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Multi-element regulation of the tropical forest carbon cycle

Alan R Townsend^{1*}, Cory C Cleveland², Benjamin Z Houlton³, Caroline B Alden⁴, and James WC White⁵

Tropical ecosystems dominate the exchange of carbon dioxide between the atmosphere and terrestrial biosphere, yet our understanding of how nutrients control the tropical carbon (C) cycle remains far from complete. In part, this knowledge gap arises from the marked complexity of the tropical forest biome, in which nitrogen, phosphorus, and perhaps several other elements may play roles in determining rates of C gain and loss. As studies from other ecosystems show, failing to account for nutrient–C interactions can lead to substantial errors in predicting how ecosystems will respond to climate and other environmental changes. Thus, although resolving the complex nature of tropical forest nutrient limitation – and then incorporating such knowledge into predictive models – will be difficult, it is a challenge that the global change community must address.

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Tropical forests are among the most important biomes on Earth, supporting perhaps 50% of all species on the planet (Losos and Leigh 2004) and providing a variety of critical resources and ecosystem services to humans, including food, fiber, clean water, sources of new medicines, and mitigation of infectious disease risk (Foley *et al.* 2007; Vittor *et al.* 2009). These forests also exchange more water and energy with the atmosphere than any other biome (Foley *et al.* 2003), account for nearly 70% of terrestrial nitrogen (N) fixation, and are responsible for ~50% of terrestrial nitrous oxide (N₂O) emissions (Panel 1). Tropical ecosystems are threatened by high rates of land-use change and multiple other human perturbations (Lewis *et al.* 2004; Nepstad *et al.*

2008; Figure 1); as a result, there have been increased efforts during the past two decades to understand and predict ecological dynamics in tropical forests at multiple scales, including the ways in which these forests cycle biogeochemical elements.

The tropical carbon (C) cycle has garnered particular interest. Although tropical forests occupy only about 12% of Earth's land surface, they account for nearly 40% of terrestrial net primary production (NPP) and contain about 25% of the world's biomass C (Panel 1). Though difficult to quantify, tropical deforestation and related land-use changes clearly account for a substantial fraction of anthropogenic carbon dioxide (CO₂) emissions each year (Ramankutty *et al.* 2007), and at least over the past two decades, intact tropical forests appear to be acting as a major CO₂ sink (Luyssaert *et al.* 2007; Stephens *et al.* 2007; Phillips *et al.* 2008; Lewis *et al.* 2009). The high rates of CO₂ exchange in tropical ecosystems, combined with their sizable C pools, also indicate that the tropics have a disproportionate ability to affect atmospheric CO₂ levels in response to changing environmental conditions (Clark 2007; Luyssaert *et al.* 2007). Thus, accurate predictions of how tropical ecosystems will respond to future environmental change are critical to effective forecasts of Earth's shifting climate (Clark 2007).

Our ability to predict pan-tropical responses to environmental disturbances, however, is challenged by the complexity of the tropical forest biome. The range in several biogeochemically relevant variables across tropical forests (rainforests to dry forests) is daunting (Figure 2 in Panel 1). Even when restricting the analysis to moist tropical forests, one finds a biome that includes extraordinary heterogeneity in both the biotic and abiotic controls over ecosystem function (Townsend *et al.* 2008) and the potential for multiple limiting nutrients (Vitousek and Sanford 1986). Together, these characteristics create conditions for a suite of possible links between the C cycle and several other biogeochemical cycles – interac-

In a nutshell:

- Tropical forests have an enormous influence on Earth's changing carbon (C) cycle
- Studies from outside the tropics demonstrate that understanding nutrient limitation is key to predicting how the C cycle will respond to environmental change
- Multiple nutrients may limit aspects of the tropical C cycle, yet most models generally consider only single-element limitation
- Nutrient interactions are largely absent from widely used projections of future atmospheric carbon dioxide levels, representing a critical gap in the ability to predict climate change

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Figure 1. Moderate Resolution Imaging Spectroradiometer (MODIS) image (dated September 2007) of widespread fires associated with deforestation across the state of Mato Grosso in the Brazilian Amazon. Worldwide, tropical forests are subjected to an increasing number of anthropogenic changes, including those related to climate, land use, atmospheric composition, and nutrient deposition.

tions that may be central to predicting future trajectories in atmospheric CO₂, but which remain largely absent from any of the current prognostic frameworks (Randerson *et al.* 2009; Thornton *et al.* 2009). Here we examine tropical forests within the context of the broader Earth system, focusing on how nutrient limitation may

control the tropical C cycle. We begin by exploring the nature of nutrient limitation in tropical forests, and then discuss its broader implications and some of the challenges inherent in improving our understanding of tropical biogeochemistry at large scales.

