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Effect of elevated CO_2 and soil fertilization on whole-plant growth and water use in seedlings of a tropical pioneer tree, *Ficus insipida* Willd.

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Summary

Seedlings of the tropical pioneer tree species *Ficus insipida* were cultivated at present-ambient and elevated (about twice-ambient) CO_2 concentrations in open-top chambers located in a forest clearing near Panama City, Republic of Panama. To examine potential chamber-specific effects on growth and transpiration, plants were also studied outside chambers at ambient CO_2 levels. Plants were grown individually in 38 litre pots containing a mixture of soil and leaf litter, either in the absence or presence of a slow-release fertilizer. Data from three experiments, lasting 7 to 9 weeks each, are presented. Transpirational water loss of plants was determined gravimetrically. Fertilized plants grew more rapidly than unfertilized plants. Elevated CO_2 strongly enhanced biomass accumulation in fertilized plants. In unfertilized plants, elevated CO_2 enhanced growth in two experiments, but not in a third. Transpiration ratios (TR, g water lost: g dry mass accumulated) of plants grown in open-top chambers ranged from 176 (elevated CO_2, plus fertilizer) to 336 (ambient CO_2, minus fertilizer). The addition of fertilizer decreased TR by 15 to 20%, irrespective of the CO_2 concentration, and elevated CO_2 reduced TR by 27 to 35%, irrespective of whether fertilizer was present or not. The reduction in TR in response to elevated CO_2 was independent of whether biomass accumulation was enhanced by elevated CO_2 or not. In all experiments in which biomass accumulation was increased at elevated CO_2, absolute water expenditure at elevated CO_2 was greater or similar to that at ambient levels – despite the lower TR at elevated CO_2. In the single experiment in which elevated CO_2 did not lead to increased growth, the absolute water expenditure of plants was lower at elevated than at ambient CO_2. There was no chamber effect on biomass accumulation, but TR of both fertilized and unfertilized plants was 19 to 31% higher inside compared to outside the open-top chambers.

Key words: Atmospheric CO_2, *Ficus insipida*, global change, growth, tropical forest, water use.

Introduction

At atmospheric CO_2 concentrations above the present ambient, a leaf will assimilate CO_2 at a lower water cost per unit CO_2 fixed (JONES 1992). This is because at a given stomatal aperture, and thus at a given rate of water flux from the leaf into the atmosphere, a greater photosynthetically driven net influx of CO_2 into the leaf can be sustained at elevated CO_2 concentrations. Most studies demonstrating increased water use efficiency (WUE, moles of CO_2 incorporated per moles of water lost) or, conversely, decreased transpiration ratio (TR, moles of water lost per moles of CO_2 incorporated) in response to elevated CO_2, are based on measurements of leaf gas exchange only. The few studies that have been conducted with whole plants also demonstrated increased efficiency of water use at elevated CO_2, as measured by reductions in the amount of water lost per unit plant dry mass produced – an index of whole-plant TR (MORRISON & GIFFORD 1984a, b; SAMARAKOON & GIFFORD, 1996a, b; ARP et al. 1998).

In an ecological context, the absolute consumption of water per plant may be more important than TR. Alterations in the cumulative transpirational water loss by plants depend on the extent to which elevated CO_2 increases plant size, and whether decreases in leaf TR at elevated CO_2 are brought about by: (1) decreases in leaf conductance combined with unaltered rates of net CO_2 fixation per unit leaf area, (2) increases in the rate of net CO_2 fixation while leaf conductance remains unaffected, or (3) changes in conductance and net CO_2 fixation intermediate between (1) and (2). A rise in the atmo-

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spheric concentration of CO_2 tends to decrease stomatal conductance in most species (NORBY et al. 1999), although leaves of some trees such as *Pinus taeda* (ELLSWORTH 1999) appear not to exhibit reductions in stomatal conductance in response to elevated CO_2.

