Sensitivity of photosynthesis and carbon sink in tropical rainforests to projected atmospheric CO$_2$ and climate change

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Introduction

Terrestrial ecosystems currently take up as much as one third of anthropogenic CO$_2$ emitted annually to the earth’s atmosphere (Schimel 1995). CO$_2$ fertilization (i.e. the stimulation in photosynthesis and plant growth by elevated atmospheric CO$_2$ concentration), forest re-growth, nitrogen deposition and climate change are believed to contribute to this C sink (Field 2001). CO$_2$ fertilization is of particular interest as it could provide a negative feedback on the growth rate of the atmospheric CO$_2$ 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 CO$_2$ 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 CO$_2$ fertilization in tropical rainforests will play a significant role in offsetting future anthropogenic CO$_2$ 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 CO$_2$ 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 m$^2$, an air volume of 35,000 m$^3$ and a soil volume of 6,000 m$^3$, 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 %.

CO$_2$ control and treatments. We controlled the CO$_2$ 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 CO$_2$ 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, CO$_2$ concentration was first increased and then decreased step-wise from 400 to 1200 ppmv. In contrast, CO$_2$ 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 CO$_2$ concentration, the amount of CO$_2$ injected, the CO$_2$ exchange amounts by the pull/push fans, and the CO$_2$ exchange due to leakage through the curtains. NEE was then deconvolved into canopy photosynthesis ($A_{\text{canopy}}$) and total respiration ($R_{\text{ecosystem}}$).

Leaf-level measurements. Leaf-level measurements of photosynthesis under different light and CO$_2$ 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
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 μmol m⁻² s⁻¹ for the canopy species and 100 μmol m⁻² 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):

\[
R_c = \frac{(dP/dC_a)(C_a/P)}{(dP/dC_a/C_a)}.
\]

\( R_c \) 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, \( \tau (\text{yr}) \). 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 yr⁻¹) is gross primary productivity at time \( t \). The net C sink, \( S \) (Gt C 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 CO₂ 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 CO₂ at the whole mesocosm scale were similar to that observed at smaller scales in experiments with leaves (Fig. 1). Photosynthetic CO₂ uptake is proportional to light for a PPFD lower than 300 μmol m⁻² 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 CO₂ uptake by leaves (Aleaf, a-b) and by the whole mesocosm (NEE, c-d) to increasing photosynthetic proton flux density (PPFD, left panels) and atmospheric CO₂ 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 CO$_2$ 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 CO$_2$ indicating that the enzyme step is in full control of CO$_2$ flux in this region. The canopy response shows a lower sensitivity to CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 CO$_2$ at 750 ppmv (S750 scenario) or a linear CO$_2$ 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 CO$_2$ (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 CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 $\beta$-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 $\tau$) in carbon cycle models (Cox et al. 2000). Of the current carbon sink, direct stimulation of GPP in that year accounts for only about 1/10th 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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