■ Nutrient limitation in tropical forests

Nutrient limitation lies at the heart of ecosystem ecology (Chapin *et al.* 1986; Vitousek 2004), and is by definition a “coupling” of biogeochemical cycles. Originally cast in the perspective of Liebig’s Law of the Minimum – which stated that plant growth would be controlled by the scarcest resource relative to demand – nutrient limitation can refer to any biogeochemical process in which the availability of one or more elements constrains the rate at which another element cycles. Biogeochemical linkages driven by nutrient limitation are a global phenomenon – occurring in all major terres-

trial, freshwater, and marine ecosystems – and are not restricted to the limitation of plant growth (eg Sterner and Elser 2002). As mentioned, nutrient limitation may not always be confined to the relative scarcity of a single element; a biogeochemical process may be co-limited by multiple nutrients and/or may experience shifting degrees of limitation by different elements at multiple timescales (Chapin *et al.* 1986; Vitousek 2004). The widespread existence of nutrient limitation also contributes to predictable patterns in element concentrations in both biotic and abiotic components of ecosystems (Reiners 1986; Sterner and Elser 2002), underscoring the fact that no major biogeochemical cycle operates in isolation. There is perhaps no better demonstration of the importance of nutrient limitation than the existence of a multibillion-dollar fertilizer industry.

The economic importance of fertilizer hints at a key point for projections of future climate change: it is not possible to fully understand the C cycle without considering the ways in which other nutrients constrain its behavior. For instance, abundant data indicate that N is a common limiting factor to NPP in Earth’s major ecosystems (Elser *et al.*

Panel 1. Tropical forests and the global C and N cycles

Tropical forests have a disproportionately large effect on the global cycles of C and N, and yet their effects at large scales also arise from the extraordinary heterogeneity in the factors affecting biogeochemical cycling associated with this biome. Here we use four metrics to exemplify both of these points: (1) net primary production (NPP), (2) plant C storage, (3) biological N fixation, and (4) soil nitrous oxide (N₂O) emissions. As depicted in Figure 2, the percentage of all four metrics relative to global terrestrial totals far exceeds that for land area. The values in the table at the bottom of Figure 2 show how these large fluxes or pools integrate across substantial ranges. Values for land area, NPP, plant C storage, and N₂O emissions are from Carnegie–Ames–Stanford approach (CASA) model simulations or databases (eg Potter *et al.* 1993, 1996), whereas those for N fixation are from the modeling framework described in Wang and Houlton (2009).

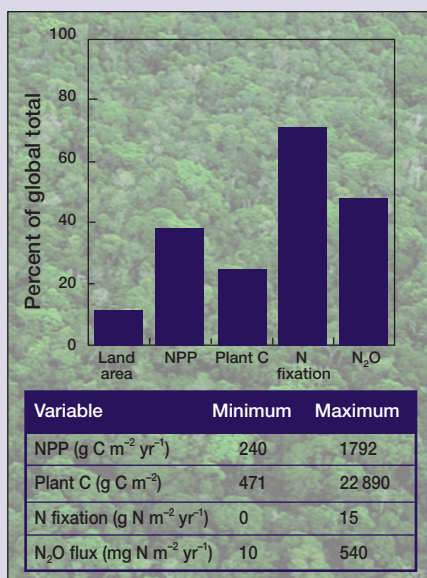


Figure 2.

