *Swietenia macrophylla* (Meliaceae), which is used as a plantation species in Panamá (Fig. 2). To ensure the results could be generalized for any arrangement of species, species were arranged differently in each pair of chambers (Fig. 2). In each arrangement, late-successional species were dispersed among the other faster-growing species. Of the nine local species studied, three were early successional, *Cecropia longipes* Pitt. (Moraceae), *Luehea seemannii* Tr. & Planch. (Tiliaceae), and *Ficus insipida* Willd. (Moraceae); three were shade-tolerant, late-successional species, *Tetragastris panamensis* (Engler) O. Kuntze (Burseraceae), *Virola surinamensis* (Rol.) Warb. (Myristicaceae), and *Calophyllum longifolium* Willd. (Clusiaceae); and three were mid-successional, *Antirrhoea trichantha* (Griseb.) Hemsl. (Rubiaceae), *Cordia alliodora* (R. & P.) Cham. (Boraginaceae) and *Anacardium excelsum* (Bertero & Balb.) Skeels (Anacardiaceae). Plants were transplanted into the chambers when they had between 50 and 500 cm^2 leaf area (Table 1). Leaf area was determined at approximately 6-week intervals throughout the 6 months of the experiment. Leaf area was estimated using regressions between measures of leaf length or width

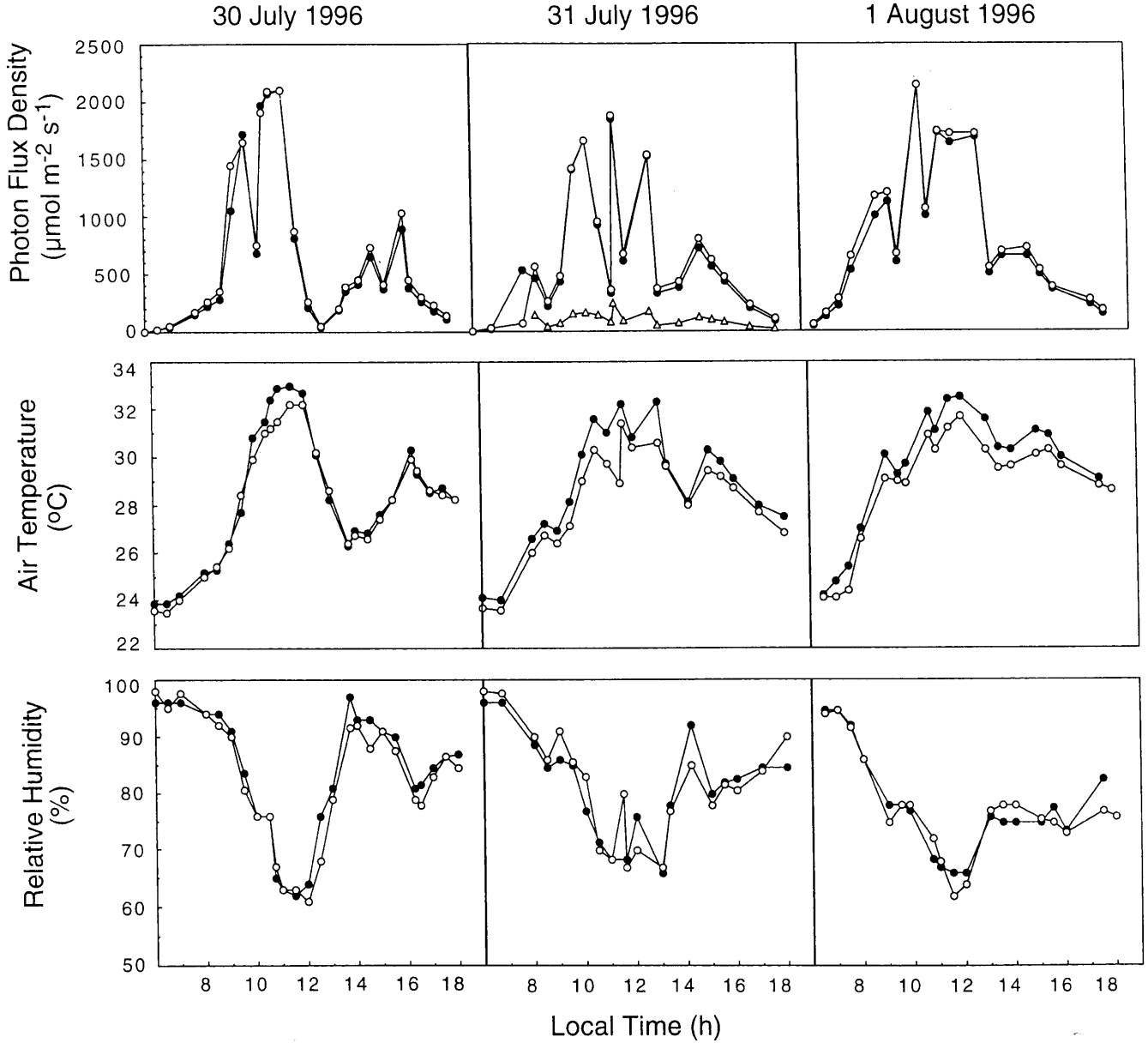

Fig. 1 Photon flux density (*upper panels*), air temperature (*middle panels*), and relative humidity (*lower panels*) inside (*filled circles*) and outside (*open circles*) the open-top chambers for 3 days toward the end of the experiment. Photon flux density under the canopy (20 cm height) within the chambers is shown for 31 July 1996 (*open triangles*). Conditions are typical for the wet season (April–November), with bright mornings followed by cloudy skies in the afternoon, and frequent thunderstorms. Air temperatures within the chambers are approximately 2°C above that outside when photon flux densities are high during the middle of the day

and leaf area for each species. The regressions were established by measuring the area of tracings of leaves of experimental plants using a LiCor leaf area meter (Li-Cor, Lincoln, Neb.). The adequacy of the regression equations was checked at each leaf census. Relative growth rates of leaf area for communities were calculated as $\ln(CHLA_2) - \ln(CHLA_1)/(t_2-t_1)$ where CHLA is the total leaf area within a chamber and t_1 and t_2 are time in days. Final leaf areas are direct measures of harvested leaves. All senesced leaves (necromass) were collected and dried throughout the experiment.

