Research Priorities for Tropical Ecosystems Under Climate Change

Workshop Report

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Co-Chairs

Jeffrey Chambers, Ph.D.
Lawrence Berkeley National Laboratory

Rosie Fisher, Ph.D.
National Center for Atmospheric Research

Jefferson Hall, Ph.D.
Smithsonian Tropical Research Institute

Richard J. Norby, Ph.D.
Oak Ridge National Laboratory

Steven C. Wofsy, Ph.D.
Harvard University

Organizers
Climate and Environmental Sciences Division

Daniel Stover, Ph.D.
Daniel.Stover@science.doe.gov
301-903-0289

Dorothy Koch, Ph.D.

Mike Kuperberg, Ph.D.

Patrick Horan, M.Sc.

This report is available at science.energy.gov/ber/news-and-resources/ and tes.science.energy.gov.

Mission

The Office of Biological and Environmental Research (BER) advances world-class fundamental research programs and scientific user facilities to support the Department of Energy's energy, environment, and basic research missions. Addressing diverse and critical global challenges, the BER program seeks to understand how genomic information is translated to functional capabilities, enabling more confident redesign of microbes and plants for sustainable biofuel production, improved carbon storage, or contaminant bioremediation. BER research advances understanding of the roles of Earth's biogeochemical systems (the atmosphere, land, oceans, sea ice, and subsurface) in determining climate so that it can be predicted decades or centuries into the future, information needed to plan for future energy and resource needs. Solutions to these challenges are driven by a foundation of scientific knowledge and inquiry in atmospheric chemistry and physics, ecology, biology, and biogeochemistry.

Images. Front cover: NASA tropical forest map by Robert Simmon, using Moderate Resolution Imaging Spectroradiometer land cover classification data. Second and fourth images on top row courtesy of Yadvinder Malhi, University of Oxford, and Jeffrey Chambers, Lawrence Berkeley National Laboratory, respectively. Other images from iStockphoto.com. Back cover: First and fourth images courtesy of Sassan Saatchi, NASA Jet Propulsion Laboratory, California Institute of Technology, and Biqing Liang, Cornell University and Academia Sinica, respectively. Other images from iStockphoto.com. Appendices image courtesy of Tana E. Wood, USDA Forest Service.

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Preface and Acknowledgements

The goal of the Research Priorities for Tropical Ecosystems Under Climate Change Workshop was to engage the scientific community in an open discussion to identify critical scientific gaps that limit the ability to represent tropical ecosystems in Earth system models (ESMs) and that demand immediate field investigations. The results of this workshop will inform the Department of Energy's Office of Biological and Environmental Research (BER) as it plans and prepares for a tropical Next-Generation Ecosystem Experiment (NGEE). The NGEE approach uses model-informed and -inspired field studies resulting in iterative refinement of high-resolution, predictive ESMs. The overall goal of BER's decade-long investment will be to investigate tropical ecosystems and their vulnerabilities to climate change and to improve the representation of these systems in ESMs. Specifically, the workshop (1) summarized past and current tropical terrestrial field and modeling research related to tropical climate change; (2) identified critical sensitivities and uncertainties in the systems; and (3) discussed the state of the science in tropical land modeling, processes poorly captured in models, and potential experiments that would test and improve tropical land model fidelity. These issues were discussed with an emphasis on three major tropical ecosystem locations that may be candidate regions for NGEE Tropics field studies: the Amazon Basin, Congo Basin, and Southeast Asia.

BER would like to thank all participants who energetically took part in workshop discussions and generously contributed their time and ideas during the two-day meeting. The workshop would not have been possible without the scientific vision and leadership of the workshop co-chairs. We are thankful for the dedicated efforts of the following members of the workshop writing team who did an exceptional job of stimulating a productive discussion and capturing new ideas and concepts that emerged: Scott Brooks, Molly Cavaleri, Jeffrey Chambers, Nick Chappell, Robin Chazdon, Mary Firestone, Rosie Fisher, Jefferson Hall, Terry Hazen, Alex Johs, Michael Keller, Charlie Koven, Liyuan Liang, Scot Martin, Melanie Mayes, Patrick Meir, Richard J. Norby, Sasha Reed, Peter Thornton, Sue Trumbore, Maria Uriarte, Steven C. Wofsy, Tana Wood, Joe Wright, and Xiaojuan Yang.

Additional contributions from Patrick Baker, Lucas Cernusak, William Hoffmann, Ariel Lugo, Yadvinder Malhi, Alistair Rogers, and Whendee Silver are greatly appreciated. We also are thankful for the excellent work of the staff from Oak Ridge National Laboratory's Biological and Environmental Research Information System who served as rapporteurs, edited, and prepared this report for publication.

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Executive Summary

Understanding Connections Between Tropical Forests and Climate

The Tropics, with approximately 40% of Earth's land surface area, critically regulate many Earth system processes. Containing great stores of biomass, tropical ecosystems represent the largest reservoir of terrestrial carbon. The Tropics also cycle more carbon dioxide (CO_2) and water than any other biome and play important roles in determining Earth's energy balance, which drives global systems of temperature and precipitation. Overall, wet tropical forests contain about 25% of the carbon in the terrestrial biosphere and account for 34% of Earth's gross primary production. This vast area, which includes the world's driest deserts and wettest forests, also harbors a large fraction of Earth's biodiversity. Despite the negative impact of widespread deforestation, tropical ecosystems continue to benefit Earth's atmosphere and climate system by mitigating climatic warming through carbon sequestration and evaporative cooling. Of great concern, however, is the vulnerability of tropical ecosystems to rapid shifts resulting from a changing climate. Significant potential thus exists for important feedbacks with CO_2, water, and energy exchange from tropical ecosystems due to climatic change.

Tropical forests are thought to be especially vulnerable to climate change compared to other regions of Earth. Unlike in temperate forests where temperatures fluctuate widely during the course of a year, temperatures in tropical forests (at a given elevation) vary little, with trees adapted to thrive in a relatively narrow thermal range. Hence, the relative impact of climatic warming likely will be greater in the Tropics because predicted changes in temperature are large compared to normal interannual variation. Moreover, increasing atmospheric temperatures may push tropical forests into climate regimes beyond those ever experienced by existing forests. Also, high-biomass tropical forests require sufficient moisture to maintain a closed canopy, and changing precipitation patterns such as a shift toward more extreme events and extended droughts potentially could push forests beyond a moisture threshold, causing widespread tree mortality. Catastrophic loss of tropical forests may be a key feedback in tropical ecosystems because widespread tree mortality would release large quantities of CO_2 back to the atmosphere, accelerating the influence of this primary driver of global warming. Major disruptions in hydrologic cycles affecting large tropical regions also would be expected.

Improving Climate Model Representation of Tropical Systems

The ability to reliably predict interactions between the Tropics and climate is imperative, given the large potential impacts of a changing climate on the structure and function of tropical forests and on the direct and indirect feedbacks they provide to the climate system. Although understanding of tropical systems is improving, their representation in climate models lags significantly behind that of temperate systems. Tropical ecosystems are responsible for numerous biases in Earth system models (ESMs), which currently disagree on the direction or degree of climate–carbon cycle feedbacks in tropical forests. Improving ESMs will require a coordinated effort by scientists from many disciplines. This urgently needed effort involves integrating new data, experimental results, and process knowledge into a fully coupled global climate model. This robust, fully coupled community model must incorporate diverse sources of information that describe the physical, chemical, and biological processes by which tropical terrestrial ecosystems affect and are affected by climate.

The U.S. Department of Energy (DOE) is strategically committed to improving the representation of terrestrial ecosystem processes in ESMs—and thereby enhancing the robustness of their climate projections—by coupling models with experimental and observational studies across relevant spatial and temporal scales. These improved predictive capabilites can then be used, for example, to better inform U.S. energy policy and climate adaptation strategies. The scientific community has determined that tropical forests are a key biome for comprehensive study, given their global and regional significance, expected sensitivity to a changing climate with large potential feedbacks to the Earth system, and inadequate representation in modeling efforts (IPCC 2007; Christensen et al. 2007; Hanson et al. 2008). Model-informed field studies in the most climate-sensitive tropical geographies can result in iterative refinement of high-resolution predictive models. These improvements can be achieved by identifying key processes from the bedrock to the top of the canopy, improving their representation in models, and exploring the vulnerabilities of tropical ecosystems to a changing climate.

Identifying Uncertainties and Gaps in Tropical Ecosystem Research

This report documents the results of the Research Priorities for Tropical Ecosystems Under Climate Change Workshop held June 4–5, 2012, in Bethesda, Maryland. The workshop's overall goal was to identify critical scientific gaps that limit the ability to represent tropical forests in ESMs and that demand immediate field investigations. Nearly 40 researchers representing a large range of tropical forest expertise participated in the meeting. During the workshop, these experts addressed key unanswered questions that are critical for determining how tropical ecosystems interact with and feed back to the climate system. The workshop featured a series of plenary talks, four breakout sessions with three parallel groups focused on broad research areas, and activities to integrate discussions among groups. Breakout sessions focused on soil biogeochemistry and hydrology, natural and anthropogenic disturbance, tropical forest ecophysiology, and cross-cutting issues. During the breakouts, participants were charged with summarizing and discussing current knowledge and understanding of these topics, the largest associated uncertainties, and general strategies for resolving those uncertainties. Underlying all topics was the recognition that they must be considered within the context of high-level constraints, such as energy and mass balance and regional-scale measurements of terrestrial-atmosphere fluxes, so that experimental results can be leveraged for modeling and simulation. Workshop participants identified a number of critical uncertainties. Considerable overlap was recognized among these broad themes, and several additional questions were discussed during the breakout sessions. The broad themes identified include:

- **Soil Biogeochemistry and Hydrology.** How are tropical soils characterized, including soil structure, soil carbon pools, and biogeochemical cycling? How will forests on different soils, saprolite, and rock respond to the same climate change drivers? How do differences in hydrology and soil, saprolite, and rock (i.e., geochemical and geomorphological) properties influence tree susceptibility to drought-induced mortality? How will, for example, local and regional soil nutrient availability respond to rising atmospheric temperature and changing precipitation combined with unique local characteristics of soil geochemistry, microbiology, ecology, and geomorphology?

