Biogeochemistry and Ecology of Terrestrial Ecosystems of Amazonia

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The last decade of research associated with the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) has led to substantial advances in our understanding of the biogeochemistry and ecology of Amazonian forests and savannas, in particular in relation to the carbon cycle of Amazonia. In this chapter, we present a synthesis of results and ideas that are presented in more detail in subsequent chapters, drawing together evidence from studies of forest ecology, ecophysiology, trace gas fluxes and atmospheric flux towers, large-scale rainfall manipulation experiments and soil surveys, satellite remote sensing, and quantification of carbon and nutrient stocks and flows. The studies have demonstrated the variability of the functioning and biogeochemistry of Amazonian forests at a range of spatial and temporal scales, and they provide clues as to how Amazonia will respond to ongoing direct pressure and global atmospheric change. We conclude by highlighting key questions for the next decade of research to address.

1. INTRODUCTION

The Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) has resulted in an unprecedented international effort to understand the functioning of the vegetation of Amazonia and its interaction with the atmosphere and hydrosphere. As a result, Amazonia is now almost certainly the best studied major tropical forest region of the world, although our journey to a comprehensive understanding of the functioning of this system is only just beginning. Some of the key questions that LBA asked in relation to the vegetation and soils of Amazonia included the following: (1) How does the structure and functioning of Amazonian forests vary across the region; what factors drive this variation? (2) How much carbon is stored in Amazonian vegetation and soils; is this carbon store increasing or decreasing in response to contemporary environmental change? (3) How does the supply of nitrogen, phosphorus, and other nutrients affect Amazonian forests and the viability and sustainability of management practices after conversion of forest to other land uses? (4) How does Amazonian vegetation respond to seasonal, interannual, and long-term drought? (5) What role does Amazonia play in global climatic teleconnections and in the budgets of the major atmospheric trace gases? (6) How are Amazonian forests changing, and how will they change in response to climate change?

In this introduction, we provide a brief overview of the major themes discussed in this section. We do not introduce the chapters in sequence but rather when appropriate to our narrative.

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2. NUTRIENT SUPPLY AND LIMITATIONS

The supply of nutrients affects forest composition and function, and also the viability of agriculture or cattle production on converted forest lands, and the rate of recuperation of forests on degraded lands. *Davidson and Martinelli* [this volume], *Luizão et al.* [this volume], *Malhi et al.* [this volume], and *Lloyd et al.* [this volume] review a range of LBA research on nutrient limitation in Amazonia. It has been suggested that the main limiting nutrient in many lowland tropical forests growing on highly weathered soils may be phosphorus rather than nitrogen. LBA research over recent years has both confirmed and refined this picture. On the regional scale, the growth rate and net primary productivity of trees in old-growth forests does seem most strongly correlated with leaf phosphorus concentration, which in turn is strongly correlated to soil phosphorus status [*Malhi et al.*, this volume; *Lloyd et al.*, this volume]. Old-growth Amazonian forests appear to have plentiful nitrogen supply, which leads to a leaky nitrogen cycle and significant emissions of gaseous N_2O from the soil [*Bustamante et al.*, this volume]. However, nitrogen limitation does appear on sandy soils, in montane regions, and perhaps also in the dry season in seasonally dry forests, when dry leaf litter and soil surface brings decomposition and mineralization to a halt [*Lloyd et al.*, this volume]. Perhaps most importantly, secondary forests appear to be nitrogen-limited because of losses of actively cycling N during the agricultural phase [*Luizão et al.*, this volume], which takes several decades of secondary forest succession to replenish [*Davidson and Martinelli*, this volume]. Agricultural systems can therefore be limited in both phosphorus and nitrogen as well as other nutrients [*Luizão et al.*, this volume]. Hence, the broad picture of phosphorus limitation in lowland Amazonian forests has been confirmed, but research has also revealed an ephemeral but important role for nitrogen limitation in the dynamics of forest and nonforest landscapes. Nutrient management is a key aspect of research on sustainable agriculture and forest management in the Amazon Basin [*Luizão et al.*, this volume].

