Oecologia (1995) 104:61–71


ORIGINAL PAPER

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# Soil and biomass carbon pools in model communities of tropical plants under elevated $CO_2$

Received: 27 July 1994 / Accepted: 21 April 1995

**Abstract** The experimental data presented here relate to the question of whether terrestrial ecosystems will sequester more C in their soils, litter and biomass as atmospheric $CO_2$ concentrations rise. Similar to our previous study with relatively fertile growth conditions (Körner and Arnone 1992), we constructed four rather nutrient-limited model communities of moist tropical plant species in greenhouses (approximately 7 $m^2$ each). Plant communities were composed of seven species (77 individuals per community) representing major taxonomic groups and various life forms found in the moist tropics. Two ecosystems were exposed to 340 µl $CO_2$ $l^{-1}$ and two to 610 µl $l^{-1}$ for 530 days of humid tropical growth conditions. In order to permit precise determination of C deposition in the soil, plant communities were initially established in C-free unwashed quartz sand. Soils were then amended with known amounts of organic matter (containing C and nutrients). Mineral nutrients were also supplied over the course of the experiment as timed-release full-balance fertilizer pellets. Soils represented by far the largest repositories for fixed C in all ecosystems. Almost 5 times more C (ca. 80% of net C fixation) was sequestered in the soil than in the biomass, but this did not differ between $CO_2$ treatments. In addition, at the whole-ecosystem level we found a remarkably small and statistically non-significant increase in C sequestration (+4%; the sum of C accretion in the soil, biomass, litter and necromass). Total community biomass more than quadrupled during the experiment, but at harvest was, on average, only 8% greater (i.e. 6% per year; n.s.) under elevated $CO_2$, mainly due to increased root biomass (+15%, $P = 0.12$). Time courses of leaf area index of all ecosystems suggested that canopy expansion was approaching steady state by the time systems were harvested. Net primary productivity (NPP) of all ecosystems – i.e. annual accumulation of biomass, necromass, and leaf litter (but *not* plant-derived soil organic matter) – averaged 815 and 910 g $m^{-2}$ $year^{-1}$ at ambient and elevated $CO_2$, respectively. These NPPs are remarkably similar to those of many natural moist tropical forested ecosystems. At the same time net productivity of soil organic matter reached 7000 g dry matter equivalent per $m^2$ and year (i.e. 3500 g C $m^{-2}$ $year^{-1}$). Very slight yet statistically significant $CO_2$-induced shifts in the abundance of groups of species occurred by the end of the experiment, with one group of species (*Elettaria cardamomum*, *Ficus benjamina*, *F. pumila*, *Epipremnum pinnatum*) gaining slightly, and another group (*Ctenanthe lubbersiana*, *Heliconia humilis*, *Cecropia peltata*) losing. Our results show that: (1) enormous amounts of C can be deposited in the ground which are normally not accounted for in estimates of NPP and net ecosystem productivity; (2) any enhancement of C sequestration under elevated atmospheric $CO_2$ may be substantially smaller than is believed will occur (yet still very important), especially under growth conditions which permit close to natural NPP; and (3) species dominance in plant communities is likely to change under elevated $CO_2$, but that changes may occur rather slowly.

**Key words** Carbon dioxide enrichment · Ecosystem C sequestration · Humid tropics · Root biomass · Species composition

## Introduction

Terrestrial ecosystems of the world, including their soils, contain approximately 2060 Gt C (Houghton and Woodwell 1989). About one-quarter (560 Gt C) of this pool is represented by terrestrial plant biomass, and about three-quarters are estimated to be stored in soils. Hence, nearly 3 times as much C is stored in terrestrial biomes than is currently present in the atmosphere (ca. 735 Gt C). Changes in the amount of C stored in these ecosystems can thus dramatically influence the concentration of $CO_2$

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in the atmosphere (e.g. Dixon et al. 1994). However, it is uncertain how rising concentrations of atmospheric $CO_2$ will affect C storage in terrestrial ecosystems.

During the 1980s, the general consensus was that terrestrial ecosystems will sequester more C as atmospheric $CO_2$ concentrations increase (e.g. Kimball 1983; Lemon 1983; Strain and Cure 1985). However, this assertion was based primarily on theory, and on results of experiments with agricultural or horticultural crop plants and seedlings of forest trees grown under non-nutrient and non-water-limiting conditions (Körner 1993). Results from longer-term field studies in natural ecosystems (Tissue and Oechel 1987; Curtis et al. 1989; Owensby et al. 1993; Cipollini et al. 1994; Oechel et al. 1994), as well as data from experiments with mesocosms containing single (Norby et al. 1992) and multi-species model plant communities (Billings et al. 1984; Körner and Arnone 1992), indicate that the potential enhancement of C sequestration at elevated atmospheric $CO_2$ is likely to be significantly lower than originally predicted.

While peak net assimilation of $CO_2$ is almost universally stimulated under elevated $CO_2$ at both the level of the leaf (e.g. Bazzaz 1990; Woodward et al. 1991; Gifford 1992) and ecosystem (e.g. Grulke et al. 1990; Drake and Leadley 1991; Körner and Arnone 1992; Diemer 1994), biomass responses in most native terrestrial systems have been absent or comparatively small. However, even in cases where a significant stimulation of biomass accumulation has been observed, a substantial amount of excess fixed C has remained unaccounted for and seems to have been sequestered in the soil (review by Körner 1995).

Evidence for this is summarized in O'Neill (1994), but includes: (1) greater responses of below-ground organs relative to responses of leaves and stems (e.g. Curtis et al. 1990; Körner and Arnone 1992; Norby et al. 1992; Rogers et al. 1994); (2) greater microbial presence and activity of both symbiotic (e.g. Phillips et al. 1976; Finn and Brun 1982; Norby 1987; O'Neill et al. 1987; Arnone and Gordon 1990; Monz et al. 1994) and non-symbiotic micro-organisms (Körner and Arnone 1992; Díaz et al. 1993; Zak et al. 1993); and (3) increases in fine root production and mortality, and thus turnover (Körner and Arnone 1992).

The only direct evidence about changes in soil C storage under elevated $CO_2$, provided by Körner and Arnone (1992) using artificial tropical ecosystems growing on relatively fertile substrate, indicated that the C content of soils (an active compost layer in this case) may even decrease under elevated $CO_2$, suggesting a possible priming effect and increased C cycling under elevated $CO_2$. In natural ecosystems, it is impossible to detect very small changes in soil C content relative to the large and spatially heterogeneous background of soil C. This is why we began with a C-free substrate in this study.

We again constructed four model ecosystems containing complex communities of moist tropical plant species to test the hypothesis that more C would be sequestered in systems maintained at elevated atmospheric $CO_2$. We attempted to simulate low levels of nutrient availability to approximate those occurring in many native terrestrial plant communities (e.g. Whittaker 1975; Chapin 1980; Jordan 1985; Vitousek and Sanford 1986). Our second objective was to quantify the potential effects of elevated $CO_2$ on the allocation of C within the ecosystems, including the distribution among plant organs and species, to help explain responses in total C sequestration.