- **Natural and Anthropogenic Disturbance.** How do changes in land use affect mass and energy fluxes to the atmosphere? How does fire interact with other environmental factors to affect closed-canopy forests and transitions to other states? What are other major natural disturbances, and how will they vary with climate change?

- **Tropical Forest Ecophysiology.** What are the direct effects of elevated atmospheric CO_2 on leaf physiology and plant and ecosystem carbon cycling and metabolism? How do tropical trees and forests respond to drought, what are the thresholds for drought-induced tree mortality, and will these responses and thresholds change as atmospheric CO_2 rises? How will trees and forest ecosystems respond to rising atmospheric temperature with a changing climate?

- **Cross-Cutting Issues.** What aspects of tropical ecosystem diversity and demography are most important for constraining ESMs? What are the physiological and climatic factors that control forest-atmosphere interactions, processes, convection, and emissions (e.g., biogenic volatile organic compounds and carbon)? What kinds of remote-sensing datasets and products, at relevant scales (landscape, regional, and continental), could inform uncertainties related to carbon energy fluxes and climate change in the Tropics?

Based on these workshop discussions, this report is broadly organized into three sections including background information (introduction and regional differences across the Tropics); responses to external forcings (elevated atmospheric CO_2, elevated temperature, drought, natural disturbances, and anthropogenic disturbance); and integrating processes (biosphere-atmosphere interactions, nutrient limitations, roots and soil biogeochemistry, and hydrology). Summary key points from these chapters include:

- **How will tropical ecosystems respond to increasing temperatures?** In the Intergovernmental Panel on Climate Change's (IPCC) Fourth Assessment Report A1B scenario, temperatures are predicted to increase by 2 to 5°C over the tropical region by 2100, representing a substantial warming (IPCC 2007; Christensen et al. 2007). The change in temperature relative to weather patterns in the 1900s is particularly important because tropical species have adapted to a very narrow thermal range. Because the current climate is at the upper end of this range, projected temperature increases during this century will increasingly expose tropical forest systems to conditions that are beyond their natural operating regime. Thus, there are no analogue environments with which to compare tropical climates in a warmer world. To improve ESM predictions of tropical ecological response to increasing temperatures, more research is required to understand temperature thresholds and sensitivities of photosynthesis and respiration, temperature-induced changes in plant carbon allocation, impacts on soil biogeochemical processes, and interactions between functional diversity and temperature. More insight is needed on how long-term responses to increased temperature relate to those observed in the short term and on the importance of temporal variation in these responses.

- **How will tropical ecosystems respond to changes in rainfall?** Atmospheric processes are among the best-developed aspects of current models. Projections from these models indicate reduced precipitation patterns and regimes across large tropical regions (such as the southern and eastern Amazon) and increased rainfall seasonality, raising concerns over the vulnerability of tropical forests to drought-induced changes in ecosystem structure and functioning. These projections also show increased rainfall over other regions such as tropical Africa. To improve the representation of tropical forests in these models, a better understanding is needed of the response of these systems to changes in water supply and, most importantly, the spatial and temporal drivers and feedbacks of drought stress and tree mortality. Similar improvements are needed for representations of soil depth, structure, and hydraulic properties; root systems; and stomatal regulation.

- **How will natural disturbance events and tree mortality increase as a result of climate forcings?** Relatively small directional shifts in tree mortality rates can significantly affect the global carbon cycle and net forest-atmosphere CO_2 exchanges. The potential for increased tree mortality from drought, fire, temperature, and windthrow is a primary concern. A major gap in the ability of models to predict disturbance regimes is the insufficient understanding of the dominant mechanisms and risks of vegetation mortality, the relationship between atmospheric convection patterns and extreme events, and functional compositional shifts related to disturbance events.

- **How will tropical ecosystems respond to increasing atmospheric CO_2 concentrations?** Although the increase in atmospheric CO_2 is unambiguous and short-term physiological responses are universal, the integrated response of forest ecosystems and the feedbacks to the atmosphere are harder to predict. Research is needed to understand the response of tropical forests to elevated CO_2, including the study of critical interactions among CO_2, water, and nutrient cycles. ESMs cannot predict the response of tropical forests to elevated CO_2 without new data on leaf-level gas exchange under tropical conditions; the role of nutrient limitations; and large-scale biomass dynamics, carbon allocation patterns, and belowground responses that alter the longer-term fate of carbon. A particularly important uncertainty is whether elevated atmospheric CO_2 will ameliorate drought responses of tropical ecosystems and alter their plant community composition.

- **What are the interactions between climate change and aerosols, particulates, and other trace gas emissions from tropical forests?** Tropical forests are large sources of biological aerosols and trace gases such as methane, nitrous oxide, and biogenic volatile organic compounds (BVOCs), which all have significant roles in the Earth system. Many unanswered questions about these compounds and their roles limit current understanding and representation of tropical ecosystems in ESMs. Key uncertainties include physiological and climatic factors that control production and emission of plant and soil methane, nitrous oxide, and BVOCs. Also needed is improved understanding of the environmental influence of forest ecosystem properties and processes including light quality, storm intensity, cloud-aerosol interactions (e.g., fire- and fungal-derived aerosols), nutrient deposition, and ozone effects.
- **How will tropical forest interactions with the Earth system shift as a result of anthropogenic disturbance and land-use change?** A significant fraction of the tropical forest cover lies in areas recovering from logging or in secondary forests and land abandoned from agriculture (FAO 2010). The consequences of this land-use change on ecosystem function remain uncertain. Thus, a key need is understanding the relationships between changes in land use (e.g., deforestation, use conversion, and recovery) and hydrology, sensible and latent heat fluxes, and impacts on soil biogeochemistry. Such insights are essential for capturing the magnitude of land-atmosphere feedbacks across a range of spatial scales in ESMs.

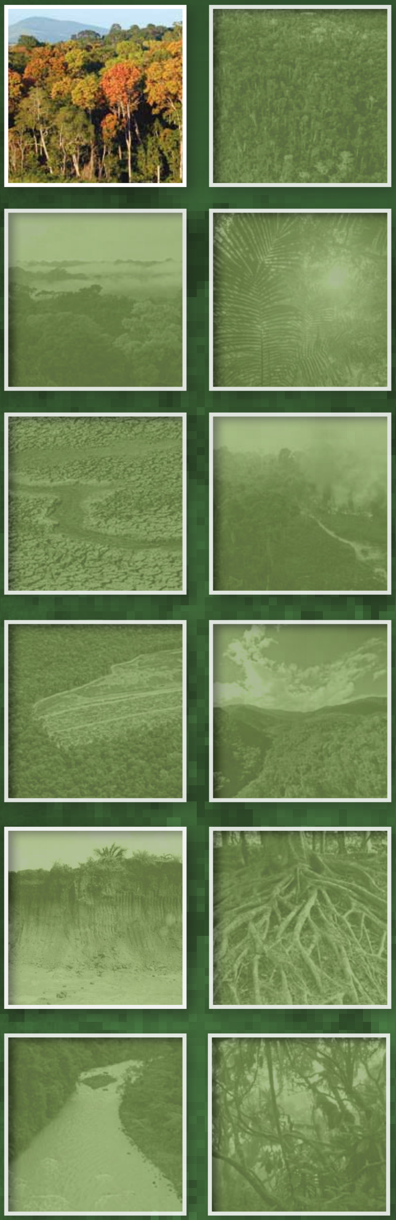
Addressing Research Uncertainties, Gaps, and Opportunities

Many of these questions are critical and relevant across the Tropics—including the Amazon, Central America and the Caribbean, the Congo Basin of Africa, and Southeast Asia—but some may be more applicable to one region than another. Choosing the best place to study these questions requires balancing numerous factors, such as a region's impact on the global system; its perceived vulnerability to climate change; the representativeness of a site relative to a larger region; and the degree to which an area has been studied, whether little or extensively. Studying one region intensively holds great value, but so too does conducting extensive research across all of the Tropics. Regardless of the geographic approach, careful coordination of the implementation, goals, and outcomes of the proposed research will be necessary to achieve the intended objectives. Science drivers are paramount, but practical issues of infrastructure support and accessibility cannot be ignored. Ultimately, good hypothesis-driven science carried out anywhere in the Tropics will be valuable in informing models about critical processes that can improve their predictive capacity.

Although the questions and uncertainties identified at the workshop and in this report are challenging, the scientific community is committed to tackling them. Research networks established across the Tropics, as well as projects led by single investigators, have elucidated many critical processes that must be studied more extensively. Observations of forest productivity, responses to periodic drought, or recovery after disturbance reveal areas in which models currently fail and require improvement. Important processes missing from models iteratively guide decisions about new knowledge to be pursued and datasets to assemble. Using these models to predict an uncertain future—one with climatic conditions never experienced by extant tropical forests—may require experimental systems that simulate those future conditions and provide a platform for model testing. A rigorous scaling framework is needed so that process studies, experiments, plot-level observations, and regional to continental scaling approaches can inform and be constrained by their simulated representation in a global land-ocean-atmosphere model. Together, these considerations describe the broad goals of a concentrated and multidisciplinary research program—such as DOE's Next-Generation Ecosystem Experiment (NGEE) in the Tropics—that closely integrates experimental approaches and modeling to maximize research investments in ecosystem science.