3. TRACE GAS EXCHANGES

Amazonia plays a major global role not only in the cycling of water, energy, and carbon, but also in important trace gases such as nitric oxide (NO), nitrous oxide (N_2O), and methane, which play important roles in atmospheric chemistry and can be major greenhouse gases. *Bustamante et al.* [this volume] review recent research findings on trace gas sources and sinks in Amazonia and the cerrado. The availability of nitrogen and the supply of water are major determinants of natural emissions of NO and N_2O. Land use change can cause a temporary increase in N_2O and NO emissions, but cattle pastures older than a few years have lower emissions than native forests, due, in part, to declines in nitrogen availability [*Luizão et al.*, this volume]. Rates of uptake of atmospheric methane also decline as pastures age and as soils become compacted. Large uncertainties in regional estimates remain regarding regional balances and the effects of land use change, and further change may occur as cattle pastures are replaced by fertilized row crop agriculture.

4. BIOGEOGRAPHY OF AMAZONIAN FORESTS AND SAVANNAS

One of the achievements of the LBA era has been a significant improvement in understanding of the regional variation in vegetation structure and dynamics, and tree community composition across the Amazon region, and how these variations are related to soil and climatic conditions [*Malhi et al.*, this volume; *Philllips et al.*, this volume; *Lloyd et al.*, this volume]. In particular, the Rede Amazonica de Inventarios Florestais (RAINFOR) long-term forest plots have described and explored a broad east-west gradient in forest function, and have shown how many traits in forest function can covary in response to shifts in environmental conditions. Lowland forests in western Amazonia tend to have higher wood productivity than those in eastern Amazonia, and thereby higher tree recruitment and mortality rates, shorter-lived trees, lower mean wood density, and thinner, more nutrient-rich leaves. Most surprisingly, perhaps, the higher productivity in western Amazonia is associated with slightly lower biomass, as forest turnover times are higher, and wood densities are slightly lower. It appears that soil fertility, and in particular phosphorus, drives this east-west gradient: soils in western Amazonia tend to be of Pleistocene or Holocene age, deposited on the floodplains of meandering rivers carrying recently eroded material off the Andes. Soils in the center and east tend to be ancient, heavily weathered, infertile Ferralsols.

The second key environmental gradient in Amazonia is the broad rainfall gradient from the high rainfall climate of the northwest to the strong seasonality of the southeast. Another LBA focus has been on the impact of this rainfall seasonality on vegetation community and on the seasonality of vegetation function. The most important transition along this gradient is from forest to savanna, and this forest-savanna boundary is broadly related to interannual frequency of intense drought. However, soil fertility also appears to have an influence, with fertile sites favoring seasonal tropical forest and infertile sites favoring savannas [*Lloyd et al.*, this volume].

5. METABOLISM AND ITS SEASONAL VARIATION

A number of aspects of LBA research have focused on gaining detailed understanding at a few focal sites. Here a broad spectrum of measurements, some of them applied for the first time in a tropical context, have painted a detailed picture of the physiology, metabolism, and cycling of carbon, nutrients, and water in these tropical forest stands. A particular feature has been the establishment of eddy covariance flux towers at a number of sites across Brazilian Amazonia (results from these are reviewed by *Saleska et al.* [this volume]; see also *Houghton et al.* [this volume] and *Lloyd et al.* [this volume]). These flux tower studies have provided new insights into the seasonality of carbon dynamics. Sites in the central Amazon appear to have little decline in forest photosynthesis in the dry season or even some enhancement of photosynthesis under cloud-free dry season conditions. Many of these forests tend to have sufficient dry season water supply in most years because of the high water holding capacity of the well-drained but clay-rich soils, which can be accessed through deep root systems [*Meir et al.*, this volume; *Lloyd et al.*, this volume]. Forests in southern Amazonia, however, appear to have greater decline to dry season photosynthesis. This pattern of seasonal variation has been broadly corroborated by observations of the Enhanced Vegetation Index derived from satellite imagery acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on the Terra and Aqua satellites [*Saleska et al.*, this volume].

