

Sensitivity of photosynthesis and carbon sink in tropical rainforests to projected atmospheric CO₂ and climate change

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Introduction

Terrestrial ecosystems currently take up as much as one third of anthropogenic CO₂ emitted annually to the earth's atmosphere (Schimel 1995). CO₂ fertilization (i.e. the stimulation in photosynthesis and plant growth by elevated atmospheric CO₂ concentration), forest re-growth, nitrogen deposition and climate change are believed to contribute to this C sink (Field 2001). CO₂ fertilization is of particular interest as it could provide a negative feedback on the growth rate of the atmospheric CO₂ concentration. Recent field measurements and model simulations indicate that a significant fraction of the terrestrial sink (approximately 1 Gt C yr⁻¹) may be attributed to CO₂ fertilization occurring in tropical rainforests (Malhi and Grace 1998). However it is crucial to understand the dynamic properties of this C sink before assuming that CO₂ fertilization in tropical rainforests will play a significant role in offsetting future anthropogenic CO₂ emissions. Previous evaluations of C sink dynamics have been limited mostly to model simulations (Tian et al. 1999; Kicklighter et al. 1999, Chamber et al. 2001), and have not been linked with experiments at appropriate spatial scales. Here we present results from an empirical evaluation of photosynthesis and carbon sink sensitivity to projected CO₂ and climate change, based on measurements in a large-scale rainforest mesocosm.

Materials and Methods

Description of the rainforest mesocosm. Our study takes advantage of the technical innovations at Biosphere 2, a 1.27 ha enclosed structure near Tucson, Arizona. With a ground area of 1,900 m², an air volume of 35,000 m³ and a soil volume of 6,000 m³, the rainforest mesocosm we used in this study contains more than 400 individual plants belonging to ~120 species as well as diverse groups of soil micro-organisms. This rainforest models after a humid tropical rainforest in South America and has been separated from the rest of Biosphere 2 using a partitioning curtain since January 1999. During the study period, the daily mean air temperature was set at 27 °C (Max. 35 °C, Min. 20 °C), with relative humidity (RH) at about 85 %.

CO₂ control and treatments. We controlled the CO₂ concentration in the rainforest mesocosm's atmosphere at each of four target levels (400, 700, 1000 and 1200 ppmv) for 4 days by either injecting CO₂ or using pull/push fans. Two experimental periods, Sept. 9-Oct. 10 of 1999 and May 1-June 5 of 2000, were selected for stable light levels. During Sept. 9-Oct. 10 of 1999, CO₂ concentration was first increased and then decreased step-wise from 400 to 1200 ppmv. In contrast, CO₂ was increased step-wise twice during May 1-June 5 of 2000.

Calculations of net ecosystem exchange (NEE). We calculated NEE over 15 min intervals for each day based on the changes in CO₂ concentration, the amount of CO₂ injected, the CO₂ exchange amounts by the pull/push fans, and the CO₂ exchange due to leakage through the curtains. NEE was then deconvolved into canopy photosynthesis (A_{canopy}) and total respiration ($R_{ecosystem}$).

Leaf-level measurements. Leaf-level measurements of photosynthesis under different light and CO₂ concentrations were measured on four canopy species (*Cecropia schreberiana*, *Ceiba pentandra*, *Arenga pinnata*, *Clitoria racemosa*) and two understory species (*Costus sp.*, *Coffea arabica*) using a LI-6400 photosynthesis

system (LICOR, Inc.). The temperature inside the chamber was 30.0 ± 0.5 °C for the canopy species and 25.0 ± 0.5 °C for the understory species, while the RH was set at 85 % for all species. The light level was $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the canopy species and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the understory plants.

Response coefficient of photosynthesis. We related our experimental results to modeling approaches using the response coefficient (R_c) of photosynthesis to C_a according to Woodrow et al. (1990):

$$R_c = (dP/dC_a) \cdot (C_a/P) = (dP/P)/(dC_a/C_a).$$

R_c is a dimensionless parameter that gives the fractional change in photosynthesis (either measured or modeled) to a fractional change in C_a , and P is photosynthetic rate at specific scale. Here, we compare R_c values calculated for commonly used approaches for modeling the response of GPP to C_a (the linear and logarithmic β -factor, Kicklighter et al. 1999) and a theoretically derived R_c for a leaf photosynthesis model based on enzyme kinetics (Farquhar et al. 1980) with our observed leaf and canopy level responses.