2007; LeBauer and Treseder 2008), and knowledge of this constraint has proven critical to understanding the potential mechanisms behind observed sinks for anthropogenic CO₂ in various temperate ecosystems (Schimel *et al.* 1997; Luo *et al.* 2004). As for moist tropical forests, resolving the role of nutrient limitation in the C cycle may arguably be even more important, not only because of the magnitude of CO₂ exchange in these forests, but also because the constraints imposed by low temperatures, water limitation, and/or reduced sunlight will often be less severe in the tropics than in temperate latitudes (eg Jolly *et al.* 2005), although recent work highlights the possibility for increased thermal limitation of NPP as temperatures throughout the tropics increase (Doughty and Goulden 2008; Clark *et al.* 2010). Indeed, the apparent paradox of high N fixation in the tropics may be because a tropical climate imposes fewer energetic constraints on the process (Vitousek *et al.* 2002; Houlton *et al.* 2008). In addition, Huston and Wolverton (2009) argue provocatively that, despite higher mean annual temperatures in the tropics, NPP actually peaks in temperate latitudes as a result of greater average nutrient constraints in low-latitude soils.

Unfortunately, identifying nutrient limitation in tropical forests and resolving its importance therein is a complex undertaking. A common generalization about lowland tropical forests is that they are phosphorus (P) limited, and multiple lines of evidence suggest that P constraints are widespread. Ultisols and oxisols are the most common soil orders in the lowland tropics (Sanchez *et al.* 1982), and these highly weathered soils are depleted of the so-called “rock-derived” nutrients, including P (Uehara and Gillman 1981). Low P availability in these soils is further exacerbated by physical and chemical properties that promote strong P sorption (Uehara and Gillman 1981), resulting in forests that are characterized by high rates of foliar P resorption, low litter and foliar P content, and high foliar N:P ratios (Vitousek and Sanford 1986; McGroddy *et al.* 2004; Townsend *et al.* 2007). Although direct tests of nutrient limitation in the tropics remain rare, some research has demonstrated P limitation of both NPP and decomposition (Vitousek 2004; Cleveland and Townsend 2006), while several recent correlative studies suggest the importance of P availability in controlling multiple aspects of the C cycle (Aragao *et al.* 2009; Quesada *et al.* 2009; Chave *et al.* 2010).

Nevertheless, a simple generalization of P limitation is clearly inadequate when applied to the entire tropical forest biome. The heterogeneity of the biome – which includes all but one of the major soil orders and features substantial ranges in temperature and precipitation (Townsend *et al.* 2008) – implies that, when taken together, multiple nutrients may limit C gain and loss. For example, N limitation is common in many montane forests (Tanner *et al.* 1998; Adamek *et al.* 2009), and may also exist in the wettest of lowland forests (Houlton *et al.* 2006; Nardoto *et al.* 2008). Furthermore, some studies

suggest that in highly weathered soils, limitation by calcium (Ca; Cuevas and Medina 1988; Paoli and Curran 2007) or potassium (K; Kaspari *et al.* 2008) may equal or exceed limitation by P. Moreover, variations in oxidation–reduction or “redox” conditions (Silver *et al.* 1999) and in inputs of elements from atmospheric deposition (Chadwick *et al.* 1999) or erosion-driven exposure of weatherable source material (Porder *et al.* 2007) can affect the relative availability of potentially limiting elements to varying degrees, depending on both the nutrient in question and the location within the biome. Viewed broadly, then, tropical forests contain myriad biogeochemical interactions that can affect C exchange and storage (Figure 3). In the following sections, we use Figure 3 as a template to review some of the most important nutrient–C interactions in tropical forests and then discuss their importance in the context of the global C cycle and climate change.

■ Nitrogen versus phosphorus

The factors that most commonly contribute to low P availability in tropical forests include intense weathering without replacement and the high P-sorption capacities of many tropical soils (Uehara and Gillman 1981). But P availability is also influenced by interactions with both the N cycle and soil oxygen (O₂) levels. When N is more readily available than P, both plants and microbes have been shown to allocate N to the production of extracellular phosphatases (enzymes that mineralize organic P), thereby increasing potential release of ester-bound P from organic matter reserves (Treseder and Vitousek 2001). Such an interaction can serve to alleviate P constraints in the short term, but may ultimately promote further N limitation over time. However, enhanced P availability can also stimulate biological N fixation, bringing additional N into the ecosystem (Houlton *et al.* 2008).