Net photosynthetic CO_2 exchange was measured on mature leaves in the final 2 weeks of the experiment using a Li-Cor 6400 portable photosynthesis measuring system. Measurements were made at approximately 2-hourly intervals over 4 full days (6:00 a.m.–6:30 p.m.). At each measurement period, two leaves from each plant of the target species were randomly selected for measurement. For *Swietenia*, two leaves from two plants per chamber were selected. Photosynthesis, PFD, and leaf temperature were measured at the CO_2 concentration at which leaves were grown. The measurements were made by clamping the cuvette on the leaf and holding the cuvette such that the leaf remained in its natural orientation. Photosynthetic rate was logged when the rate became constant, usually within 1 min. During each individual measurement, PFD was constant. Photosynthetic light response curves (Fig. 5) were generated using the variation in light levels that occurred throughout the days of measurement. Leaf temperatures varied between 23 and 41° C depending on ambient air temperature and exposure to PFD.

All plants were harvested after 6 months within 5 days. Intact root systems were excavated by hand using a high-pressure water hose. After harvest, all plant material was initially placed into a

drying oven for 1 h at 120°C. After the initial heating of the plant material it was dried to a constant weight at 60°C before weighing.

Relative growth rate (RGR) for individual species was calculated as $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ where W_2 and W_1 are the dry weights at the end and the beginning of the experiment respectively, and $t_2 - t_1$ is the duration of the experiment in weeks. Net assimilation rate (NAR) was calculated as $[(W_{t_2} - W_{t_1})/(t_2 - t_1)]/[LA_{t_2} - LA_{t_1})/(\ln LA_{t_2} - \ln LA_{t_1})]$ where LA_{t_2} and LA_{t1} are the leaf area at the end and the beginning of the experiment, respectively. The leaf area ratio (LAR), specific leaf area (SLA), leaf weight ratio (LWR) and root:shoot ratio were calculated from final dry weight measures of biomass and leaf area. Net primary production of the communities was calculated as $(CHW_{t_2} + \text{necromass} - CHW_{t_1})/(t_2 - t_1)$, where $CHWt_2$ and CHW_{t_1} are the total dry weight of plants within the chambers at the end and the beginning of the experiment, respectively. Leaf area index for the communities was calculated at the end of the experiment as CHLA/1.77 (the internal diameter of the open-top chambers, excluding peripheral airducts of the ventilation system was 1.5 m). Community characteristics of RGR, NAR, LWR, SLA, and root:shoot ratio were calculated using biomass dry weight and leaf area from the community as a whole (i.e., all plants summed).

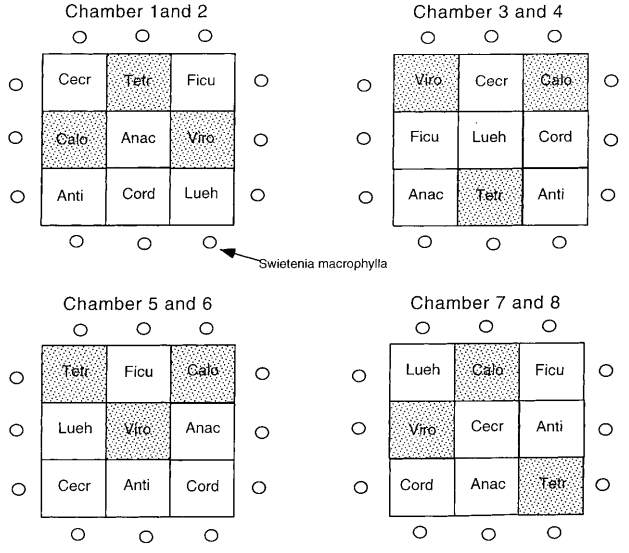

Fig. 2 Planting arrangement within the open-top chambers. Squares are 30 × 30 cm. For each planting arrangement, one chamber was exposed to elevated levels of CO_2 and the other to ambient levels of CO_2. In each arrangement, late-successional species were dispersed among the other faster-growing species. Of the nine local species studied, three were early successional: *Cecr Cecropia longipes* Pitt. (Moraceae), *Lueh Luehea seemannii* Tr. & Planch. (Tiliaceae), and *Ficu Ficus insipida* Willd. (Moraceae); three were shade-tolerant, late-successional species (*shaded squares*): *Tetr Tetragastris panamensis* (Engler) O. Kuntze (Burseraceae), *Viro Virola surinamensis* (Rol.) Warb. (Myristicaceae), and *Calo* is *Calophyllym longifolium* Willd. (Clusiaceae); and three were mid-successional: *Anti* is *Antirrhoea trichantha* (Griseb.) Hemsl. (Rubiaceae), *Cord Cordia alliodora* (R. & P.) Cham. (Boraginaceae), and *Anac Anacardium excelsum* (Bertero & Balb.) Skeels (Anacardiaceae). The position of *Swietenia macrophylla* (Meliaceae), an exotic in Panamá, is shown with *open circles*