Description of carbon sink model. To simply illustrate the dynamics of the interaction of GPP and respiration and the resulting sink, we constructed a model with one pool carbon (M). Respiration, R , depends linearly on M , $R = k \cdot M$, where k is a first order rate constant. This rate constant is the inverse of the mean residence time of C in M , or turnover time, τ (yr). The time evolution of the C mass, $M(t)$ (Gt C), is then given by the following differential equation:

$$dM(t)/dt = -M(t)/\tau + GPP(t)$$

where t denotes time in years and $GPP(t)$ (Gt $C \text{ yr}^{-1}$) is gross primary productivity at time t . The net C sink, S (Gt $C \text{ yr}^{-1}$), during one year can then be approximated by:

$$S_t = GPP_t - R_t = GPP_t - M_{t-1} / \tau$$

where S_t is the C sink in the year $[t-1, t)$, M_{t-1} is the biomass at time $t-1$. We evaluated the dynamics of the CO_2 fertilization carbon sink in global rainforests for two scenarios of change in C_a . Both scenarios are based on observed C_a from 1860 to 1990; after 1990, C_a was assumed to increase linearly with time at 1.5 ppmv yr^{-1} (L1200), or to increase more rapidly at first but eventually stabilize at 750 ppmv (S750). Further we assumed either no temperature increase associated with a C_a increase or a 2.5 °C increase with a doubling of C_a from 350 to 700 ppmv (ca. 0.007 °C ppmv^{-1}). To calibrate the turnover time and the initial biomass we fitted the model to the biomass in 1985 reported by Amthor et al. (1995).

Results and Discussion

Photosynthetic responses at different scales. Responses of photosynthetic rates to light and CO_2 at the whole mesocosm scale were similar to that observed at smaller scales in experiments with leaves (Fig. 1). Photosynthetic CO_2 uptake is proportional to light for a PPFD lower than $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ at both scales. Although the canopy response is the daily sum but the leaf level responses are instantaneous responses, all curves show similar saturation responses to increasing C_a .

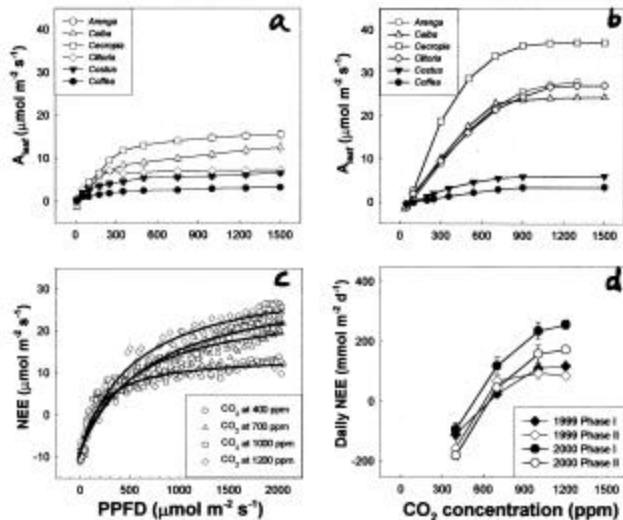


Figure 1. Responses of photosynthetic CO_2 uptake by leaves (A_{leaf} , a-b) and by the whole mesocosm (NEE, c-d) to increasing photosynthetic proton flux density (PPFD, left panels) and atmospheric CO_2 concentration (right panels) within the tropical rainforest mesocosm of Biosphere 2. NEE values in Fig. 1c were 15-min means while those in Fig. 1d were the daily sum over the photo period. Relatively higher daily sum NEE values observed in 2000 than in 1999 (Fig. 1d) were likely the results of much higher daily integrated light.

Response coefficient of photosynthesis. Our measurements suggest that the sensitivity of photosynthesis decreases with increasing CO₂ concentration and biological organization level (data not shown). The linear β -factor does not represent the saturation of this response with increasing C_a (decreasing values of R_c). The logarithmic β -factor represents this saturation response better, and while the modeled sensitivity declines with C_a , it cannot be parameterized to match the observed response over the range of the observations used in this study. The R_c values of the leaf and enzyme responses are nearly identical below about 600 ppmv CO₂ indicating that the enzyme step is in full control of CO₂ flux in this region. The canopy response shows a lower sensitivity to CO₂ than the leaf or the modeled biochemical formulations for all C_a , and this is interpreted as indicating that other processes (probably light availability at different points in the canopy) are co-limiting the rate of CO₂ fixation. These differences in response with the scale of observations provide information on subtle changes in the controlling processes that should be addressed in models that scale from the enzyme to ecosystem.

Dynamics of C sink in tropical rainforests. Our model simulations indicate that the response coefficient of photosynthesis to C_a (R_c), the future trajectory of C_a and the associated temperature change all have profound effects on the temporal dynamics of the C sink in global rainforests (Fig. 2).

