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Responses to Elevated Carbon Dioxide in Artificial Tropical Ecosystems

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Carbon, nutrient, and water balance as well as key plant and soil processes were simultaneously monitored for humid tropical plant communities treated with CO_2-enriched atmospheres. Despite vigorous growth, no significant differences in stand biomass (of both the understory and overstory), leaf area index, nitrogen or water consumption, or leaf stomatal behavior were detected between ambient and elevated CO_2 treatments. Major responses under elevated CO_2 included massive starch accumulation in the tops of canopies, increased fine-root production, and a doubling of CO_2 evolution from the soil. Stimulated rhizosphere activity was accompanied by increased loss of soil carbon and increased mineral nutrient leaching. This study points at the inadequacy of scaling-up from physiological baselines to ecosystems without accounting for interactions among components, and it emphasizes the urgent need for whole-system experimental approaches in global-change research.

Greater carbon sequestering by terrestrial ecosystems, increasing amounts of leaf area per unit of land area, reduced water consumption, and greater efficiency of mineral nutrient capture are some of the common predictions for plant and ecosystem behavior in a future world with high levels of CO_2 (*1–5*). We evaluated these assumptions in an experiment with closed ecosystems of tropical rain forest plants of various life forms arranged in complex communities.

The only available data about in situ CO_2 responses of a natural terrestrial ecosystem, Alaskan tundra (*6*), revealed no such growth stimulation, whereas semiaquatic salt-marsh vegetation, whose nutritional situation is comparable to agricultural conditions, not surprisingly showed positive biomass responses similar to those found in crops (*7, 8*). Forests, which make up about 90% of the global biomass, have not yet been studied under artificially enhanced CO_2 levels, and current predictions of their behavior in a CO_2-rich world are based on data largely derived from experiments with isolated seedlings (*4, 9*). Before success is realized from long-term and large-scale CO_2 enrichment experiments on natural forests (*10*), investigations with experimental ecosystems provide an excellent means for the assessment of CO_2 effects in highly structured ecosystems. We selected a humid tropical ecosystem because this biome represents about 40% of the global biomass and because plant responses to CO_2 are predicted to be more pronounced under high temperatures (*11*).

We constructed four such model ecosystems by enclosing identically structured populations of 15 tropical plant species (*12*) in 17-m^3 polyethylene-covered houses. Plants in each house shared a common soil volume of 1.3 m^3 and ground area of 6.7 m^2. The two to six individuals of each species in each ecosystem were located in exactly the same position in the four houses. Soils consisted of a mixture of silicate sand and vermiculite, overlain by a thin layer of leaf and bark compost, which was supplemented with 20 g per square meter of timed-release fertilizer pellets. Houses were situated in a climate-conditioned greenhouse at the University of Basel, Switzerland, and received natural daylight. Closed air-circulation systems changed the air in each house 11 times per hour and included activated charcoal filters and dew point and temperature controllers with dehumidifying water traps. The experimental ecosystems were not designed to mimic a specific natural situation but to represent model stands with a characteristic vertical stratification.

All ecosystems were allowed to stabilize under low CO_2 levels (340 μl of CO_2 per liter of air) for 30 days before the experiment. No differences in stand structure {for example, leaf area index [LAI; area of leaves (m^2) per square meter of ground] and mean height of individual plants} were apparent among houses after this stabilization period. Daytime CO_2 was maintained at 340 μl of CO_2 per liter in two of the houses, while the other two received 610 μl of CO_2 per liter during the experiment. The experiment was terminated after 3 months, 1 month after the LAI stabilized at a value typical for humid tropical forests (*13*).

Total ecosystem biomass at both CO_2 levels more than doubled within 3 months (from about 700 to 1500 g of dry mass per square meter); thus, the experimental conditions supported vigorous growth. Despite this increase, neither the biomass of the entire ecosystem nor that of the individual species (*14*) responded significantly to elevated CO_2 (Table 1), although a slight positive effect was detected. This result is in contrast to that of Ziska *et al.* (*15*), who reported dramatic stimulation of growth in tropical plants isolated in pots that contained rich soil. However, in the long run, marginal gains, such as those found here under elevated CO_2, could still result in more rapid maturation of stands.