Temporal variations in both N and P availability develop at multiple timescales, leading to shifts in which element may be more limiting to NPP (eg Vitousek *et al.* 2010). Over geological timescales, soil formation and weathering processes tend to drive a shift in N versus P availability, such that N limitation is more likely in ecosystems on younger substrates, whereas P becomes scarce in older, more highly weathered soils (Walker and Syers 1976; Vitousek 2004). This transition contributes to the scarcity of P in many lowland forests (see above), as well as the tendency toward N limitation in montane systems (Tanner *et al.* 1998; Adamek *et al.* 2009), where soils are often younger and less intensely weathered. However, this geological transition alone cannot explain all of the observed patterns in N versus P limitation; rather, the ultimate outcome depends on a suite of processes that determine the balance between N and P inputs, losses, and biological demand (Vitousek *et al.* 2010), factors that shift over human as well as geological time scales.

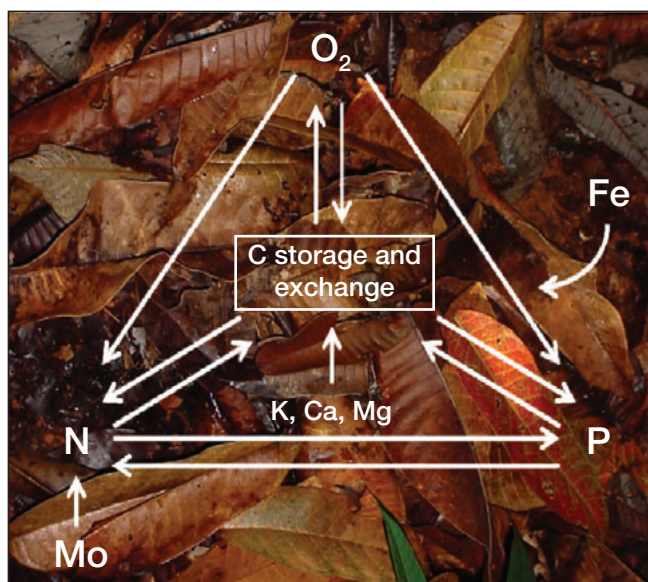


Figure 3. Multiple interactions among biogeochemical cycles can affect the tropical C cycle, including the consequences of varied soil O_2 levels, interactions between the N and P cycles, base cation deficiency, and micronutrient controls over N fixation and P sorption. Details on the key interactions are provided in the primary text.

In the eastern Amazon, Davidson *et al.* (2007) noted that deforestation causes a shift – from P limitation in mature forests, to N limitation in converted pastures and early successional forests, and to increasing P constraints as forests once more mature. This pattern may be explained by greater N losses – relative to those of P – resulting from forest conversion, followed by longer-term restoration of N pools via enhanced N fixation. On shorter time scales, episodic soil anoxic events could simultaneously promote N fixation (O_2 is toxic to the N-fixing enzyme nitrogenase) and drive increases in P availability via anaerobic decomposition (iron [Fe] reduction) that effectively liberates P sorbed by Fe(III) oxides (Chacon *et al.* 2006; Liptzin and Silver 2009). Through yet another set of coupled interactions, low soil O_2 inhibits organic matter decomposition, driving decreases in N and P mineralization and leading to plant–soil feedbacks that can cause more persistent low-fertility conditions (Schuur 2001).

Finally, the rich biodiversity of many tropical systems can, in itself, further complicate attempts to determine what nutrient is limiting to a given ecological process in tropical forests. Leguminous trees, for instance, are common throughout the tropics (Crews 1999); because of their symbioses with N-fixing bacteria, such trees are capable of enhancing N availability within the ecosystem. At the same time, legumes may be subject to greater relative P constraints than are many other tree families (Vitousek *et al.* 2002). Yet the capacity to fix N may allow legumes to invest more N into acquiring P via higher production of phosphatases (Houlton *et al.* 2008), which could in turn enhance P availability in general.

Moreover, biotic controls clearly extend beyond this functional type; variation in foliar N and P demand and resorption across species within a single soil type in the tropics often far exceeds geologically driven shifts across soil types (Townsend *et al.* 2007), suggesting that P versus N limitation may vary by species even at the local scale. Hedin *et al.* (2009) also argued that spatial and temporal differences in N and P availability can contribute to shifting patterns of nutrient limitation within different portions of a single ecosystem.