CHAPTER 1

Introduction



Introduction

The Tropics—the region of Earth between 23.4° latitude north and south of the equator—have widely diverse ecosystems, including some of the driest deserts and wettest forests on the planet. Tropical forests, which comprise about half of Earth's total forest area, are characterized by their warm and wet climate, generally nutrient-poor soils, and high biological diversity. These forests hold more biomass and cycle more carbon and water than any other biome and play critical roles in determining Earth's energy balance. Land-use activities in the Tropics are responsible for most of the net nonfossil flux of carbon dioxide (CO_2) to the atmosphere. These fluxes, along with significant emissions of aerosols and other compounds from tropical forests, play important roles in determining the atmospheric chemical environment. The potential for extreme drought with a warming climate over large portions of the tropical forest biome could lead to significant carbon fluxes to the atmosphere associated with tree mortality. Moreover, because the Tropics occur at the high temperature extremes of the current climate, a warmer climate will push these ecosystems toward states not experienced in recent history. These critical features result in strong potential feedbacks among tropical forests, the atmosphere, and global cycles of carbon and water. The ability to better predict these feedbacks under a changing climate requires improving the representation of tropical forests in Earth system models (ESMs).

Report Structure and Organization

To identify critical scientific gaps that limit the ability to represent tropical ecosystems in ESMs, the U.S. Department of Energy's (DOE) Office of Biological and Environmental Research (BER) held the Research Priorities for Tropical Ecosystems Under Climate Change Workshop in June 2012. Nearly 40 experts in tropical ecosystem science addressed key questions important for determining how tropical forests interact with and feed back to the climate system. The workshop featured a series of plenary talks, four breakout sessions with three parallel groups focused on broad research areas, and activities to integrate discussions among groups. Breakout sessions focused on soil biogeochemistry and hydrology, natural and anthropogenic disturbance, tropical forest ecophysiology, and cross-cutting issues. This report summarizes these discussions and presentations and is broadly organized into three sections:

- **Background Information**, including this introduction and a description of regional differences across the Tropics (Chapter 2, p. 7).
- **Responses of Tropical Forests to External Forcings**, such as elevated atmospheric CO_2 (Chapter 3, p. 13), temperature (Chapter 4, p. 23), drought (Chapter 5, p. 33), natural disturbance (Chapter 6, p. 43), and anthropogenic disturbance and land use (Chapter 7, p. 51).
- **Integrating Processes**, such as biosphere-atmosphere interactions (Chapter 8, p. 55), nutrient limitations (Chapter 9, p. 63), belowground processes including roots and soil biogeochemistry (Chapter 10, p. 69), and hydrology (Chapter 11, p. 77).

Also featured in this report is a summary section reiterating the main workshop themes (Chapter 12, p. 85), followed by a description of BER's Next-Generation Ecosystem Experiment (NGEE) approach (Appendix 1, p. 92). Next are the workshop agenda, breakout session details, participants list (Appendix 2, p. 95), and bibliography (Appendix 3, p. 101).

Because of the focus on improving ESMs mechanistically, this report emphasizes understanding ecosystems at a functional scale. Ecosystem-scale carbon balance is an emergent property, representing the sum total of all processes. Since it is not represented directly, this report does not have a section devoted to the subject, even though measurements of net carbon fluxes could be very important as integral constraints.

Significance of Tropics to Earth System and Climate

Tropical forests are a central component of the Earth system. Global gross primary productivity (GPP) is estimated at 122 Pg of carbon per year (C yr^{-1}), and of that total, 41 Pg (34%) are assimilated by tropical forests, with an additional 31 Pg (25%) taken up by tropical savannahs and grasslands (Beer et al. 2010). Total aboveground carbon storage in terrestrial ecosystems is about 560 Pg (Schlesinger 1997), with 190 Pg (34%) in tropical forests alone (Saatchi et al. 2011). Deforestation and forest degradation in the Tropics account for 12 to 20% of total global anthropogenic CO_2 emissions, reducing tropical forest carbon stocks annually by 1 to 2 Pg in the 1990s and early 2000s (DeFries et al. 2002; Houghton 2003; van der Werf et al. 2009).

Given the importance of tropical forests to the global carbon cycle, any changes in their extent, structure, or functioning will have consequences for the trajectory of atmospheric CO_2 and associated climate forcing. Carbon flux studies using observations from permanent forest plots indicate that mature tropical forests represent a net global sink of 1.3 Pg C yr^{-1} (Lewis et al. 2009a), or more than 50% of the total estimated global terrestrial carbon sink (Canadell et al. 2007). However, because plot networks sample only a small fraction of vast regions over a limited period of time, disturbances at timescales of decades or longer may not be adequately sampled, potentially leading to overestimates of biomass increase (Davidson et al. 2012; Chambers et al. 2009; Lloyd, Gloor, and Lewis 2009). Tower-based eddy flux studies show contrasting carbon balance estimates for Amazon forests (Pyle et al. 2008; Gatti et al. 2010; Araújo et al. 2002; Malhi et al. 1998; Kruijt et al. 2004) that are highly dependent on a number of data-processing assumptions (Miller et al. 2004).

Tropical forests also are large sources of biogenic volatile organic compounds (BVOCs) and aerosols from biomass burning, which both play significant roles in Earth system functioning (Andreae et al. 2002; Martin et al. 2010). Changes in forest flooding and soil moisture associated with seasonal changes in precipitation and under drought cause biogeochemical shifts in reduction-oxidation (redox) conditions and related emissions of non-CO_2 greenhouse gases (GHGs) such as methane and nitrous oxide (Melack et al. 2004; Silver 1998; Davidson 1993).

Tropical forests have other impacts on the climate system in addition to their indirect effects through the carbon cycle and GHG emissions. For example, climate model simulations indicate that tropical forests decrease air temperature and increase regional precipitation compared to pastureland (Bonan 2008; Shukla, Nobre, and Sellers 1990). The cooling effect of high rates of evapotranspiration offsets the warming associated with low albedo (Bala et al. 2007). Furthermore, the influence of tropical forests on climate may extend to other regions through atmospheric teleconnections (Bonan 2008; Avissar and Werth 2005; Nepstad et al. 2008). Land-use changes and forest fragmentation in the Tropics can alter atmospheric circulation patterns and cloud formation processes (Cox et al. 2004; Laurance 2004; Wang et al. 2009).

Vulnerability of Tropical Forests to Climate Change

Several aspects of tropical ecosystems suggest they will be particularly vulnerable to climate change. First, high-biomass tropical forests occur where sufficient precipitation, warm temperatures, and adequate soil fertility enable tall trees (exceeding ~20 m) to form relatively contiguous crowns, reducing understory light levels to a small fraction of incoming solar radiation. Because this forest type generally requires more than 1,000 mm of precipitation per year to maintain a closed-canopy state, shifts in precipitation regimes with a warming climate may draw some forests below this threshold. This would result in structural and compositional shifts toward more open or lower-statured forests with less biomass as susceptible trees succumb to drought-induced mortality.

Secondly, since many tropical forests already are among the warmest and wettest environments on Earth, projected warming scenarios indicate that these ecosystems will be pushed to new states that have no current analogues (Williams, Jackson, and Kutzbacht 2007). The predicted changes in temperature are large compared to normal interannual variation in the Tropics, further exacerbating potential adverse effects

of warming. Nonlinear shifts in ecosystem structure and atmosphere-biosphere exchanges of GHGs, aerosols, water, and energy could be the result. Changes in temperature, precipitation regimes, nitrogen deposition, and the quantity and quality of organic matter inputs to soils likely will alter rates of GHG production and consumption. The sensitivity of photosynthetic metabolism and the acclimation of plants to temperature extremes are emerging as critical processes for modeling tropical forests (Booth et al. 2012). However, there is no clear consensus on the response of tropical tree species to the temperature regimes expected this century (Corlett 2011).

Shifts in precipitation and higher temperatures can affect numerous ecosystem processes and their interactions, including soil nutrient cycling, soil organic matter turnover, heterotrophic and autotrophic respiration, and plant carbon allocation patterns (Wood, Cavaleri, and Reed 2012). Moreover, many of these processes will interact with increased land use and fire frequency in the Tropics, intensifying climate change effects (Davidson et al. 2012; Nepstad et al. 1999). Ultimately, current understanding of tropical ecosystems indicates that a warming climate will significantly affect ecosystem processes. Changes in these processes in turn could alter the role tropical forests play in critical global biogeochemical cycles, resulting in potentially strong feedbacks to the climate system.

Representation of Tropical Forests in Earth System Models

Although the understanding of tropical forests is improving, their representation in ESMs lags significantly behind that of temperate forests, as evidenced by, for example, the wide variation in estimates of tropical forest productivity (Beer et al. 2010). The Coupled Climate–Carbon Cycle Model Intercomparison Project (C^4MIP) compared 11 coupled ESMs and found differences among the models in land uptake of CO_2 for 2100, ranging from a large sink of 10 Pg C yr^{-1} to a source of 6 Pg C yr^{-1} (Friedlingstein et al. 2006). Most of this variability arose from differences in how tropical forests responded to CO_2 fertilization, increased temperature, and changing precipitation patterns. In particular, widespread drought-driven tree mortality in the Amazon Basin (Cox et al. 2004) was a conspicuous difference among models. With respect to modeling trees, treatment of key processes is poor even for temperate forests, challenging efforts to understand how carbon allocation, root deployment, nutrient uptake, and tree mortality will affect ecosystem structure and functioning and atmospheric exchanges. A fundamental reason for this limitation is that ESMs traditionally have used a "big-leaf" approach with specified parameters for photosynthesis, allocation, turnover, and other processes. This approach does not resolve the dynamics of individuals and therefore can only treat mortality and competitive vegetation interactions in a rudimentary way. These issues are magnified in tropical forests with tall deep canopies, high diversity, and complex ecosystem processes. Further uncertainty arises because tropical forests are near potential thresholds such as the high-temperature photosynthesis optimum, leading to widely divergent model behavior (Booth et al. 2012). Additionally, representation of the long-term ecosystem-scale effects of environmental forcings (e.g., temperature and CO_2) typically is based on results from short-term physiological studies. This introduces biases into models by not accounting for potential acclimation responses or interactions with other environmental resources such as nitrogen or phosphorus. Thus, tropical ecosystems are responsible for large uncertainties in ESMs. In fact, models even disagree on the direction of the climate–carbon cycle feedback for tropical forests (Friedlingstein et al. 2006).