## Material and methods

### Construction of artificial communities and environmental conditions

Equivalent model ecosystems similar to those described by Körner and Arnone (1992) were constructed in each of four large-scale (17 $m^3$; 2.0–2.5 m tall) clear plastic houses (Körner et al. 1994). Plant communities were composed of seven species representing major taxonomic groups and various life forms found in the moist tropics. These were: the dicot tree species *Cecropia peltata* (early successional, Cecropiaceae, 16 individuals per community) and *Ficus benjamina* (later successional, Moraceae, 6); the rhizomatous monocots *Ctenanthe lubbersiana* (Maranthaceae, 14), *Elettaria cardamomum* (Zingiberaceae, 15), and *Heliconia humilis* (Musaceae, 16); and the ground creepers *Ficus pumila* (5) and *Epipremnum pinnatum* (Araceae, 5). Thus, each community was made up of a total of 77 plants on a ground area of 6.7 $m^2$. The two tree species (*Cecropia peltata* and *Ficus benjamina*) were planted at regular spacing in each community. Locations of individuals of all other species were chosen randomly for the first community planted and then replicated identically in the remaining three communities. Root systems of plants were washed free of potting soil before individuals were transplanted in the ecosystems.

All plants in each community shared a common air space and a common soil substrate of unwashed quartz sand (1.7 $m^3$, 25 cm depth). Soils were inoculated with fresh tropical soil from a moist lowland forest in Costa Rica (32 g dry soil equivalent $m^{-2}$ ground). All systems received ambient sunlight (reduced in intensity by 30–40% by the glasshouse roof depending on time of day) as well as supplemental light during cloudy periods and in winter (October to March) from high intensity 1000 W broad spectrum mercury vapour lamps (Powerstar, Osram). Photon flux density (PFD) measured at midday on sunny days immediately above the tops of canopies during summer months ranged from 800 to 1200 (1600 peak) μmol $m^{-2}$ $s^{-1}$. During the winter midday PFD ranged from 360 to 800 μmol $m^{-2}$ $s^{-1}$. Side light was screened out to 90% in each of the communities. Temperature in all ecosystems was similar ranging between 22 and 34°C during daylight hours in the summer months, and between 21 and 27°C in the winter months. Night-time temperatures in the summer were between 20 and 24°C, and in the winter between 19 and 22°C. Vapour pressure deficit ranged between 4 and 7 hPa during the day and between <1 and 2 hPa at night.

Plant communities were allowed to recover from transplanting shock for 32 days. During this period, all ecosystems were maintained at a $CO_2$ concentration of 340 μl $l^{-1}$. On 3 July 1992 (day 1), the $CO_2$ concentration in two of the plastic houses was increased to daytime concentrations averaging 610 μl $l^{-1}$, while the concentrations in the other two houses were continued at 340 μl $l^{-1}$. After 530 days (15 December 1993) all communities were harvested. Night-time $CO_2$ concentrations were about 200 μl $l^{-1}$ higher than these daytime levels, and it took approximately 2 h in the early morning for canopy photosynthesis to scrub the air back to daytime set points. On day 1, leaf area index (LAI) in all communities was 0.9, and the height of the plant canopy was about 35 cm.

**Table 1** Schedule followed for application of: (1) Osmocote timed-release fertilizer, (2) organic matter (*DSPR* dried shredded plant remains), and tropical soil inoculum (*TSI*)

| Day | Item added | Dry weight equivalent added ($g\ m^{-2}$) | Corresponding N and C added | |
|---|---|---|---|---|
| | | | ($g\ N\ m^{-2}$) | ($g\ C\ m^{-2}$) |
| 0 | Osmocote | 17.74 | 2.662 | <0.01 |
| 5 | DSPR | 59.25 | 0.595 | 25.33 |
| 6 | TSI | 32.09 | 0.196 | 3.06 |
| 15 | DSPR | 59.25 | 0.595 | 25.33 |
| 22 | Osmocote | 17.74 | 2.662 | <0.01 |
| | DSPR | 59.25 | 0.595 | 25.33 |
| 31 | DSPR | 59.25 | 0.595 | 25.33 |
| 118 | DSPR | 59.25 | 0.595 | 25.33 |
| 126 | DSPR | 59.25 | 0.595 | 25.33 |
| 128 | Osmocote | 17.74 | 2.662 | <0.01 |
| 208 | Osmocote | 17.74 | 2.662 | <0.01 |
| 333 | Osmocote | 17.74 | 2.662 | <0.01 |
| Total added | | | 17.076 | 151.98 |
| Annual equivalent | | | 118 kg N $ha^{-1}$ | 1047 kg C $ha^{-1}$ |

## Soils, nutrients and watering

Osmocote 3-month timed-release fertilizer (17.7 $g\ m^{-2}$; i.e. 2.66 g N $m^{-2}$) was applied to the sand substrate on the day that $CO_2$ treatment began. The same amount was added in 1–3 month intervals over the first 333 days of $CO_2$ treatment which resulted in a total N input of 13.3 g N $m^{-2}$ (Table 1). Additional nutrients and organic matter were provided over the first 126 days of the 530 day experiment to the surface of the sand in the form of dried shredded plant material obtained from our previous experiment with artificial tropical plant communities (Körner and Arnone 1992; total amount of N and C added was 17.1 g $m^{-2}$ and 152 g $m^{-2}$, respectively). The combination of all nutrient additions was equivalent to an annual rate of 118 kg N $ha^{-1}$ (Table 1), 78% of which was in available form (i.e. Osmocote-N). We calculated this fertilizer addition rate to achieve a net primary productivity (NPP: plant community biomass increment plus shoot litter produced plus standing above-ground dead material) equivalent to approximately half of that observed in our previous study (Körner and Arnone 1992), where NPP extrapolated to 1 year at 340 µl $CO_2$ $l^{-1}$ was 37% greater than the global average NPP for tropical forests (2000 g $m^{-2}$ $year^{-1}$; Whittaker 1975), and NPP at 610 µl $CO_2$ $l^{-1}$ was 67% greater. We considered the dried shredded plant material to represent a well-defined initial amount of soil organic matter (SOM) and C in the soil compartment.

Simulated (and metered) rainfalls of deionized water occurred every 2–4 days. All communities received equal watering, and the amount was designed to slightly more than balance water losses occurring through evapotranspiration at ambient $CO_2$. This resulted in maintenance of soils near field capacity in all ecosystems, and in substantial drainage which was used for nutrient analyses (see Körner and Arnone 1992; Körner et al. 1994). Drainage water was not recycled to ecosystems as it was in our previous study.

## Destructive and non-destructive sampling of plants and soils

Several containerized individuals of each species from the planting stock were installed in soils of each community when the other plants were planted into the common soil. These potted plants were harvested at the beginning of the $CO_2$ treatments to provide us with initial biomass and LAI. No dead material was attached to plants at the start of the experiment. Net litter production over the 530 day experiment was defined as the amount of leaf and stem detritus present on the ground surface at harvest. SOM was calculated as twice the mass of C measured in the soil of each ecosystem over the entire soil volume. Mean plant height, number of leaves per plant, and leaf area per plant for each species were measured (and LAI calculated) at the beginning of the experiments, on day 115 (and in some cases on day 377), and at the harvest.

