

Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon

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The fixation and storage of C by tropical forests, which contain close to half of the globe's biomass C, may be affected by elevated atmospheric CO₂ concentration. Classical theoretical approaches assume a uniform stimulation of photosynthesis and growth across taxa. Direct assessments of the C balance either by flux studies or by repeated forest inventories also suggest a current net uptake, although magnitudes sometimes exceed those missing required to balance the global C cycle. Reasons for such discrepancies may lie in the nature of forest dynamics and in differential responses of taxa or plant functional types. In this contribution I argue that CO₂ enrichment may cause forests to become more dynamic and that faster tree turnover may in fact convert a stimulatory effect of elevated CO₂ on photosynthesis and growth into a long-term net biomass C loss by favouring shorter-lived trees of lower wood density. At the least, this is a scenario that deserves inclusion into long-term projections of the C relations of tropical forests. Species and plant functional type specific responses ('biodiversity effects') and forest dynamics need to be accounted for in projections of future C storage and cycling in tropical forests.

Keywords: carbon sequestration; biodiversity; elevated CO₂; lianas; tropics

1. INTRODUCTION

Among the various facets of global change, the enrichment of the atmosphere with CO₂, now at concentrations slightly above 370 p.p.m., is unquestioned. There are two main mechanisms through which this rapidly progressing change can affect biota.

The first effect, which is indirect, operates through the climate system. This is covered by other contributions in this issue. To the extent that climatic changes would include more disturbances (extreme events, storms) these would tend to enhance biomass turnover and reduce standing C stocks. Gradual influences, such as atmospheric warming seem to be of less significance in the tropics, but changes in rainfall patterns would have major influences.

The second effect of elevated CO₂ concentrations is direct and influences C fixation by plants. As forest-forming tropical trees use the C₃ pathway of photosynthesis, their carboxylation machinery is not CO₂ saturated at current concentrations. Hence, rising concentrations of CO₂ can stimulate photosynthesis per unit of leaf area. Whether this leads to more growth, and if it does, to more net C binding, is an open question and will depend on a suite of factors other than CO₂ concentration, and in particular on differential responses of plant species, which may lead to new community composition and ecosystem functioning. The consequences of enhanced growth rates on C stocks are unclear. Alternatively, if there are recruitment waves with concomitant tree mortality lagging behind, then a transitory build up of C stocks is possible

(see Lewis *et al.* 2004). However, because fast growing, shorter-lived species tend to produce less dense wood (e.g. *Cecropia*, *Ochroma*, many Bombacaceae) than slow growing, longer-lived species, faster turnover could actually reduce the standing C pool (Phillips & Gentry 1994).

Direct influences of elevated atmospheric CO₂ concentrations on tropical plants have been reviewed by Arnone (1996) and Körner (1998). Here, I discuss the potential effects on species diversity and forest dynamics. To start with I will recall two key issues, which concern the most widespread misconceptions in the interpretation of the responses of plants to CO₂ enrichment in the published literature: the link between CO₂ assimilation and growth, and the link between growth and C sequestration. These are of particular importance for the discussion of overall forest responses.

2. A STIMULATION OF ASSIMILATION DOES NOT NECESSARILY MEAN THAT THERE IS MORE GROWTH

Since the discovery 200 years ago that plants take up C from the atmosphere rather than from soil (De Saussure 1804, 1890), there has been a widespread misconception of a direct proportionality between the rate of leaf photosynthesis and growth. This is not the place to review the relevant literature, but it should be sufficient to recall that if there were such straightforward links, agricultural research programmes would not have given up selecting for cultivars with high photosynthetic capacity *ca.* 30 years ago. In the world's most economically important crop, for instance, wheat, there is no such link (Evans & Dunstone 1970; Gifford & Evans 1981; Saugier 1983; Watanabe *et al.* 1994). Rather, whether plants produce a lot or little biomass over a certain period of time depends on how,

One contribution of 17 to a Theme Issue 'Tropical forests and global atmospheric change'.