Another particular problem for model development in tropical systems is the absence of many important model validation products available for temperate ecosystems. For example, results from large-scale manipulation experiments in the Tropics are only sparsely available for some drivers (e.g., drought and nutrients) and completely lacking for others (e.g., CO_2 and temperature). Although improvements in model structure are possible and ongoing, additional datasets with which to test models also are needed. This need is typified by studies associated with the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) flux tower program, which unambiguously illustrated that the majority of models erroneously represented moisture-stressed behavior in the dry season for Amazonian forests. The LBA research led to significant changes to the

parameterization and structure of multiple ESM land surface schemes.

Similar problems arise when considering the lack of representation of key soil and ecosystem processes in ESMs, particularly for tropical forests. Critical redox processes, nutrient availability (especially phosphorus), soil organic matter dynamics, and soil structure and rooting depth are absent or poorly represented in most models. These limitations hinder the ability to model and predict how climate and land-use changes will affect net productivity and GHG fluxes from these ecosystems. Fully coupled, well-tested ESMs ultimately are needed to better understand global climate change during the 21st century, and improving the treatment of tropical forests in these models is essential for enhancing predictions at regional, continental, and global scales.

Geographical Considerations

Within the broader Tropics occupying latitudes between the Tropic of Cancer (23.4°N) and Tropic of Capricorn (23.4°S) are three regions with unique biota and geological history:

- **Neotropical** (NEO) ecozone of South America, Central America, and the Caribbean.
- **Afrotropical** (AFR) ecozone of sub-Sahara Africa.
- **Indo-Malay-Australasia** (IMA) tropical ecozone including regions of India, Southeast Asia, and southern China separated from Australia and New Guinea by Wallace's Line.

Within these zones are large, relatively contiguous areas of tropical forest in the Amazon, Congo, and Southeast Asia. The soils in these regions are diverse, with Oxisols (a soil type absent in temperate zones) dominating the tropical forests of the Amazon and Congo and Ultisols dominating those of Southeast Asia (for details, see Chapter 10, Belowground Processes: Roots and Soil Biogeochemistry, p. 69). Because of their large potential feedbacks with the climate system, this report primarily is focused on the high-biomass forests in these three regions (hereafter referred to as "tropical forests") and the areas that may shift toward or away from this high-biomass state.

Neotropical Region

Among the forests in this area (South America, Central America, and the Caribbean), those of the Amazon Basin represent the single largest block of intact tropical forests and alone comprise ~40% of total tropical forest biomass (Saatchi et al. 2011). The Amazon Basin also includes vast floodplains with remarkable seasonal variation in spatial extent. In several studies, the inundated areas along the Amazon River varied from a minimum of 25,000 km^2 in November to a maximum of 65,000 km^2 in June. Flooded forests increased from 5,000 to 35,000 km^2, accompanied by a large increase in associated methane emissions (Melack et al. 2004; Hess et al. 2003). Ter Steege et al. (2006) describe two major floristic gradients across Amazonia. The first stretches from the Guiana Shield to southwestern Amazonia and corresponds with a soil fertility gradient; the second spans from Columbia to southeastern Amazonia, representing a broad moisture gradient that corresponds with increasing dry season length. The forests of Central America and the Caribbean share many floristic similarities with those in the Amazon but occur on younger, more fertile soils with less overall diversity. With the exception of Panama, Central American and Caribbean forests experience regular hurricanes and more recently have been affected by forest fires that accompany severe El Niño drying periods (Cochrane 2002). Strong environmental gradients occur over relatively small spatial scales in Central America and the Caribbean, and forests are embedded in a complex matrix of human settlement.

Afrotropical Region

African forests include those of Madagascar, the Congo River and adjacent drainages in Gabon and neighboring countries, and West Africa located within several hundred kilometers of the coast. West African coastal forests are highly fragmented and degraded, but those of the Congo Basin represent the second-largest intact block of tropical forests after the Amazon (Pan et al. 2011). Within the center of the Congo Basin are approximately 220,000 km^2 of swamp forest, and other forests dominated by a single tree species (*Gilbertiodendron dewevrei*) occupy large areas (Vande weghe 2004; Devers, Vande weghe, et al. 2006). Central African forests do not experience tropical cyclones but are subject to large storm

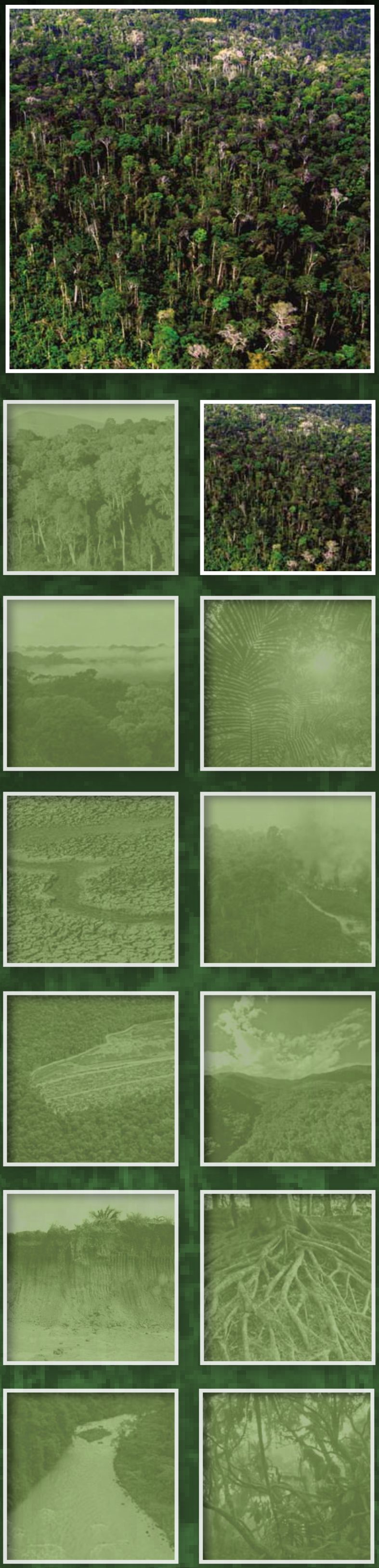
events. Additionally, African forests experience droughts and exceptionally wet years associated with El Niños and La Niñas. Lewis et al. (2009a) recently added a large set of plots to a pantropical network to monitor biomass in African tropical forests. They estimate that these forests accounted for 34% of a net 1.3 Pg C yr^{-1} tropical forest carbon sink (with NEO and IMA forests representing 47% and 19%, respectively).

Indo-Malay-Australasia Tropical Region

In contrast to all NEO and AFR forests where Leguminoseae is the dominant plant family, Southeast Asian forests are dominated by trees in the Dipterocarpaceae family, which are completely absent from NEO and AFR. Dipterocarps have a disproportionate influence on ecosystem properties and dynamics across the region because of their abundance and large size. Dipterocarps also are among the most highly prized timber species across much of the region, which has led to intense logging pressure in many IMA forests. Across the IMA region are steep gradients in total rainfall, rainfall seasonality, soil type and age, and land-use history. Drought is an important climatic feature of the region, particularly over the past 2,500 years with the onset of the El Niño–Southern Oscillation (ENSO). The intense ENSO-associated droughts of 1982–83 and 1997–98 led to widespread fires and tree mortality even in the region's wettest forests (Leighton and Wirawan 1986; Potts 2003; Phillips et al. 2010). Other remarkable features of this region are the peat swamps, primarily in Borneo and Peninsular Malaysia. Recent studies estimate that drainage and burning of peat forests in this area were responsible for a flux of ~0.3 Pg C yr^{-1}, comprising ~25% of total global carbon emissions from tropical forests (Harris et al. 2012; van der Werf et al. 2008; Hooijer et al. 2010).

DOE's Role in Improving Predictions of Tropical Forest Response to Climate Change

BER includes programs focused on terrestrial ecosystems and ecological processes that are globally or regionally significant, expected to be sensitive to climate change, and insufficiently understood or inadequately represented in ESMs. Tropical ecosystems meet these criteria, and improving their representation in models is critically needed for enhancing the robustness of global climate predictions, which in turn will better inform future research, energy policy, and adaptation strategies. To achieve these advances, BER is strategically committed to coupling models with experimental and observational campaigns across relevant spatial and temporal scales. Developing a better predictive capacity for how climate feedbacks from tropical forests will respond to a changing climate will require an interdisciplinary approach such as BER's Next-Generation Ecosystem Experiment activity. NGEE would serve as a powerful tool for understanding tropical ecosystems and provide the framework for their improved representation in climate modeling efforts. The NGEE program anticipates coupling focused manipulative experiments, extensive observational studies, and mechanistic forest ecosystem simulation models to ultimately improve ESMs. DOE is uniquely positioned to address this critical research need based on its (1) historical successes in developing long-term manipulation studies like the Free-Air CO_2 Enrichment (FACE) experiments, (2) major investments in developing and assessing ESMs, and (3) leadership-class computational capabilities.



CHAPTER 2

Regional Differences in Tropical Forest Response to Climate Change

Regional Differences in Tropical Forest Response to Climate Change

Tropical forests cover about 19.5 million km^2 of Earth's surface and are responsible for 34% of global terrestrial gross primary productivity (Beer et al. 2010). They can be broadly divided into wet, moist, and dry forests but also include significant areas in swamps or montane forests. Based on their geological history and floristic composition, tropical forests are broadly classified into the Neotropical (NEO) region of South America, Central America, and the Caribbean; the Afrotropical (AFR) region of sub-Sahara Africa; and the Indo-Malay-Australasia (IMA) tropical region that includes parts of India, Southeast Asia, southern China, and New Guinea. Although assessments of the extent of tropical forests vary substantially depending on the methodology and technologies used (Wright 2005), Saatchi et al. (2011) estimate that tropical forests with 10% to 30% minimum canopy-cover thresholds span about 2,500 to 1,700 million hectares (Mha), respectively. Using the 30% canopy-cover threshold, NEO, AFR, and IMA forests comprise 890, 450, and 336 Mha, respectively. Saatchi et al. (2011) further define high-biomass tropical forests as those with aboveground biomass exceeding 100 Mg ha^{-1}. This study notes that although high-biomass forests are less extensive than low-biomass ones, they contain 83%, 59%, and 82% of total biomass in NEO, AFR, and IMA forests, respectively (see Fig. 2.1, this page).