This study focuses on the effects of elevated CO_2 on water use by tropical plants, and builds on previous growth studies with individual plants and plant arrays of tropical tree species (WINTER & VIRGO 1998; LOVELOCK et al. 1998, 1999a, b; WINTER & LOVELOCK 1999; WINTER et al. 2000, 2001). Here, seedlings of a fast-growing early-successional tree species, *Ficus insipida* (CROAT 1978) were cultivated in large pots at ambient and elevated CO_2, either in the absence or presence of soil fertilizer. High soil water availability was maintained during all experiments. Measurements of cumulative transpiration and biomass accumulation demonstrated that both nutrient availability and atmospheric CO_2 concentration markedly affect the absolute water use per plant as well as the relative water use per unit of biomass gained.

Materials and methods

Plant material

Seedlings of *Ficus insipida* Willd. were established from seeds in a screenhouse and transplanted into 38 litre Rubbermaid Round Brute containers (upper diameter 36.5 cm; lower diameter 32 cm; height 44 cm; Consolidated, Twinsburg, OH) covered with lids. Pots contained 1.75 kg of charcoal at their base to improve drainage, 28 kg of a 1:1 mixture (v/v) of sieved, dark, air dried top soil and leaf litter, and 9 l of water. Two kg of gravel (particle size 1.1 ± 0.6 cm, n = 13) were layered onto the soil surface to reduce evaporation. Half of the plants received 80 g each Osmocote-Plus controlled release fertilizer (N-P-K 16-8-12 and Mg, Fe, Mn, Cu, Mo, and B; Scotts-Sierra, Maryville, OH). Lids had a 3.4 cm diameter hole in the middle through which the plants grew. Two additional holes carried PVC T-type tubes to facilitate gas exchange between soil surface and atmosphere while preventing rain water from entering the pots (Fig. 1). At the onset of each experiment, seedlings were approximately 5.5 cm high and had a dry mass of approximately 0.16 g.

Study site and chamber design

The study was conducted in a large forest clearing of the seasonally dry tropical forest of Parque Natural Metropolitano, close to Panama City, Republic of Panama. Annual rainfall is about 1740 mm with a pronounced dry season extending from late December to early May. Following an initial pilot study, three experiments (lasting 7 to 9 weeks each) were performed between July 1998 and May 1999, two during the wet season and one during the dry season. Plants were grown in octagonal, rain-shielded open-top chambers of about 2 m across. Aluminum frames provided structural support for 1.25 m high plastic film side walls and also supported horizontally positioned translucent shields of plexiglas (1.8×2.2 m) on their tops (2.5 m height) to minimize exposure of plants to direct rainfall. The chamber bottom was inserted 30 cm into the ground so that the surface of the plant containers was almost level with the soil surface. Chambers were either supplied with ambient air or air containing elevated levels of CO_2 (300 to 400 ppm above ambient). Ambient CO_2 concentrations typically showed distinct diel courses with minima of about 350 ppm in the early afternoon and maxima of typically 400 to 430 ppm at dawn. CO_2 supply equipment and air ventilation systems have been described previously (WINTER et al. 2000a). Possible chamber effects were assessed by studying plants inside chamber aluminum support structures without plastic covered side walls.

Fig. 1. Seedling of *Ficus insipida* growing through a central opening in the lid of an experimental pot. Two additional openings in the lid carry T-shaped tubes which facilitate soil gas exchange with the atmosphere while preventing rain water from entering the pots.

Transpiration, dry matter, leaf area

The weight of plant containers was determined initially at 7 day intervals, and later at 3 day intervals using a Sartorius Balance QS64B, capacity 64 kg (Thomas, Swedesboro, NJ). Lost water was replaced after each measuring cycle to bring the pots to their initial weight (42 kg). Transpiration was calculated from the difference in weight loss of pots plus plants and control pots without plants, and corrected for biomass (fresh weight) increase. At the end of each experimental period, plants were divided into roots, stems and leaves and dried at 60 °C for dry matter determination. Leaf areas were measured with a LI-3100 Area Meter (Li-Cor, Lincoln, NE).