Eddy covariance measurements have enabled quantification of bulk ecosystem photosynthesis and respiration, and their sensitivity to seasonal and interannual environmental variation. At the same time, numerous studies of the various component processes of production and respiration have painted a detailed picture of the stand-level cycle of carbon production, allocation, respiration, and decomposition [*Malhi et al.*, this volume]. When compared, the "top-down" flux tower or soil gas-exchange estimates and "bottom-up" component measurements tend to be surprisingly consistent. These studies highlight that wood production, the main subject of carbon-focused studies, accounts for only a small fraction (about 10%) of the ecosystem, carbon cycle. More generally, the carbon-use efficiency, the fraction of gross photosynthesis that ends up producing new organic tissue, is as low as 30% in old-growth forests on infertile soils in eastern Amazonia, but may rise to about 50% after disturbance, and also may rise with increasing soil fertility (phosphorus concentration). Both belowground and aboveground productivity appear to rise as soil fertility increases, with little shift in relative allocation, but disturbance appears to cause a disproportionate allocation aboveground. The emerging picture is that shifts in carbon allocation may be as important as shifts in photosynthesis and bulk respiration in determining the wood productivity, biomass, and structure of tropical forests, but our understanding of the determinants of allocation is much more limited. Another interesting feature is that the highest forest net primary productivity measured, to date, in Amazonia has been for forest growing on the highly fertile terra preta soils, created by pre-Columbian indigenous communities [*Malhi et al.*, this volume; *Luizão et al.*, this volume].

6. RESPONSE TO DROUGHT

Perhaps one of the most remarkable components of LBA was the implantation of large-scale rainfall manipulation experiments: two droughting experiments in mature forests at Tapajós and Caxiuanã, and a dry season watering experiment at a secondary forest at Castanhal. *Meir et al.* [this volume] synthesize the outcomes of these experiments and their implications for our understanding of the drought response of the Amazon forest. The two drought experiments showed that in the first few years, the forest ecophysiology showed surprising resilience to drought, partially through access to adequate water within the top few meters of the soil surface, through some access to deeper soil water stores through deep roots and through the closure of leaf stomata to limit water loss. Soil respiration shows either no change or a slight decline with imposition of drought, and overall, short-to-medium-term drought did not seem to cause a substantial carbon efflux from the forest to the atmosphere. This resilience seems to have a limit, though, and after a few years of drought, there was a pulse of mortality at both sites. However, the immediate physiological mechanism of this mortality is not known. The most likely explanations are that ongoing depletion of soil water reserves leads to hydraulic failure within plant vessels, or that the trees experience "carbon starvation," as respiration costs outpace photosynthetic intake, or other factors such as pathogens. The imposition of drought also greatly increased the flammability of the near-ground region, and it is likely that the spread of fire would have a greater role than ecophysiological drought resilience in determining the response of Amazonian forests to drought.

7. CARBON STORES

Tropical forests are one of world's largest reservoirs of carbon, but the exact magnitude of this store remains a focus of research. The question of carbon storage has moved from being one of purely academic interest to one of policy relevance, as global attention focuses on the impacts of carbon emissions from deforestation on global climate change and potential mechanisms to pay for this carbon to remain in living, healthy forests. Uncertainty in forest biomass is the largest uncertainty term in estimating emissions from deforestation [*Houghton et al.*, this volume]. Major sources of uncertainty include lack of sufficient data (from forest harvests) on the allometric relationship between tree biomass and tree dimensions, differences in methodology that make cross-site comparison of biomass estimates difficult, and the sheer challenge of extrapolating from even a few hundred sample sites to a region as vast as Amazonia. Over the past decade, significant progress has been made on all fronts (as described by *Malhi et al.* [this volume]). Allometric relationships have been developed and tested in central and eastern Amazonia based on rigorous and careful harvesting of over 300 trees. Use of the Amazon-wide RAINFOR network has allowed for a consistent methodology to be applied to examine regional variations in biomass. Application of remote sensing and climatic data layers has allowed for more information-rich spatial extrapolation. These recent efforts suggest that about 120 Pg C is stored in live biomass in Amazonia. There are further steps to be taken, such as development of allometries for other forest types or regions of Amazonia, the expansion and merging of the forest inventory and remote sensing approaches, and the incorporation of new remote sensing products such as latest-generation radar and lidar.

Amazonian forests also contain substantial stores of carbon in and on the soil. *Trumbore and de Camargo* [this volume] review what is known about these stores and their stability or otherwise (with further insights given by *Malhi et al.* [this volume] and *Lloyd et al.* [this volume]). Carbon in the dead wood and litter layer can be a substantial and fairly labile store of carbon, as much as the labile stores in the soil. The deeper soil (below 10 cm) holds large, fairly stable reserves of carbon in forms that have mean ages of many centuries, and in deep soils, this soil carbon store can be greater than the live biomass carbon store. These stores are, however, unlikely to show a major response to climate change on a century timescale. In understanding the response of tropical forest soils to climate or land use change, it is essential to take the very different residence times of different soil carbon pools into account; failure to do so can lead to substantial overestimation of the sensitivity of soil carbon reserves.

