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Marked growth response of communities of two tropical tree species to elevated CO_2 when soil nutrient limitation is removed

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Summary

As part of an ongoing project to understand the effects of elevated atmospheric CO_2 on plants in complex, tropical communities, we studied biomass accumulation in a simplified model seedling community consisting of two species of tropical trees (*Ficus insipida*, a fast growing pioneer species, and *Virola surinamensis*, a slow-growing, shade-tolerant late successional species). The plants were grown at ambient and elevated (about two times ambient) CO_2 concentrations using open-top chambers at a field site in Panama. Communities grew in heavily fertilized soil. Compared to a previous experiment with model communities of *F. insipia* and *V. surinamensis* grown on unfertilized soil (WINTER et al., Flora [2000] 195, 289) application of soil fertilizer markedly accelerated community growth rates at ambient CO_2, and biomass accumulation was enhanced by an additional 52% at elevated CO_2. In contrast, elevated CO_2 had no significant effect on biomass accumulation in unfertilized communities. Communities growing on fertilized soil showed greater biomass allocation into leaves, i.e. higher leaf weight ratios (LWRs) than did communities on unfertilized soil. Higher LWRs were related to lower root: shoot ratios and together with greater specific leaf areas (area per unit leaf mass), largely a consequence of lower leaf starch contents, resulted in higher leaf area ratios (LARs). While elevated CO_2 caused the relatively low LARs in unfertilized communities to decrease further, by strongly increasing leaf starch levels and decreasing specific leaf areas, these leaf characteristics changed only slightly in fertilized communities exposed to elevated CO_2. Thus, by maintaining relatively high LARs at elevated CO_2, fertilized plants were able to effectively use enhanced CO_2 concentrations for increased carbon gain and growth. Leaves of plants on fertilized soil were characterized by relatively low C : N ratios which were largely unaffected by CO_2 concentration. In contrast, C : N ratios in leaves of unfertilized plants were higher than those of fertilized plants and increased in response to elevated CO_2.

Key words: CO_2 exchange, elevated CO_2, growth, nutrients, trees, tropical forest

Introduction

The possible effects of the ongoing increase in global atmospheric CO_2 concentration (HOUGHTON 1997) – currently about 1.5 ppm per year – on plants and ecosystems have been the subject of intensive research. Hundreds of studies have focused on the responses of northern temperate zone plants to elevated CO_2 (KOCH & MOONEY 1995; KÖRNER & BAZZAZ 1996; WARD & STRAIN 1999); relatively few studies have been conducted with tropical plants (OBERBAUER et al. 1985; REEKIE & BAZZAZ 1989; ZISKA et al. 1991; KÖRNER & ARNONE 1992; ARNONE 1996; FARNSWORTH et al. 1996; LOVELOCK et al. 1997, 1999; RODEN et al. 1997; KÖRNER 1998; WINTER & VIRGO 1998; WÜRTH et al. 1998; WINTER & LOVELOCK 1999). Studies of CO_2 responses of tropical plants in situ are particularly scarce. In two recent open-top chamber experiments with tropical model plant communities at a field site in Panama, neither community biomass accumulation nor the proportion to which individual species contributed to community biomass accumulation were significantly affected at elevated as compared to ambient CO_2 (LOVELOCK et al. 1998; WINTER et al. 2000). Plants grown under elevated CO_2 showed greater net assimilation rates (NAR, increase in plant dry mass per unit leaf area per unit of time), and greater rates of leaf net CO_2 fixation, but this did not result in markedly enhanced growth because of decreases in the total leaf area per total plant dry mass (LAR) at elevated CO_2. In the study of LOVELOCK et al. (1998), model communities consisted of 10 different species, 9 of which were represented by

only one individual per community. Plants grew in relatively compact, poorly drained and nutrient depleted natural soil. Open-top chambers were installed on existing terrain at a forest edge. Because of small, unavoidable microsite-related differences in soil conditions between chambers, growth of plants within a given CO_2 treatment (ambient or elevated) varied as much as did growth between CO_2 treatments. In a subsequent study at the same site (WINTER et al. 2000), greater consistency between chambers was accomplished by replacing the natural soil with uniform soil from another site, which also reduced soil compaction, improved drainage and slightly increased soil nutrient content. To further increase uniformity between replicate treatments, the number of species was reduced to two (an early successional species, *Ficus insipida*, and a late successional species, *Virola surinamensis*), and plant density was substantially increased. Results of these two experiments were similar, showing no (LOVELOCK et al. 1998) or barely discernable (WINTER et al. 2000) stimulation of community biomass accumulation at elevated CO_2.

The design of the study presented here is identical to that of WINTER et al. (2000), except that we eliminated growth limitations due to soil nutrient availability by adding large amounts of full-strength fertilizer to the soil. We demonstrate that, under these conditions, model tropical communities show markedly increased biomass accumulation under elevated as compared to ambient CO_2. Furthermore, CO_2 effects on leaf physiological characteristics markedly differed from those observed previously with unfertilized plants.

Materials and methods

Open-top chamber set-up and microclimate conditions have previously been described in detail (WINTER et al. 2000) (Fig. 1). Four octagonal chambers (about 2 m across; 2.5 m high) were supplied with ambient air, and four with air containing elevated levels of CO_2 (about 300 to 400 ppm above ambient). Typically, the CO_2 concentration of ambient air varied between slightly above 400 ppm in the early morning hours and about 350 ppm in the afternoon. The upper 30 cm of natural soil was replaced with sieved, dark, top-horizon soil from another site (for soil analysis, see WINTER et al. 2000) to increase comparability between chambers. Osmocote-Plus controlled release fertilizer (N-P-K 16-8-12 and Mg, Fe, Mn, Cu, Mo, and B; Scotts-Sierra, Marysville, OH) (2 kg per chamber) was evenly distributed on the soil surface at the beginning of the experiment and

Fig. 1. Open-top chambers with communities of *Ficus insipida* and *Virola surinamensis* during the final part of the 16 week experiment. Left, community at ambient CO_2; right, community at elevated CO_2.