## Carbon content of plant tissue and soil; net ecosystem productivity

C content of leaf, stem and root subsamples from individual plants were measured at the start of the experiment (using the potted reference plants) and at harvest with a CHN analyser (Model 932, LECO Instruments, St. Joseph Mich., USA). In addition, the C content of bulk coarse and fine root samples from each ecosystem was measured. Total organic soil C content at the start and end of the experiment was determined using the chromic acid digestion procedure (Wilde et al. 1979) on ten 4-cm-diameter soil cores taken over the entire depth in each community at randomly selected locations. We used Whittaker's (1975) definition of net ecosystem productivity (NEP), namely: the increase in the organic matter content of the ecosystem per $m^2$ per year which includes the increase in biomass, above-ground litter and SOM (converted from soil C content measurements made at days 0 and 530).

## Statistical analyses

A nested statistical design and ANOVAs were used to assess the effects of $CO_2$ treatment, plant species and the species × $CO_2$ interaction for all parameters in Table 2, on a data set consisting of mean values for each species and each house ($7 \times 8 = 28$). In most cases these data required transformation (log) to comply with ANOVA principles of equal variance. A nested design was required since the $CO_2$ effect was confounded with the ecosystem effect (i.e. green*house*, two houses within each $CO_2$ treatment). Thus, the $CO_2$ mean square term (1 *df*) was tested against the house-within-$CO_2$ mean square term (2 *df*) for each dependent variable. The species effect (6 *df*) was tested against the residual mean square term (12 *df*). The linear model procedure in the GENSTAT statistical package (Lawes Agricultural Trust, Rothamsted Experimental Station) was used for the ANOVAs.

To compare the $CO_2$ effect on pooled data from the ecosystems (e.g. LAI, total leaf biomass per ground area, total biomass per ground area; Tables 2, 3), we used both the parametric Student *t*-test and the non-parametric Mann-Whitney *U*-test with a sample size of two (i.e. two ecosystems per $CO_2$ level). In cases where the variance within $CO_2$ treatments (between houses within $CO_2$ treatments) was very unequal, and where transformation did not correct the inequality, the non-parametric test was used for the interpretation of the data. This was particularly the case for root biomass per ground area (Table 2).

**Table 2** Ecosystem biomass, standing dead, and net litter accumulation after 530 days exposure to ambient (340 $\mu l l^{-1}$) and elevated (610 $\mu l l^{-1}$) atmospheric carbon dioxide (mean±SE). *P* values indicate the probability that the mean *net accretion* in mass for a given component (i.e. harvest mass minus starting mass[a]) are the same using: (1) unpaired Student *t*-tests ($P_t$), and (2) non-parametric Mann-Whitney *U*-tests ($P_u$); both tests with $n$=2 (two ecosystems)

| | Ambient $CO_2$ | | Elevated $CO_2$ | | Mean difference at harvest[b] | $P_t$ | $P_u$ |
|---|---|---|---|---|---|---|---|
| | ($g\ m^{-2}$) | (% total biomass) | ($g\ m^{-2}$) | (% total biomass) | | | |
| Biomass | | | | | | | |
| Above-ground | 616 ±5 | (47.8) | 624 ±8 | (44.6) | +1.3 | 0.45 | 0.44 |
| Leaves | 197 ±14 | (15.3) | 202 ±7 | (14.4) | +2.5 | 0.76 | 1.00 |
| Green leaves | 176 ±9 | (13.7) | 171 ±10 | (12.2) | −2.8 | 0.78 | 0.44 |
| Yellow leaves | 20.9±5.6 | (1.6) | 31.1±3.7 | (2.2) | +48.8 | 0.27 | 0.12 |
| Stems | 419 ±19 | (32.5) | 422 ±1 | (30.2) | +0.7 | 0.89 | 1.00 |
| Roots | 674 ±11 | (52.2) | 774 ±74 | (55.4) | +14.8 | 0.31 | 0.12 |
| >2 mm ∅ | 520 ±13 | (40.3) | 572 ±38 | (40.9) | +10.0 | 0.32 | 0.12 |
| ≤2 mm ∅ | 154 ±1 | (11.9) | 202 ±36 | (14.5) | +31.2 | 0.31 | 0.12 |
| Total biomass | 1290 ±6 | (100.0) | 1398 ±66 | (100.0) | +8.4 | 0.25 | 0.12 |
| Necromass | | | | | | | |
| Standing dead | 52 ±15 | | 50 ±26 | | −3.7 | 0.96 | 1.00 |
| Above-ground litter | 114 ±11 | | 146 ±4 | | +18.1 | 0.12 | 0.12 |
| Total necromass | 166 ±4 | | 196 ±22 | | +18.1 | 0.31 | 0.12 |

[a] Starting conditions: total biomass: 273 $g\ m^{-2}$; green leaf biomass 43 $g\ m^{-2}$; stem biomass 71 $g\ m^{-2}$; total root biomass 159 $g\ m^{-2}$; no yellow leaf biomass or necromass

[b] Percentage of mean at ambient $CO_2$ when measured in $g\ m^{-2}$

**Table 3** Effects of elevated $CO_2$ concentrations on leaf area index (*LAI*) of the seven species, and their contribution to LAI of entire communities, measured at the start and harvest of the 530 day experiment (Mean±SE). $P_t$ and $P_u$ are the probabilities that the means for ambient and elevated $CO_2$ treatments ($n$=2 for both tests) for each species are the same ($P_t$ unpaired Student *t*-test, $P_u$ non-parametric Mann-Whitney *U*-test)

| Species | Start | Harvest | | Mean difference at harvest | $P_t$ | $P_u$ |
|---|---|---|---|---|---|---|
| | | Ambient $CO_2$ | Elevated $CO_2$ | | | |
| LAI ($m^2$ leaves $m^{-2}$ ground) | | | | (% of Ambient)[b] | | |
| Monocots | | | | | | |
| *Elettaria cardomomum* | 0.20 | 2.51±0.08 | 2.65±0.16 | +6 | 0.53 | 0.44 |
| *Ctenanthe lubbersiana* | 0.32 | 0.47±0.01 | 0.23±0.11 | −51 | 0.16 | 0.12 |
| *Heliconia humilis* | 0.09 | 0.51±0.05 | 0.42±0.03 | −18 | 0.24 | 0.12 |
| *Epipremnum pinnatum* | 0.03 | 0.03±0.00 | 0.03±0.00 | 0 | 0.50 | 0.44 |
| Dicots | | | | | | |
| *Cecropia peltat*[a] | 0.16 | 0.03±0.02 | 0.01±0.00 | −55 | 0.43 | 0.44 |
| *Ficus benjamina* | 0.08 | 0.39±0.13 | 0.47±0.04 | +21 | 0.60 | 1.00 |
| *F. pumila* | 0.02 | 0.03±0.00 | 0.07±0.02 | +94 | 0.32 | 0.12 |
| Species contribution to community LAI (%) | | | | (Δ %) | | |
| Monocots | | | | | | |
| *Elettaria cardomomum* | 22.6 ↑[a] | 63.3 ±0.5 | 68.2 ±1.6 | +4.9 | 0.10 | 0.12 |
| *Ctenanthe lubbersiana* | 35.4 ↓ | 11.8 ±0.1 | 6.2 ±3.0 | −5.6 | 0.20 | 0.12 |
| *H. humilis* | 10.4 ↓ | 12.8 ±1.7 | 10.8 ±0.3 | −2.0 | 0.36 | 0.12 |
| *Epipremnum pinnatum* | 3.4 ↓ | 0.74±0.06 | 0.67±0.01 | −0.1 | 0.43 | 0.44 |
| Dicots | | | | | | |
| *Cecropia peltata* | 17.3 ↓ | 0.73±0.43 | 0.33±0.04 | −0.4 | 0.44 | 0.44 |
| *F. benjamina* | 8.6 ↑ | 9.7 ±2.8 | 12.1 ±0.5 | +2.4 | 0.49 | 0.44 |
| *F. pumila* | 2.3 ↑ | 0.88±0.16 | 1.7 ±0.55 | +0.8 | 0.29 | 0.12 |