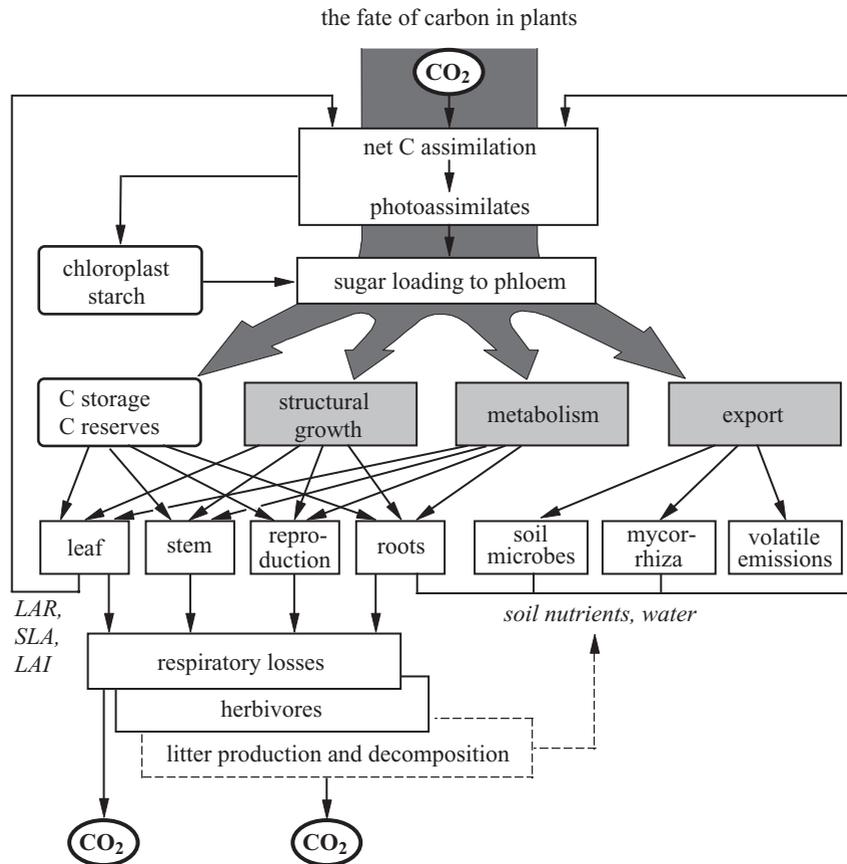


Figure 1. A schematic representation of the fate of C in trees. The diagram illustrates a variety of pathways along which photosynthates may be distributed. The resultant C allocation ultimately determines the rate of biomass accumulation. (Reproduced from Körner (2003c) with permission from *Journal of Ecology*. Copyright © 2003 Blackwell Science.)

for a given rate of assimilation, plants handle assimilates (investment), how dense their tissues are (costs) and how long these function and how growth is timed (developmental controls). Moreover, it is almost trivial to recall that all organisms need to keep a certain balance of elements in their tissue, hence, the investment of one chemical element (e.g. C) always requires the investment of some others, which must be available. If other elements are in short supply, plants may still assimilate more C in response to elevated CO_2 , but this C will tend to dilute other elements and then will channel C away from structural growth (figure 1 illustrates some options). It is obvious that actual plant responses to elevated CO_2 will always reflect the availability of resources other than C. For experimentalists this means that their experimental design to a large extent predefines the resulting responses to CO_2 enrichment. To draw meaningful conclusions on plant responses to elevated CO_2 , these must be studied under the relevant nutrient conditions. These may be a full nutrient solution in horticulture, or a poor, depleted soil in some natural systems. Obviously, such results are not interchangeable (Körner 1995) and must strictly be statistically separated when examining data in the literature. Most available meta-analyses do not stratify data in this way (Körner 2003a) and, thus, results tend to reflect the proportions of growth conditions under which the data were collected.

In essence, this means that one cannot expect proportionality between the increase of CO_2 concentration of

the atmosphere, the degree of photosynthetic stimulation and the rate of growth of plants. In the ideal case, one would observe the growth response *in situ* over the 60–80 years it may take for the current, already 30% increased CO_2 concentration to arrive at a 100% increase compared with pre-industrial conditions—obviously not an option if predictions are to be made right now. Researchers have tried to circumvent this problem by adopting experimental conditions that approximate life in a tropical forest and expose plants to a stepped increase in CO_2 , in the hope of obtaining at least a picture of the likely direction and nature of such responses.