Microclimate

Microclimate conditions were monitored inside and outside open-top chambers with Li-190SA quantum sensors (Li-Cor, Lincoln, NE), ASPTC aspirated fine wire thermocouples, Vaisala relative humidity sensors (HMP45C probe), and 014A wind speed sensors (all from Campbell Scientific, Logan, UT). Sensors were connected to dataloggers (LI-1000, Li-Cor; CR 10, Campbell). Evaporation was measured with an Etgage Model A evaporator covered with Style # G2 Gore-Tex (Etgage Company, Loveland, CO). Comparative measurements on Barro Colorado Island, Panama, showed that the Etgage simulated reasonably well evaporation from the free water surface of a standard class A evaporation pan (Fig. 2). The Etgage tends to underestimate Pan evaporation during rainy days by up to approximately 15% probably due to the wetting of the Gore-Tex cover. However, after 640 days of concurrent operation on Barro Colorado Island, Panama, the Etgage had underestimated Pan evaporation by only 5.2%.

Figure 3 depicts microclimate measurements during the second of two experiments conducted during the wet season. Average daily PFD was 21.4 mol m^{-2} (plastic film covered side walls, rain shield), 20.8 mol m^{-2} (no plastic film covered side walls, but rain shield), and 21.8 mol m^{-2} (outside, no chamber structures, no rain shield). Plants inside open-top chambers

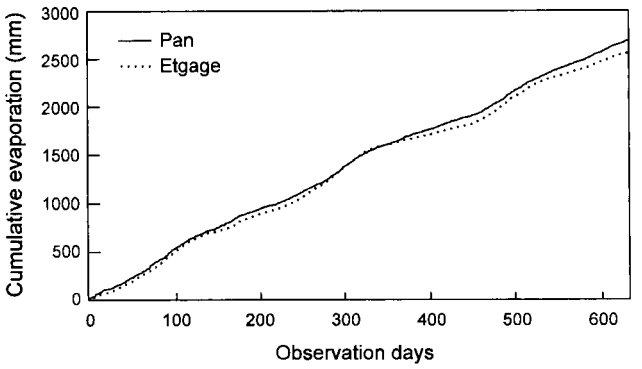

Fig. 2. Free water evaporation from a Etgage evaporimeter as compared to a class A pan. Measurements were conducted on Barro Colorado Island (Republic of Panama) between 1996 and 1999.