Particular differences among the three regions can influence tropical forest response to a warming climate and changing atmospheric conditions. Overall, the complex gradients in soil properties, total rainfall and seasonality, species composition, disturbance regimes, and land-use history among regions will affect forest response to climate change. These factors all contribute to a rich diversity of forest types across the Tropics and to complex aggregations of forest types within landscapes. This chapter describes a number of factors likely to have important effects on the differential responses of tropical forests at regional to continental scales.

Variations in Soil Fertility, Structure, Hydrology, Topography

A large range of soil types are found within tropical forests, including soils derived from volcanic origin

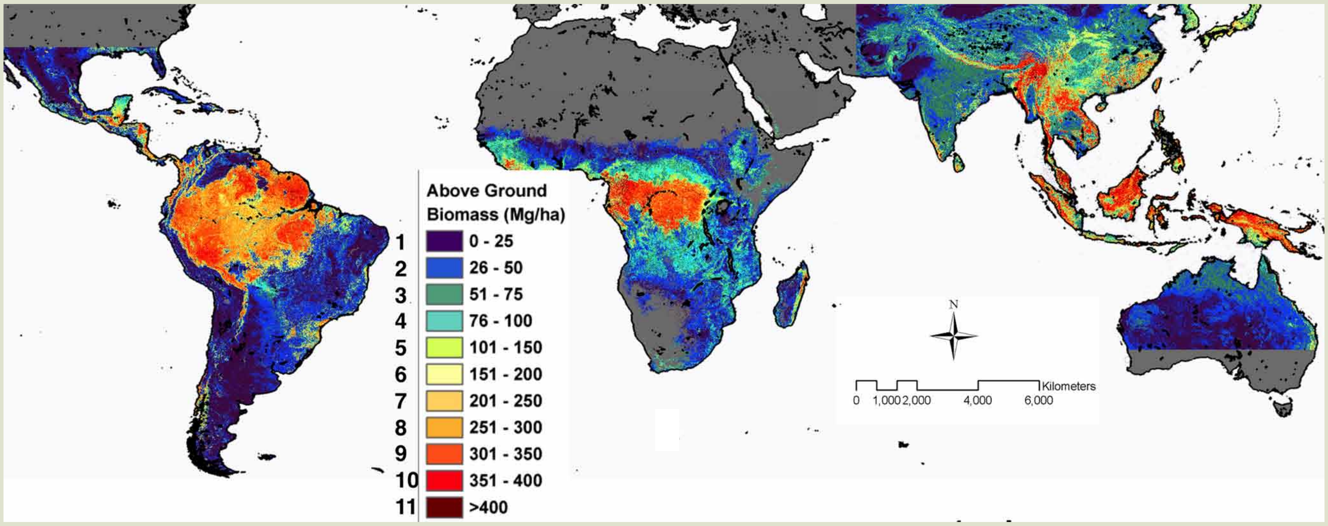


Fig. 2.1. Distribution of Forest Aboveground Biomass. [From Saatchi, S. S., et al. 2011. "Benchmark Map of Forest Carbon Stocks in Tropical Regions Across Three Continents," *PNAS* **108**(24), 9899–904.]

such as those in the Hawaiian Islands, widespread heavy clay Oxisols in Africa and South America, and white sand formations in the Amazon Basin. With other state variables such as precipitation, temperature, and topography held constant, differences in soil properties can drive dramatic changes in forest structure and ecosystem processes (Amundson and Jenny 1997). Within the Amazon Basin, for example, soils are highly complex, ranging from relatively fertile soils of anthropogenic origin to deep white sands (Quesada et al. 2011). Amazon forests on white sand formations vary from tall closed-canopy forests with a shallow saturated zone to low-biomass shrublands called "campinaranas" ("caatinga" and "heath forests") when the water table occurs at depth (Anderson 1981). The soils of many forests in Central America and the Caribbean are younger and have been significantly affected by land-use activities. Overall, Oxisols and Ultisols are the dominant soil types among tropical regions globally but are relatively rare in extratropical ecosystems. Because tropical soils vary considerably from those in temperate forests (for which ecosystem models were largely developed), efforts to improve their treatment in terrestrial models should be a high priority.

A better understanding is needed of how regional variability in soil properties interacts with rising temperatures, shifts in precipitation, and elevated carbon dioxide (CO_2) concentration to affect forest structure and ecosystem processes. These insights are essential for improving predictions of regional differences in the response of tropical forests to a changing atmosphere and warming climate. Achieving this understanding will require better regional mapping of key soil parameters (e.g., parent material, texture, hydraulic conductivity profiles, bedrock features, saprolite layers, and water table depth) as well as rigorous evaluation of terrestrial model representation of processes that change across key gradients in soil properties. For example, how do forest productivity and biomass density change along a gradient in soil texture from a heavy clay Oxisol to a deep white sand soil with all other factors held constant? Addressing this and other key tropical soil questions will be critical for improving terrestrial ecosystem components of Earth system models (ESMs).

Shifts in Precipitation and Temperature Patterns with a Warming Climate

Regional climate projections from the Intergovernmental Panel on Climate Change's (IPCC) multimodel data (MMD) A1B scenario predict increased tropical surface temperatures ranging from ~3 to 5°C for Southeast Asia, the Amazon, and West Africa by 2100 (IPCC 2007). This increase in temperature will push tropical forests into temperature regimes that do not currently exist, resulting in "no-analogue" climates. The MMD A1B scenario also predicts generally increased annual precipitation for West Africa and Southeast Asia, though with decreases over some areas in Southeast Asia from December to February. Decreased precipitation also is projected over much of the southern and eastern Amazon, particularly from June to August, which corresponds to the region's annual seasonal drought period. This potential intensification of the drought period across significant portions of the Amazon Basin is a critical topic for additional research. Increased severity of droughts also could lead to more frequent forest fires (Cochrane 2003), especially when associated with land-use forest fragmentation in the Amazon (Soares et al. 2012), Central America (Cochrane 2002), and West Africa (Hawthorne 1995). Both regular seasonal drought and intense episodic drought affect tropical forest ecosystem structure and functioning. Baltzer et al. (2008, 2009) demonstrated how drought variability drives plant species distributions in tropical Asia, with the transition from aseasonal to more seasonal environments. The intense droughts of 1982–83 and 1997–98 associated with the El Niño–Southern Oscillation led to widespread fires and tree mortality, even in the most aseasonal forests in the region (Leighton and Wirawan 1986; Potts 2003). The interaction of human land-use change and increasing atmospheric temperatures may exacerbate the effects of drought in the coming decades and lead to widespread loss or degradation of tropical forests vulnerable to drought with a warming climate. The extent to which various regions will respond differently to the same drivers is unclear, as is current understanding of how changes in temperature, rainfall, and CO_2 interact with variation in ecosystem properties such as soil and species composition.

Addressing these uncertainties will require comprehensive multidisciplinary research approaches.

Functional and Phylogenetic Differences in Plant Species Responses

Other factors being equal, regional differences in tropical species composition, particularly trees, can affect regional responses to a warming climate. For example, many Southeast Asian forests are dominated by a single plant family (Dipterocarpaceae) that is virtually absent from Africa and Latin America, and Dipterocarps have a disproportionate influence on ecosystem properties and dynamics because of their abundance and large size. Thus, for a given set of conditions, Asian forests have higher biomass (Yamakura et al. 1986) and may respond differently to changes in temperature and precipitation. Tropical forests also vary dramatically in tree diversity. Although tree species are highly diverse in most tropical forests, typically averaging hundreds of tree species per hectare, there are some notable exceptions. For example, in equatorial forests of Africa, the tree species *Gilbertiodendron dewevrei* can dominate thousands of square kilometers (Vande weghe 2004). In the Neotropics, limited forest areas are mono-dominated by *Dicymbe corymbosa*, *Eperua falcata*, *Mora gonggrijpii*, and *Peltogyne gracilipes* (Henkel 2003). Finally, the tropical forests of Hawaii are dominated by a single tree species, *Metrosideros polymorpha*. In the Amazon, ter Steege et al. (2006) describe a number of floristic gradients that correspond with soil fertility, dry season length, and disturbance regimes. Overall, differences in community composition of plant species and phylogenies among tropical forest regions reflect a variety of factors that affect survivorship, including the potential for differential adaptation to potential stress factors such as drought and soil fertility. These differences should be considered in selecting sites for field studies and in developing robust models for improved prediction of tropical forest response to climate change.

Differences in species composition and functional types among tropical forests may partially explain some contrasting observations. Analysis of tree growth rates in Costa Rica, Panama, Malaysia, and the central Amazon found either decreases in tree growth rates or no discernible change (as yet) over the last two to three decades (Clark et al. 2003; Feeley et al. 2007; Laurance et al. 2009). These observations run counter to what might be expected if global changes are leading to increased forest biomass accumulation. Several authors have noted an increase in lianas (woody vines) in Neotropical forests in recent decades (Phillips et al. 2005; Schnitzer and Bongers 2011; Wright et al. 2004), but limited evidence from Africa does not indicate an increase there (Schnitzer and Bongers 2011). Lianas compete with trees for light, nutrients, and moisture but store relatively little carbon. As such, the increased tree mortality and decrease in productivity associated with increasing lianas could profoundly affect tropical forest carbon cycling (Schnitzer and Bongers 2011). The effects of lianas may be particularly important early in forest development, during which lianas can rapidly attain high densities and significantly reduce tree recruitment, density, diversity, and survival (Schnitzer and Carson 2010). Research has yet to determine whether the observed increase in lianas results from a changing atmosphere or some other factor and whether they are increasing in tropical secondary forests. Regardless of the cause, lianas likely have a much stronger effect in tropical forests now than in recent history because their density, biomass, and productivity have increased considerably in some forests over the past 30 years (Schnitzer and Bongers 2011).