Carbohydrate analysis

For analysis of carbohydrates, mature leaves were harvested at dawn and dusk. Directly after harvesting, leaf tissue was placed in liquid nitrogen. Leaves were then freeze dried for storage. Dried samples were finely powdered in a sample mill (MM2, Retsch, Idar-Oberstein, Germany) and extracted with hot water. Aliquots of this extract were analyzed by high-pressure liquid chromatography (HPLC) on an anion-exchange column (Carbopac PA100, 250 × 4 mm, Dionex, Sunnyvale, CA). Low-molecular-weight carbohydrates and polyols were eluted by 50 mM NaOH at 32°C and detected by PAD (pulsed amperometric detection; ED40, Dionex). For determination of starch content, 20 mg of the finely ground powder was extracted with 1 ml distilled water at room temperature, centrifuged, and the pellet reextracted with 1 ml of 80% ethanol and 1 ml 90% ethanol at 60°C for 5 min. The pellets were dried and incubated with 8 μkat heat-stable α-amylase (from *Bacillus licheniformis*, Sigma, St Louis, Mo.) in 1 ml distilled water at 85°C for 30 min. The samples were centrifuged and 100-μl aliquots of the supernatant incubated with 160 nkat amyloglucosidase (from *Aspergillus niger*, Boehringer-Mannheim, Mannheim, Germany) in 0.5 ml of 20 mM sodium acetate (pH 4.6) at 55°C. The reaction was terminated after 30 min by addition of 0.5 ml chloroform. Glucose and other water-soluble sugars were quantified in aliquots of the supernatants by HPLC-PAD (Carbopac PA100, 250 × 4 mm, 150 mM NaOH at 32°C).

Statistical analysis

Differences in characteristics of communities growing under elevated and ambient CO_2 were assessed using paired *t*-tests. Chamber 3 was excluded from the analysis because the *C. longipes* plant from that chamber was abnormally small, reaching only 59 cm in height after 25 weeks, compared to an average height of 150 cm for the

Table 1 Mean (± SE) initial biomass (dry weight), height, and leaf area of ten species of tropical tree seedlings (n = 3–5)

	Plant charactersitic		
	Biomass (g)	Height (cm)	Leaf area (cm^2)
(A) Early successional			
Cecropia longipes	4.91 ± 0.43	12.5 ± 2.0	574 ± 50
Ficus insipida	4.80 ± 0.43	28.0 ± 1.0	525 ± 30
Luehea seemannii	3.51 ± 0.38	23.5 ± 1.5	280 ± 32
(B) Mid-successional			
Anacardium excelsum	4.29 ± 0.62	16.0 ± 1.0	387 ± 43
Antirrhoea trichantha	1.83 ± 0.12	18.0 ± 1.0	316 ± 5
Cordia alliodora	5.61 ± 0.51	18.0 ± 1.0	549 ± 71
(C) Late successional			
Calophyllum longifolium	4.65 ± 0.23	26.0 ± 1.0	308 ± 27
Tetragastris panamensis	1.86 ± 0.13	17.5 ± 0.5	160 ± 7
Virola surinamensis	2.54 ± 0.32	15.0 ± 2.5	182 ± 23
(D) Surrounding species			
Swietenia macrophylla	0.20 ± 0.01	16.0 ± 0.5	46 ± 5

other plants. For the analysis of community characteristics, exclusion of chamber 3 also leads to the exclusion of its pair, chamber 4.

To assess the response to CO_2 of individual species, data for nine species (excluding *S. macrophylla*) were analyzed by analysis of variance (ANOVA). Within the ANOVA model, species were considered random and were nested within successional status (either early, mid- or late successional) which was considered a fixed effect. CO_2 concentration was also considered a fixed effect. All plants from chamber 3 were excluded. The data were also analyzed when plants from both chamber 3 and 4 were excluded. Results were similar and thus the data from plants in chamber 4 were included in the analysis. Adequacy of the model was checked by assessing plots of studentized residuals on predicted values. Data in which the variance was not constant over its range were logarithmically transformed before the analysis. This occurred for root:shoot ratio, final leaf area, total dry weight, SLA, leaf nitrogen concentrations and NAR.

Results

Community level responses

Growth of leaf area over time was slightly decreased in communities growing under elevated CO_2 (Fig. 3). At harvest, final leaf area within the chambers and the leaf area index were lower in communities grown under elevated CO_2 (Table 2). Final biomass, net primary production, and necromass accumulated over the 6 months of the experiment did not differ among elevated- and ambient-CO_2-grown communities (Table 2), although there was variation among pairs of open-top chambers. Necromass was approximately 10% of the net primary production under both elevated- and ambient-CO_2 concentrations (Table 2).

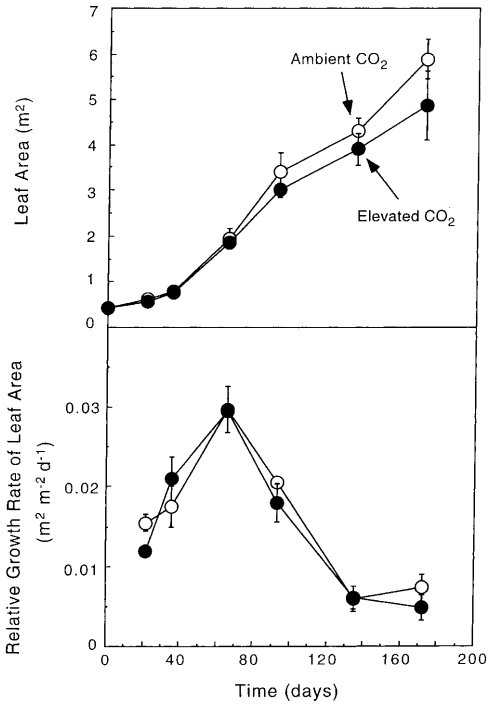

Fig. 3 Growth of mean community leaf area (*upper panel*) and relative growth rate of mean community leaf area (*lower panel*) over the experiment. Communities were grown under elevated CO_2 (*filled circles*) and ambient CO_2 (*open circles*). Values are means ± SE for $n = 4$ for communities grown under ambient CO_2 and $n = 3$ for communities under elevated CO_2