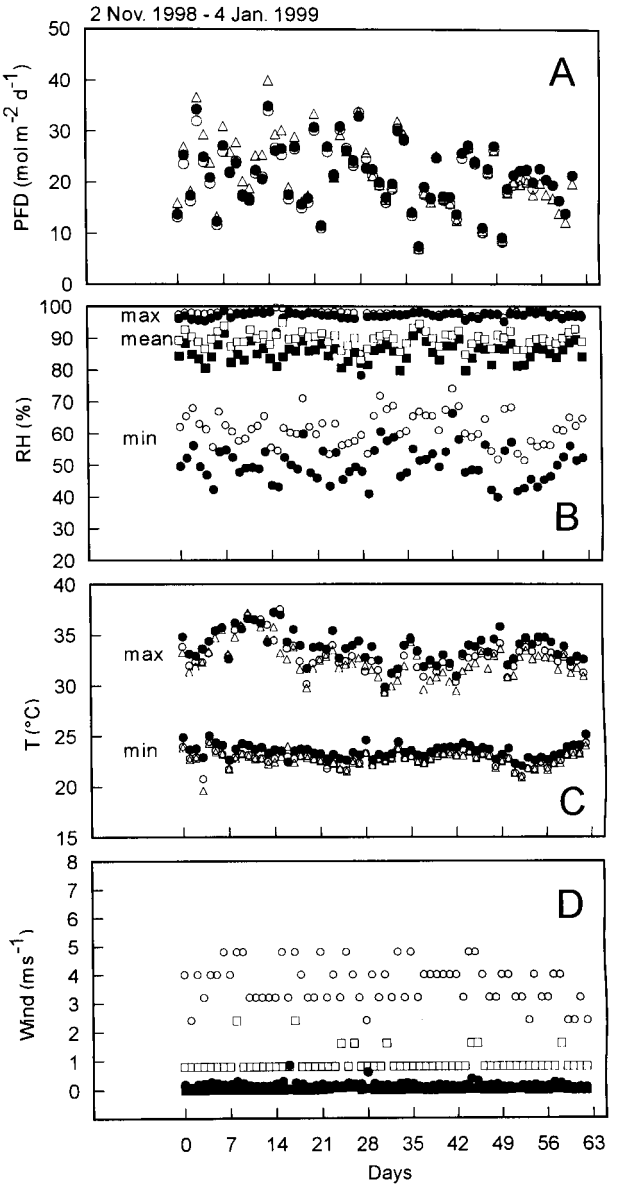

Fig. 3. Microclimate conditions during the late wet season (Experiment II). A: PFD inside open-top chambers plus rain shield (closed circles); inside chamber support structures (no plastic-film side walls) plus rain shield (open circles); and outside the chambers (no support structures, no rain shield) (open triangle). B: Minimum and maximum daily relative humidity (RH) inside open-top chambers (closed circles) and inside chamber support structures minus plastic-film side walls (open circles). Mean RHs inside open-top chambers are indicated by closed squares, and inside chamber support structures minus plastic-film side walls by open squares. (C) Maximum and minimum daily temperatures inside open-top chambers (closed circles); inside chamber support structures (no plastic-film side walls) plus rain shield (open circles); and outside the chambers (no support structures, no rain shield) (open triangles). (D) Daily maximum (open symbols) and mean (closed symbols) wind speeds inside open-top chambers (squares) and outside chambers (circles).

Table 1. Effect of elevated CO_2 and fertilizer treatment on growth and water use of *Ficus insipida*. Plants were either grown in open-top chambers (+ chamber) or outside open-top chambers (– chamber). Values are means ± SD (n = 6).

Treatment	Area increase (cm^2)	Dry mass increase (g)	Water transpired (g)	Transpiration ratio (g water g^{-1} dry mass)
Experiment I (wet season, 20 July – 14 Sept 1998, 8 weeks)				
Minus Fertilizer				
Ambient CO_2, – chamber	1068 ± 286	9.04 ± 2.36	2078 ± 579	229 ± 21
Ambient CO_2, + chamber	1341 ± 314	10.64 ± 2.58	3198 ± 890	299 ± 26
Elevated CO_2, + chamber	1844 ± 680	19.43 ± 5.42	4195 ± 1028	219 ± 17
Plus Fertilizer				
Ambient CO_2, – chamber	4081 ± 583	39.65 ± 5.31	8428 ± 1128	213 ± 5
Ambient CO_2, + chamber	4610 ± 816	40.46 ± 7.02	10288 ± 1965	254 ± 10
Elevated CO_2, + chamber	5953 ± 876	62.76 ± 8.46	11559 ± 1496	185 ± 7
Experiment II (late wet season, 2 Nov 1998–4 Jan 1999, 9 weeks [minus fertilizer]; 2 Nov–21 Dec 1998, 7 weeks [plus fertilizer])				
Minus Fertilizer				
Ambient CO_2, – chamber	913 ± 212	8.26 ± 2.35	2059 ± 485	253 ± 15
Ambient CO_2, + chamber	983 ± 149	8.29 ± 1.00	2713 ± 270	329 ± 24
Elevated CO_2, + chamber	898 ± 164	10.37 ± 1.92	2157 ± 428	213 ± 19
Plus Fertilizer				
Ambient CO_2, – chamber	2902 ± 480	23.61 ± 5.10	5018 ± 1005	213 ± 6
Ambient CO_2, + chamber	3106 ± 684	23.12 ± 5.21	6073 ± 1425	262 ± 11
Elevated CO_2, + chamber	4172 ± 473	42.39 ± 4.39	7468 ± 780	176 ± 3
Experiment III (dry season, 1 Mar 1999–19 Apr 1999, 7 weeks)				
Minus Fertilizer				
Ambient CO_2, – chamber	1332 ± 397	11.73 ± 3.72	3565 ± 995	309 ± 35
Ambient CO_2, + chamber	1589 ± 385	14.43 ± 2.87	4846 ± 1025	336 ± 16
Elevated CO_2, + chamber	2428 ± 266	26.88 ± 3.49	6122 ± 732	228 ± 7