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covered with a 2 cm thick layer of leaf litter cut into 2–3 cm^2 fragments. After 8 weeks another 2 kg of fertilizer was added to each chamber. (These fertilizer levels are beyond those typically used in agricultural practice, but resulted in lavish growth of experimental plants, ensuring that nutrient supply was non-limiting.) Soil compaction, measured with a soil compaction tester (Dickey-john, Auburn, IL) at the end of the experiment, was 11 ± 7, 24 ± 16, and 48 ± 34 psi at 7.5, 15 and 22.5 cm depths (mean ± SD, n = 9–10), respectively. Wooden boards inserted 30 cm into the ground around the chamber edges prevented roots from growing beyond the confines of the chambers. Each chamber contained 18 seedlings of *Ficus insipida* Willd., an early successional species (ZOTZ & WINTER 1996), and 18 seedlings of *Virola surinamensis* (Rol.) Warb., a late successional species (CROAT 1978). Plants were narrowly spaced and arranged in a regular pattern (WINTER et al. 2000), with 20 seedlings (10 *F. insipida*, 10 *V. surinamensis*) forming the edge of the model plant communities, and 16 seedlings (8 *F. insipida*, 8 *V. surinamensis*) growing in the centre of the plant communities. At the onset of the experiment, plants were up to 20 cm tall. *F. insipida* and *V. surinamensis* had total dry masses of 0.19 ± 0.06 g and 2.32 ± 0.41 g per seedling, respectively. The 16 week-experimental period, beginning on 25 August, 1997, coincided largely with the wet season. Diurnal courses of net CO_2 exchange were measured at regular intervals throughout the experiment (WINTER et al. 2000). Final plant harvest, biomass determination, growth analysis, carbohydrate analysis and C : N analysis were as described previously (WINTER et al. 2000). The mean relative growth rate (RGR) was calculated as $(\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_2 and W_1 are the dry masses at the end and the beginning of the experiment, respectively, and t_2-t_1 is the duration of the experiment in weeks. Mean net assimilation rate (NAR) was calculated as $[(W_2 - W_1)(\ln LA_2 - \ln LA_1)]/[(LA_2 - LA_1)(t_2 - t_1)]$, where LA_2 and LA_1 are the leaf areas at the end and at the beginning of the experiment, respectively. The specific leaf area (SLA) is the leaf area per unit leaf dry mass. The leaf weight ratio (LWR) is the leaf dry mass divided by total plant dry mass. The leaf area ratio (LAR) is the total leaf area divided by total plant dry mass. The leaf area index (LAI) represents the leaf area per unit ground area. Differences in characteristics of communities were assessed using student's t-test.

Diurnal courses in PFD, temperature and relative humidity (RH) inside and outside of open-top chambers on a sunny day near the end of the experiment are shown in Fig. 2. PFD was measured with a quantum sensor LI-190SA connected to a LI-250 light meter (LI-COR, Lincoln, NE, USA). Air temperature and RH were measured with an Assmann psychrometer (Oaklon

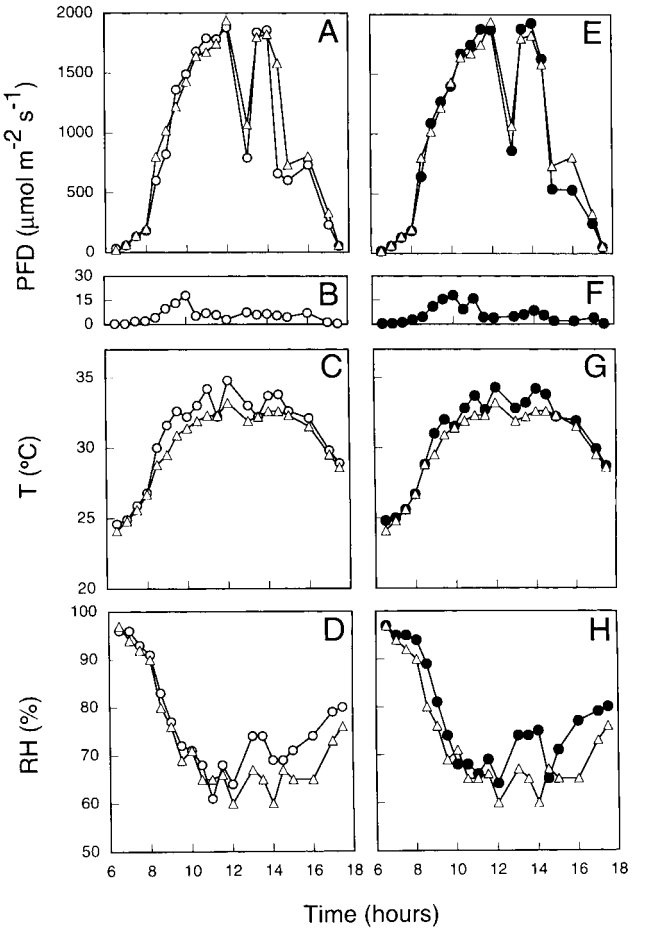

Fig. 2. Diurnal courses in PFD (A, B, E, F), air temperature (C, G) and relative humidity, RH (D, H) inside (circles) and outside (open triangles) open-top chambers supplied with ambient air (A, B, C, D) or air enriched in CO_2 (E, F, G, H) during the penultimate week of the experiment. PFD was measured above the community canopy (= above the *Ficus insipida* overstorey, A and E) and at the level of the *Virola surinamensis* understorey (about 35 cm height, B and F). Temperature and RH were measured at a height of 1.5 m.

37210 series, Cole Palmer, IL, USA). Similar to previous experiments at the same field site, air temperature inside chambers was about 2 °C higher than ambient at times of maximum solar radiation (Fig. 2C and G). Daytime RH was higher inside the chambers than outside. Deviations from ambient were slightly more pronounced for communities at elevated CO_2 than at ambient CO_2 (Fig. 2D and H), because communities at elevated CO_2 had more leaf area than those at ambient CO_2.

Abbreviations: LAR, leaf area ratio; LWR, leaf weight ratio; NAR, net assimilation rate; PFD, photosynthetic photon flux density; RGR, relative growth rate; RH, relative humidity; SLA, specific leaf area.

Results

Community growth response

Model plant communities grew vigorously, particularly at elevated CO_2 (Figs. 1 and 3). In just 16 weeks, community biomass and community leaf area increased >60 fold at ambient CO_2, and 100 and 83 fold at elevated CO_2, respectively (Table 1). Final biomass and leaf area of communities were 52% and 37% greater at elevated than at ambient CO_2, respectively. The strong increases in leaf area translated into extremely high leaf area indices: about 9 at ambient and 12 at elevated CO_2 at the end of the experiment. Necromass (dead leaves) was 6% of biomass production at both CO_2 concentrations. Root: shoot ratios did not differ between treatments. Mean relative growth rate of communities at elevated CO_2 increased by 10%, and was related to an increase in NAR of 17%, which was counteracted by a decrease in LAR of 10% (Table 1). This relatively small decrease in LAR was primarly caused by a small decrease in SLA.

Species growth response

Responses to elevated CO_2 shown for *F. insipida* and *V. surinamensis* in Table 1 are based on comparisons of the sum of all plants of each species per chamber. *F. insipida* contributed 96.9% and 97.4% to community biomass and community leaf area at ambient and elevated CO_2, respectively. Thus, biomass accumulation, leaf area increase, SLA, LAR and LWR of *F. insipida* closely resembled the values obtained for the entire communities. In contrast to *F. insipida*, which formed the community overstorey and reached heights of approximately 1.5 m (ambient CO_2) to 1.7 m (elevated CO_2) (Table 2), *V. surinamensis* grew slowly, attained heights of 0.35 m (ambient CO_2) and 0.38 m (elevated CO_2), and remained in the community understorey. PFD in the centre of the community understorey was only about 1% of the PFD received by outer-canopy leaves of the *F. insipida* overstorey (Fig. 2A, B, E, F). Despite the relatively low growth rates of *V. surinamensis* (RGR = 0.05 g g^{-1} wk^{-1} at ambient CO_2 versus RGR = 0.421 g g^{-1} wk^{-1} in *F. insipida*; Table 1) biomass accumulation and leaf area production of *V. surinamensis* were significantly higher (29% and 19%, respectively) at elevated CO_2 (Table 1), although relative increases in *V. surinamensis* were smaller than in *F. insipida* (53 and 37%, respectively). Similar to the community response, increases in RGR of *F. insipida* at elevated CO_2 were paralleled by proportionally greater increases in NAR, and by small decreases in LAR and SLA. Increases in RGR of *V. surinamensis* in response to elevated CO_2 were paralleled by increases in NAR of