Variation in Regional Disturbance Regimes

Natural disturbances that cause tree mortality in tropical forests include drought, storms (e.g., wind and lightning), fire, flooding, and other processes such as pest and pathogen outbreaks and monocarpy (for details, see Chapter 6, Natural Disturbance and Recovery, p. 43). Each of these agents of mortality also exhibits regional variability and may respond differently to a changing climate. Examples of this variability are tropical forests affected by cyclonic storms, such as hurricanes in the Caribbean and Central America, typhoons in Southeast Asia, and tropical cyclones in the Southern Hemisphere including northeastern Australia. Several studies indicate an increase in the intensity of tropical cyclones with

a warming climate (Emanuel 1987, 2005; Webster et al. 2005), although complex interactions with upper-atmosphere wind sheer can prevent cyclonic development (Hoyos et al. 2006). However, given conditions conducive to storm development, higher sea surface temperatures generally result in more intense tropical cyclones.

In addition to the expected intensification of tropical cyclones, a general increase in storm intensity and extremes in precipitation and wind speed are robust climate change predictions (IPCC 2007). More powerful storms under a warming climate may cause higher tree mortality rates and more dynamic disturbance regimes, leading to an increase in naturally regenerating secondary forests and shifts in ecosystem carbon balance toward lower-biomass forests. However, little is known about how disturbance regimes of tropical forests will change regionally with a warming climate, and efforts are needed to quantify baseline regimes for different regions and to monitor changes in disturbance patterns. Important objectives include distinguishing among mortality processes in field and remote-sensing studies and developing mechanistic disturbance algorithms for terrestrial models.

The effects of land use in tropical forests also vary considerably among regions. In the Amazon, for example, a deforestation crescent from near the city of Belem in the northeast of Brazil to Rio Branco in the southwest represents most land-use activity and biomass burning (Skole and Tucker 1993). However, large tracts of tropical forests in the central and western Amazon are among those least disturbed by direct human activity. In Africa, western coastal forests are highly fragmented and degraded, but those in the Congo Basin are relatively intact. Similar regional variability in human disturbance occurs in Southeast Asian forests. The intensity of anthropogenic impacts on tropical forests also differs considerably across regions, ranging from low-level resource extraction to selective logging to widespread deforestation and biomass burning for agricultural activities. Atmospheric pollutants also exhibit strong regional variability. An important activity thus would be to determine which specific anthropogenic activities are affecting ecosystem processes among regions with respect to key interactions with the climate system.

CHAPTER 3

Responses of Tropical Forests to Elevated CO_2

Responses of Tropical Forests to Elevated CO_2

Overview

The rise in atmospheric carbon dioxide concentration [CO_2] is unprecedented, rapid, and ubiquitous. Unlike some aspects of global change for which the magnitude, direction, and location of the change is uncertain, the rise in CO_2 is global and, unfortunately, almost certain to continue for decades to come. Current projections—based on assumptions about energy use, population growth, and other physical, biological, and socioeconomic factors—indicate that atmospheric [CO_2] will increase from its present-day value of 392 parts per million (ppm) in 2011 to more than 800 ppm by 2100 (Intergovernmental Panel on Climate Change A2 emissions scenario, www.ipcc-data.org/ddc_co2.html). Because atmospheric CO_2 is the primary substrate for all terrestrial productivity, this substantial increase undoubtedly will affect the metabolism of tropical forests worldwide. The qualitative and quantitative expression of the effects, however, is largely unknown, representing a major source of uncertainty that limits the capacity to understand tropical ecosystem processes, assess their vulnerabilities to climate change, and improve the representation of these systems in Earth system models. Much is known about the effects of elevated concentrations of CO_2 (eCO_2) on biochemical and physiological processes in leaves, including leaves of tropical trees under tropical conditions. However, these primary responses (e.g., photosynthesis) do not necessarily reveal the integrated responses of ecosystem productivity, carbon cycling, and biotic interactions. Growth studies of tropical tree species have been conducted with seedlings and young saplings, but no single mature tropical tree has ever been exposed to eCO_2 under natural forest conditions (Körner 2009). In temperate forest ecosystems, free-air CO_2 enrichment (FACE) experiments have revealed many higher-order responses and emphasized the importance of interactions and feedbacks between CO_2 and other environmental resources, stand development, and integration across time and space (Norby and Zak 2011). No such experiments have been conducted in tropical forests. Moreover, substantial differences in the plant species, forest structure, soils, and climate of temperate and tropical forests severely limit the ability to use results from temperate-zone studies to predict tropical forest responses. The current generation of land surface models, as applied to tropical forests, highlights the gulf between what is known about tropical forest responses to rising atmospheric CO_2, what remains uncertain, and what must be done to resolve the uncertainty and improve predictive capacity.

Insights from Models

Forest inventory analysis has indicated increasing aboveground biomass and net primary productivity (NPP) in tropical forests over the past several decades. Some analyses suggest this increase may be attributable to rising CO_2 (Lloyd and Farquhar 2008; Lewis et al. 2009b), but other studies conclude that different factors are the more likely cause of biomass increases observed at the plot scale (Chambers and Silver 2004; Clark, Clark, and Oberbauer 2010). Attributing the driver of past changes in forest biomass is never straightforward because of multiple, uncontrolled environmental and stand development factors that are confounded with past increases in atmospheric CO_2. Adding to the difficulty is the problem of reliably estimating regional-scale changes in aboveground biomass and the potential divergence between changes in aboveground biomass and total NPP. Using an individual-based tree growth model, Chambers et al. (2004a) suggested that tree growth would need to be extremely sensitive to CO_2 for stand-level increases in aboveground biomass to match observed increases in central Amazon forests over the past several decades. A more important challenge now for improving the ability to predict responses to future climate change is to understand and better represent in models the response of tropical forests to increases in atmospheric CO_2 over the coming decades.

Responses of temperate trees in FACE experiments make clear that aboveground biomass is not a sufficient metric for evaluating forest responses

to eCO_2 and their feedbacks to the atmosphere. Significant increases in NPP and carbon storage can occur without any increase in aboveground woody biomass (Norby et al. 2005; Iversen et al. 2012). Global models that incorporate a whole-ecosystem analysis illustrate the potential importance of eCO_2 to tropical carbon cycling and the feedbacks from the Tropics to climate. Carbon cycle predictions of different dynamic global vegetation models (DGVMs) are consistent with contemporary global land carbon budgets but can diverge considerably when forced with the future climate predicted by general circulation models and emission scenarios. However, models agree that including effects of eCO_2 in the simulations counteracts carbon losses caused by climate change, resulting in the land being a net sink for carbon rather than a net source over the 21st century (Sitch et al. 2008). The Tropics are especially important in such simulations, and the response of tropical forests has been explored in detail. One DGVM, the LPJ model, predicted a 35% increase in NPP for tropical forests at an atmospheric CO_2 concentration of 550 ppm relative to that at 370 ppm (see Fig. 3.1, this page; Hickler et al. 2008).

The effects of eCO_2 on NPP of evergreen forests in the Amazon were simulated with two ecosystem models (Biome-BGC and LPJ) and compared with modeled effects of climate and increased shortwave radiation (Hashimoto et al. 2010). Both models showed a monotonous positive trend in NPP corresponding with increasing atmospheric CO_2. However, observed trends of increasing normalized difference vegetation index (NDVI) had a distinct seasonal variation that was matched in the models by the response to increasing shortwave radiation but not by the response to increasing CO_2. Hence, the authors concluded that the positive trend in

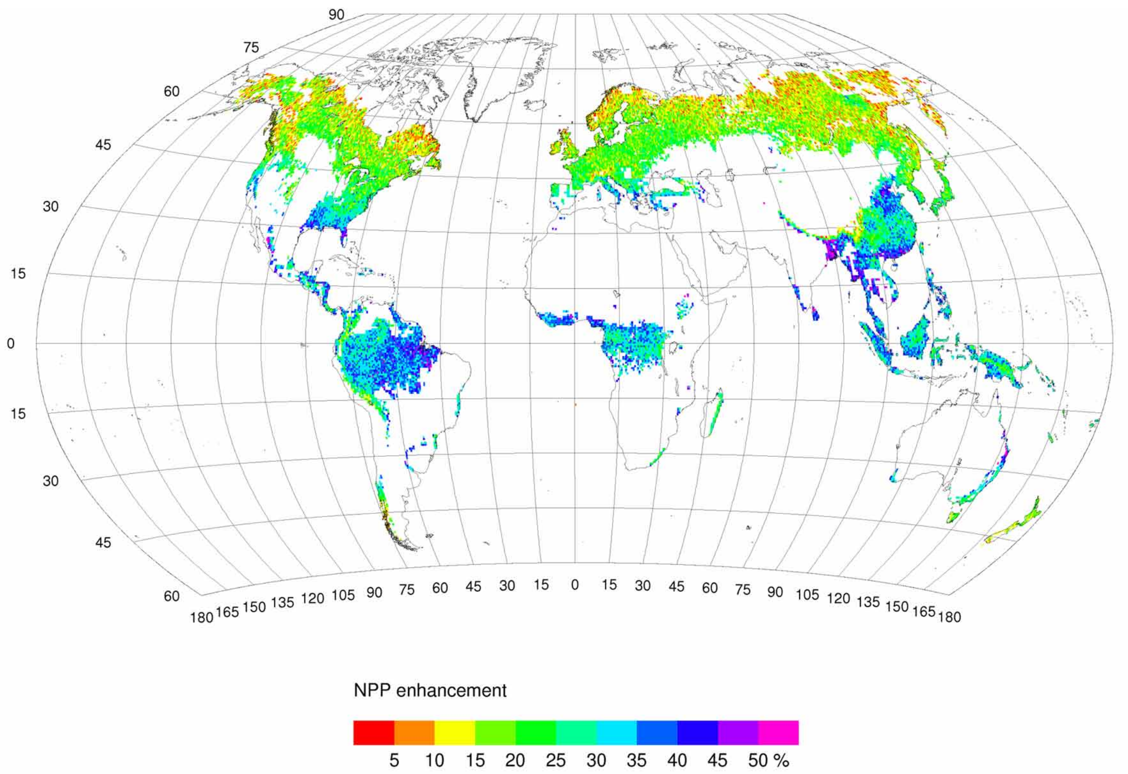


Fig. 3.1. Geographic Pattern of NPP Enhancement Resulting from a Step Increase of CO_2 from Ambient to 550 ppm as Simulated by the LPJ Model. [From Hickler, T., et al. 2008. "CO_2 Fertilization in Temperate FACE Experiments Not Representative of Boreal and Tropical Forests," *Global Change Biology* **14**(7), 1531–42. © 2008 Blackwell Publishing Ltd.]