experienced only slightly higher temperatures. Average maximum temperatures were 33.9 °C (side walls, rain shield), 33.1 °C (rain shield, no side walls), and 32.5 °C (outside). Average minimum temperatures were 23.5 °C (side walls, rain shield), 22.7 °C (rain shield), and 22.7 °C (outside). Minimum average RHs during daytime were lower inside chambers surrounded by plastic film (50.4%) than in the absence of plastic film (61.5%). Outside open top chambers, wind speeds were on average 0.19 m s^{-1} (daily mean) and 3.7 m s^{-1} (daily maxima). Wind speeds were lower inside chambers surrounded by plastic film than outside, although 014A wind speed sensors did not reliably measure the jets of air emitted from the chamber air-ventilation system (perforated octagonally-shaped PVC air ducts along the inner chamber walls at the base of the chambers). The air jets were distributed in a circular manner and leaves close to the lid of pots were exposed to wind speeds of 0.1 to 0.7 m s^{-1}, as measured with a thermal air velocity sensor (model 8355, TSI Inc., MN).

During the dry season (experiment III), average daily PFD was 28.9 mol m^{-2} (plastic film covered side walls, rain shield), 29.4 mol m^{-2} (no plastic film covered side walls, but rain shield), and 34.5 mol m^{-2} (outside). Average maximum temperatures were 35 °C (side walls, rain shield), 34.2 °C (rain shield, no side walls), and 33.6 °C (outside). Average minimum temperatures were 22.9 °C (side walls, rain shield), 21.9 °C (rain shield), and 21.8 °C (outside). Minimum average RH was 41.7% inside open-top chambers (side walls, rain shield), and 49.5% when the plastic side walls were removed. Outside open-top chambers daily mean wind speeds were on average 0.29 m s^{-1} and daily maxima were on average

Table 2. P values derived from student's t-test on results shown in Table 1. Data are compared for "ambient CO_2, – chamber" versus "ambient CO_2, + chamber" (chamber), and for "ambient CO_2, + chamber" versus "elevated CO_2, + chamber" (CO_2). ns = not significant ($P > 0.05$).

Treatment	Area increase	Dry mass increase	Water transpired	Transpiration ratio
Experiment I				
Minus Fertilizer				
Chamber	ns	ns	<0.05	<0.001
CO_2	ns	<0.01	ns	<0.001
Plus Fertilizer				
Chamber	ns	ns	ns	<0.001
CO_2	<0.05	<0.001	ns	<0.001
Experiment II				
Minus Fertilizer				
Chamber	ns	ns	<0.05	<0.001
CO_2	ns	ns	<0.05	<0.001
Plus Fertilizer				
Chamber	ns	ns	ns	<0.001
CO_2	<0.05	<0.001	ns	<0.001
Experiment III				
Minus Fertilizer				
Chamber	ns	ns	ns	ns
CO_2	<0.01	<0.001	<0.05	<0.001

4.69 m s^{-1}. Average daily mean wind speeds as measured with the 014A sensor inside open-top chambers were 0.05 m s^{-1} and average daily maxima were 1.11 m s^{-1}.

Abbreviations: PFD, photon flux density (400–700 nm); p_a, ambient CO_2 partial pressure; p_i, intercellular CO_2 partial pressure; RH, relative humidity; SD, standard deviation; TR, whole plant transpiration ratio (g water transpired g^{-1} dry mass produced), unless specified as leaf TR (moles water transpired moles $^{-1}$ CO_2 fixed); WUE, water use efficiency.