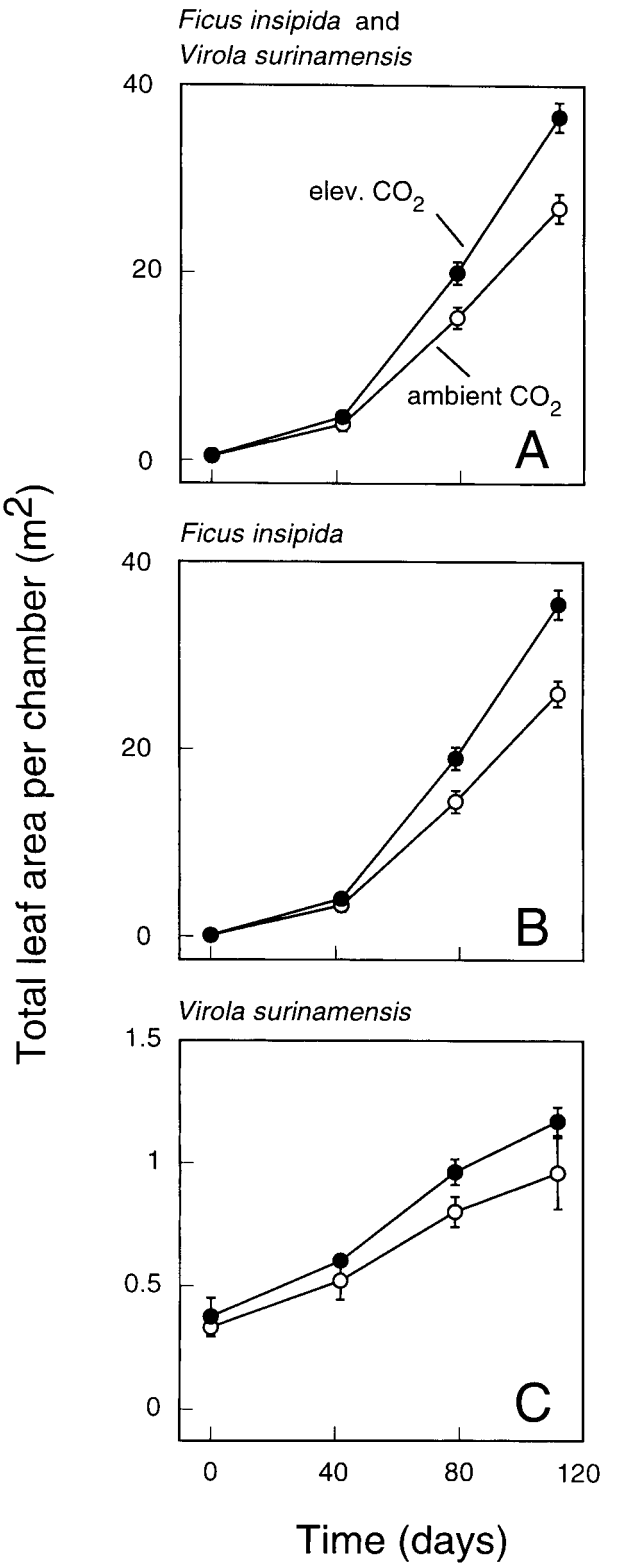

Fig. 3. Time course of increase in community leaf area at ambient (open symbol) and elevated (closed symbol) CO_2. Data are means ± SD (n = 4). A, leaf area of total community; B, leaf area of all plants of *Ficus insipida* per community; C, leaf area of all plants of *Virola surinamensis* per community.

Table 1. Biomass in communities of *Ficus insipida* and *Virola surinamensis* after 16 weeks growth at ambient (A) and elevated (E) concentrations of CO_2. Values refer to the total of all 36 plants per chamber (I), to the sum of all 18 plants of *F. insipida* per chamber (II) and to the sum of all 18 plants of *V. surinamensis* per chamber (III), respectively. Values are means ± SD (n = 4).

Community characteristics	CO_2 concentration			P
	Ambient	Elevated	E/A	
I. *Ficus insipida* and *Virola surinamensis*				
Total biomass (kg)	2.977 ± 0.131	4.534 ± 0.438	1.52	< 0.001
Leaves (kg)	1.113 ± 0.049	1.615 ± 0.084	1.45	< 0.001
Stems (kg)	1.185 ± 0.073	1.910 ± 0.242	1.61	< 0.01
Roots (kg)	0.679 ± 0.030	1.009 ± 0.116	1.49	< 0.01
Necromass (kg)	0.191 ± 0.062	0.284 ± 0.038	1.49	< 0.05
Root : shoot (kg kg^{-1})	0.296 ± 0.014	0.286 ± 0.012	0.97	n.s.
Leaf area (m^2)	26.79 ± 1.51	36.66 ± 1.57	1.37	< 0.001
Leaf area index (m^2 m^{-2})	9.01 ± 0.50	12.26 ± 0.52	1.36	< 0.001
Relative growth rate (g g^{-1} wk^{-1})	0.262 ± 0.003	0.288 ± 0.006	1.10	< 0.001
Net assim. rate (g m^{-2} wk^{-1})	28.83 ± 0.50	33.81 ± 2.28	1.17	< 0.01
Specific leaf area (m^2 kg^{-1})	24.19 ± 0.67	22.72 ± 0.44	0.94	< 0.01
Leaf area ratio (m^2 kg^{-1})	9.04 ± 0.21	8.12 ± 0.47	0.90	< 0.05
Leaf weight ratio (kg kg^{-1})	0.374 ± 0.004	0.358 ± 0.016	0.96	n.s.
II. *Ficus insipida*				
Total biomass (kg)	2.884 ± 0.121	4.415 ± 0.437	1.53	< 0.001
Leaves (kg)	1.067 ± 0.044	1.556 ± 0.084	1.46	< 0.001
Stems (kg)	1.157 ± 0.069	1.872 ± 0.241	1.62	< 0.01
Roots (kg)	0.661 ± 0.030	0.986 ± 0.117	1.49	< 0.01
Necromass (kg)	0.187 ± 0.061	0.279 ± 0.037	1.49	< 0.05
Root : shoot (kg kg^{-1})	0.298 ± 0.014	0.287 ± 0.013	0.96	n.s.
Leaf area (m^2)	25.95 ± 1.38	35.49 ± 1.57	1.37	< 0.001
Relative growth rate (g g^{-1} wk^{-1})	0.421 ± 0.003	0.448 ± 0.006	1.06	< 0.001
Net assim. rate (g m^{-2} wk^{-1})	39.93 ± 0.70	47.14 ± 3.23	1.18	< 0.01
Specific leaf area (m^2 kg^{-1})	24.33 ± 0.68	22.82 ± 0.44	0.94	< 0.01
Leaf area ratio (m^2 kg^{-1})	8.99 ± 0.20	8.07 ± 0.48	0.90	< 0.05
Leaf weight ratio (kg kg^{-1})	0.370 ± 0.004	0.354 ± 0.016	0.96	n.s.
III. *Virola surinamensis*				
Total biomass (kg)	0.092 ± 0.011	0.119 ± 0.008	1.29	< 0.01
Leaves (kg)	0.046 ± 0.006	0.059 ± 0.003	1.28	< 0.05
Stems (kg)	0.028 ± 0.004	0.037 ± 0.004	1.32	< 0.05
Roots (kg)	0.018 ± 0.001	0.023 ± 0.002	1.28	< 0.001
Necromass (kg)	0.004 ± 0.001	0.005 ± 0.001	1.25	n.s.
Root : shoot (kg kg^{-1})	0.247 ± 0.029	0.242 ± 0.013	0.98	n.s.
Leaf area (m^2)	0.98 ± 0.13	1.17 ± 0.06	1.19	< 0.05
Relative growth rate (g g^{-1} wk^{-1})	0.050 ± 0.007	0.066 ± 0.004	1.32	< 0.01
Net assim. rate (g m^{-2} wk^{-1})	5.27 ± 0.77	6.91 ± 0.56	1.31	< 0.05
Specific leaf area (m^2 kg^{-1})	21.10 ± 0.6	20.00 ± 0.7	0.95	n.s.
Leaf area ratio (m^2 kg^{-1})	10.59 ± 0.5	9.84 ± 0.4	0.93	n.s.
Leaf weight ratio (kg kg^{-1})	0.502 ± 0.010	0.492 ± 0.005	0.98	n.s.