Response of successional groups and species

Leaf area growth of each individual species followed a similar trend as the whole community, with leaf area being similar or slightly reduced when plants were grown under elevated CO_2 (Fig. 4, Table 3). Biomass accumulation and height were similar under both elevated and ambient CO_2 for all species (Tables 3, 4). Leaf area, biomass, and necromass of early successional species (*C. longipes*, *F. insipida*, and *L. seemannii*) dominated the communities (Fig. 4). Average RGR and tissue senescence (necromass) over the 6-month experiment were not significantly influenced by elevated CO_2 (Tables 3, 4). The LAR (leaf area expressed as a proportion of the total biomass), which is a measure of the investment species make to their carbon-assimilating organs, was decreased in high-CO_2-grown plants (Tables 3, 4). The LAR tended to be lower in early and mid-successional species under elevated CO_2 than in the slow-growing late-successional species. A reduced LAR under elevated CO_2 was due to a significant reduction in the biomass invested in leaves (LWR), and also due to reduced SLA (Table 3). The net carbon assimilation rate (NAR), which is a measure of the efficiency with which leaf area is used for carbon gain, was generally higher in plants grown under elevated CO_2 compared to those

Table 2 Comparison of mean (±SE) biomass accumulation and growth among communities of tropical plants grown at ambient or elevated CO_2 for 25 weeks ($n = 3$)

Community characteristic	Ambient CO_2	Elevated CO_2
Total biomass (g)	1502 ± 174	1406 ± 182
Roots	479 ± 59	438 ± 34
Leaves	366 ± 36	326 ± 44
Stems	657 ± 96	641 ± 122
Necromass (g)	169 ± 11	165 ± 14
Leaf area (m^2)	5.81 ± 0.60	4.80 ± 0.70
Leaf area index	3.22 ± 0.33	2.71 ± 0.40
Net primary production		
(1000 kg ha^{-1} $year^{-1}$)	19.2 ± 2.1	18.1 ± 2.3
(g m^{-2} wk^{-1})	36.9 ± 4.1	34.7 ± 4.4
Relative growth rate (g $g^{-1}wk^{-1}$)	0.148 ± 0.005	0.146 ± 0.005
Leaf area ratio (cm^2 g^{-1})	39.0 ± 2.4	34.0 ± 1.8
Specific leaf area (cm^2 g^{-1})	158 ± 3	146 ± 3
Leaf weight ratio (g g^{-1})	0.245 ± 0.009	0.232 ± 0.006
Net assimilation rate (mg cm^{-2} wk^{-1})	3.84 ± 0.33	4.30 ± 0.20
Root:shoot (g g^{-1})	0.471 ± 0.036	0.470 ± 0.059
Leaf N (mg g^{-1})	1.37 ± 0.07	1.16 ± 0.07
Leaf C:N ratio	39.7 ± 1.5	48.0 ± 2.5

Table 3 Growth and biomass partitioning of ten tropical tree species grown under elevated or ambient CO_2. For the first nine species, values are means ± SE for four plants under ambient CO_2 and three plants under elevated CO_2. Swietenia *macrophylla* values are for 48 plants under both ambient and elevated CO_2