[a] Direction of change in a species' contribution to community LAI over the course of the experiment

[b] Percentage of mean at ambient $CO_2$ when measured in $g\ m^{-2}$

## Results

### Ecosystem responses

#### *Carbon storage*

Total ecosystem C stores increased more than 11-fold over the course of the experiment, from a starting level of 270 g C $m^{-2}$ (118 g C $m^{-2}$ in biomass, 152 g C $m^{-2}$ in the dried shredded plant material applied to the ground surface) to 3362 ± 294 g C $m^{-2}$ and 3503 ± 58 g C $m^{-2}$ in ecosystems exposed to ambient and elevated $CO_2$, respectively (Fig. 1). By harvest, ecosystems maintained at elevated $CO_2$ had sequestered (accreted) 4% more C on average (n.s.) than those maintained at ambient $CO_2$ (includes C in: biomass, litter, and soil). Biomass in all ecosystems accounted for ca. 17% of the total C sequestered over the course of the experiment, while above-ground litter and necromass accounted for ca. 2%. The amount sequestered in the soil accounted for approximately 81%, and this also did not differ between $CO_2$ levels (Fig. 1). The slight increases in the largest ecosystem compartments – root biomass and the soil – contributed most to the 4% increase in the mean ecosystem C pool at the end of the experiment under elevated $CO_2$.

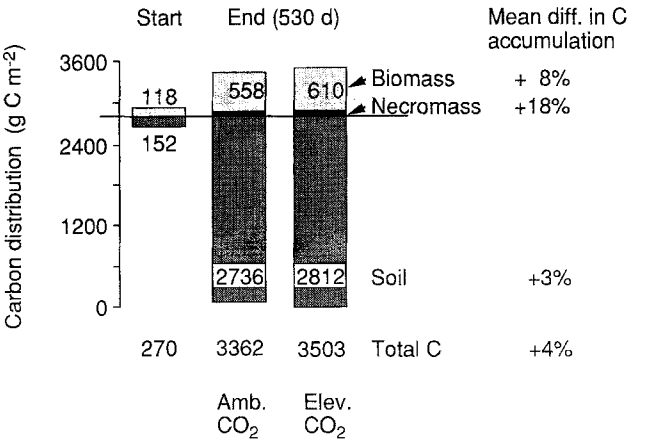


**Fig. 1** Total carbon pool sizes of ecosystems maintained at either ambient (340 µl $l^{-1}$) or elevated (610 µl $l^{-1}$) $CO_2$ for 530 days, expressed per $m^{-2}$ of ground (mean ±SE of two ecosystems for each $CO_2$ level). Necromass includes above-ground litter and standing dead plant tissues. Percentage values represent the relative effects of elevated $CO_2$ on mean *net carbon accretion* for the various ecosystem compartments. The probabilities ($P$ values) that means of $CO_2$ treatments for each compartment are equal are based on: (a) unpaired Student's $t$-tests ($P_t$), and (b) non-parametric Mann-Whitney $U$-tests ($P_u$), n = 2 for both tests. Biomass: $P_u = 0.12$, $P_t = 0.25$; necromass: $P_u = 0.12$, $P_t = 0.31$; soil: $P_u = 1.00$, $P_t = 0.83$; total ecosystem: $P_u = 0.44$, $P_t = 0.69$

#### *Net ecosystem productivity*

Patterns of community biomass accretion were also reflected in patterns of NEP over the 530 day experiment expressed as g organic matter accretion $m^{-2}$ $year^{-1}$, including biomass, above-ground litter and SOM accretion). NEP under elevated $CO_2$ averaged 4329 ± 379 g $m^{-2}$ $year^{-1}$, 5% greater (n.s.) than the average measured under ambient $CO_2$ (4129 ± 68 g $m^{-2}$ $year^{-1}$) (Table 2; Fig. 1 – assume 1.0 g SOM contains 0.5 g C). Thus, by harvest, approximately 82–84% of the total net *amount* of organic matter *accretion* to the ecosystems by photosynthesis was found in the soil compartment (excluding live root biomass), 14–15% in biomass, and the remaining fraction in leaf litter and standing above-ground necromass, regardless of $CO_2$ treatment (Table 2; Fig. 1).

### Community development

#### *Leaf area index*

Mean community LAI (including yellow/senescing leaves) quadrupled over the 530 day experiment from a 0.9 starting level in all ecosystems to 4.0 ± 0.2 under ambient $CO_2$ and 3.9 ± 0.1 under elevated $CO_2$ by harvest (Fig. 2). LAI of ecosystems treated with both ambient and elevated $CO_2$ increased rapidly over the first 115 days of the experiment, but increased more slowly at later intervals and began leveling off by harvest (Fig. 2). LAI of green leaves alone reached 3.6 ± 0.2 at ambient $CO_2$ and

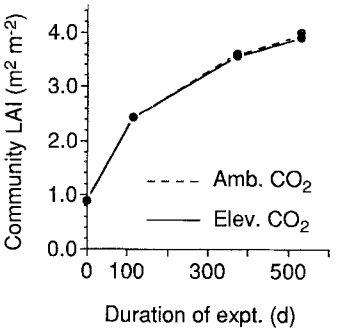


**Fig. 2** Time courses of leaf area index (LAI) for communities exposed to either ambient (340 µl $l^{-1}$) or elevated (610 µl $l^{-1}$) $CO_2$ for 530 days (mean ±SE of two ecosystems for each $CO_2$ level)

3.3 ± 0.1 under elevated $CO_2$; thus the senescent leaf fraction (yellow leaves) tended to be greater under elevated $CO_2$ ($P = 0.12$, Table 2). The absence of $CO_2$-induced changes in LAI at the community level was also generally reflected in lack of significant $CO_2$ effects at the individual species level (Fig. 3). However, the overall pattern of LAI development was a product of relative increases and decreases in leaf area of species groups under elevated $CO_2$, "decliners" (*Cecropia peltata*, *Ctenanthe lubbersiana*, *Heliconia humilis*) and "gainers" (*Ficus benjamina*, *F. pumila*, *Elettaria cardomomum*), with the latter dominating the overall community LAI (Table 3). *Epipremnum pinnatum* and *F. pumila* contributed less than 6% to community LAI at the beginning of the experiment and less than 3% at the end, but LAI of *Epipremnum pinnatum* remained unaffected by $CO_2$ while that of *F. pumila* was stimulated (Table 3).