similar magnitude. LAR and SLA were only slightly lower, on average, at elevated as compared to ambient CO_2; unlike *F. insipida* the decreases were not significant in *V. surinamensis*. As in *F. insipida*, root : shoot ratios of *V. surinamensis* did not change in response to elevated CO_2 (Table 1). The biomass ratio (*F. insipida* per chamber : *V. surinamensis* per chamber) increased from 31.4 ± 2.6 to 37.1 ± 4.3 (mean ± SD, n = 4) in response to elevated CO_2, but the increase was not significant at the 5% level.

Edge versus central plants

F. insipida plants growing at the edge of communities produced about 1.8 times more biomass and leaf area than plants in the centre, irrespective of CO_2 concentration, but there was no difference in height between edge and central plants at a given CO_2 concentration (Table 2). The percentage increase in biomass accumulation in response to elevated CO_2 was similar for edge and central plants of *F. insipida* (54 and 51%, respectively). Decrease in RGR of plants in the centre was accompanied by a decrease in NAR, a consequence of lower PFDs in the centre, while LAR, SLA and LWR changed little (data not shown). Relative changes in growth characteristics (increases in RGR and NAR, decreases in LAR, SLA and LWR) were similar at elevated as compared to ambient CO_2 for edge and central plants, respectively (data not shown).

Plant position within communities also affected growth of *V. surinamensis*, but to a lesser extent than that of *F. insipida*. Biomass of plants of *V. surinamensis* in the centre of communities was 25% (ambient CO_2) and 32% (elevated CO_2) lower than at the edge (Table 2). Significant increases in average biomass of *V. surinamensis*, caused by elevated CO_2, were only observed in edge plants (33%), and not in central plants. In response to elevated CO_2, the biomass ratio *F. insipida* : *V. surinamensis* (based on the sum of all plants per species in the centre or at the edge, respectively) increased, on average, from 34.8 ± 1.8 to 39.9 ± 4.6 (15%) at the edge, and from 26.3 ± 4.5 to 32.4 ± 5.8 (23%) in the centre, but in both cases, increases were not statistically significant.

Table 2. Biomass, dry matter allocation and other growth characteristics per plant after 16 weeks growth of *Ficus insipida* and *Virola surinamensis* at ambient (A) and elevated (E) CO_2 concentrations. Values are means ± SD of 4 samples (n = 4). Each sample represents the average of 10 or 8 plants at the edge and in the centre of plant communities, respectively, from each chamber. E/A refers to the ratio "response at elevated CO_2 : response at ambient CO_2" of plants at the edge and in the centre, respectively. Edge/Centre refers to the ratio "response of edge plants: response of central plants" at ambient and elevated CO_2, respectively.

Parameter	CO_2	Plant location		
		Edge	Centre	Edge/Centre
I. *Ficus insipida*				
Height (m)	Ambient	1.48 ± 0.05	1.48 ± 0.01	1.00
	Elevated	1.70 ± 0.09	1.75 ± 0.06	0.97
	E/A	1.15	1.18	
Total biomass (g)	Ambient	200 ± 10	111 ± 5	1.80
	Elevated	307 ± 39	168 ± 27	1.83
	E/A	1.54	1.51	
Root : shoot (g g^{-1})	Ambient	0.308 ± 0.018	0.282 ± 0.022	1.09
	Elevated	0.293 ± 0.016	0.279 ± 0.017	1.05
	E/A	0.95	0.99	
Leaf area (cm^2)	Ambient	17776 ± 819	10220 ± 790	1.74
	Elevated	24617 ± 2101	13590 ± 2102	1.81
	E/A	1.38	1.33	
II. *Virola surinamensis*				
Height (m)	Ambient	0.36 ± 0.01	0.34 ± 0.05	1.06
	Elevated	0.39 ± 0.01	0.38 ± 0.02	1.03
	E/A	1.08	1.12	
Total biomass (g)	Ambient	5.8 ± 0.6	4.3 ± 0.8	1.35
	Elevated	7.7 ± 0.7	5.2 ± 0.4	1.48
	E/A	1.33	1.21	
Root : shoot (g g^{-1})	Ambient	0.255 ± 0.024	0.265 ± 0.038	0.96
	Elevated	0.254 ± 0.026	0.266 ± 0.026	0.95
	E/A	1.00	1.00	
Leaf area (cm^2)	Ambient	590 ± 51	486 ± 106	1.21
	Elevated	737 ± 57	543 ± 62	1.36
	E/A	1.25	1.12	

Table 3. Starch and soluble sugar content in leaves of *F. insipida* and *V. surinamensis* during the final week of growth at ambient and elevated CO_2 concentrations. Values are means ± SD of 4 samples (n = 4), each of which represents the average of 2 measurements of different plants at the edge and in the centre of plant communities, respectively, from each chamber. Samples were taken from upper canopy leaves (edge, centre) and from midcanopy leaves (centre only, midcanopy). ND = not detected.