One of the key determinants of carbon fixation by ecosystems is the amount of photosynthetic machinery per unit area of land, commonly expressed as the LAI. Elevated CO_2 has been shown to enable plants to achieve greater relative carbon gains under low irradiances (*4, 16, 17*), and therefore greater leaf retention on plants in the shade would be expected, leading to greater LAIs (*18*). The LAI in our study, measured with an electronic canopy analyzer (*19*), increased linearly in all ecosystems during the first 60 days from 3.4 to approximately 7, after which it leveled off (Fig. 1). Steady-state LAI was accompanied by the onset of leaf litter production, which was

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Table 1. Effect of elevated CO_2 levels on final biomass and litter production (measured in grams per square meter). Mean ± SE of two houses for each CO_2 level (ambient and elevated CO_2) are shown. With the use of the two-tailed *t* test, *P* gives the probability that the results from the two CO_2 treatments are not the same. Biomass partitioning is represented as a percent of the total system biomass which is calculated as the mean of two houses. The biomass of roots ≤1 mm in diameter was measured for the entire soil depth with the use of mesh in-growth cylinders. Air circulation systems were regularly switched between ambient and elevated CO_2 houses to minimize the potential effects of systematic errors.

Component	Treatment				Mean difference (% change in actual biomass)	*P*
	Ambient CO_2		Elevated CO_2			
	Amount of biomass	% of total biomass	Amount of biomass	% of total biomass		
Biomass (total)	1408 ± 5	100.0	1558 ± 52	100.0	+11	0.1022
Aboveground	1165 ± 7	82.7	1241 ± 51	79.6	+ 6	0.2741
Leaf	391 ± 7	27.7	413 ± 6	26.5	+ 5	0.1371
Stem	774 ± 14	55.0	828 ± 45	53.1	+ 7	0.3658
Roots	243 ± 2	17.3	318 ± 2	20.4	+30	0.0011
Diameter ≤1 mm	32 ± 5	2.3	52 ± 3	3.3	+63	0.0658
Diameter 1 to 3 mm	103 ± 3	7.3	141 ± 2	9.1	+37	0.0068
Diameter >3 mm	108 ± 1	7.7	125 ± 6	8.0	+16	0.1113
Litter production	8.4 ± 0.0		11.6 ± 0.0		+38	0.0002

greater under elevated CO_2 (Table 1). Final LAI and light extinction (1 to 2% reaching the ground) (Fig. 2) were similar to those reported for closed forest canopies in Puerto Rico and Malaysia (*13*).

Leaves in ecosystems exposed to elevated CO_2 levels contained twice as much total nonstructural carbohydrates (TNC; 18% versus 8% of dry mass) as those grown under ambient CO_2 levels. Thus, TNC-free leaf biomass under elevated CO_2 levels was actually 6% less (not significant) than that of leaves under ambient CO_2 levels. TNC accumulation increased dramatically with height in the canopy, and up to one-third of total leaf dry matter was composed of TNC in plants exposed to high levels of CO_2 (Fig. 2). Monocots tended to accumulate less than dicots even when leaves from the same canopy layer were compared. No evidence of carbohydrate dissipation from sun-exposed to shaded leaves of the same plant was observed. Accumulation of TNC under elevated CO_2 levels has been also observed in a number of crop plants (*20, 21*), but this vertical stratification has not been described. In the houses with elevated CO_2, top-canopy leaves that contained the largest amounts of starch were also more yellow in *Ficus benjamina* and *Tetrastigma voinerianum* than in counterparts in the houses with ambient CO_2 levels. This observation suggests that increased CO_2 levels under full illumination can have an adverse effect, as has been shown to occur in some potted crop plants under higher CO_2 concentrations [1000 μl of CO_2 per liter (*22, 23*)] than used here.

There are several reasons that carbohydrates might overflow in CO_2-fertilized leaves (*24*): (i) reduced activity of carbon sinks, (ii) restriction of assimilate transport, or (iii) limitation of phosphorylation in the chloroplasts. Factors that have been shown to result in some of these conditions, which lead to increased TNC accumulation in leaves, are nutrient shortage (*21*) and the restriction of root growth by pot volume (*25*) and by soil penetration resistance (*26*). Because plants in our experiment grew in a large, common volume of soil unlikely to restrict root growth, the next logical step was to evaluate the extent to which plants were limited in the amount of available nutrients (nitrogen in particular).

Total nutrient pool size remained constant because nutrients lost in drainage water were recycled (nitrogen losses from denitrification were assumed to be negligible compared to the size of the nitrogen pool). Nitrogen uptake by plants was the same at both CO_2 levels, although more nitrogen was allocated to roots and less to leaves under elevated CO_2 levels (Table 2). Similar observations have been reported for temperate, forest-tree species (*27*).