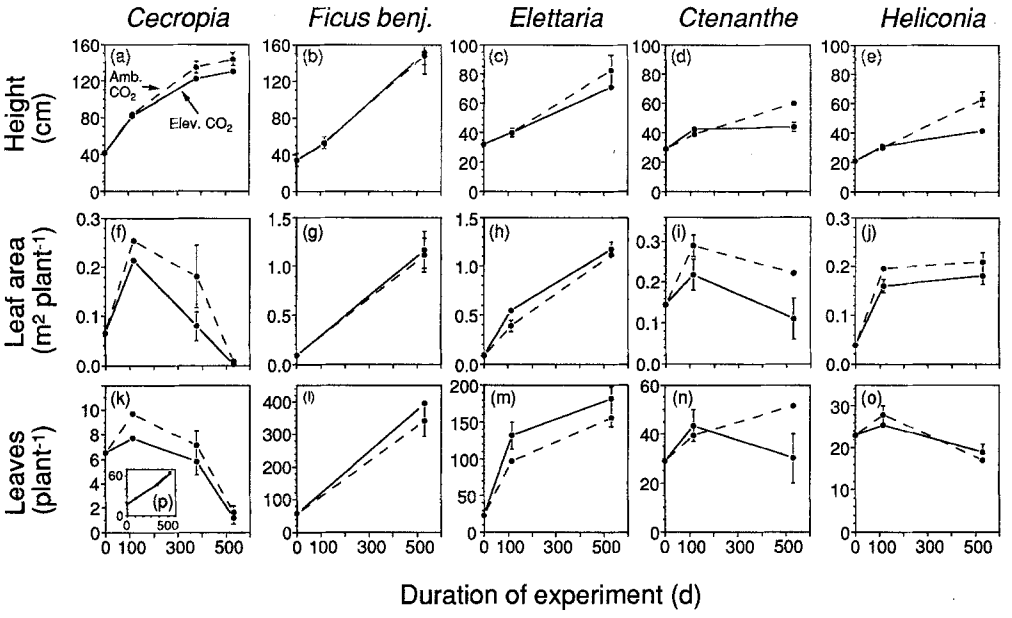


**Fig. 3a–o** Changes in morphology of the five most dominant species (see text for full names) in model plant communities exposed to either ambient (340 µl $l^{-1}$) or elevated (610 µl $l^{-1}$) $CO_2$ for 530 days (mean ±SE of two ecosystems for each $CO_2$ level). **p** (*inset*) Cumulative leaf production by *Cecropia peltata* (*y*-axis) over time in days (*x*-axis). Note the different scales used on the *y*-axes (*dashed lines* ambient $CO_2$, *solid lines* elevated $CO_2$)

*Shoot dynamics*

The height of the plant canopy increased from 35 cm at the start of the experiment to a maximum of approximately 180 cm (*Cecropia peltata* and *F. benjamina*) by harvest. The early successional tree species, *Cecropia peltata*, dominated the overstory for the first half of the experiment (Fig. 3), and quickly occupied the soil with long, shallow, fine roots. Significant height growth and leaf production in *Cecropia peltata* occurred simultaneously (Fig. 3a, p). Growth of *Cecropia peltata* began to slow considerably in the second third of the experiment when the later successional tree species, *F. benjamina*, as well as the monocots *Elettaria cardomomum*, *Ctenanthe lubbersiana* and *H. humilis*, became well established and gained an increasing share of the soil and the leaf canopy (Fig. 3). *Cecropia peltata* continued to produce new leaves, even up to the harvest (Fig. 3p), despite the increasing below-ground competition from the other species in the community. However, competition from these four other species appears to have resulted in marked reductions in the height growth of *Cecropia peltata*, as well as in dramatic reductions in the actual number of leaves and leaf area on these plants, under both $CO_2$ levels (Fig. 3a, f, k). By the end of the experiment, *Elettaria cardomomum* enjoyed a massive lateral expansion in all communities and dominated the LAI (Table 3). *F. benjamina*, originally shaded by the *Cecropia peltata* leaf canopy, extended its stems to the tops of the canopies in the last third of the experiment and continued to steadily increase its number of leaves and leaf area (Fig. 3b, g, l). In addition to *Cecropia peltata*, *Ctenanthe lubbersiana* and *H. humilis* showed signs of becoming suppressed by *F. benjamina* and *Elettaria cardomomum* in all ecosystems as early as day 115 (Fig. 3).

*Biomass accumulation*

The biomass, including roots, of all communities increased from a starting value of 273 g $m^{-2}$ (43 g $m^{-2}$ in leaves, 71 g $m^{-2}$ in stems, and 159 g $m^{-2}$ in roots) to 1290 g $m^{-2}$ under ambient $CO_2$ and 1398 g $m^{-2}$ under elevated $CO_2$ (i.e. 8% greater at high $CO_2$; Table 2). The mean net *biomass increment* under elevated $CO_2$ was almost 11% greater after 530 days. These effects were only very marginally significant ($P$ = 0.1269, *U*-test; $P$ = 0.2481, t-test). The tendency for increased biomass under elevated $CO_2$ appeared to be mainly due to increases in root biomass (+15% overall, +31% for fine roots alone – $P$ = 0.1269, *U*-test; Table 2). Remarkably, stem and green leaf biomass accretion at the level of the entire community was not affected by elevated $CO_2$. Overall, means for above-ground parameters were very similar between $CO_2$ treatments, with surprisingly small variances (Table 2). One exception to this was the mean mass of yellow (senescing) leaves at harvest, which was small in absolute terms but markedly greater in relative terms (49%) under elevated $CO_2$ ($P$ = 0.1269, *U*-test; $P$ = 0.2481; *t*-test; Table 2).