Species Carbohydrate (mg g^{-1} dry mass)	CO_2	Plant location, time of day					
		Edge		Centre		Centre, midcanopy	
		dawn	dusk	dawn	dusk	dawn	dusk
Ficus insipida							
Insoluble							
Starch	Ambient	15.5 ± 10.0	31.3 ± 17.9	8.8 ± 0.9	39.6 ± 8.3	3.1 ± 3.7	4.2 ± 5.1
	Elevated	49.8 ± 23.7	83.4 ± 26.8	21.6 ± 14.4	67.7 ± 22.7	1.1 ± 0.1	4.2 ± 5.3
Soluble							
Glucose	Ambient	11.9 ± 6.8	16.9 ± 14.4	10.8 ± 5.7	23.2 ± 22.9	9.3 ± 6.2	14.0 ± 13.9
	Elevated	7.8 ± 0.9	14.7 ± 7.4	9.0 ± 2.0	16.6 ± 6.9	7.4 ± 1.2	12.1 ± 5.3
Fructose	Ambient	8.9 ± 4.3	13.3 ± 9.5	9.4 ± 3.9	16.3 ± 11.1	11.2 ± 7.6	13.2 ± 11.2
	Elevated	5.7 ± 0.9	11.6 ± 4.4	6.3 ± 1.3	12.8 ± 5.3	7.2 ± 0.6	10.6 ± 4.7
Sucrose	Ambient	49.2 ± 18.8	74.4 ± 25.0	47.2 ± 15.3	74.8 ± 20.5	49.2 ± 18.6	66.7 ± 19.2
	Elevated	42.1 ± 13.2	73.0 ± 16.4	32.5 ± 5.7	65.4 ± 18.4	31.2 ± 16.8	54.3 ± 25.4
Raffinose	Ambient	1.1 ± 0.6	1.6 ± 1.1	1.0 ± 0.4	2.0 ± 1.5	1.0 ± 0.4	1.1 ± 0.6
	Elevated	0.8 ± 0.6	1.3 ± 0.7	0.5 ± 0.1	1.2 ± 0.5	0.8 ± 0.3	1.5 ± 1.0
Stachyose	Ambient	ND	ND	ND	0.4 ± 0.5	0.1 ± 0.2	0.3 ± 0.5
	Elevated	ND	ND	ND	ND	0.1 ± 0.1	0.3 ± 0.4
myo-Inositol	Ambient	11.8 ± 4.2	11.0 ± 3.2	12.4 ± 4.6	12.5 ± 6.0	4.6 ± 2.0	5.0 ± 2.2
	Elevated	9.1 ± 3.4	11.5 ± 3.5	8.4 ± 2.3	11.8 ± 4.4	2.6 ± 0.7	3.3 ± 1.0
Total soluble	Ambient	82.9 ± 32.8	117.2 ± 49.6	80.8 ± 29.4	129.1 ± 57.7	75.3 ± 34.1	100.2 ± 44.1
	Elevated	65.4 ± 18.7	112.0 ± 29.3	56.8 ± 11.0	107.7 ± 35.1	49.3 ± 17.8	81.9 ± 37.8
Sol. + insol.	Ambient	98.4 ± 36.9	148.5 ± 44.9	89.6 ± 29.8	168.8 ± 51.0	78.5 ± 38.8	104.3 ± 45.0
	Elevated	115.2 ± 26.4	195.4 ± 50.3	78.4 ± 20.7	175.4 ± 53.9	50.4 ± 17.7	86.1 ± 42.5
Virola surinamensis							
Insoluble							
Starch	Ambient	13.7 ± 12.4	8.0 ± 2.7	4.2 ± 0.6	5.2 ± 2.0		
	Elevated	22.9 ± 14.2	23.7 ± 22.8	4.5 ± 1.2	4.7 ± 3.8		
Soluble							
Glucose	Ambient	12.8 ± 5.7	20.3 ± 10.2	26.7 ± 11.2	29.9 ± 11.9		
	Elevated	14.0 ± 2.5	15.1 ± 1.9	17.2 ± 8.5	20.6 ± 4.6		
Fructose	Ambient	6.0 ± 2.0	10.4 ± 4.4	14.1 ± 7.5	12.4 ± 4.0		
	Elevated	6.2 ± 0.9	8.8 ± 1.5	6.5 ± 4.0	11.5 ± 4.4		
Sucrose	Ambient	20.2 ± 7.5	25.7 ± 14.1	14.0 ± 4.2	11.8 ± 8.6		
	Elevated	14.2 ± 7.3	16.6 ± 6.1	11.7 ± 6.5	4.5 ± 0.6		
Raffinose	Ambient	1.9 ± 1.9	1.3 ± 0.5	1.2 ± 0.5	1.0 ± 0.5		
	Elevated	1.0 ± 0.4	1.1 ± 0.4	0.7 ± 0.4	0.8 ± 0.4		
Stachyose	Ambient	0.9 ± 0.7	0.8 ± 0.5	0.5 ± 0.3	0.4 ± 0.3		
	Elevated	1.1 ± 0.3	1.1 ± 0.7	1.3 ± 0.4	1.2 ± 0.4		
myo-Inositol	Ambient	5.1 ± 4.0	4.3 ± 2.3	3.8 ± 1.9	3.3 ± 1.2		
	Elevated	3.7 ± 0.6	3.7 ± 1.6	2.2 ± 0.8	2.2 ± 0.6		
Total soluble	Ambient	46.8 ± 20.9	62.8 ± 30.9	60.3 ± 22.3	58.7 ± 18.6		
	Elevated	40.1 ± 10.1	46.4 ± 10.7	39.5 ± 13.9	40.8 ± 10.4		
Sol. + insol.	Ambient	60.5 ± 31.7	70.8 ± 33.3	64.4 ± 22.4	63.9 ± 17.0		
	Elevated	63.1 ± 5.4	70.1 ± 19.2	44.0 ± 13.1	45.5 ± 14.0		

Carbohydrates, C : N, and photosynthesis

In upper canopy leaves of edge and central plants of *F. insipida*, starch levels ranged from about 1 to 8% depending on time of day and CO_2 concentration (Table 3). At ambient CO_2, starch content increased from about 1 to 4% of leaf dry mass during the course of the day, while diurnal increases from 2 to 8% were observed at elevated CO_2. Soluble sugars, the majority of which was sucrose, represented between 5.7 and 13% of leaf dry mass. This was not altered by CO_2 concentration and also tended to increase diurnally. In shaded leaves from the midcanopy of central plants of *F. insipida*, starch content was less than 1% of leaf dry mass and was not affected by CO_2 concentration, while soluble sugars accounted for between 5 and 10% of leaf dry mass, indicating that soluble sugars were less affected by shade than were starch levels.

Carbohydrate levels were much lower in leaves of *V. surinamensis* than in upper canopy leaves of *F. insipida*. Starch content in *V. surinamensis* ranged from 0.4 to 2.4%, and soluble sugar content from 4 to 7%. The two major soluble sugars present were glucose and sucrose, with glucose exceeding sucrose levels in central plants of *V. surinamensis*.

N content was between 4.3 and 4.9% of leaf dry mass in upper canopy leaves of *F. insipida* and C : N ratios were 9 to 10 (Table 4). In shaded midcanopy leaves, N was slightly reduced to below 4% of leaf dry mass and C : N was increased to above 11. N content in leaves of *V. surinamensis* was about half that of *F. insipida*, and C : N about twice as high as in *F. insipida*.

At elevated CO_2, light saturated rates of net CO_2 uptake of *F. insipida* approached about 40 µmol $m^{-2}s^{-1}$, whereas at ambient CO_2 rates reached about 20 µmol $m^{-2}s^{-1}$ (Fig. 4; and additional data, not shown). Maximum rates of net CO_2 uptake in *V. surinamensis* were about 8 (elevated CO_2) and 6 µmol $m^{-2}s^{-1}$ (ambient CO_2), respectively (Fig. 4; and additional data, not shown).

Discussion

Among the three field studies performed thus far on responses of tropical model plant communities to elevated CO_2, this is the first to demonstrate markedly enhanced biomass accumulation at elevated CO_2. In two previous field experiments at the same study site in Panama (LOVELOCK et al. 1999; WINTER et al. 2000), plant communities grew on non-fertilized soil; elevated CO_2 did not significantly enhance community biomass accumulation. The application of commercial soil fertilizer in the current experiment resulted in considerably accelerated growth at ambient CO_2; elevated CO_2 concentra-

Table 4. C and N content in leaves of *Ficus insipida* and *Virola surinamensis* during the final week of growth at ambient and elevated CO_2 concentrations. Values are means ± SD of 4 samples (n = 4), each of which represents the average of 2 measurements of different plants at the edge and in the centre of plant communities, respectively, from each chamber. Samples were taken from upper canopy leaves (edge, centre) and from midcanopy leaves (centre only, midcanopy).