The net result of all of these interactions is a dynamic balance in which nutrient limitation ultimately is driven not only by relative inputs and losses, but also by evolved differences in demand and nutrient acquisition strategies among organisms, as well as by connections between the N and P cycles themselves. The links between the N and P cycles can cause ecosystems to approach roughly equal constraints by each element (Vitousek *et al.* 2010), an equilibration that may exist in a broader array of terrestrial ecosystems than once thought (Elser *et al.* 2007). However, the tropics – on account of the abundance of P-poor soils, tremendous potential for N fixation, and inherent high levels of biodiversity – appear particularly likely to contain complex and shifting patterns of P and N availability at multiple scales.

■ Nitrogen, phosphorus, or something else?

Nitrogen and P are not the only limiting nutrients that might ultimately affect the C cycle. A comparison of several tropical forests – all found on P-poor soils – illustrates the difficulty in determining what nutrient regulates C cycling in the tropics. First, consider the geologically oldest site in the Hawaii Long Soil Age Gradient (LSAG; Vitousek 2004), a forest growing on a stable, remnant volcanic shield surface on the island of Kauai. Using this and other LSAG sites, researchers clearly demonstrated a transition from N to P limitation as soils weather and age over geologic time (Vitousek 2004), a pattern consistent with theoretical predictions for shifts in nutrient limitation with soil formation (eg Walker and Syers 1976). These results suggest that P limitation may also prevail in other tropical forests growing on old soils.

However, Cuevas and Medina (1988) found that in a Venezuelan forest growing on an oxisol, roots responded as strongly to Ca additions as to P additions. Likewise, in the forests of Borneo's Gunung Mulu National Park, biomass increases appear related to both P and Ca availability (Paoli and Curran 2007). Data from another site – a long-term fertilization experiment on nutrient-poor soils in a lowland forest in Panama – revealed an even more complex set of interactions; there, fertilization had no effect on total litterfall, but N additions stimulated the production of reproductive tissues, whereas K, P, and micronutrient additions enhanced decomposition in various ways (Kaspari *et al.* 2008). In the same Panamanian site, molybdenum (Mo) additions stimulated N fixation

(Barron *et al.* 2009), illustrating yet another way in which multiple element cycles can be coupled in tropical systems and potentially play out in ways that affect the tropical C cycle. Lastly, in a lowland Costa Rican forest growing on an ultisol, N additions stimulated root growth, whereas P additions stimulated heterotrophic CO₂ production (Cleveland and Townsend 2006).

The results from the Costa Rican and Panamanian sites (1) highlight the potential for different elements to limit distinct C-cycle processes, even within the same site, and (2) hint at a larger set of barriers to understanding how nutrient availability regulates the tropical C cycle. Measurements of whole-system NPP are difficult to obtain in many ecosystems, but especially so in tropical forests – for reasons ranging from the high species diversity, to the varied but important presence of lianas, to the frequent unsuitability of traditional ground-based methods (such as the use of dendrometer bands), and to the notorious challenges of documenting root production (Clark *et al.* 2001). Also, the use of eddy covariance techniques to estimate net CO₂ exchange is particularly challenging in tropical forests, resulting from both logistical constraints and difficulties in accurately quantifying night-time airflow (Loescher *et al.* 2006; Campos *et al.* 2009) among other reasons. These challenges, combined with evidence that different nutrients can constrain different aspects of C flow within the same site, underscore the critical need for considering tropical C cycling in a multi-element perspective.

Even when restricting the analysis to Hawaii, the picture is not as simple as that implied by the original LSAG studies. For example, foliar P content increases markedly from the stable soils of the P-limited Kauai LSAG site to soils associated with nearby forests on steeper slopes – a product of higher soil erosion rates uncovering fresh parent material that is not accessible to forests on the stable shield surface (Vitousek *et al.* 2003). Also, studies across the entire LSAG show that, as expected, in situ rock sources of base cations are lost by weathering more rapidly than P is lost, but that high inputs of cations from sea-salt deposition drive the older forests toward P limitation rather than cation limitation (Chadwick *et al.* 1999; Vitousek 2004). In sites such as the previously described Venezuelan forest where replenishment of nutrients from marine sources occurs less frequently, cation limitation may be more likely (Chadwick *et al.* 1999).