Although total biomass more than doubled during the experiment for both control

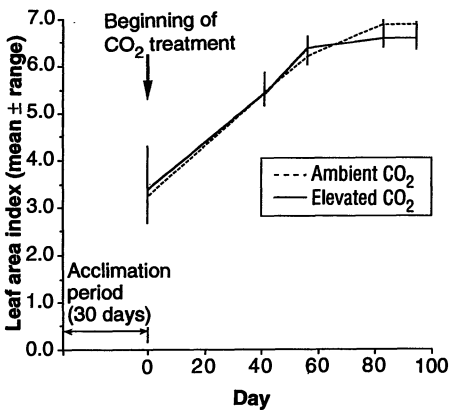

Fig. 1. Leaf canopy development under ambient and elevated CO_2 levels. The LAI is measured in area of leaves (m^2) per square meter of ground.

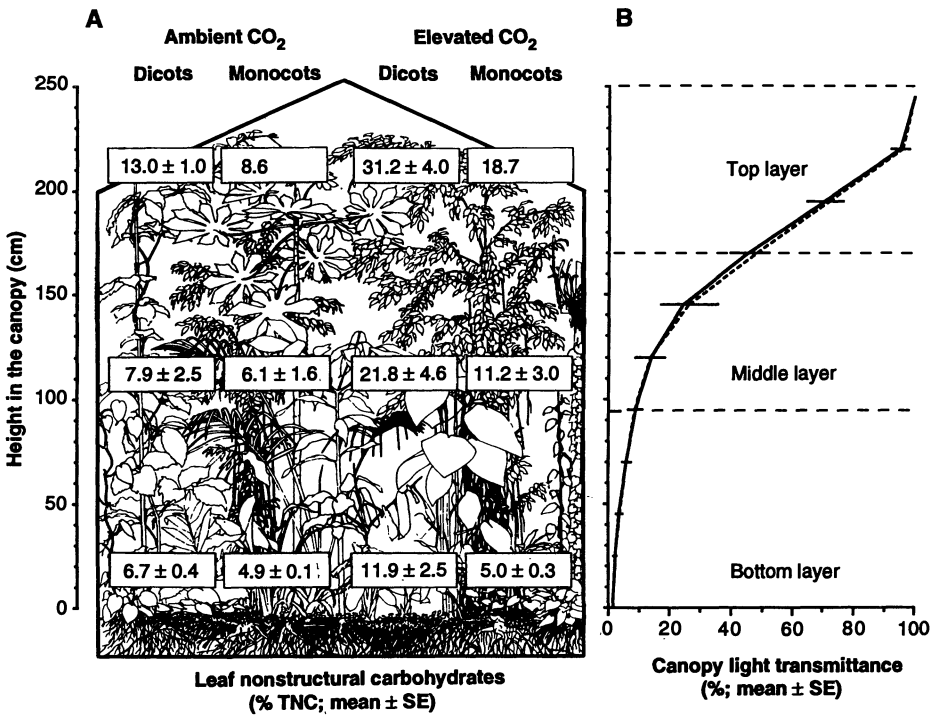

Fig. 2. Increases in leaf nonstructural carbohydrate (TNC) with increasing height in the canopy (**A**) corresponding to irradiance at the end of the experiment (**B**). Side light was shaded with green plastic slats around each house.

and elevated CO_2 treatments, one could argue that soil nutrient limitations may have precluded a significant biomass response to the elevated CO_2. However, this does not seem to have been the case because ions of all major nutrients were abundant in percolation water after all watering in which the soil was saturated (Table 3). Amounts of nitrate, potassium, and phosphate in percolation water of ecosystems with high CO_2 levels were twice as high as those in ecosystems with low CO_2 levels. Hence, although mineral nutrients were not supplied to permit luxury consumption, they were available at sufficient levels to have allowed for a CO_2 stimulation of growth.

Another possible explanation for the unexpectedly small stimulation of biomass production under elevated CO_2 levels could be a downward adjustment of photosynthesis (*20, 25, 28*). Actual canopy CO_2 uptake measured at the end of the experiment was almost twice as high in houses with elevated CO_2 levels as in those with ambient CO_2 levels. However, uptake rates of canopies in both CO_2 treatments, after an accounting for CO_2 evolution from the soil, were identical (7.5 μmol of CO_2 per square meter of ground per second) when CO_2-rich ecosystems were exposed to ambient CO_2 for short periods. This result indicated that no downward adjustment had occurred. Also, leaf diffusive conductances and stomatal densities did not differ between treatments (*14*).