Species, Position, CO_2 conc.	C (% dry mass)	N (% dry mass)	C : N
Ficus insipida			
Edge			
Ambient CO_2	43.47 ± 0.28	4.59 ± 0.17	9.5 ± 0.4
Elevated CO_2	43.01 ± 0.32	4.32 ± 0.24	10.0 ± 0.5
Centre			
Ambient CO_2	43.91 ± 0.16	4.92 ± 0.25	9.0 ± 0.5
Elevated CO_2	43.72 ± 0.34	4.75 ± 0.39	9.3 ± 0.7
Centre, midcanopy			
Ambient CO_2	42.62 ± 0.26	3.80 ± 0.09	11.3 ± 0.3
Elevated CO_2	42.23 ± 0.91	3.63 ± 0.36	11.9 ± 1.1
Virola surinamensis			
Edge			
Ambient CO_2	49.40 ± 0.83	2.42 ± 0.14	20.6 ± 1.3
Elevated CO_2	49.11 ± 0.48	2.30 ± 0.13	21.5 ± 1.3
Centre			
Ambient CO_2	49.46 ± 0.30	2.78 ± 0.06	17.9 ± 0.3
Elevated CO_2	49.66 ± 0.52	2.39 ± 0.36	21.2 ± 3.4

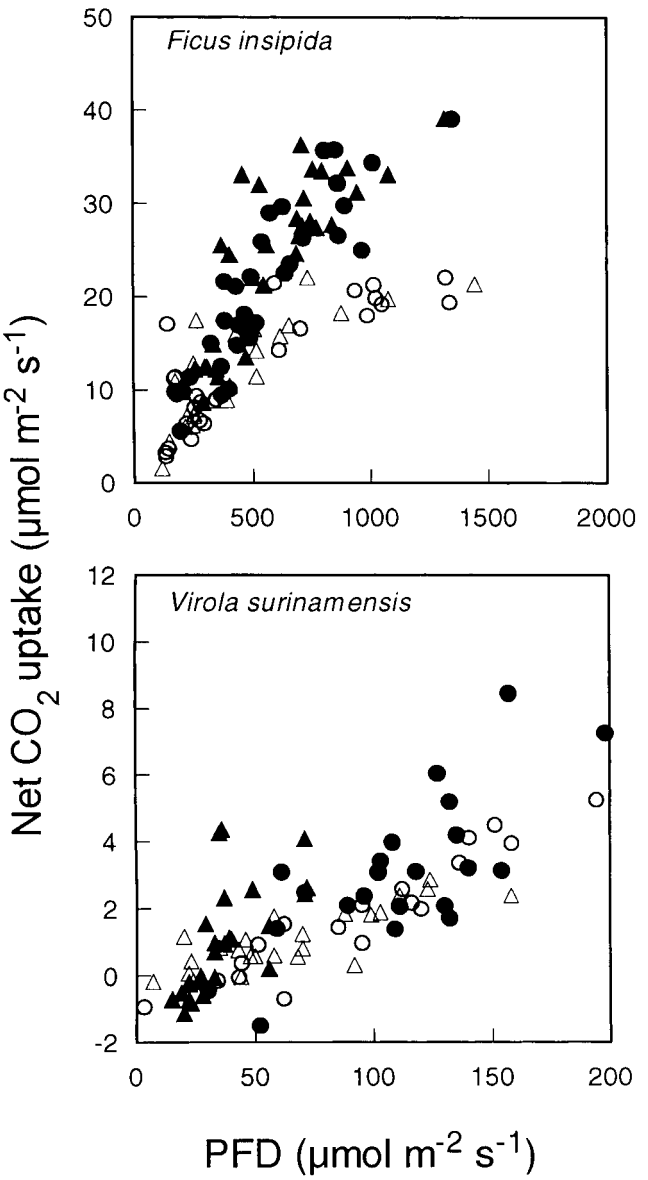

Fig. 4. Rates of photosynthetic net CO_2 uptake for leaves of *Ficus insipida* and *Virola surinamensis* at ambient (open symbols) and elevated CO_2 (closed symbols) from plants at the edge (circles) and centre (triangles) of communities. Plants growing at ambient CO_2 were assayed at ambient CO_2, and plants growing at elevated CO_2 were assayed at elevated CO_2. Natural variation in sunlight during diurnal cycles was used to generate PFD response curves. Data shown were obtained during the 8th week of the experiment.

tion led to an additional 52% increase in biomass accumulation as compared to ambient CO_2. The results of these three studies suggest that the ability of plant communities to positively respond to elevated CO_2 increases as soil nutrient conditions improve.

Both the *F. insipida* overstorey and the *V. surinamensis* understorey contributed to increased community biomass accumulation at elevated CO_2, but absolute increases in biomass at elevated CO_2 were much greater for *F. insipida* than for *V. surinamensis*. Relative biomass increases were also greater in *F. insipida* (53%) than in *V. surinamensis* (29%). A tendency toward increased responsiveness to elevated CO_2 by the pioneer species *F. insipida* as compared to the late successional species *V. surinamensis* was also indicated by greater average biomass ratios (sum of all *F. insipida* per chamber : sum of all *V. surinamensis* per chamber) at elevated as compared to ambient CO_2, although differences were not significant possibly because n equaled only 4. Tropical forest inventories show trends towards increased forest turnover rates and increased abundance of gap-dependent species during recent decades (PHILLIPS & GENTRY 1994).

Compared to the previous open-top chamber experiment, that applied the same species composition and plant density as the current experiment but used unfertilized soil (WINTER et al. 2000), growth under non-limiting nutrient conditions strongly reduced root : shoot ratios and increased the leafiness of plants. Root : shoot ratios decreased from >0.5 in unfertilized communities to approx. 0.3 in fertilized communities, LARs more than doubled, and SLAs increased, concomitant with reduced leaf starch contents, although comparisons are complicated because plant sizes and experimental durations were not the same. Without fertilizer addition, community NAR strongly increased in response to elevated CO_2 (36%), but this did not result in increased growth, because of marked reductions in LAR (WINTER et al. 2000). In contrast, under nutrient-rich conditions, increases in leaf photosynthesis rates (Fig. 4) and community NAR translated into significantly increased growth at elevated CO_2, because community LAR decreased relatively little during growth under elevated CO_2.

LAR responses to nutrient and CO_2 regime were related to the way in which nutrient status modified responses of SLA and starch content to elevated CO_2, particularly in *F. insipida* which contributed most to community biomass. While the elevated CO_2 treatment resulted in strong decreases in SLA (and marked increases in starch content) in non-fertilized *F. insipida* (WINTER et al. 2000), the generally higher SLAs of fertilized *F. insipida* decreased only marginally at elevated CO_2, mainly because starch content was much less affected by CO_2 concentration in fertilized than in non-fertilized plants. In an analogous manner, CO_2 concentration exerted essentially no influence on the relatively low C : N ratios observed in fertilized plants, while in non-fertilized plants, which had much higher C : N ratios than fertilized plants, C : N ratios markedly increased at elevated CO_2.