This simple comparison among several forested regions is not intended to be comprehensive, but rather to illustrate a broader point: as in any ecosystem, nutrient limitation will depend on a balance between inputs, outputs, and organismal demand. Although in higher-latitude zones the balance historically points toward N limitation, the tropics as a whole contain a suite of elements whose abundances vary in space and time over multiple scales, all of which have the potential to affect at least portions of the C cycle. Neither do we suggest that tropical forests are always more biogeochemically heterogeneous than

are ecosystems at higher latitudes, nor do we argue that only the tropics require consideration of potential limiting nutrients other than N. However, we contend that, when viewed collectively, the tropics contain: (1) abundant evidence for multiple possible limiting elements; (2) exceptional heterogeneity in key controls over nutrient cycling (*sensu* Townsend *et al.* 2008); and (3) an overall lack of data as compared with data from many non-tropical biomes. Many studies in higher-latitude ecosystems have indicated that understanding nutrient limitation can be essential to making accurate predictions of biosphere–atmosphere CO₂ exchange. The tropics present a distinctive set of challenges to such understanding, one that the global-change scientific community has not yet fully met.

■ How does tropical nutrient limitation matter at large scales?

The importance of tropical forests in the global C cycle is undeniable. High rates of deforestation and forest degradation continue to add substantial amounts of CO₂ to the atmosphere (Ramankutty *et al.* 2007). At the same time, multiple studies suggest that intact tropical forests may be acting as a major sink for excess CO₂ (Luyssaert *et al.* 2007; Stephens *et al.* 2007; Phillips *et al.* 2008; Lewis *et al.* 2009), while others highlight the potential for the tropical C cycle to change markedly with even small shifts in climate (Betts *et al.* 2008; Nepstad *et al.* 2008; Phillips *et al.* 2009; Clark *et al.* 2010). The influence of the tropics at the global scale can be seen in estimates of net CO₂ exchange between the biosphere and atmosphere over the past two decades (Figure 4); interannual variation in such an exchange is commonly about 1–2 petagrams (Pg) of C per year, with a range that exceeds 4 Pg – or roughly half of current global fossil-fuel emissions.

These and other factors have led to tropical forests taking center stage in recent climate policy negotiations; for example, the United Nations' Reducing Emissions from Deforestation and Forest Degradation (REDD) program is seen as a path not only to protecting biodiversity, but also to reducing CO₂ emissions from deforestation and perhaps to enhancing C sequestration (Stickler *et al.* 2009). Yet both prediction and management of tropical forest C cycling rely on a solid understanding of the underlying mechanisms, and therein lies a potential problem: direct tests of nutrient–C interactions in the tropics are scarce, and none of the widely used climate or C-cycle models fully encapsulate the coupled biogeochemical interactions that are likely to affect tropical C exchange.

Is this truly a problem? Evidence from the temperate zone suggests it is. In the 1980s and early 1990s, multiple analyses of C–climate feedbacks in terrestrial ecosystems highlighted the potential for warming to drive a net loss of C to the atmosphere, producing a positive feedback to additional warming (eg Woodwell 1990). But subsequent modeling and experimental studies showed that when the