*Biomass allocation*

The distribution of biomass among various organs (also viewed at the level of the plant community) was remarkably unaffected by elevated $CO_2$, given the substantial overall biomass accumulation which occurred during the experiment. Some slight trends are shown in Table 2 (3.2% more in roots and 3.2% less in above-ground organs at high $CO_2$). Changes in total community biomass partitioning over the course of the experiment across both $CO_2$ treatments also were rather small. As plants grew bigger, stems increased their share of total ecosystem biomass (26% at the start of the experiment in-

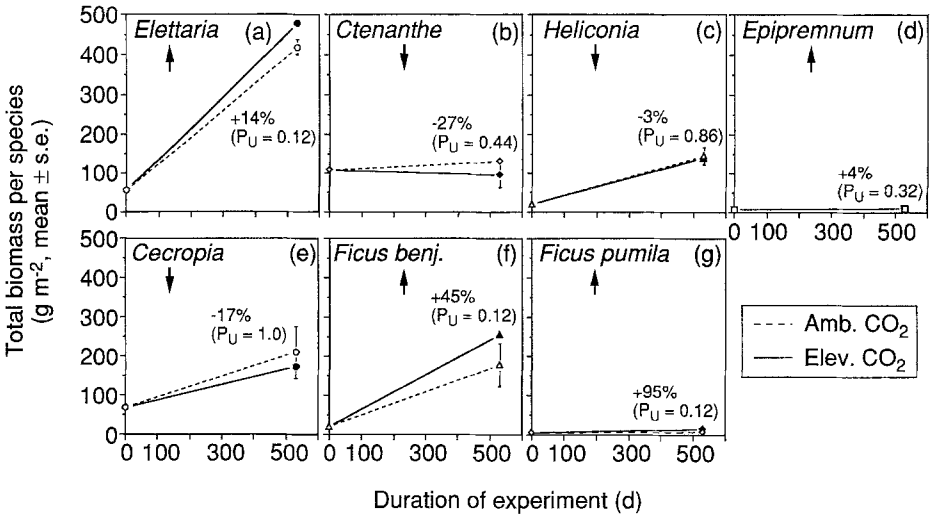


**Fig. 4a–g** Changes in total biomass (including coarse roots in "root balls") of each species (see text for full names) in communities exposed to either ambient (340 µl l$^{-1}$) or elevated (610 µl l$^{-1}$) $CO_2$ for 530 days expressed per m$^{-2}$ of ground (mean ±SE of two ecosystems for each $CO_2$ level). *Arrows* indicate the direction of change under elevated $CO_2$ in harvest means. Fine roots (≤2 mm diameter) are not included in the total biomass; however, they represented only ca. 20% of total biomass. ANOVA *P* values were: $CO_2$ effect – 0.0047; species effect – <0.0001; $CO_2$ × species effect – 0.3742

**Table 4** Above-ground biomass of species and biomas distribution among species in communities after 530 days exposure to ambient and elevated atmospheric carbon dioxide (mean±SE). *P* values indicate the probability that the mean *net accretion* in mass for a given component (i.e. harvest mass minus starting mass[a]) are the same using: (1) unpaired Student *t*-tests ($P_t$), and (2) non-parametric Mann-Whitney *U*-tests ($P_u$); *n*=2 (two ecosystems) for both tests

| | Ambient $CO_2$ | | Elevated $CO_2$ | | Mean difference at harvest[b] | $P_t$ | $P_u$ |
|---|---|---|---|---|---|---|---|
| | (g m$^{-2}$) | (% total biomass) | (g m$^{-2}$) | (% total biomass) | | | |
| Community above-ground biomass | 616±5 | (100.0) | 624±8 | (100.0) | +1.3 | 0.45 | 0.44 |
| Monocots | | | | | | | |
| *Elettaria cardomomum* | 229±12 | (37.2) | 250±9 | (40.1) | +9 | 0.29 | 0.12 |
| *Ctenanthe lubbersiana* | 62±1 | (10.1) | 37±16 | (6.0) | –40 | 0.27 | 0.12 |
| *Heliconia humilis* | 54±10 | (8.7) | 44±4 | (7.0) | –18 | 0.46 | 0.44 |
| *Epipremnum pinnatum* | 5±1 | (0.9) | 5±0 | (0.9) | 0 | 0.98 | 1.00 |
| Total monocots | 350±2 | (56.9) | 337±3 | (54.0) | –4 | 0.08 | 0.12 |
| Dicots | | | | | | | |
| *Cecropia peltata* | 143±49 | (23.1) | 117±9 | (18.7) | –18 | 0.66 | 1.0 |
| *Ficus benjamina* | 119±42 | (19.3) | 160±2 | (25.7) | +35 | 0.42 | 0.44 |
| *Ficus pumila* | 4±1 | (0.7) | 10±4 | (1.6) | +136 | 0.32 | 0.12 |
| Total dicots | 266±7 | (43.1) | 288±11 | (46.0) | +8 | 0.24 | 0.12 |

[a] Starting above-ground biomass: community 114 g m$^{-2}$, 100%; *Elettaria cardomomum* 20 g m$^{-2}$, 17.7%; *Ctenanthe lubbersiana* 33 g m$^{-2}$, 28.9%; *H. humilis* 8.4 g m$^{-2}$, 7.4%; *Epipremnum pinnatum* 4.8 g m$^{-2}$, 4.2%; *Cecropia peltata* 37 g m$^{-2}$, 32.3%; *F. benjamina* 9.5 g m$^{-2}$, 8.4%; *F. pumila* 1.2 g m$^{-2}$

[b] Percentage of mean at ambient $CO_2$ when measured in g m$^{-2}$

creased to 33% and 30% for ambient and elevated $CO_2$, respectively) while roots (initially 58%, decreased slightly to 52 and 55%, respectively, at harvest) and leaves (initially 16% decreased slightly to 15 and 14%, respectively, at harvest) composed a slightly smaller fraction of the total at the end. Thus, roots, stems and leaves grew in relatively constant proportion to each other under both ambient and elevated $CO_2$.

### *Leaf and litter production*

Total leaf production (biomass of green and yellow leaves plus mass of above-ground litter) under elevated $CO_2$ was slightly (12%, $P$ = 0.12) greater than that observed under ambient $CO_2$ (Table 2). Leaf senescence and litter production tended to be greater at high $CO_2$ (Table 2), at least when assessed at harvest. Mean total above-ground necromass at harvest was 18% ($P$ = 0.1213) greater in elevated $CO_2$ ecosystems, with leaf litter accounting for most of this effect.

### Species-level biomass responses

The biomass of all species in all communities increased over the course of the experiment, but to widely varying degrees for different species (Fig. 4). Mortality of indi-

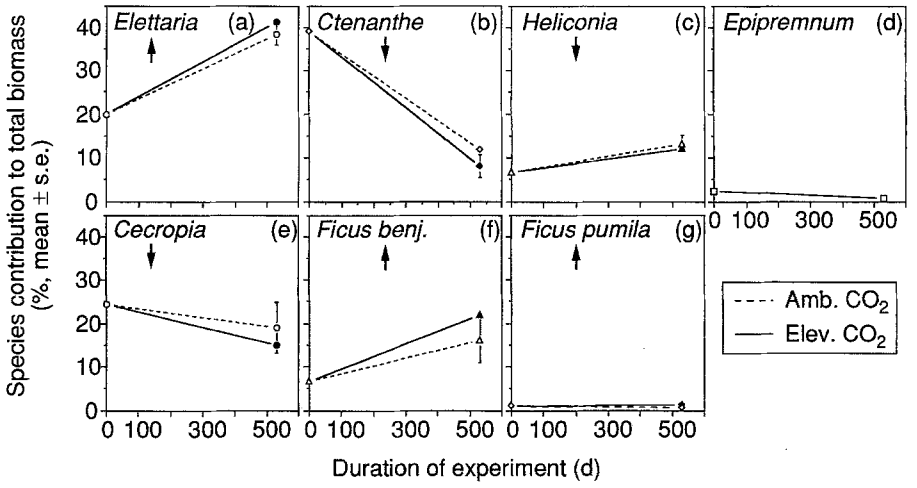


**Fig. 5a–g** Changes in individual species' contribution to total community biomass (including coarse roots still attached to the plant when it was uprooted) in communities exposed to either ambient (340 µl $l^{-1}$) or elevated (610 µl $l^{-1}$) $CO_2$ for 530 days (mean ±SE of two ecosystems for each $CO_2$ level). Arrows indicate the direction of change under elevated $CO_2$ in harvest means