Results

CO_2 effects on growth, cumulative transpiration, and TR

Fertilized plants at elevated CO_2 consistently showed greater biomass increases relative to plants at ambient CO_2 levels (Table 1 and results from pilot study [not shown]). Cumulative transpiration was, on average, higher at elevated CO_2 in fertilized plants, but differences were not statistically significant ($P > 0.05$; student's t-test, Table 2). Elevated CO_2 led to marked reductions in TR by about 30% (experiments I and II, Tables 1 and 2).

Responses of biomass accumulation to elevated CO_2 in unfertilized plants were variable. In two experiments (I and III), unfertilized plants showed >80% greater dry mass at elevated CO_2, whereas in experiment II, total plant dry mass did not change significantly (Table 1). In all cases, TR decreased at elevated CO_2 by between 27% and 35%. As with fertilized plants, faster growth in unfertilized plants at elevated CO_2 was always accompanied by greater average cumulative transpiration (Table 1, experiments I and III), although cumulative transpiration of unfertilized plants at ambient and elevated CO_2 was only significantly different in experiment III (Table 2). In experiment II, in which biomass remained unaltered in response to elevated CO_2, cumulative transpiration was significantly lower in plants at elevated CO_2 compared to plants at ambient CO_2 (Tables 1 and 2).

Fertilizer effect on TR

Plants grown in fertilized soil showed a markedly decreased TR compared to plants in unfertilized soil, independent of CO_2 concentration. At ambient CO_2, reductions in TR observed in experiments I and II were 15 and 20%, respectively, for plants inside chambers, and 9 and 16% for plants outside chambers. At elevated CO_2, corresponding fertilizer-related reductions in TR for plants inside chambers were 16% and 17%, respectively.

Chamber effect on growth and TR

Dry matter accumulations at ambient CO_2, both in the absence and presence of fertilizer, did not differ between plants grown inside and outside of chambers ($P > 0.05$; Tables 1 and 2). However, cumulative transpiration inside chambers was higher, and TR was between 8% (dry season) and 14 to 24% (wet season) lower for plants

Table 3. Evaporation (mm water) from the surface of an Etgage evaporator inside and outside open-top chambers during three experiments conducted at different times of the year.

Experiment	Time of year	Treatment	Evaporation (mm wk^{-1})
I	Wet season	Inside	26.6 ± 0.7[a]
		Outside	23.1[b]
II	Late wet season	Inside	23.9 ± 0.6[a]
		Outside	20.5[b]
III	Dry season	Inside	37.5 ± 0.4[a]
		Outside	36.0[b]

[a] average of results from 4 Etgages ± SD; [b] average of results from two Etgages.

inside chambers ($P < 0.001$; Table 2). Correspondingly, evaporation from Etgage evaporimeters was 15 to 17% higher inside chambers compared to outside during the wet season, but only 4% higher during the dry season (Table 3). Marked seasonal changes in TR were observed for plants outside chambers in the absence of fertilizer. During the two wet season experiments (I and II), TR was 229 and 253, respectively, and increased to 309 during the dry season experiment (experiment III). Evaporation from Etgage evaporimeters inside chambers was approximately 50% higher during the dry season than during the wet season (Table 3). Evaporation outside chambers increased by 65% during the dry season.

Discussion

Our results on TR in *Ficus insipida* do not suffer from two complications frequently encountered in TR studies using containers, especially those from the early literature: the lack of separation of soil evaporation from transpiration and the incomplete sampling of roots for whole-plant dry matter determination. For example, root mass was not included (except for root crops) in the classic studies by BRIGGS, SHANTZ and PIEMEISEL (cf. SHANTZ & PIEMEISEL 1927) in Colorado, which upon re-evaluation decades later illustrated marked differences in TR between C3 and C4 plants. Furthermore, the study presented here was conducted under close-to-natural tropical field conditions, whereas several recent studies on TR of other species have been performed in glasshouses or environmental growth chambers where the driving forces for transpirational water loss may differ substantially from those in the field. Thus, only coarse comparisons can be made between TR obtained for *Ficus insipida* and those reported in the literature for other species.