Treatment by species	Plant characteristic										
	Biomass (g)	Necromass (g)	Height (cm)	Leaf area (cm^2)	Relative growth rate ($g\ g^{-1}\ wk^{-1}$)	Leaf area ratio ($cm^2\ g^{-1}$)	Net assimilation rate ($mg\ cm^{-2}\ wk^{-1}$)	Specific leaf area ($cm^2\ g^{-1}$)	Leaf weight ratio ($g\ g^{-1}$)	Leaf N ($mg\ g^{-1}$)	Leaf C:N ratio
(A) Early successional											
Cecropia longipes											
Ambient CO_2	443 ± 60	84.9 ± 8.2	170 ± 4	13 304 ± 2 375	0.179 ± 0.005	30.0 ± 3.37	6.21 ± 0.78	179.6 ± 11.3	0.167 ± 0.015	24.7 ± 4.0	19.9 ± 3.8
Elevated CO_2	401 ± 77	99.6 ± 15.7	149 ± 17	9 985 ± 1 907	0.175 ± 0.007	25.4 ± 4.4	7.27 ± 1.15	180.5 ± 2.0	0.141 ± 0.024	21.4 ± 1.4	21.1 ± 1.3
Ficus insipida											
Ambient CO_2	260 ± 42	18.1 ± 3.3	193 ± 5	8 389 ± 800	0.158 ± 0.006	33.3 ± 2.4	4.87 ± 0.53	146.1 ± 7.7	0.228 ± 0.010	19.9 ± 1.0	20.1 ± 0.7
Elevated CO_2	240 ± 27	17.5 ± 4.0	177 ± 9	5 229 ± 627	0.156 ± 0.004	21.8 ± 0.3	7.16 ± 0.19	128.2 ± 2.7	0.170 ± 0.005	17.8 ± 2.9	23.7 ± 4.1
Luehea seemannii											
Ambient CO_2	273 ± 42	23.3 ± 2.9	156 ± 5	11 983 ± 1 399	0.173 ± 0.006	45.1 ± 4.8	3.96 ± 0.43	171.0 ± 2.5	0.263 ± 0.024	18.1 ± 0.4	25.4 ± 0.6
Elevated CO_2	333 ± 87	20.9 ± 4.8	141 ± 12	12 999 ± 3 443	0.179 ± 0.011	38.7 ± 2.1	4.64 ± 0.29	161.3 ± 3.8	0.240 ± 0.009	15.9 ± 0.1	28.4 ± 0.3
(B) Mid-successional											
Anacardium excelsum											
Ambient CO_2	105 ± 16	7.2 ± 1.9	91 ± 13	5 638 ± 741	0.126 ± 0.007	55.0 ± 4.5	2.36 ± 0.29	124.1 ± 4.0	0.442 ± 0.028	11.4 ± 0.5	40.9 ± 1.9
Elevated CO_2	117 ± 7	3.5 ± 1.2	95 ± 8	5 499 ± 327	0.132 ± 0.003	47.2 ± 1.1	2.80 ± 0.10	107.6 ± 4.1	0.439 ± 0.009	9.5 ± 0.9	49.7 ± 4.8
Antirrhoea trichantha											
Ambient CO_2	89.2 ± 19.0	9.8 ± 2.9	125 ± 13	4 531 ± 1 043	0.152 ± 0.009	49.8 ± 3.8	3.09 ± 0.19	207.5 ± 11.8	0.239 ± 0.006	14.3 ± 0.5	33.1 ± 1.3
Elevated CO_2	94.4 ± 15.0	9.3 ± 2.4	129 ± 19	3 645 ± 613	0.157 ± 0.006	38.8 ± 3.3	4.11 ± 0.41	178.0 ± 6.1	0.218 ± 0.020	12.1 ± 0.6	38.9 ± 1.6
Cordia alliodora											
Ambient CO_2	59.6 ± 9.8	9.1 ± 2.1	100 ± 15	1 974 ± 438	0.092 ± 0.008	33.0 ± 4.3	2.94 ± 0.47	181.0 ± 6.3	0.185 ± 0.029	14.6 ± 1.2	28.9 ± 3.1
Elevated CO_2	50.4 ± 5.7	9.4 ± 1.6	84 ± 8	1 063 ± 961	0.088 ± 0.005	21.1 ± 0.5	4.15 ± 0.31	173.7 ± 2.1	0.122 ± 0.001	12.4 ± 1.9	34.4 ± 6.5
(C) Late successional											
Calophyllum longifolium											
Ambient CO_2	16.9 ± 0.8	2.0 ± 0.2	44 ± 2	587 ± 71	0.052 ± 0.002	34.7 ± 4.0	1.55 ± 0.20	84.4 ± 3.5	0.408 ± 0.033	6.9 ± 0.5	71.4 ± 8.2
Elevated CO_2	13.7 ± 0.8	1.9 ± 0.2	36 ± 4	449 ± 25	0.043 ± 0.002	32.7 ± 0.5	1.31 ± 0.07	77.3 ± 1.7	0.424 ± 0.011	5.5 ± 0.5	89.4 ± 1.3
Tetragastris panamensis											
Ambient CO_2	8.9 ± 1.9	0.2 ± 0.1	19 ± 2	371 ± 75	0.059 ± 0.010	41.9 ± 1.8	1.43 ± 0.26	121.3 ± 1.5	0.346 ± 0.015	8.3 ± 0.4	52.6 ± 7.5
Elevated CO_2	9.0 ± 1.8	0.1 ± 0.1	19 ± 1	344 ± 83	0.062 ± 0.009	37.4 ± 2.3	1.63 ± 0.16	123.2 ± 7.9	0.305 ± 0.022	7.2 ± 0.6	62.5 ± 2.4
Virola surinamensis											
Ambient CO_2	12.6 ± 1.8	0.3 ± 0.1	24 ± 3	494 ± 62	0.063 ± 0.006	39.2 ± 1.0	1.62 ± 0.17	147.1 ± 5.7	0.268 ± 0.017	9.2 ± 0.5	52.4 ± 2.4
Elevated CO_2	13.3 ± 2.7	0.5 ± 0.2	24 ± 4	410 ± 62	0.065 ± 0.008	31.8 ± 4.0	2.13 ± 0.43	118.3 ± 3.3	0.268 ± 0.030	6.8 ± 0.2	69.8 ± 2.3
(D) Surrounding species											
Swietenia macrophylla											
Ambient CO_2	12.9 ± 0.6	1.3 ± 0.2	45 ± 1	856 ± 42	0.257 ± 0.002	67.7 ± 2.1	3.96 ± 0.12	67.6 ± 2.1	0.427 ± 0.008	11.0 ± 0.9	43.4 ± 3.9
Elevated CO_2	12.3 ± 0.8	1.8 ± 0.5	41 ± 1	665 ± 54	0.252 ± 0.003	53.4 ± 1.8	4.97 ± 0.17	53.4 ± 1.8	0.405 ± 0.010	7.3 ± 0.3	62.2 ± 2.9

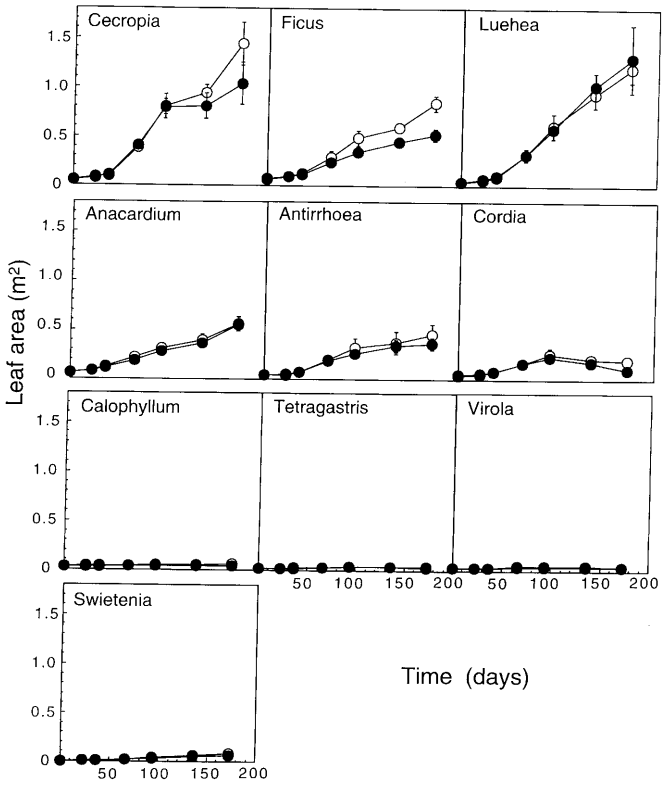

Fig. 4 Growth of leaf area of early successional species (*upper panels*), mid-successional species (*middle panels*), late-successional species (*lower panels*), and of the border species *Swietenia macrophylla* (*lower-far-left panel*) under elevated CO_2 (*filled circles*) and ambient CO_2 (*open circles*). Values are means ± SE for $n = 4$ individuals under ambient CO_2 and $n = 3$ for individuals under elevated CO_2, except for *S. macrophylla*, where $n = 48$ individuals under ambient CO_2 and $n = 36$ for individuals under elevated CO_2