8. THE CARBON BALANCE OF AMAZONIA

Quantifying the carbon balance of Amazonia has been an aspiration of LBA because it enables understanding of the possible carbon sequestration service provided by forests and the carbon emission damage being done by deforestation and degradation. It also opens a door into more mechanistic understanding of how Amazonia will respond to twenty-first century climate change. *Houghton et al.* [this volume] review the evidence informing our understanding of the contemporary carbon balance of Amazonia. A few key features stand out. First, deforestation is clearly a substantial source of CO_2 to the atmosphere. Second, long-term observations of intact old-growth Amazonian forests suggest that they are increasing in biomass and absorbing carbon (the latter result still generates some controversy, which is discussed by *Phillips et al.* [this volume] and *Trumbore and de Camargo* [this volume]). An acceleration of biomass production, perhaps stimulated by increasing atmospheric CO_2 or increased diffuse radiation, could lead to a modest soil carbon sink, but the heavily weathered forest soils of eastern Amazonia are unlikely to be significant sinks of C [*Trumbore and de Camargo*, this volume].

The deforestation carbon emission and intact forest carbon absorption are of similar magnitude and may approximately cancel each other out, resulting in a net carbon balance close to zero [*Houghton et al.*, this volume]. Atmospheric approaches, ranging from global analyses of carbon dioxide concentration to short-time scale local aircraft studies through to eddy covariance flux towers, they each have their methodological issues and have thus far failed to conclusively quantify the net carbon balance of the region [*Houghton et al.*, this volume]. A clear next step forward would be a long-term, multisite atmospheric sampling campaign using tall towers and/or aircraft combined with surface observations of biomass change and forest carbon cycling, and detailed remote sensing estimations of monthly carbon emissions from fires. Such a plan is underway through the LBA programs Balanço Regional de Carbono na Amazonia (BARCA) and Amazon Integrated Carbon Analysis (AMAZONICA), and may finally provide a conclusive answer to the carbon balance question.

9. CHANGES IN INTACT VEGETATION OVER TIME

If old-growth Amazonian forests are increasing in biomass, this begs the question why they are doing so, and what implications this has for the ecology and functioning of these forests. *Phillips et al.* [this volume] discuss these issues. A particularly remarkable feature is that forests appear to have accelerated in both tree growth and death rates, resulting in a reduction in overall turnover times. This in turn is likely to affect forest composition and ecology, favoring faster-growing disturbance species over slow growing species. The authors argue that the overall pattern and broad extent of the change suggests that a global atmospheric driver (probably either CO_2 or changing light quality) may be the most likely cause. Whatever the cause, *Phillips et al.* [this volume] underline that even the most remote Amazonian forests are changing and will continue to change as greenhouse gas concentrations and temperatures continue to rise. Understanding the nature, causes, and consequences of this change is one of the great challenges facing Amazon forest ecologists this century.

10. CONCLUSION

In summary, a decade of LBA-associated research has led to substantial advances in understanding of the ecology and biogeochemistry of Amazonian forests, savannas, and converted landscapes. Only now are researchers in a position to step back and synthesize these findings, and this book represents a major milestone in that process. This process will continue, as will new research spawned by these findings and new research programs implemented by the cadre of scientists that have been trained through LBA. Inevitably, this research throws up as many questions as it answers. Here are a few: If phosphorus does limit forest productivity, what physiological process is it limiting? How will response to twenty-first century environmental change vary across species, and what implications does this have for forest composition and ecology? How would a potential twenty-first century temperature rise in excess of 4°C affect the forests and their fauna? What is the potential for agricultural intensification on better managed soils, perhaps borrowing lessons from the terra preta soils? How will the combination of changing climate and changing land use and interactions of these two trends affect fire susceptibility of forests and future forest-savanna transitions? How will climate change and land use change affect the quantity and quality of water draining from Amazonian lands? What is the carbon balance of Amazonia, and how does it change in drought years? Will newer approaches enable us to map forest biomass from satellites? All of these questions need answers, and some need urgent answers. The challenge is set for this coming decade of scientific research to deliver.

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