3. A STIMULATION OF GROWTH DOES NOT NECESSARILY MEAN ENHANCED CARBON SEQUESTRATION

An equally difficult issue to communicate to a broad concerned audience is the difference between rates and pools. Analogous to economy, rates of C incorporation (growth rate) do not in a simple way scale to the stock of C (the capital). The total C capital per unit land area is the net result of input (growth) and output (decay) or more precisely (as long as no C is lost through runoff) the difference between net CO_2 fluxes into and out of the system, NEE, as it is measured in C flux studies from towers. The key point here is time. Over certain periods of time the accumulation of biomass by a tree (growth) enhances its C capital, the reason why we have foresters. On a

landscape-wide scale the capital would only change if all trees were growing continuously. In reality, all trees eventually die or get harvested. If birth and death rates are balanced and the demography of trees is such that a steady forest cover is ensured, the overall biomass C pool would be constant, despite the fact that most trees are growing. Natural regeneration waves or forest plantation management can cause growth to be synchronized over large areas so that at landscape scales C pools may cycle in regular patterns. In this case, whether net C uptake or release is recorded depends on when one makes the measurements. As the accumulation of biomass is slow, but collapse and breakdown are often very fast, there is a far greater likelihood of finding forests with net C uptake than forests with a net C release although, at the landscape level, the balance may be zero (Körner 2003b). Given average tree lifespans of 200 years in a natural forest and 30 years in a vigorous plantation, the ratio between areas with a net C fixation to areas with a net C release (death of a tree or groups of trees) could be 200 : 1 in a uniform natural forest and 30 : 1 in a plantation forest. A key aspect is the size of the regenerating patches. The larger they are, the more severe the problem becomes. Very small patches (gaps) may be nested at random positions in a hectare size test plot. However, their dynamics must also be random, not to distort the picture. Such conditions are difficult to ascertain. A random positioning of measurement stations will always reflect the spatial and temporal regeneration and mortality pattern. Whether findings of net biomass increase in forests based on inventory data (Lewis *et al.* 2004; Baker *et al.* 2004) will scale to realistic landscape level responses will always depend on the representativeness of patch dynamics and age structure. Once breakdown waves and wave regeneration occur, the probability of a plot being installed in an area that is accumulating C is many times greater than the probability of a plot being installed in an area in which there is net C release. If C release is not by microbial activity but by fire, there may be only 2 days in a millennium to witness the release, and during most of the rest of the time one would detect accumulation. For gap-mediated dynamics, the larger the plot and the smaller and more random in time the gaps, the more representative the data obtained will be. Given that C release will always remain a very stochastic phenomenon, the integration over time remains a challenge and the 'space for time model' (e.g. using larger measurement towers) still has its limits.

These constraints are critical for ascertaining CO₂ enrichment effects on tropical forests. Answers will remain scale dependent, as trivial as this may sound. The question is, what sort of answers can we expect at which types of scale? I see three domains as follows.

- (i) The plant-based study of growth and development (scale of less than 10 m²).
- (ii) The plot-based study of community dynamics (scale of less than 1 km²).
- (iii) The landscape-based study of C balance (scale of less than 100 km²).

For scaling reasons, (i) and (ii) will never produce direct answers about the landscape C balance, and (iii) will not provide answers on biodiversity effects. After a short

account on the global dimension of missing C, I will focus on experimental data obtained for (i), and I will try to draw conclusions for (ii), which may have implications for (iii). Needless to say, no experimental CO₂ enrichment data (beyond anthropogenic levels) exist for (ii) and (iii).

4. MISSING CARBON AND THE TROPICAL FOREST

At global scales, the C cycle cannot be closed, because human society annually emits more CO₂ than is added to in either the atmospheric or the upper oceanic pools. This 'missing C' of 1–2 Gt C is generally assumed to disappear into the terrestrial biota, including the tropics. If we consider all vegetation-covered land on Earth (*ca.* 100 million km², disregarding deserts and cropland), the annually missing C is 10–20 g m⁻². This is a very small signal to detect, in view of the 10–20 kg of C m⁻² stored in most soils and the similar amount of C tied up in biomass in the case of forests (Körner 2000). If the 'missing C' would exclusively be sequestered to forests and woodlands, which is very unlikely, the relevant land area would be *ca.* 48 million km² (17 million km² in the humid tropics) and the required net flux would be roughly twice as high.