vidual plants in all ecosystems was extremely low so changes in biomass do not represent changes in plant density (one of the 77 individuals planted in each community died – all from *Ctenanthe lubbersiana* – over the 530 days.) Largest increases in biomass (i.e. harvest biomass/starting biomass) were observed in *F. benjamina* and *Elettaria cardomomum*, followed by *H. humilis*, *Cecopia peltata*, *F. pumila*, *Epipremnum pinnatum*, and *Ctenanthe lubbersiana*. In general, height and leaf canopy responses (Fig. 3) were mirrored in biomass responses (Fig. 4).

ANOVA on plant biomass (including the "root ball") at harvest revealed a highly significant effect of $CO_2$ ($P = 0.0047$) and species ($P < 0.0001$) but no significant $CO_2$ × species interaction (Fig. 4). This result indicates that elevated $CO_2$ induced larger gains in plant biomass of one group of species (*Elettaria cardomomum*, *F. bejamina* and *F. pumila*) and smaller gains, or no changes, in another group of species (*Cecropia peltata*, *Ctenanthe lubbersiana*, *H. humilis* and *Epipremnum pinnatum*) (Fig. 4); which helps explain the non-significant effects of elevated $CO_2$ on biomass accumulation at the community level. The lack of a significant interaction indicates that no species alone showed a statistically significant positive or negative response to elevated $CO_2$. ANOVAs on shoot biomass (i.e. above-ground biomass; using species means in Table 4) and on coarse root biomass (excavated "root balls"; data included in the >2 mm diameter root category in Table 2) at harvest showed neither a significant $CO_2$ effect nor a significant $CO_2$ × species effect. All of these ANOVAs suggest that elevated $CO_2$ only exerted significant effects when as much of the whole-plant biomass as possible was represented.

No significant shifts in individual species' *contribution* to total community biomass were observed at elevated $CO_2$ at harvest (Fig. 5). Species which tended to gain in share of total community biomass (= 100%) at elevated $CO_2$ over the course of the experiment were: *F. benjamina* (+5.6%), *Elettaria cardomomum* (+2.9%), and *F. pumila* (+0.6%). Species suffering losses in average share at elevated $CO_2$ were: *Cecropia peltata* (-4.1%), *Ctenanthe lubbersiana* (–3.7%), and *H. humilis* (–1.2%). No shifts in species' contribution to community above-ground biomass were observed either (Table 4).

## Discussion

We present data for rather complex ecosystems in which multiple interactions among species were allowed to occur. The small differences in responses to elevated $CO_2$ in these large-sized experimental units, compared to those commonly used, certainly constrained us with respect to replication. However, we believe they provided more realistic growth conditions for mixes of species differing in morphology. We could have used smaller experimental units to increase our sample size, but then would have had to contend with large edge effects or work with juvenile plant material, aspects for which no statistical analysis accounts.

The results of this experiment must also be seen in light of the comparatively long treatment duration under moist tropical growth conditions. This allowed as much time for potential treatment effects to materialize as would 3 years (i.e. growing seasons) of experimentation with a temperate deciduous ecosystem, or 6 years in a tundra ecosystem. The amount of mineral nutrients we provided to our ecosystems needs to be viewed in this context, clearly ranking our experiment at the low-nutrient end of related studies.

### Ecosystem carbon storage

An overwhelming fraction of C passed through the biomass into the soil compartment in all ecosystems (Fig. 1). For each mole of C sequestered in biomass, almost 5 moles were sequestered in the soil. This translates into a mean net ecosystem $CO_2$ fixation rate per day of 2.3 µmol $CO_2$ $m^{-2}$ leaf $s^{-1}$ at ambient $CO_2$ and 2.4 µmol $CO_2$ $m^{-2}$ leaf $s^{-1}$ at elevated $CO_2$, assuming an average green LAI of 2.45 in all communities integrated over the entire experiment (i.e. LAI at start 0.9, at end 4.0).

It appears that photosynthesis of the whole canopy over the entire experimental period was only marginally stimulated by elevated $CO_2$. No differences in respiration of soil (R. Stocker, unpublished data) or shoots (J.A. Arnone and M. Gruber, unpublished data) were observed between $CO_2$ treatments after 1 year of treatment. Stimulation of soil $CO_2$ evolution in our first experiment (Körner and Arnone 1992) may have been due to an enhanced breakdown of SOM in the compost (i.e. priming effect) which may also be confined to the initial phase of space (i.e. site) occupation and exponential growth. Losses of C and nutrients in drainage water from all ecosystems during the current experiments were negligible (J.A. Arnone and Ch. Körner, unpublished data), again suggesting that the increased leaching observed under elevated $CO_2$ in our earlier study (Körner and Arnone 1992) was due to a stimulation of decomposition of rather rich substrate.

The fact that approximately 80% of the C that was fixed by leaf canopies of all communities (and not respired back to the atmosphere) ended up in the soil C pool profoundly demonstrates the importance of incorporating below-ground portions of ecosystems in analyses of the effects of rising $CO_2$ on C sequestration. Elevated $CO_2$ apparently did not result in more efficient use of organically bound nutrients (i.e. in litter) or increase recapture of nutrients sequestered to the large pool of new SOM. In fact, it appears that mineral nutrients were immobilized in the SOM. The lack of stimulation of soil $CO_2$ evolution in this experiment and the huge amount of C that remained in the soil suggest that C cycling may not be as greatly enhanced under elevated $CO_2$ in native plant communities growing on such infertile soils as we had concluded from our first study (Körner and Arnone 1992). Although we observed no effect of elevated $CO_2$ on ecosystem C storage, it is important to point out that even as small an increase as the one we observed between the means (+4% over 1.5 years), scaled-up to the globe, would more than account for the 2 Gt of "missing C" (e.g. Houghton and Woodwell 1989) believed to be stored in terrestrial ecosystems of the world. This also raises serious questions about the ability of ecologists to experimentally detect – much less predict – such small, but ecologically rather relevant, changes in ecosystem C storage under elevated $CO_2$ concentrations, particularly when the background C levels are high.

## Community biomass responses and net ecosystem productivity

An overall slight trend toward greater biomass accumulation was observed under elevated $CO_2$ after 530 days of treatment which was similar to the effect observed in our earlier experiment with model ecosystems of moist tropical plants after only 94 days of treatment (Körner and Arnone 1992). The main differences between the previous experiment and the current study are that nutrient supply and plant size were significantly less at the beginning of and during the current experiment, and that its duration was almost 6 times as long as the previous study.