shortwave radiation is most likely the driver of both the observed increasing trend in NDVI and the corresponding observed increases in aboveground biomass in the Amazon Basin for the period from 1984 to 2002 (Hashimoto et al. 2010). The study, however, acknowledged that FACE experiments in temperate systems showed that increases in NPP under eCO_2 occurred without increases in leaf area index (LAI) or, presumably, NDVI (Norby et al. 2005).

In addition to direct effects on NPP, eCO_2 also could influence the trajectory of biome shifts. Scheiter and Higgins (2009) simulated the vegetation of the grassland-savanna-forest complex of Africa using a DGVM with process-based and adaptive modules for phenology, carbon allocation, and fire. C_4 photosynthesis of tropical grasses is carbon saturated at ambient CO_2, and C_3 photosynthesis is not. Thus, with increases in CO_2 concentration, the model simulates a change in the relative performance of grasses and trees resulting in a substantial increase in tree dominance and a replacement of savannas by deciduous woodlands. Lapola et al. (2009) used a potential vegetation model (CPTEC-PVM2) that performs well at delimiting the forest-savanna border in South America to analyze the effect of different scenarios of CO_2 and climate. When a CO_2 fertilization effect was fully considered, there were no substantial changes in Amazonia, but in the absence of CO_2, climate change caused a pronounced shift to drier biomes, indicating that eCO_2 could moderate the possibility of biome shifts caused by climate change. Numerous uncertainties were noted, however, giving rise to a call for long-term experimental studies exploring the effects of eCO_2 on the productivity and canopy conductance of tropical ecosystems (Lapola et al. 2009).

The possibility of climate change causing a substantial loss of Amazon rainforest cover and carbon stocks and amplifying the climate–carbon cycle feedback has been suggested (Cox et al. 2000). Galbraith et al. (2010) tested the importance of changes in precipitation relative to other environmental drivers, including CO_2. Three DGVMs (HyLand, LPJ, and TRIFFID) agreed that modeled responses to increased temperature were as important, or more important, than reduced precipitation in causing loss of plant biomass carbon. Similar to the results of Lapola, eCO_2 mitigated much of the climate-driven losses in the models (see Fig. 3.2, p. 17). Acknowledged uncertainties in the representation of the CO_2 effect include nutrient limitations, which were not included in these models, and possible effects of eCO_2 on species composition (Galbraith et al. 2010).

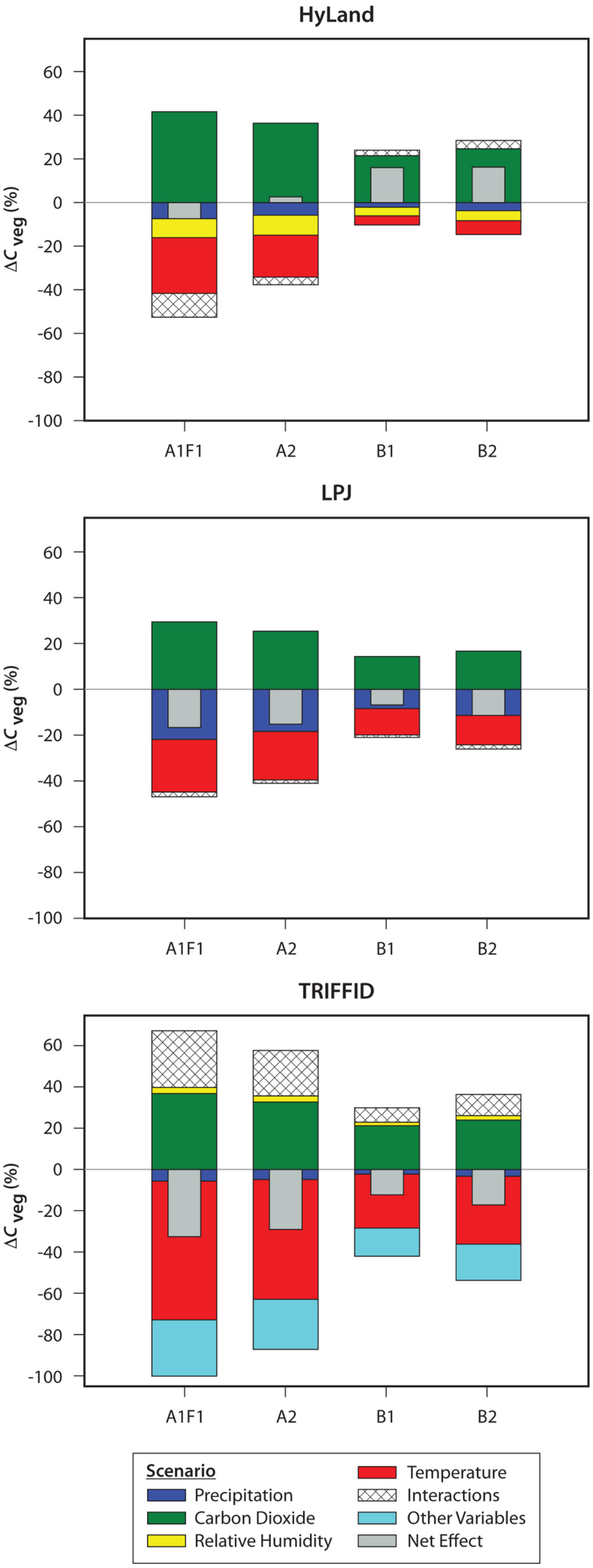
As discussed below, these model predictions are based on very limited information and omit what are likely to be critical modifying processes (e.g., the phosphorus cycle). At best, the model results represent testable hypotheses that can guide experimental design (Cernusak et al., in review). Understanding the critical points of uncertainty in the models with regard to representation of eCO_2 responses will identify important research gaps.

Known Responses to Elevated CO_2

The initial interaction between any green plant and CO_2 occurs through the biochemical process of photosynthesis. Hence, most all terrestrial carbon cycling models appropriately start with an expression of leaf-level photosynthesis, employing a modified version of the Farquhar et al. photosynthesis model (Farquhar, Caemmerer, and Berry 1980; Collatz et al. 1991). Photosynthetic responses to eCO_2 are very well described. For example, eCO_2 generally causes the CO_2 assimilation rate (A) to increase (Lloyd and Farquhar 1996; Drake, Gonzalez-Meler, and Long 1997), and the A of tropical woody plants has a larger potential to respond positively to eCO_2 than that of plants in cooler climates. As temperature increases, the specificity of the primary carboxylating enzyme RuBisCO for fixing CO_2 instead of O_2 decreases along with the solubility of CO_2, leading to increased photorespiration (Farquhar, Caemmerer, and Berry 1980; Long 1991). Increasing the $[CO_2]$ around RuBisCO suppresses photorespiration, thereby stimulating A. In the abovementioned model by Hickler et al. (2008), the geographic difference in the simulated proportional stimulation of productivity largely was caused by variations in photorespiration.

A second primary effect of eCO_2 is to reduce stomatal conductance to water vapor through partial stomatal closure (Morison 1985; Ainsworth and Rogers 2007). This response has been observed in short-term studies and persists over time under field conditions. Stomatal conductance (g_s) decreased 21% in eCO_2

Fig. 3.2. Contribution of Environmental Factors to Simulated Changes in Amazonian Vegetation Carbon (C_{veg}) for Four Special Report on Emissions Scenarios (SRES) in Three Dynamic Global Vegetation Models. Main effects and the sum of all interaction terms, as quantified in the factorial ANOVA, are shown. The overall net effect of including all factors is represented as the inner gray bar. [Adapted from Galbraith, D., et al. 2010. "Multiple Mechanisms of Amazonian Forest Biomass Losses in Three Dynamic Global Vegetation Models Under Climate Change," *New Phytologist* **187**(3), 647–65.]



across all open-top chamber experiments with young, temperate-zone trees (Medlyn et al. 2001). FACE experiments have confirmed the persistence of this primary physiological response to eCO_2 in some experiments, but the magnitude of the response varied widely (4% to 44%; Warren et al. 2011). Lower g_s results in a lower transpiration rate, reducing the evaporative cooling of the leaf and causing an increase in leaf temperature. Stomatal closure also occurs with unfavorable environmental conditions, such as hot, sunny days that lead to a high leaf–to–air vapor pressure deficit. Under such conditions many tropical forest trees display a midday depression in both g_s and A, responses that have been documented at both the leaf level (Koch, Amthor, and Goulden 1994; Ishida, Toma, and Marjenah 1999; Kosugi et al. 2009) and canopy scale (Goulden et al. 2004). Thus, as atmospheric CO_2 rises over the coming century, higher vapor pressure deficit caused by higher leaf temperatures could curtail the positive response of A to eCO_2. However, no controlled experiments have investigated CO_2 and temperature interactions in the Tropics.