Through their longer growing season, tropical forests (which store *ca.* 40% of the globe's biomass C; Brown & Lugo 1982; Soepadmo 1993) may suck up a relatively greater fraction of this missing C, but per unit of time in the growing period (per week, per month) their productivity is similar to any other humid forest in the world (Körner 1998). Recent estimates of C release from tropical forest destruction suggest lower rates than previously thought (Achard *et al.* 2002), reducing the globally missing C fraction to 1 Gt C or less, of which more than half can perhaps be explained by forest regrowth in parts of the temperate zone (Canadell & Pataki 2002). This would reduce the remaining mean C sequestration per unit of tropical forest area to potentially immeasurable quantities. In the following, I will try to explain why it may be more promising and significant for the understanding of the consequences of CO₂ enrichment for tropical forests to search for plant and community responses to CO₂, than to search for missing atmospheric C. I will illustrate that such biotic responses are likely to overrun classical concepts of ecosystem C binding which are based on photosynthesis responses. My prediction is that 'Rio' will determine what 'Kyoto' had hoped to solve: it will in large part be biodiversity, i.e. species specific or functional type responses to atmospheric change, which will determine the ecosystem C balance. The humid tropical forest is likely to be among the first systems where this will be seen, simply because the 12 month growing season and sufficient moisture should allow significant effects to materialize faster than elsewhere.

5. DIFFERENTIAL RESPONSES BY SPECIES OR PLANT FUNCTIONAL TYPES TO ELEVATED CARBON DIOXIDE CO-DETERMINE CARBON STOCKING

Experimental CO₂ enrichment work conducted in the tropics or with tropical plants until recently had been summarized by Arnone (1996) and Körner (1998). In essence, CO₂ has always been found to stimulate photosynthesis,

led to greater carbohydrate accumulation in plant tissues (Würth *et al.* 1998b) and often also depleted nitrogen concentrations. Growth of tropical plants was found to be stimulated only when they were grown with ample nutrients or in isolation and/or deep shade. Under a fertile but highly competitive re-growth situation, a complex model community of tropical plants showed enhanced C turnover (greater litter production and C release from soil) but little growth stimulation (Körner & Arnone 1992). Microcosms composed of a suite of tropical tree seedlings also revealed no overall growth response, but species-specific responses in height growth, which ultimately would alter community structure (Reekie & Bazzaz 1989). When seedlings of two commonly dominant tropical tree species were grown to a height of almost 2 m in a high light environment in open-top chambers in the tropics, they either showed no growth response to CO₂ when grown in unfertilized substrate (Winter *et al.* 2000), or showed a massive stimulation, when fertilized (Winter & Lovelock 1999; see also Winter *et al.* 2001). A broad screening for CO₂ responsiveness across early and late successional tropical tree species revealed that, under favourable growth conditions, it is the early successional species with high relative growth rate that take advantage and not the late successional species (Winter & Lovelock 1999).

Deep shade has been found to be the situation under which the CO₂ responses of plants are most dramatic. The explanation is very simple. Plants can use low light intensities far better when exposed to a CO₂-enriched atmosphere, and the light compensation point of photosynthesis shifts to lower light intensities. *In situ* tests had revealed relative stimulations of growth of seedlings in Panama (Barro Colorado Island) by up to 50% in only 15 months of growth under *ca.* 0.5% of maximum midday photon flux density (a mean of 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Würth *et al.* 1998a).

Responses among the tested species differed, but did not reveal any relationships to plant functional types such as shrub or tree, or nitrogen-fixing or not. Remarkably, there was no indication of a greater stimulation in the leguminous tree *Tachigali versicolor* (which was visibly nodulated) compared with the lauraceous tree *Beilschmiedia pendula*. It is still very doubtful whether enhanced nutrient availability (assuming this was the case for the legume) can stimulate tree recruitment under such deep shade conditions. A cross-continental test with a common treatment design revealed very little or no effect of nutrient addition to the understorey in a Swiss temperate and montane forest, a laurophyll forest in the Canary Islands and a humid tropical forest in Panama (S. Hättenschwiler, M. S. Jiménez, A. Gonzalez and Ch. Körner, unpublished data). The one exception to this in deep shade was one tropical liana species, which took advantage from nutrient addition (Hättenschwiler 2002). Responses may also depend on the degree and type of mycorrhizal infection, as was shown *in situ* for the already-mentioned *Beilschmiedia* by Lovelock *et al.* (1996).