A large portion of the assimilates produced in excess of what occurred as starch in canopies in the houses with high CO_2 levels appeared to have been allocated to sinks below the ground level. Fine-root biomass (Table 1) was significantly greater at elevated CO_2 levels, a frequently reported observation (*29, 30*), and CO_2 efflux from soils almost doubled (Table 4). Efflux rates measured in houses with ambient CO_2 levels (1.9 μmol of CO_2 m^{-2} ground s^{-1}) were similar to the mean (2.0 μmol of CO_2 m^{-2} ground s^{-1}) calculated for annual rates for 13 different tropical forests reported by Raich and Nadelhoffer (*31*). Greater fine-root mass would account for some of the increase in efflux found in our ecosystems at high CO_2 levels, but much of the CO_2 must have arisen from stimulated microbial activity that was a result of increased fine-root turnover or root exudation (*32*), as indicated by one-third greater soil xylanase and protease activity in houses with high CO_2 levels (*33*). Increased turnover of fresh root tissue (for example, release of xylose) and exudation of soluble substrate (carbohydrates and amino acids) possibly stimulated the breakdown of soil organic matter and would explain why cumulative soil carbon losses were three times greater at the end of the experiment under elevated CO_2 levels (Table 4). Elliott *et al.* (*34*) also reported CO_2-stimulated rates of soil CO_2 efflux in shortgrass prairie microcosms. The average daily consumption of water by the experimental ecosystems did not differ between CO_2 treatments. This substantiates the lack of differences observed in LAI and leaf diffusive conductance between the different CO_2 treatments and agrees with data of Reekie and Bazzaz (*35*).

We find it alarming that CO_2 fertilization can promote losses of soil carbon and the release of mineral nutrients similar to the effects achieved when sugar is added to soils (*36*). These effects may lead to long-lasting depletion of mineral nutrients if unbound ions are leached from the rhizosphere. There is a danger that such processes may be masked in the short term, because elevated CO_2 has been shown to

Table 2. Effect of elevated CO_2 levels on final system nitrogen distribution [grams of N per square meter of ground (g N m^{-2}); mean ± SE of two houses for each CO_2 level (ambient and elevated) are shown; *P* is as in Table 1. The CHN analyzer was used for plant tissue, and Kjeldahl procedures were used for total soil N]. Starting soil nitrogen for all houses was 39.9 ± 0.2 g N m^{-2}, which included 2.9 g N m^{-2} in 3-month time-release Osmocote pellets (Sierra, Heerlen, the Netherlands).

Component	Treatment		Mean difference (%)	*P*
	Ambient CO_2	Elevated CO_2		
N in biomass (total)	10.47 ± 0.02	10.46 ± 0.09	0	0.8914
Aboveground	8.76 ± 0.11	8.18 ± 0.09	− 7	0.0551
Leaf	5.54 ± 0.03	5.05 ± 0.02	− 9	0.0054
Stem	3.22 ± 0.14	3.13 ± 0.07	− 3	0.6234
Roots	1.71 ± 0.09	2.28 ± 0.01	+33	0.0245
Diameter ≤1 mm	0.45 ± 0.05	0.68 ± 0.05	+51	0.0021
Diameter 1 to 3 mm	0.73 ± 0.02	1.00 ± 0.01	+37	0.0034
Diameter >3 mm	0.53 ± 0.01	0.60 ± 0.05	+13	0.2939
Litter	0.09 ± 0.00	0.12 ± 0.00	+33	0.0002
Soil (total)	34.68 ± 0.24	34.43 ± 0.01	− 1	0.4125

Table 3. Effect of elevated CO_2 levels on nutrients (measured in milligrams per square meter) in ecosystem percolation water over the course of the experiment sampled after soil-saturating "rains"; N, nitrogen; P, phosphorus. Mean ± SE of two houses for each CO_2 level (ambient and elevated) are shown; *P* is as in Table 1. Analysis methods: ammonium (NH_4^+), Indophenol method (Berthelot's reaction); nitrate (NO_3^-), ion chromatography; phosphate (PO_4^{-3}), molybdenum blue; K^+, flame photometry; Mg^{2+}, atomic absorption.