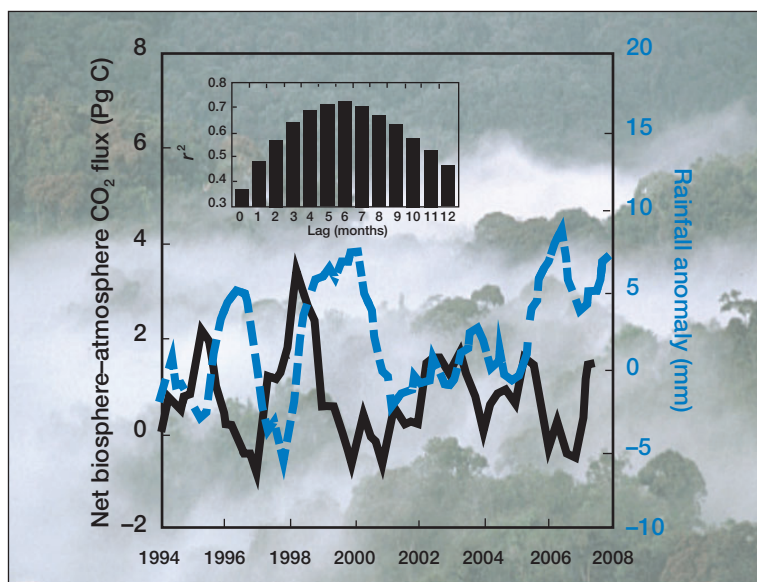


Figure 4. Twelve-month running mean of net biosphere-atmosphere CO₂ flux between 23.5°N and 23.5°S latitudes (black line) and monthly average precipitation anomalies (blue line) for the same latitude bands. Net terrestrial CO₂ flux estimates were (1) calculated as a residual of atmospheric CO₂ observations from National Oceanic and Atmospheric Administration (NOAA) Global Monitoring Division sites, (2) smoothed, and (3) interpolated (eg Masarie and Tans 1995). We compiled fossil-fuel and cement production data using data from the Carbon Dioxide Information Analysis Center, and removed ocean fluxes from atmospheric observations using the Le Quére *et al.* (2007) Ocean Parallelise (OPA) General Circulation Model, coupled to the PISCES-T biogeochemistry model of Buitenhuis *et al.* (2006). Because this budgeting technique is performed from a top-down perspective, terrestrial C exchange from deforestation, reforestation, and other land-use changes is inherently included in the overall net terrestrial value shown. Monthly precipitation anomalies were obtained from the NOAA National Climatic Data Center's Global Historical Climatology Network, and were weighted by net assimilation for each month and 5° grid cell through the Simple Biosphere model (SiB; Suits *et al.* 2005), before being averaged to create a time series for the latitudinal band of interest. Inset: correlations (r^2) between the net CO₂ exchange and precipitation anomalies, after invoking a range of monthly lags from 0–12 months.

N cycle was included in such analyses, very different results occurred (Schimel *et al.* 1997). Similarly, early estimates of CO₂ fertilization did not include considerations of nutrient-based controls; once these were addressed, both forecasted and measured C storage differed markedly from those of initial projections (Luo *et al.* 2004).

At the global scale, Hungate *et al.* (2003) demonstrated that all of the scenarios for future C storage – from the Intergovernmental Panel on Climate Change's Third Assessment Report – likely exceed the available N supply necessary to achieve such storage. Similarly, Wang and Houlton (2009) noted that N fixation in the tropics holds considerable leverage over C storage and climate change, with all of the fully coupled climate–C-cycle models underestimating future warming. Moreover, Finzi *et al.* (2011) outline how the rate and extent of future cli-

mate change may exceed many current predictions because those forecasts do not consider basic nutrient constraints. Finally, research by Thornton *et al.* (2009) – one of the first attempts to bring nutrients into a coupled climate–C-cycle model – also demonstrated that N limitation has a significant effect on climate predictions. More than a decade ago, Schimel *et al.* (1997) put it this way: “Comprehensive analyses of the role of ecosystems in the carbon cycle must consider mechanisms that arise from the interaction of the hydrological, carbon, and nutrient cycles in ecosystems”.

Yet, typically, such interactions are not explicitly considered when projecting the tropical C cycle. A simple analysis of the net tropical CO₂ exchange (Figure 4) highlights the potential information gap, as well as the ways in which coupled biogeochemical cycles may drive the observed patterns in C balance. From decades of study, we know that climate alone is often a remarkably good predictor of ecosystem function, and indeed, a correlation between temperature and the CO₂ exchange reveals a highly significant relationship ($r^2 = 0.49$) – but one that still explains just under half of the variability in tropical biosphere-atmosphere CO₂ exchange over the past two decades. A similar correlation with precipitation yields even less explanatory power ($r^2 = 0.37$). Combining both temperature and precipitation (as actual evapotranspiration or in multiple regressions) does not markedly improve the predictive power of climate.