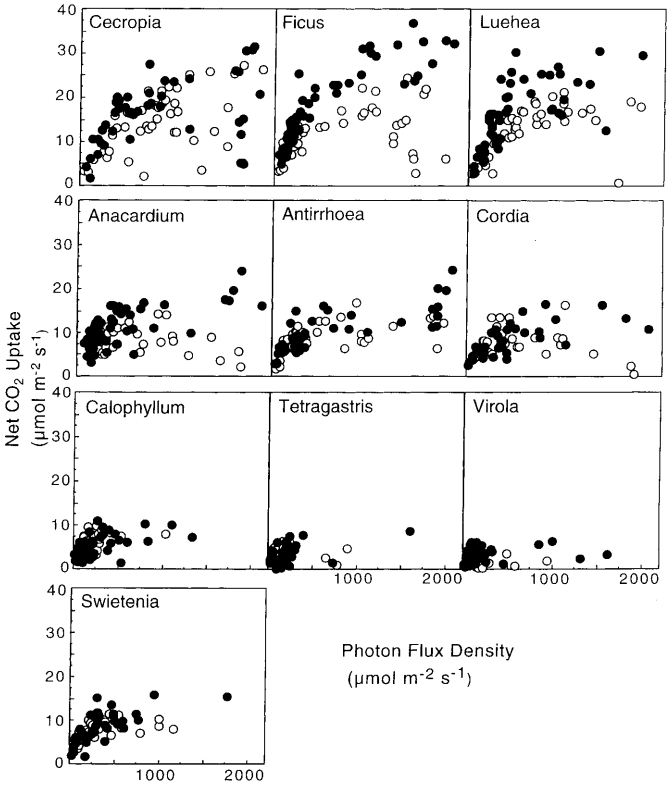

Fig. 5 Net CO_2 uptake of individual species over the range of photon flux densities occurring naturally within the open-top chambers during the day. Values are for plants growing under elevated CO_2 (*filled circles*) and ambient CO_2 (*open circles*), where early successional species are represented in the *upper panels*, mid-successional species in the *middle panels*, late-successional species in the *lower panels*, and net CO_2 uptake of the border species *Swietenia macrophylla* in the *lower-far-left panel*

grown at ambient levels, particularly in early and mid-successional species (Table 3).

Rates of net CO_2 uptake measured at the end of the experiment were generally greater in elevated CO_2 in the early and mid-successional species compared to the late-successional species (Fig. 5). Differences in photosynthetic rates among early successional species growing under elevated and ambient CO_2 were particularly evident at high light levels where leaf temperatures were also high (between 35 and 41°C). By the end of the 6-month experiment, late-successional species received low levels of light within the chambers because of shading by the early successional species. Photosynthetic rates of late-successional species did not differ among high- and low-CO_2-grown plants (Fig. 5)

Leaf chemical composition

Concentrations of leaf nitrogen were greatest in early successional species, followed by mid- and then late-successional species (Table 3). Leaf nitrogen concentrations were reduced in all plants grown under elevated CO_2 (Tables 3, 4). Leaf N concentration expressed on a leaf area basis showed similar patterns as values expressed on a dry weight basis (data not shown). The C:N ratio of leaf tissue also differed among species from different successional groupings (Tables 3, 4). The C:N ratio of early successional leaf tissue varied between 20 and 30, for mid-successional species between 30–50, while for late-successional species values ranged from 50 to 90. Increases in the C:N ratio when growing under elevated CO_2 occurred in all species, but increases in the C:N ratio were greatest in late-successional species.

Measures of leaf carbohydrate concentrations showed that starch concentrations within leaves varied among species, ranging from 2 to 10% of dry weight when growing under ambient CO_2 (Table 5). Growth under elevated CO_2 approximately doubled leaf starch concentrations for all species. Despite this increase in the absolute levels of starch within leaves under elevated CO_2, there was no increase in the daily accumulation of starch (evening – predawn levels) due to elevated CO_2. Levels of soluble sugars within leaves also differed among species, ranging between 2 and 14% of dry weight (Table 5). Growth under elevated CO_2 had little

Table 4 Summary of ANOVA results of growth and biomass partitioning of nine tropical tree species grown under elevated or ambient CO_2 concentrations for 25 weeks. *F* values are given and significance indicated by $*P \leq 0.15$; $**P \leq 0.05$; $***P \leq 0.001$; *ns* not significant

Source of variation	*df*	Plant Characteristic										
		Biomass	Necromass	Height	Leaf area	Relative growth rate	Leaf area ratio	Net assimilation rate	Specific leaf area	Leaf weight ratio	Leaf N	Leaf C:N ratio
CO_2	1	ns	ns	5.63*	6.62**	ns	51.45***	11.76**	10.05**	7.75**	140.89***	70.27***
Successional status	2	89.58***	14.48***	43.30***	33.91***	24.42**	ns	23.29**	ns	ns	35.89***	20.60**
Species	6	5.92***	11.41***	11.52***	12.74***	16.22***	12.45***	4.17**	66.71***	45.88***	5.39***	10.09***
Successional status × CO_2	2	ns	ns	ns	ns	ns	5.99**	3.15*	ns	ns	3.94*	14.26**
Species × CO_2	6	ns	ns	ns	ns	ns	ns	ns	2.10*	ns	ns	ns
Error	45											

effect on the concentration of soluble sugars within leaves.