TR for *Ficus insipida* growing outside open-top chambers ranged from 229 to 309 g H_2O g^{-1} dry mass; these values are at the lower extreme of TR observed in C3 plants from other environments (Kansas, Utah, Israel, Queensland; summarized in FISCHER & TURNER 1978; see also OSMOND et al. 1980 and LARCHER 1994). This result is not unexpected given that our study was performed in the humid tropics where free water evaporation is relatively low. Variations in TR between C3 plants from different sites are generally believed to be due to differences in the water vapour pressure drop between the leaves and the surrounding air (TANNER 1981; KRAMER 1983). The effect of air water vapour deficit on TR is also evident in our experiments by generally higher TR for plants inside chambers as compared to those outside, and by higher TR during the dry season (experiment III) compared to the wet season for plants outside chambers (experiments I and II, Table 1). No seasonal effect on TR was detected for plants inside chambers, where the interpretation of transpirational driving forces based on Etgage evaporation data was complicated by local effects of the air ventilation system on leaf transpiration rates.

Soil fertilization reduced TR in *Ficus insipida*. This result is consistent with results from leaf gas exchange studies that have shown that photosynthetic CO_2 uptake operates at lower p_i/p_a ratios (intercellular/ambient CO_2 partial pressure) in nitrogen rich compared to nitrogen poor leaves (K. WINTER, unpublished data with *Arbutus unedo*). At a given leaf to air water vapour gradient, the p_i/p_a ratio during photosynthesis correlates with the amount of water lost per unit CO_2 fixed (FARQUHAR et al. 1989). Furthermore, leaves of cotton maintained at ambient CO_2 and cultivated with an ample supply of nitrogen showed a 21% lower ratio of transpiration rate to CO_2 assimilation rate compared to plants grown with small nitrogen supply (WONG 1979). Photosynthesizing leaves tend to maintain a relatively constant p_i/p_a ratio over a wide range of CO_2 assimilation rates (WONG et al. 1979), but this relationship is not a strict one. Recent growth studies in glasshouses also provided evidence for decreased TR in fertilized versus nitrogen-stressed *Picea glauca* (LIVINGSTON et al. 1999) and in high nitrogen treated *Arrhenatherum, Molinia* and *Rumex* (ARP et al. 1998), whereas no effect of nitrogen nutrition on TR was observed in *Calluna* and *Vaccinium*. Nitrogen availability did not consistently affect TR in *Pseudoroegneria spicata* and *Gutierrezia microcephala* (POLLEY et al. 1999). Some earlier reports in the agronomic literature of decreases in evapotranspiration relative to dry matter production as a result of soil fertilization may have been related to reduced soil evaporation (FISCHER & TURNER 1978).

Despite the observed decreases in TR in response to high CO_2, in most experiments the absolute loss of water per plant either remained unchanged or increased because of increases in plant size. Nonetheless, in experiment II (minus fertilizer) the decrease in TR at elevated CO_2 was accompanied by a significant reduction in cumulative transpiration per plant, because plant size did not markedly increase at elevated CO_2. This result may have implications about responses of tropical forest ecosystems to predicted future increases in atmospheric CO_2. Even if regenerating trees within tropical forests do mature more rapidly under conditions of elevated CO_2, because of limitations such as soil nutrients, future tropical forest ecosystems would not necessarily attain a greater standing above-ground biomass per unit ground area than today. If this is so, the major effect of enhanced CO_2 could well be a significant reduction in forest transpiration, potentially affecting rainfall patterns and soil water availability, particularly for plants in

the forest understorey, although such effects may subsequently be modified by feedback responses of the ecosystem.

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