CO₂-stimulated growth should improve seedling survival in the understorey, but could also cause young lianas to be more likely to escape the forest shade. We now have evidence that this is a plausible scenario. Three species of tropical lianas grown competitively in their natural substrate in a dynamic climate simulator, which mimics

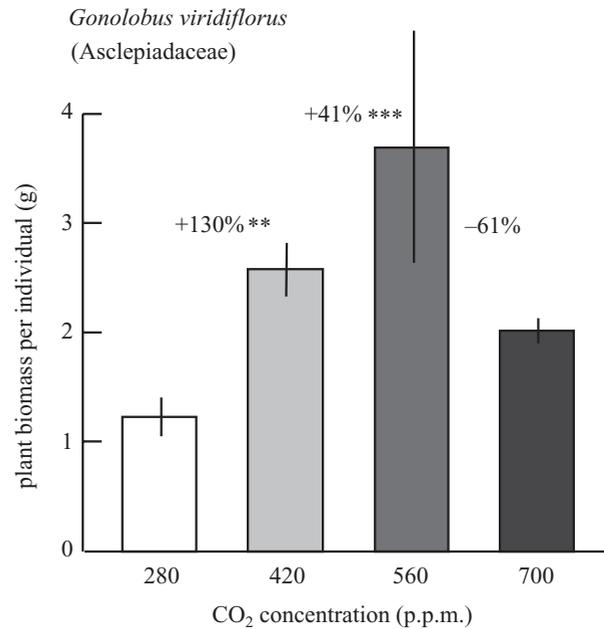


Figure 2. The biomass response of a tropical liana species at seven months growth under three different levels of atmospheric CO₂ concentrations, starting from pre-industrial CO₂ concentration. Note the nonlinear response and the largest relative stimulation in the range of current CO₂ concentrations (from data by Granados & Körner (2002)).

the tropical understorey temperature and humidity, yielded greater CO₂ responses (in relative terms) when exposed to very low light (one example is shown in figure 2).

The growth of these lianas was strongly stimulated (more than 100%), particularly when responses at elevated CO₂ concentrations were compared with growth rates at 280 p.p.m., the pre-industrial CO₂ concentration. The most dramatic effect occurred between 280 and 420 p.p.m., i.e. within the range of concentrations plants are experiencing now and during the past 100 years. At higher CO₂ concentrations the responses were smaller and became even reversed above 560 p.p.m. These data suggest that lianas are likely to take a significant advantage from currently ongoing atmospheric CO₂ enrichment. Have lianas become more successful in recent decades? According to new analyses by Phillips *et al.* (2002) the answer seems yes. Their demographic data suggest enhanced growth and biomass of tropical lianas, and the greater vigour of lianas is a strong candidate for explaining faster tree turnover (Phillips & Gentry 1994; Phillips *et al.* 2004). It is well known that lianas play a key role in tropical forest dynamics (Laurance *et al.* 2001; Schnitzer & Bongers 2002). If lianas as a single functional type would take greater advantage from atmospheric CO₂ enrichment, this biodiversity effect could potentially shift tropical forests from later to earlier successional stages, irrespective of whether trees also become stimulated by elevated CO₂ or not. Early successional forests store much less C than old-growth, late successional forests.

Paradoxically then, growth stimulation can potentially lead to a reduction in forest C storage. This example underlines the significance of differential effects on species or functional plant types under CO₂-enriched atmospheric

conditions. The next experimental step needed would be *in situ* tropical forest CO₂ enrichment, using the technical tools developed and successfully tested for mature temperate forests (Pepin & Körner 2002). As far as the first two seasons' results of these tests in a diverse, 35 m tall forest near Basel show, species do indeed respond differently to elevated CO₂. Hence, the overall ecosystem response will depend on the species present.

6. CARBON DIOXIDE AND FOREST WATER RELATIONS

In this paragraph I am entering almost unexplored terrain. Beyond its potential influence on the climate and its established direct effects on plant photosynthesis, the concentration of CO₂ in the atmosphere has a third effect: elevated CO₂ reduces the width of stomatal pores in many plants. This is commonly explained by an optimization strategy of plants, keeping CO₂ uptake and vapour loss in balance, so that C gain per unit of water lost is maximized (Farquhar & Von Caemmerer 1982). A reduction in leaf transpiration in response to CO₂ enrichment would have far-ranging consequences at landscape level, with more moisture retained in the ground and less used to humidify the atmosphere. Both of these effects create positive feedback. High soil moisture and lower vapour pressure deficit could enhance transpiration and reduce the consequences of the leaf level response (Field *et al.* 1995; Körner 2000). This is a theoretical prediction. The reality for temperate forests so far tells us that there is no uniform behaviour among different tree species in this respect. Some species exhibit the expected response (many, but not all broad-leaved deciduous species), whereas others (in particular evergreen conifers) do not (Ellsworth *et al.* 1995; Medlyn *et al.* 2001).