Discussion

Community response to elevated CO_2

This is the first study demonstrating that increasing CO_2 concentrations do not result in increased biomass accumulation by tropical plants when they are grown under natural conditions. Net primary productivity of the communities within the open-top chambers was not affected by elevated CO_2, and was within the range observed in tropical forests (range from 10 000 to 32 000 kg ha^{-1} $year^{-1}$, mean of 18 000 kg ha^{-1} $year^{-1}$; Cannell 1982). Variation in biomass among chambers over the site was greater than effects due to elevated CO_2; therefore, local variations in soil physical and biological characteristics had an overriding influence on the communities. From this result, we predict that future variations in climate may have a greater influence on forest productivity than global increases in CO_2 concentration. Our results are similar to those of other investigators, who also found that elevated CO_2 had no influence on biomass accumulation in model tropical ecosystems grown in glasshouses (Reekie and Bazzaz 1989; Körner and Arnone 1992; Arnone and Körner 1995). Small, or no change in biomass accumulation under elevated CO_2 conditions was also observed in field experiments with *Populus* (Ceulemans and Mousseau 1994), in natural grassland (Schäppi and Körner 1996), and temperate forest communities (Cipollini et al. 1993). These studies are in contrast to results of studies with tropical plants in pots (e.g., Oberbauer et al. 1985; Hogan et al. 1991; Ziska et al. 1991; Winter and Lovelock, in press), and also to studies of other natural (e.g., Drake 1992; Norby et al. 1992; Würth et al., in press) and managed (e.g., Idso et al. 1991) ecosystems, all of which have shown enhancements in productivity under elevated CO_2. One explanation as to why plants in some experiments do not show enhancements in productivity under elevated CO_2 is that resources other than carbon are limiting growth under elevated CO_2 (Körner 1993).

Tropical ecosystems commonly have highly weathered, nutrient-poor soils (Vitousek and Sanford 1986), that can be particularly deficient in phosphorus (Yavitt et al. 1993), as was the case in the current experiment. Soil nutrient limitations could therefore be potentially important in influencing the extent of biomass accumulation under elevated CO_2 in tropical ecosystems. However, in a nutrient-poor temperate ecosystem, elevated CO_2 substantially increased biomass accumulation (Norby et al. 1986), indicating that there may be some interaction between soil nutrient concentrations and elevated CO_2 that is ecosystem dependent (Berntson and Bazzaz 1996).

Recent evidence suggests that below-ground processes are important in determining plant community

Table 5 Non-structual carbohydrate concentrations (starch and soluble carbohydrates) of leaves of ten tropical tree species grown under elevated or ambient CO_2 concentrations for 25 weeks. For the first nine species, values are means ± SE for four plants under ambient CO_2 and three plants under elevated CO_2. *Swietenia macrophylla* values are for 48 plants under both ambient and elevated CO_2

Treatment by species	Starch (% dry weight)		Soluble sugars (% dry weight)	
	Morning	Evening	Morning	Evening
(A) Early-successional				
Cecropia longipes				
Ambient CO_2	2.64 ± 0.42	10.09 ± 1.74	5.20 ± 0.78	7.17 ± 0.76
Elevated CO_2	5.03 ± 0.63	12.06 ± 1.08	5.41 ± 0.83	5.40 ± 0.27
Ficus insipida				
Ambient CO_2	5.50 ± 1.33	8.77 ± 2.10	12.22 ± 0.69	14.39 ± 0.70
Elevated CO_2	12.59 ± 2.06	17.59 ± 2.37	9.21 ± 1.21	10.18 ± 0.22
Luehea seemannii				
Ambient CO_2	3.90 ± 0.80	8.76 ± 1.30	4.17 ± 0.15	6.77 ± 0.60
Elevated CO_2	9.12 ± 1.53	13.63 ± 1.77	4.43 ± 0.11	5.86 ± 0.25
(B) Mid-successional				
Anacardium excelsum				
Ambient CO_2	3.54 ± 0.27	5.45 ± 0.36	4.09 ± 0.18	5.90 ± 0.76
Elevated CO_2	5.88 ± 0.83	9.96 ± 1.81	4.41 ± 0.23	6.31 ± 0.99
Antirrhoea trichantha				
Ambient CO_2	1.04 ± 0.29	3.75 ± 0.51	1.78 ± 0.25	2.63 ± 0.20
Elevated CO_2	2.72 ± 0.40	4.94 ± 0.78	2.01 ± 0.51	2.74 ± 0.49
Cordia alliodora				
Ambient CO_2	2.21 ± 0.33	3.75 ± 0.64	2.02 ± 0.36	2.72 ± 0.38
Elevated CO_2	4.58 ± 2.25	6.27 ± 2.39	2.35 ± 0.31	3.06 ± 0.85
(C) Late successional				
Calophyllum longifolium				
Ambient CO_2	2.84 ± 0.57	3.00 ± 0.58	2.98 ± 0.36	3.65 ± 0.25
Elevated CO_2	4.35 ± 0.52	4.98 ± 0.56	3.99 ± 0.54	3.35 ± 0.15
Tetragastris panamensis				
Ambient CO_2	2.80 ± 0.51	3.49 ± 0.64	6.54 ± 0.36	6.22 ± 0.27
Elevated CO_2	4.10 ± 0.85	5.96 ± 0.92	4.84 ± 0.92	6.46 ± 0.18
Virola surinamensis				
Ambient CO_2	4.95 ± 2.06	3.39 ± 0.90	5.56 ± 0.25	7.13 ± 0.55
Elevated CO_2	9.46 ± 1.75	5.95 ± 1.16	4.81 ± 0.55	7.02 ± 0.65
(D) Surrounding species				
Swietenia macrophylla				
Ambient CO_2	2.89 ± 0.79	4.57 ± 0.92		
Elevated CO_2	14.43 ± 1.30	12.18 ± 1.40		

responses to elevated CO_2, through changes in rhizodeposition (Cardon 1994), root symbiont activity (e.g., Morgan et al. 1994; Klironomos et al. 1996; Zanetti et al. 1996; Lovelock et al. 1997), and other microbial activity (Diaz et al. 1993; Zak et al. 1993; O'Neill 1994; Klironomos et al. 1996; Hungate et al. 1997). Moreover, in a grassland community growing under elevated CO_2, increases in soil respiration accounted for the dissipation of most of the additional carbon fixed in photosynthesis (Luo et al. 1994; Hungate et al. 1997), demonstrating that changes below ground can effectively counteract any increases in net CO_2 uptake above ground.