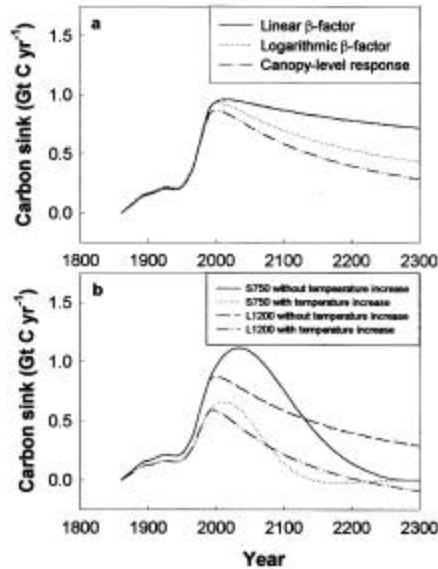


Figure 2. The simulated temporal change in the strength of CO₂ fertilization carbon sink in global rainforests from 1860 to 2300 based on the canopy-level response function and two type β -factor functions assuming a linear CO₂ increase of 1.5 ppmv yr⁻¹ until 1200 ppmv (L1200 scenario)(a) and the simulated C sink based on the canopy response assuming either a stabilizing CO₂ at 750 ppmv (S750 scenario) or a linear CO₂ increase of 1.5 ppmv yr⁻¹ until 1200 ppmv (L1200 scenario) under either no temperature change or a 2.5 °C increase with a doubling CO₂ (b).

These trajectories can be understood by noting that approximately $S_t \sim R_c * GPP * (dC_a/C_a) * \tau$. From 1860 to 1960 the modeled CO₂ sink is quite small -- because the rate of increase in C_a was slow. The strong increase in C sink since 1960 resulted from the significant growth rate of atmospheric CO₂ from the 60's to the present. Thus, the present sink may be a comparatively recent phenomenon. Future behavior of this sink depends strongly on the rate of growth in C_a and the consequent change in R_c . Imposing a linear rate of growth beginning in 1990 causes the sink to peak and begin to decline slowly as R_c declines with increasing C_a . This decline is more pronounced when the canopy response rather than a β -factor is used, reaching about 50% of its current value by 2300 (Fig. 2a). Assuming that growth of C_a carries an associated temperature change results in a lower present estimate of the sink and a more rapid decline, reaching 50% of its current value before the end of this century (Fig. 2b). When CO₂ is assumed to stabilize

at 750 ppmv, the sink peaks then declines to zero as C_a reaches a stable value. The areas under the curves in Fig. 2 could be used to estimate total amount of C stored in global rainforests, which translates directly to anthropogenic CO_2 that could be released before C_a reaches the ceiling of 750 ppmv. C storage using the linear β -formulation is larger (227 Gt C) than that simulated assuming the observed canopy response (146 Gt C) and much larger than that simulated assuming both CO_2 saturation and climate change (48 Gt C). The latter corresponds to less than 6 years of fossil fuel use at current rates or to a 27 ppmv lower final value of C_a .

Although our model is highly simplified, its simple structure is useful for exploring the effects of different assumptions on the CO_2 response of photosynthesis and the consequence of global warming on carbon sink dynamics. Further, while our short-term measurements of canopy response to CO_2 may not capture important second order effects such as photosynthetic acclimation (Sage et al. 1989) or chronic nutrient stress (Oren et al. 2001), the values for GPP , biomass, and the carbon sink derived from our simulations are within accepted ranges. Therefore, we suggest that our estimates of the future carbon sink are plausible and conservative. Based on our analyses, we anticipate that the current C sink strength in tropical rainforests will be likely to increase over next few decades, reach a peak, start to decrease and eventually vanish (Fig. 2). If global warming occurs as predicted, the sink strength will be reduced, and the year when the sink strength starts to decrease will be reached much earlier.

In conclusion, our study illustrates the key importance of a correctly representing ecosystem carbon dynamics and respiration (our parameter τ) in carbon cycle models (Cox et al. 2000). Of the current carbon sink, direct stimulation of GPP in that year accounts for only about $1/10^{\text{th}}$ of the total, while the remainder is related to stimulation of GPP in previous years and to delays in the flow of respired carbon through ecosystems. To date, most experimental work has focused on the supply side (responses of GPP), while the slower, but equally important dynamics of carbon cycling within ecosystems and their response to temperature change have received little attention. We propose that large-scale mesocosms inside Biosphere 2 with mass balance capabilities are ideally suited for conducting such studies of ecosystem carbon dynamics.

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