However, further analysis of the relationship between net tropical CO₂ exchange and rainfall shows the existence of lags in the apparent response of the C cycle to pan-tropical anomalies in precipitation (Figure 4, inset). Specifically, the predictive power of rainfall anomalies more than doubles when one applies a 6-month lag to the correlation. The mechanisms behind

this response are unknown, but multi-month lags are consistent with both theoretical and measured responses in ecosystems in which the underlying mechanism is mediated by nutrient cycles. As Schimel *et al.* (1997) indicated, a climate anomaly can drive a change in nutrient supply, which in turn can drive transient responses in both NPP and respiration. In the tropics, as depicted in Figure 4, positive rainfall anomalies appear to drive a subsequent net release of CO₂ from the biome as a whole, possibly suggesting that redox-driven constraints on nutrient mineralization (eg Schuur 2001) become stronger during high rainfall periods, thereby affecting NPP more than they affect respiration. Nonetheless, some data indicate that periods of high rainfall can strongly stimulate respiration by delivering both C and nutrients in dissolved form to soils (Cleveland and

Townsend 2006). In addition, recent evidence suggests that high rainfall can drive substantial CO₂ production via the anaerobic oxidation of organic matter coupled to Fe reduction (Liptzin and Silver 2009; Dubinsky *et al.* in press).

Regardless of the ultimate mechanisms, relationships between climate and the C cycle are not always direct and simple, but rather can be strongly affected by coupled biogeochemical feedbacks that may occur over multiple time scales (eg Schimel *et al.* 1997; Figure 4). Indeed, lags between rainfall and CO₂ exchange were also demonstrated at the eddy-flux scale in the central Amazon (Saleska *et al.* 2003), perhaps reflecting interactions between C, O₂, and nutrients (Figure 3). Such complex climate interactions may also play out via the process of N fixation; Wang and Houlton (2009) showed the potential for temperature-driven declines in tropical N inputs under various climate-change scenarios, which in turn could alter the C balance of tropical forests in the future.

■ Where do we go from here?

Calling for greater attention to nutrient interactions with the tropical C cycle is one thing, but achieving the necessary understanding and developing appropriate modeling tools are quite another. Many members of the global-change scientific community are well aware of the potential importance of nutrient limitation to large-scale analyses of tropical ecosystems and are taking steps to include nutrients in coupled C–climate models (eg Sokolov *et al.* 2008; Gerber *et al.* 2009; Thornton *et al.* 2009). The tropics simply pose a range of challenges that exceed those of other forested regions, including the scarcity of in situ manipulative experiments, multiple potentially important biogeochemical connections, and the notable complexity in both biotic and abiotic drivers of ecosystem function (*sensu* Townsend *et al.* 2008). As suggested above, we do not even know which nutrient or nutrients limit NPP and C storage in most tropical forests, or to what extent nutrients will affect ecosystem responses to global climate change in this biome collectively.

Filling those knowledge gaps will not come easily. Manipulative experiments in the tropics are notoriously challenging and often expensive to conduct, for reasons that include high biodiversity, physical inaccessibility of sites, and political barriers. Yet, with sustained and prioritized effort, major progress is achievable – as recent syntheses from the joint Brazil–NASA Large-Scale Biosphere–Atmosphere Experiment in Amazonia program (Keller *et al.* 2009) and UK-based RAINFOR and AFRITRON projects (eg Aragao *et al.* 2009; Lewis *et al.* 2009; Phillips *et al.* 2009) illustrate. Promising research tools – which can help to overcome the inherent complexity of the tropics, including new approaches in airborne remote sensing (Asner 2009) and in regional inversions of atmospheric data (Stephens *et al.* 2007) – have also been developed in recent years. These and other

techniques that can effectively integrate the extraordinary complexity of the tropical forest biome over large scales should greatly enhance the ability to monitor and predict the tropical C cycle; their development and application should be a priority for the global-change research community.

In some ways, the situation is akin to where the scientific community stood decades ago with regard to temperate forest analyses. As evidenced during the ensuing years, ignoring nutrient-based controls can lead to markedly inaccurate predictions about ecosystem responses to a changing environment. As a community, we need to take this history lesson to heart, and prioritize both field- and modeling-based approaches that can advance the understanding of coupled biogeochemical cycles in tropical ecosystems. The importance of the tropics in determining global-scale changes of societal relevance is uncontested; rather, the grand challenge is to improve our ability to predict how this biome may change in the decades to come.

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