Nutrients	Treatment		Mean difference (%)	*P*
	Ambient CO_2	Elevated CO_2		
NH_4^+-N	0.78 ± 0.59	0.37 ± 0.12	− 53	0.5090
NO_3^--N	1.58 ± 0.40	3.78 ± 0.93	+139	0.0551
PO_4^{-3}-P	16.59 ± 4.60	37.00 ± 8.64	+123	0.0636
K^+	7.62 ± 2.03	20.39 ± 6.31	+168	0.0831
Mg^{2+}	1.34 ± 0.61	1.34 ± 0.64	0	0.9993

Table 4. Effect of elevated CO_2 levels on below-ground carbon at the end of the experiment. Mean ± SE of two houses for each CO_2 level (ambient and elevated) are shown; *P* is as in Table 1. Methods: fine-root length, line intersection method (samples taken from in-growth cylinders); soil CO_2 efflux, mobile cuvettes and infrared gas analysis; soil carbon of pooled samples from each house, dichromate oxidation.

Component	Treatment		Mean difference (%)	*P*
	Ambient CO_2	Elevated CO_2		
Fine-root length (meters per square meter of ground)				
Diameter ≤ 1 mm	3152 ± 629	5304 ± 158	+ 68	0.0800
Diameter >1 mm	380 ± 37	461 ± 68	+ 21	0.4058
Soil CO_2 efflux (μmol of CO_2 m^{-2} ground s^{-1})	1.9 ± 0.2	3.6 ± 0.2	+ 89	0.0176
Soil carbon content (g C m^{-2})				
Start	1280 ± 23			
Absolute loss in 94 days	75 ± 10	300 ± 35	+300	0.0261
% loss of starting C in 94 days	5.9 ± 0.6	23.6 ± 3.3	+300	0.0346

stimulate growth, at least temporarily, even under serious nutrient shortage (*29*, *37*).

Another concern raised by our results is that the deleterious levels of starch produced in leaves in the top of canopies under elevated CO_2 levels may cause alterations in dominance relations in plant communities as CO_2 rises. Accumulation of TNC appears to be a result of a specific local dissipation problem at the cellular or chloroplast level because we see no obvious reason for reduced sink activity or long-distance transport problems in the ecosystems with high CO_2 levels. This was indicated by significant increases in the allocation of carbon to the rhizosphere (Tables 1 and 4) and a lack of TNC concentration gradients in stem tissue in plants growing under elevated CO_2 (*14*).

Finally, our results challenge thinking about the biological effects of a doubling of atmospheric CO_2 levels. Observed over long periods, natural ecosystems are believed to have a nearly balanced carbon budget, with photosynthetic uptake equal to respiratory release of CO_2 (*38*). As a result, the ecosystem CO_2 compensation point should be close to ambient CO_2 levels, as was found in the arctic tundra (*39*). It is uncertain how rapidly ecosystem CO_2 compensation points will adjust to rising CO_2 levels. If ecosystem compensation points have not tracked the rapid increases in atmospheric CO_2 levels over the past 100 years, present ambient levels may already represent a massive CO_2 overload to some ecosystems. Our data indicate that elevated CO_2 may not necessarily lead to greater carbon sequestering by terrestrial ecosystems, but that it will likely result in greater carbon turnover.

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The Present Is Not the Key to the Past: A Polar Forest from the Permian of Antarctica

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An in situ Upper Permian fossil forest in the central Transantarctic Mountains near the Beardmore Glacier includes 15 permineralized trunks in growth position; the paleolatitude of the site was approximately 80° to 85° south. Numerous leaves of the seed fern *Glossopteris* are present in the shale in which the trunks are rooted. The trunks are permineralized and tree rings reveal that the forest was a rapidly growing and young forest, persisting in an equable, strongly seasonal climate—a scenario that does not fit with some climate reconstructions for this time period.

Fossil forests represent an important data source that can be utilized to reconstruct past climates. High-latitude fossil forests are rare, with instances known from Cretaceous deposits on Alexander Island (Antarctic peninsula) (*1*) and Paleocene-Eocene sediments on Axel Heiberg Island (Canadian Arctic) (*2*). These sites provide an opportunity to examine forest density and productivity at high-latitude sites in the past. The preservation of the wood also allows for an analysis of tree ring data. When combined with data from compression-impression floras, vegetation reconstruction is greatly enhanced. This biological input represents an important parameter that can be used to calibrate climate models based primarily on physical data.

During our 1991 to 1992 field season, we examined an in situ fossil forest on a flat bench at the top of the northward extending ridge of Mount Achernar (Fig. 1). The forest is exposed over an area of about 20 by 12 m (84°22′23″S, 164°37′56″E; Buckley Island Quadrangle) (*3*). Fifteen stumps are preserved in growth position and occur within shaley floodplain deposits (*4*) in the upper part of the Buckley Formation. Based on palynomorphs recovered at nearby sites (*5*), the age of this deposit is considered to be Late Permian.

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