Increases in the C:N ratio of leaf tissue in communities growing under elevated CO_2, with no increase in the amount of tissue produced (Table 2), could result in reduced litter quality, thereby exacerbating nutrient limitations to plant growth (Berntson and Bazzaz 1996 and references therein; Cotrufo and Ineson 1996), have a strong influence on herbivores (e.g., Traw et al. 1996; Lawler et al. 1997), and also possibly affect organisms of higher trophic levels (L. Coley, personal communication).

The reduction in leaf area index of the communities grown under elevated CO_2 (Table 2) has also been observed in temperate forest trees grown under elevated CO_2 (Hättenschwiler and Körner 1996; Hättenschwiler et al. 1997). This change may alter light transmittance in developing canopies, and through this lessen competitive interactions in regenerating forest stands (Wayne and Bazzaz 1997). Additionally, reductions in leaf area index of forests could lead to reductions in canopy water use (Hättenschwiler et al. 1997).

Response to elevated CO_2 by species with different successional status

Successional groupings and species varied in their RGRs (Figs. 3, 4). However, under elevated CO_2 there was no enhancement of RGR for any successional grouping or individual species (Tables 3, 4). These results are contrary to those of other studies where species with high growth rates are observed to have

greater enhancements in growth under elevated CO_2 compared to slower-growing species (Poorter 1993; Schäppi and Körner 1996; Potvin and Vasseur 1997; Roden et al. 1997). Elevated CO_2 did however modify biomass allocation patterns, with the extent of modification being partially dependent on the successional status of the species, but also varying within a successional grouping. In early and mid-successional species, the proportion of leaf area to total biomass (LAR) was reduced when plants were grown under elevated CO_2. In late-successional species, LAR, and SLA were similar under elevated and ambient CO_2. This may have occurred because of their slow growth rates. During the 6 months of the experiment, the late-successional species approximately doubled their leaf area, but measures of LAR and SLA could still have been dominated by their initial, "pre-elevated CO_2" leaf area. Reductions in LAR in early and mid-successional species were mainly due to the development of thicker leaves (lower specific leaf weight), rather than to changes in the proportion of biomass invested in leaves, although there were exceptions (Table 3). For example, in *Cecropia*, the LAR was not reduced under elevated CO_2 but the LWR was decreased. Variation such as this indicates that despite some consistent patterns among species within a successional grouping, species responded individualistically to elevated CO_2. This has also been observed in species of differing successional status from forests in northern latitudes (Bazzaz and Miao 1993), and underlies the as yet poor predictive power of the current understanding of the mechanistic basis for species responses to elevated CO_2 (Körner 1996).

The mechanisms leading to changes in biomass allocation patterns (reduced LAR and increased leaf mass per area), which result in limited growth enhancements in some species under elevated CO_2, are not known. One mechanism suggested to limit growth enhancements in plants under elevated CO_2 is reduced sink strength for carbon fixed in photosynthesis (Wong 1990; Arp and Drake 1991; Farrar and Williams 1991). Sink strength can be limited when low soil nutrient concentrations reduce meristem growth (Conroy et al. 1988; Wong et al. 1992; Rogers et al. 1996), when there are physical restrictions to root growth, for example limited rooting volume (Thomas and Strain 1991; McConnaughay et al. 1993) or compacted soil (Masle et al. 1990), and when the potential for storage of carbohydrates is low (Drake et al. 1997). Variation in the change in biomass allocation among species and successional status in response to elevated CO_2 could therefore be due to the relative differences in tolerance of reduced sink strength for carbohydrates among successional groupings of species. For example, in the nutrient-poor soils used in this experiment, early successional species may have experienced a relatively greater reduction in sink strength compared to late-successional species, perhaps because of lower levels of arbuscular mycorrhiza, faster depletion of soil nutrient resources, and/or because of their limited capacity to store carbohydrates in stems or roots or as secondary metabolites. Our results may indicate that species respond differently to elevated CO_2 not only because of differences in growth rates, but also because of differences in a whole range of characteristics, including nutrient acquisition strategies and carbohydrate storage capacities (Diaz 1995).

A decreased LAR usually leads to reduced growth rates, unless the reduction in leaf area is balanced by an increase in the net carbon assimilation rate of the leaf area. This was the case for the early and mid-successional species (Tables 3, 4), and was reflected in the enhancement in net photosynthetic carbon gain on a leaf area basis under elevated CO_2 in these species (Fig. 5). Enhanced net photosynthesis under elevated CO_2 was particularly evident at high levels of solar radiation and concomitant high leaf temperatures. Suppression of photorespiration, particularly at high temperatures, in plants under elevated CO_2 would have occurred, and may indicate an important interaction between high leaf temperatures and elevated CO_2 on carbon gain in tropical plants in the future (Drake et al. 1997).

Leaf nitrogen concentrations were reduced, and leaf starch concentrations increased under elevated CO_2 in all species, as has been widely observed (Poorter et al. 1997 and references therein). While changes in leaf starch concentrations were similar for all species under elevated CO_2, decreases in leaf nitrogen concentrations under elevated CO_2 were slightly more pronounced in late-successional species (Tables 3, 4). Elevated CO_2 had a stronger influence on the C:N ratio of leaves, with the C:N ratio of late-successional species being relatively more enhanced than those of early and mid-successional species under elevated CO_2. In a study of decomposition of senesced leaves produced under elevated CO_2, Hirschel et al. (1997) found that decomposition rates of leaf litter were not altered in elevated-CO_2-grown leaves. However, the C:N ratio of the initial green leaves (prior to senescence and decomposition) was also not significantly affected by growth under elevated CO_2. The difference in C:N ratios of leaf tissue among successional groupings in the work described here, if it is still apparent in senesced litter tissue (Hirschel et al. 1997), combined with no enhancement in the amount of biomass produced under elevated CO_2 may result in the production of lower-quality leaf litter and nutrient immobilization due to microbial activity (Berntson and Bazzaz 1996) in forests dominated by late-successional species.

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