Although the present and two previous studies (LOVELOCK et al. 1998; WINTER et al. 2000) provide

compelling evidence for interacting effects between soil nutrient status and atmospheric CO_2 on plant growth, there is absolutely no consensus amongst researchers regarding the question of whether or not soil nutrient availability alters the propensity of plants to exhibit increased growth rates at elevated CO_2. Literature surveys have led to conclusions in favour (CEULEMANS & MOUSSEAU 1994; POORTER et al. 1996) and against (IDSO & IDSO 1994; LLOYD & FARQUHAR 1996) the concept that nutrient limited plants are less responsive to increases in CO_2 than are well-fertilized ones, although in the majority of cases, elevated CO_2 tends to be most effective in leading to increased biomass accumulation when growth conditions are favourable (CEULEMANS & MOUSSEAU 1994). Even so, poor nutrient availability does not preclude growth enhancements at elevated CO_2. In several studies, the ratio "RGR at elevated CO_2: RGR at ambient CO_2" changed little or not at all under low versus high nitrogen conditions (WONG 1979; 1990; NORBY et al. 1986; LLOYD & FARQUHAR 1996). In this context, DRAKE et al. (1997) emphasize the benefits associated with increased efficiency of nitrogen use at elevated CO_2 when soil nitrogen resources are severely limiting (NORBY et al. 1986). LLOYD & FARQUHAR (1996) argue that, mechanistically there is no reason to assume that nitrogen limited plants, and slow-growing plants in general (POORTER 1993) would be less responsive to elevated CO_2 than well nourished, rapidly growing plants. The authors present a model indicating that, depending on the rate of N-saturated net CO_2 uptake at ambient CO_2, plants with low nitrogen availability can show either higher or lower relative growth enhancements than well-fertilized plants.

A simple explanation that may help to interpret observations of contrasting plant growth responses to elevated CO_2 in studies with varying soil nutrient supply, could be the greater difficulty of precisely assessing biomass ratios of slowly growing plants as compared to rapidly growing plants. When absolute changes in biomass are small due to unfavourable growth conditions, variability of relative growth responses of replicate plants and communities is often exacerbated, a complication that demands particularly large sample sizes. It should also be noted that in our field studies of tropical model communities, relationships between photosynthesis, growth and edaphic conditions at ambient and elevated CO_2 were more complex than in the examples discussed by LLOYD & FARQUHAR (1996) because in our experiments nitrogen nutrition was not the only parameter affecting plant growth; soil drainage, soil compaction and the level of soil nutrients other than nitrogen also varied.

The theory of growth analysis predicts that treatments that increase RGR of a plant at present ambient CO_2 concentrations such as enhanced nutrient availability do not automatically lead to greater stimulation of growth at elevated CO_2. For example, if (i) elevated CO_2 would lead to the same sustained percentage increase of net CO_2 assimilation and hence net biomass gain per unit leaf area per unit of time, for plants with a low RGR and for plants with a high RGR, respectively, and if (ii) patterns of biomass allocation (i.e. LAR) within each CO_2 treatment would not change, then, over a given time interval, plants with a low basal RGR would attain the same biomass ratio (biomass at elevated CO_2: biomass at ambient CO_2) as plants with the high RGR, although the difference (RGR at elevated CO_2 – RGR at ambient CO_2) would increase for plants with an inherently higher RGR (cf. POORTER 1993). The biomass ratio will change however, if elevated CO_2 affects either the rate of CO_2 fixation and/or LAR differently in plants with a high and a low RGR. For example, if plants with a high RGR were less prone to photosynthetic downregulation under elevated CO_2 than plants with a low RGR (SAGE 1994), then the biomass ratio would be greater in high RGR plants. Alternatively, and as is shown in our studies, if LAR decreases less over time in response to elevated CO_2 in high RGR plants, as compared to low RGR plants, then the biomass ratio would also be higher in high RGR plants.

Drawing analogies between CO_2 and PFD, LLOYD & FARQUHAR (1996) correctly state that being „nitrogen limited" does not mean that a plant is unresponsive to changes in other growth modulating factors such as light. However, nitrogen-limited leaves are usually constrained in their ability to use high PFDs for CO_2 uptake since photosynthesis saturates at lower PFDs and light saturated rates of photosynthesis are lower in nitrogen-poor than in nitrogen-rich leaves (Medina 1971). Similarly, CO_2 response curves of nitrogen limited and nitrogen rich leaves often show greater absolute increases in carbon gain between ambient CO_2 and saturating CO_2 levels in nitrogen-rich than in nitrogen limited leaves (WONG 1979), indicating a greater capacity (sink strength) of well-nourished plants to exploit elevated CO_2 for increased carbon gain. Thus increased soil nutrient availability, by favouring high rates of CO_2 assimilation and a high LAR, may indeed promote the ability of plants to exhibit enhanced rates of biomass accumulation in response to elevated CO_2, at least in the short-term, rather than merely improving an investigator's ability to experimentally demonstrate CO_2 related augmentation of growth.

Responses of tropical model communities to elevated CO_2 were previously assessed in two major glasshouse studies at the University of Basel, Switzerland (KÖRNER & ARNONE 1992; ARNONE & KÖRNER 1995). Depending on nutrient availability, community LAI increased from either about 3.5 to 7 in 94 days (nutrient rich soil; KÖRNER & ARNONE 1992), or from about 1 to 4 in 530

days (nutrient poor soil; ARNONE & KÖRNER 1995). In neither case did elevated CO_2 significantly increase biomass accumulation of communities. In the experiment reported here, which led to marked increases in community biomass at elevated CO_2, soil nutrient supply was much higher than in either of the Basel experiments. While N content did not exceed 2.2% of leaf dry mass in any of the species investigated by KÖRNER & ARNONE (1992), N-content was greater than 2.3% (*V. surinamensis*) and 4.3% (upper canopy leaves of *Ficus insipida*) at ambient and elevated CO_2 in the study presented here. Communities also grew much more rapidly in this open-top chamber study than in the Basel glasshouse experiments, e.g., LAIs increased from 0.15 to 9 (ambient CO_2) and 12.3 (elevated CO_2), respectively, over the course of 112 days. Such high values of LAI considerably exceed LAIs reported for mature moist tropical forests (5–8, WADSWORTH 1997) and are probably related to non-limiting soil nutrient supply combined with the absence of surrounding vegetation from open-top chamber communities which received more light (edge effect) than if they were segments of a larger stand. Since surrounding vegetation was also absent in the previous experiment without soil fertilizer (WINTER et al. 2000), a comparison of the effect of nutrient addition on these otherwise identically composed plant communities remains valid.