In situ data for mature tropical forest stomatal responses are available for CO₂-enriched canopy leaves, studied with a canopy crane in Panama (figure 3). Surprisingly, no CO₂ effect on stomata was observed, even though the CO₂-enrichment signal left a strong fingerprint of stable C isotopes in the CO₂-enriched leaves, proving that the gas did affect the leaves. *Fagus sylvatica* (beech), the most important European deciduous forest species, shows the same absence of a stomatal response, but other temperate tree species do save moisture under elevated CO₂ (for instance *Carpinus betulus* (hornbeam), S. Keel, unpublished data). It is almost certain that such interspecific differences will also occur in tropical forests. The consequence is a species-dependent patchiness of soil moisture, which will lead to losers and winners during dry periods of reduced moisture supply. It may well be that such CO₂-induced species-specific changes in water relations will overrun a potential direct CO₂ fertilization effect on trees, as seems to be the case for grassland (Volk *et al.* 2000). We urgently need to address these CO₂-linked water relation questions, using this new technique of CO₂ enrichment for tall forests. The relative abundance of savers and spenders of water in a CO₂-enriched world will feed back onto the climate system, causing the atmosphere either to become drier or remain unaffected. Needless to say this has consequences for the large-scale export of moisture from humid to drier regions through water vapour. Given

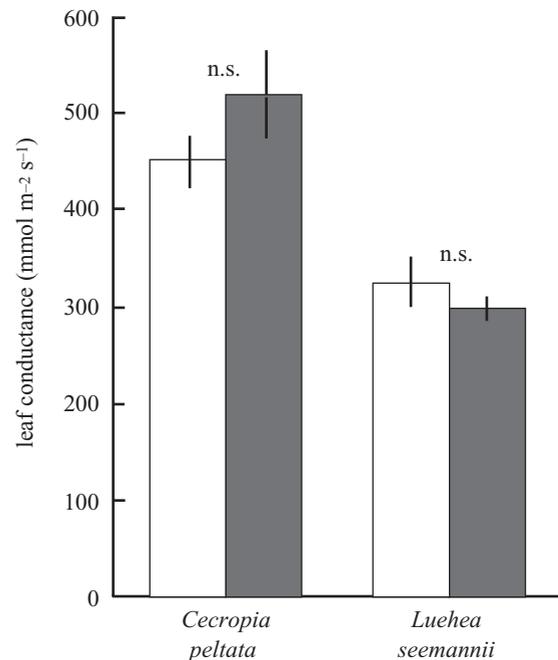


Figure 3. Stomatal responses to *in situ* CO₂ enrichment in the canopy of a tropical forest in Panama. Leaves or branches were continuously exposed to CO₂-enriched air for several days to weeks, and stomatal conductance was measured with a porometer. Open bars, ambient CO₂; filled bars, elevated CO₂. (Data from Körner & Würth (1996) and Lovelock *et al.* (1999).)

that species differ in their moisture response, biodiversity may also play a key role in these macroclimatic processes.

7. CONCLUSIONS

The consequences of atmospheric CO₂ enrichment for forests are commonly modelled from first principles, e.g. photosynthetic responses. This short account attempted to show the importance of differential responses of species or plant functional types to elevated CO₂ in predicting tropical forest responses to atmospheric CO₂ enrichment. I tried to explain why I think that direct C accounting at the plot level can be heavily biased towards higher than true C fixation because of relatively uniform uptake in space and time, but rather stochastic C release patterns. Once differential CO₂ responses of key forest taxa come into play, a greater stimulation of one type of taxa (e.g. lianas) can reduce lifespan in others (e.g. trees). Although there are few data to support such conclusions, currently available experimental findings make them appear plausible. Moreover, a more dynamic tropical forest seems a realistic scenario and would be in line with some long-term inventory data (Phillips *et al.* 2004). Faster tree turnover can reduce the C stock even under conditions of enhanced productivity. Interaction between biodiversity and forest dynamics needs to be considered when making projections about the role of tropical forests in the global C cycle in a CO₂-rich future.

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GLOSSARY

NEE: net ecosystem carbon exchange