In the previous experiment, the biomass accretion in 94 days of almost exponential growth extrapolated to 365 days was equivalent to an NPP (i.e. biomass increase plus the leaf litter found at harvest, but not including root litter production or SOM) of approximately 2780 g $m^{-2}$ $year^{-1}$ under ambient $CO_2$ to 3377 g $m^{-2}$ $year^{-1}$ under elevated $CO_2$. In the current study, NPP calculated over a 530 day period (which included the relatively slowly expanding late phase of ecosystem development) and expressed on an annual basis was 815 g $m^{-2}$ $year^{-1}$ and 910 g $m^{-2}$ $year^{-1}$ for ambient and elevated $CO_2$, respectively (using values in Table 2); approximately 82% and 92%, respectively, of the low end of the range (1000 g $m^{-2}$ $year^{-1}$) of NPPs reported in Whittaker (1975) for tropical forests. Comparisons between the two experiments are otherwise difficult because of their widely differing time scales, initial plant sizes (biomass and LAI), and soils.

Since *changes* in soil C pools were precisely known in the current experiment, we were able to estimate true NEPs reasonably accurately. In contrast to the NPPs we observed, NEPs were more than 2 times greater than the average NPP reported by Whittaker (1975; Whittaker's estimates do not account for SOM). One would, however, expect the NEP of a system at the beginning of its expansion stage to be higher than at later stages. As resources (light and nutrients) become more limiting with increased site occupancy, NEP should decline, as appears to have taken place in our study in all ecosystems toward the end of the experiment. The high NEPs in all ecosystems, and the otherwise small increase in biomass, strongly suggest enormous rates of tissue mortality, especially fine roots, in the current experiment. No reliable data are available against which to compare either these large C inputs to the soil or the NEPs of our ecosystems.

Although nutrient limitations in this experiment may appear severe, they may be quite representative of conditions in many native tropical plant communities growing on moderate to low fertility sites (e.g. Vitousek and Sanford 1986; Arnone et al. 1995). We intended (and succeeded in our intent) that our fertilizer addition rate would result in a more representative (i.e. smaller) NPP (see Whittaker 1975) than that observed in our previous study (Körner and Arnone 1992). However, we did not expect such enormous NEPs to occur, and that so much of the C assimilated would be sequestered in the soil for so long. This level of sequestration indicates that a large amount of other nutrients were also sequestered in the soil. Assuming that all of the N supplied in the Osmocote fertilizer was available initially (13.3 g N $m^{-2}$ ground) (Table 1), plant communities took up approximately 80–90% of that N under both $CO_2$ treatments (J.A. Arnone and Ch. Körner, unpublished data). Nutrient losses in drainage water were negligible (<0.1% of that supplied; J.A. Arnone and Ch. Körner, unpublished data), and gaseous losses can be assumed to be rather

small. It should be noted that leaf N concentrations at harvest were also quite normal, ranging from 16 to 29 mg N $g^{-1}$ dry mass (Arnone et al. 1995).

The responses of various plant organs to elevated $CO_2$ (Table 2) are in accordance to previous findings (e.g. Strain and Cure 1985; Körner and Arnone 1992; Rogers et al. 1994), with root biomass showing slightly greater stimulation at elevated $CO_2$ (Table 2), at least in the early growth phase on previously uninhabited ground. Leaf weight ratios (data not shown) were also consistently lower under elevated $CO_2$ (ANOVA $CO_2$ effect: $P = 0.03$) reflecting reductions in allocation to C-assimilating organs and increases in allocation to nutrient-assimilating organs.

## Species shifts

The very small $CO_2$-induced shifts in species contribution to total biomass are somewhat surprising given the long duration of the experiment and given the likelihood that at least one species of the diverse set of species would have responded more strongly than any actually did (Table 4; Figs. 4, 5). These data also suggest that in relatively low productivity systems more time may be required for potential changes in species abundance to become apparent. In the communities we designed, it appears that *F. benjamina* and *Elettaria cardomomum* may ultimately enjoy greater dominance at elevated $CO_2$ than they will at ambient $CO_2$, and that *Cecropia peltata* may disappear faster from elevated $CO_2$ communities than it might from ambient $CO_2$ communities (Figs. 4, 5).

Pronounced changes in species abundance have been observed in systems with relatively high productivity [fast growth (e.g. Carter and Peterson 1983; Patterson et al. 1984; Zangerl and Bazzaz 1984; Wray and Strain 1987; Bazzaz and Garbutt 1988; Reekie and Bazzaz 1989; Nie et al. 1992)], which may either be the result of ample resource supply (e.g. nutrients), choice of plant species' strategies, developmental stage of plants used, or length of the experiment. The salt marsh communities studied by Curtis et al. (1989) and Arp et al. (1993), and the prairie communities studied by Owensby et al. (1993), are examples of moderately productive systems showing substantial changes in species dominance at high $CO_2$. Low productivity systems tend to show small or no changes in species dominance at high $CO_2$ [e.g. Oechel and Strain (1985) in native tundra communities; Williams et al. (1988) in serpentine grassland plant assemblages; Schäppi and Körner (1995) in alpine grassland communities]. Our current experiment falls in this last category, even though the length of exposure to $CO_2$ treatments, plus the favourable temperature and moisture conditions, might correspond to six growing seasons in the tundra and two growing seasons in the salt marsh or prairie. Much longer periods of exposure to contrasting $CO_2$ concentrations may be required under conditions of low resource availability to detect any significant species-specific shifts in abundance.

Thus, our results show that in these complex communities of tropical plants, neither C storage nor C turnover are substantially stimulated at elevated $CO_2$ under conditions of low nutrient availability (even though very small, experimentally undetectable increases are certainly ecologically important on a global scale!). Elevated $CO_2$ *did* result in *groups of species* either gaining or losing their share of community biomass, while changes at the level of the individual species appeared to be slow and were not apparent even by the end of the experiment. We would also suggest that the results of this study with nutrient-limited systems may be quite representative of the magnitude of changes to elevated atmospheric $CO_2$ that might be expected in the many nutrient-poor native terrestrial ecosystems of the world.

**Acknowledgements** We thank our colleagues in the Department of Botany for their assistance in establishing, maintaining and harvesting the model ecosystems and plant communities (P. Blumer, P. Bockmühl, J. Bollinger, F. Ehrsam, B. Erny, M. Gruber, B. Gschwindemann, S. Hättenschwiler, A. Kocyan, A. Müller, J. Paulsen, S. Peláez, R. Pfeifer, C. Rötzel, B. Schäppi, R. Schneider, P. Schocher, O. Schürmann, R. Schweizer, B. Steulet, R. Stocker, L. Strasser, J. Zaller, C. Ziegler, L. Zimmermann). F. Montagnini kindly provided us with the native tropical soil inoculum. P. Stoll, A. Meyer and B. Schäppi advised us on statistical analyses. P. Leadley and two reviewers provided helpful comments on previous versions of this manuscript.

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