Conclusion

Taken together, the present and two previous field experiments (LOVELOCK et al. 1998; WINTER et al. 2000) show that soil nutrient conditions can strongly modify responses of communities of juvenile tropical trees to elevated CO_2. In the short term, over a period of several months, pronounced increases in biomass accumulation in response to elevated CO_2 were only demonstratable in communities growing under conditions of unlimited nutrient supply. These communities maintained relatively high LARs at elevated CO_2, which allowed them to effectively use increased leaf net CO_2 assimilation rates, observed under elevated CO_2, for increased biomass accumulation. In contrast, in previously studied communities growing on unfertilized soil, relatively low LARs that already existed at ambient CO_2, were further reduced under conditions of elevated CO_2, largely because of pronounced decreases in SLA resulting from the build-up of starch in leaves. Thereby, potentially positive effects of increased rates of net CO_2 uptake per unit leaf area on community growth were minimized under elevated CO_2. Large-scale CO_2 enrichment studies (MCLEOD & LONG 1999) that extend over several years and thoroughly consider site-specific edaphic conditions and soil carbon pools, are needed to further assess the extent to which regenerating tropical forest systems are affected by rising atmospheric CO_2 concentrations.

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References

ARNONE III, J. A. (1996): Predicting responses of tropical plant communities to elevated CO_2. In: KÖRNER, C. & BAZZAZ, F. A. (eds.): Carbon dioxide, populations, and communities. – Academic Press, San Diego, 101–121.

ARNONE III, J. A. & KÖRNER, C. (1995): Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. – Oecologia **104:** 61–71.

CROAT, T. B. (1978): Flora of Barro Colorado Island. – Stanford University Press, Stanford.

CEULEMANS, R. & MOUSSEAU, M. (1994): Effects of elevated atmospheric CO_2 on woody plants. – New Phytol. **127:** 425–446.

DRAKE, B. G.; GONZALES-MELER, M. A. & LONG, S. P. (1997): More efficient plants: a consequence of rising atmospheric CO_2? – Annu. Rev. Plant Physiol. Plant Mol. Biol. **48:** 609–639.

FARNSWORTH, E. J.; ELLISON, A. M. & GONG, W. K. (1996): Elevated CO_2 alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). – Oecologia **108:** 599–609.

HOUGHTON, J. (1997): Global warming. – Cambridge University Press, Stanford.

IDSO, K. E. & IDSO, S. B. (1994): Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. – Agricultural and Forest Meteorology **69:** 153–203.

KOCH, G. W. & MOONEY, H. A. (eds.) (1996): Carbon dioxide and terrestrial ecosystems. – Academic Press, San Diego.

KÖRNER, C. (1998): Tropical forests in a CO_2-rich world. – Climate Change **39:** 297–315.

KÖRNER, C. & ARNONE III, J. A. (1992): Responses to elevated carbon dioxide in artificial tropical ecosystems. – Science **257:** 1672–1675.

KÖRNER, C. & BAZZAZ, F. A. (eds.) (1996): Carbon dioxide, populations, and communities. – Academic Press, San Diego.

LLOYD, J. & FARQUHAR, G. D. (1996): The CO_2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO_2 concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. – Funct. Ecol. **10:** 4–32.

LOVELOCK, C. E.; KYLLO, D.; POPP, M.; ISOPP, H.; VIRGO, A.; WINTER, K. (1997): Symbiotic vesicular-arbuscular mycorrhizae influence maximum rates of photosynthesis in tropical tree seedlings grown under elevated CO_2. – Aust. J. Plant Physiol. **24:** 185–194.

LOVELOCK, C. E.; WINTER, K.; MERSITS, R. & POPP, M. (1998): Responses of communities of tropical tree species to elevated CO_2 in a forest clearing. – Oecologia **116:** 207–218.

LOVELOCK, C. E.; POSADA, J. & WINTER, K. (1999): Compensatory growth and photosynthesis under elevated CO_2 after defoliation of developing leaflets of seedlings of a tropical tree, *Copaifera aromatica*. – Biotropica **31:** 279–287.

MCLEOD, A. R. & LONG, S. P. (1999): Free-air carbon dioxide enrichment (FACE) in global change research: a review. – Adv. Ecol. Res. **28:** 1–56.

MEDINA, E. (1971): Effect of nitrogen supply and light intensity during growth on the photosynthetic capacity and carboxydismutase activity of leaves of *Atriplex patula* ssp. *hastata*. – Carnegie Inst. Wash. Yearb. **70:** 551–559.

NORBY, R. J.; O'NEILL, E. G. & LUXMOORE, R. J. (1986): Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. – Plant Physiol. **82:** 83–89.

OBERBAUER, S. F.; STRAIN, B. R. & FETCHER, N. (1985): Effect of CO_2 enrichment on seedling physiology and growth of two tropical tree species. – Physiol. Plant. **65:** 352–356.

PHILLIPS, O. L. & GENTRY, A. H. (1994): Increasing turnover through time in tropical forests. – Science **263:** 954–958.

POORTER, H. (1993): Interspecific variation in the growth response of plants to an elevated CO_2 concentration. – Vegetatio **104/105:** 77–97.

POORTER, H.; ROUMET, C. & CAMPBELL, B. D. (1996): Interspecific variation in the growth response of plants to elevated CO_2: a search for functional types. In: KÖRNER, C. & BAZZAZ, F. A. (eds.): Carbon dioxide, populations, and communities. – Academic Press, San Diego, 375–412.

REEKIE, E. G. & BAZZAZ, F. A. (1989): Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. – Oecologia **79:** 212–222.

RODEN, J. S.; WIGGINS, D. J. & BALL, M. C. (1997): Photosynthesis and growth of two rain-forest species in simulated gaps under elevated CO_2. – Ecology **78:** 385–393.

SAGE, R. F. (1994): Acclimation of photosynthesis to increasing atmospheric CO_2: The gas exchange perspective. – Photosynthesis Res. **39:** 351–368.

WADSWORTH, F. H. (1997): Forest production for tropical America. – USDA Forest Service, Agriculture Handbook 710.

WARD, J. K. & STRAIN, B. R. (1999): Elevated CO_2 studies: past, present and future. – Tree Physiol. **19:** 211–220.

WINTER, K. & VIRGO, A. (1998): Elevated CO_2 enhances growth in the rain forest understory plant, *Piper cordulatum*, at extremely low light intensities. – Flora **193:** 323–326.

WINTER, K. & LOVELOCK, C. E. (1999): Growth responses of seedlings of early and late successional tropical forest trees to elevated atmospheric CO_2. – Flora **194:** 221–227.

WINTER, K.; GARCIA, M.; LOVELOCK, C. E.; GOTTSBERGER, R. & POPP, M. (2000): Responses of model communities of two tropical tree species to elevated atmospheric CO_2: growth on unfertilized soil. – Flora **195:** 289–302.

WONG, S. C. (1979): Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. – Oecologia **44:** 68–74.

WONG, S. C. (1990): Elevated atmospheric partial pressure of CO_2 and plant growth. II. Non-structural carbohydrate content in cotton plants and its effect on growth parameters. – Photosynthesis Res. **23:** 171–180.

WÜRTH, M. K. R.; WINTER, K. & KÖRNER, C. (1998): In situ responses to elevated CO_2 in tropical forest understory plants. – Funct. Ecol. **12:** 886–895.

ZISKA, L. H.; HOGAN, K. P.; SMITH, A. P. & DRAKE, B. G. (1991): Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. – Oecologia **86:** 383–389.

ZOTZ, G. & WINTER, K. (1996): Diel patterns of CO_2 exchange in rainforest canopy plants. In: MULKEY, S. S.; CHAZDON, R. L. & SMITH, A. P. (eds.): Tropical forest plant ecophysiology. – Chapman & Hall, New York, 89–113.