In young, rapidly growing tree seedlings, an increase in leaf-level photosynthesis under eCO_2 generally results in an increase in growth, especially when accompanied by increased leaf area (Curtis and Wang 1998; Norby et al. 1999). Although the number of observations of tropical trees under eCO_2 is much fewer than that of temperate trees

(Körner 2009), results seem to be similar: eCO_2 can stimulate growth of young tropical trees (e.g., Cernusak et al. 2011). Similar interactions between eCO_2 and other resources have been observed in young tropical trees and temperate-zone trees. For example, the relative growth increase in two tropical tree species in response to eCO_2 was larger for plants grown under water deficit than for well-watered plants (Cernusak et al. 2011). Growth of tropical trees grown in local soil and under local climatic conditions was strongly stimulated by eCO_2 but only if fertilizer was added to the soil (Winter and Lovelock 1999).

In summary, the basic physiological responses of tropical trees to elevated CO_2 are similar to widely observed responses of temperate-zone trees. However, based on the much more extensive experimentation done with temperate trees, the primary responses of leaf-level photosynthesis and stomatal conductance, along with growth responses of young, individual trees, are insufficient for informing predictions of the integrated response of a forest ecosystem to eCO_2.

Major Uncertainties in Tropical Forest Response

FACE experiments in temperate forest ecosystems were valuable for testing hypotheses about forest response to eCO_2 based on insights gained from earlier studies (Norby and Zak 2011). Although no FACE experiments have been conducted in the Tropics, the lessons from temperate FACE experiments can highlight some critical areas of uncertainty that must be resolved to improve predictions of tropical ecosystem responses to atmospheric and climatic change.

In four temperate closed-canopy tree plantations across a wide range of productivity, NPP increased 23% (median response) in response to 550 ppm CO_2 (Norby et al. 2005). In closed-canopy (non-expanding) stands with relatively low LAI, much of the response to eCO_2 was related to increased light absorption, whereas in high LAI stands, the increase in NPP under eCO_2 was attributable to increased light-use efficiency. NPP represents the input of organic matter into an ecosystem but by itself does not predict ecosystem carbon storage, a process dependent on how carbon is partitioned to different plant and soil pools and the turnover times of those pools. FACE experiments have differed in this regard. For example, in one experiment, NPP stimulation occurred primarily in woody biomass, while in another forest, fine-root productivity was preferentially stimulated. Woody biomass has a substantially longer residence time (slower turnover) than fine roots (DeLucia, Moore, and Norby 2005), but some of the carbon deposited into soil by fine-root turnover may be retained in long-lived or protected pools (Iversen et al. 2012). Evaluation of tropical forest responses to eCO_2 thus must include analysis of NPP distribution to all pools, not just aboveground biomass. Analyzing root system responses is particularly important because of the many intersection points between roots and carbon, water, and nutrient cycles in ecosystems.

Temperate-zone experiments revealed the importance of nutrient availability and feedbacks between carbon and nitrogen cycles in modifying response to eCO_2. Even though nitrogen availability in three FACE experiments was demonstrably limiting to tree growth, nitrogen uptake increased in eCO_2, and NPP increased commensurately (Finzi et al. 2007). However, as one forest stand developed, nitrogen availability declined (especially in eCO_2), as did the stimulation of NPP in eCO_2 (Norby et al. 2010). Such interactions between eCO_2 and nitrogen have been predicted by models (Comins and McMurtrie 1993).

Many tropical forests may not be nitrogen limited, but strong evidence indicates that tropical photosynthesis is phosphorus limited (Vitousek 1984; Lloyd et al. 2001; Reich, Oleksyn, and Wright 2009). Although many questions remain about how phosphorus affects plant metabolism, enough is known to develop a semimechanistic phosphorus model on photosynthesis. With additional data from tropical trees, the effects of leaf phosphorus concentration on photosynthesis can be incorporated into models using a linear function based on Reich et al. (2009). New modeling approaches also are needed to simulate phosphorus availability, including its potential increase to trees under eCO_2 through stimulations of rhizosphere phosphatase activity (Wasaki et al. 2005), mycorrhizal establishment and activity (Lovelock et al. 1997), and deeper fine-root distribution (Iversen 2010).

Interactions between eCO_2 and water availability and use have been investigated in temperate ecosystems and could be highly important to tropical forests in a future high-CO_2 world. By increasing photosynthesis or decreasing water use via reduction in stomatal conductance (or both), water-use efficiency (WUE; carbon uptake per unit water loss) usually increases in response to eCO_2. Depending on other factors, especially leaf area responses, increased WUE may or may not result in decreased water use (Norby and Zak 2011), but increased WUE potentially could confer increased drought tolerance to trees in eCO_2 (Cernusak et al., in review). Increased soil moisture has been associated with eCO_2 in some experiments, with subsequent effects on soil respiration and nutrient turnover (Hungate et al. 1997).

Interactions between CO_2 and light derive from the effect of eCO_2 to increase light-use efficiency and decrease the light compensation point (Long and Drake 1991). Although plants in the deep shade of a closed tropical forest will have slow growth, their relative response to eCO_2 can be dramatic (Würth, Winter, and Körner 1998). Hence, eCO_2 has the potential to facilitate the expansion of plants into deeper shade (Körner 2009) and alter the species composition that results after a canopy opening. This issue is critical in determining the response of LAI and the associated change in land-atmosphere interactions under high CO_2 conditions. Controls on maximum LAI in vegetation models often are very crude "caps" on maximum leaf area and typically do not take into account the carbon balance of each leaf layer and the viability of leaf production in shade (Fisher et al. 2010). The models therefore generate highly varying responses to CO_2 fertilization because of this issue and the highly variable rules governing model allocation to plant tissues.

Despite details available on leaf-level photosynthesis, some remaining uncertainties could be particularly important in the Tropics. For example, stomatal and nonstomatal limitations on A are expected to increase with rising leaf temperatures in tropical canopies. However, the extent to which this temperature interaction will dampen the response of A and gross primary production (GPP) to rising $[CO_2]$ in tropical forests is not known. Some research also has suggested that eCO_2 could enhance the heat tolerance of tropical tree leaves (Hogan, Smith, and Ziska 1991), but this hypothesis requires experimental testing. Leaf-scale studies on temperate species have consistently shown that mesophyll conductance strongly impacts photosynthesis with an effect comparable to that of g_s (Niinemets et al. 2009). Sun et al. (in review) conducted a model simulation that suggested mesophyll conductance can cause a 24% reduction of model-estimated GPP in tropical rainforests. However, measurements of mesophyll conductance on tropical species are rare, and the validity of model parameters for such conductance in tropical species is unknown.

Few data are available describing differential sensitivity to eCO_2 among tropical species, but if such differences exist, they could represent a significant influence on forest structure resulting from revegetation of a forest gap or abandoned agricultural land. Lianas (woody vines) are increasing in Neotropical forests, representing one of the first large-scale compositional changes documented for old-growth tropical forests. Some research indicates lianas may be particularly sensitive to eCO_2 (Schnitzer and Bongers 2011), but other explanations unrelated to global change also have been offered for why they may be increasing (Wright, Hernandez, and Condit 2007). Nevertheless, a specific liana response to eCO_2 is an important hypothesis to test because more vigorous lianas—and their effects on tree mortality and growth suppression—would have far-reaching consequences for carbon storage (Phillips et al. 2002). The potential ramifications of increasing lianas are huge because these vines alter both tropical forest diversity and ecosystem functioning. At the community level, lianas affect tree species coexistence and diversity by competing more intensely with some tree species than others and thus will likely alter tree species composition. At the ecosystem level, lianas affect forest carbon and nutrient storage and fluxes. A decrease in forest carbon sequestration might be the most important consequence of liana increases. Lianas also reduce tree growth and increase tree mortality, thus reducing forest-level carbon storage. The increase in lianas, which have much less wood than trees, compensates only partially for the amount of carbon lost in the displaced trees. Because tropical forests contribute approximately one-third of global terrestrial carbon stocks and NPP, the effect of

increasing lianas for tropical forest carbon cycles may have serious consequences at the global scale.

Woody legumes are another plant functional type abundant in tropical forests and may be especially responsive to eCO_2 (Thomas et al. 1991; Tissue, Megonigal, and Thomas 1997; Cernusak et al. 2011).

Key Uncertainties and Research Opportunities

Underlying the need to gain a better understanding of CO_2 effects on tropical forests are several factors: (1) the certainty of tropical forests growing in and responding to increasing atmospheric CO_2 concentrations during this century, (2) importance of CO_2 fertilization effects in land process models and the climate models to which they are coupled, and (3) high uncertainty and lack of data about CO_2 effects and interactions in the Tropics. Efforts addressing these uncertainties are needed as part of a coordinated program to improve the ability to predict the responses of tropical forests to climate change and their feedbacks to the atmosphere and climate. Four research gaps are especially critical:

- **Will NPP of tropical forests increase in response to future concentrations of CO_2?** Retrospective analyses of tropical forest carbon stocks and tree growth have been inadequate for answering this question. Such analyses considered just part of the carbon budget (aboveground biomass), and they attempted to detect a response to a much smaller increase in CO_2 (e.g., from 330 to 380 ppm) than will be occurring in future decades. Furthermore, retrospective analyses cannot separate CO_2 effects from the confounding responses to many other uncontrolled environmental variables. Hence, failing to unambiguously detect a response to past increases in CO_2 says little about the potential for rising CO_2 to affect the metabolism and ecology of tropical forests. Getting NPP responses right in models requires new data and understanding of leaf-level gas exchange under tropical conditions, modification of those responses by temperature and nutrient (especially phosphorus) interactions, and integration of leaf-level responses across complex canopies and landscapes.
- **Will increased NPP increase ecosystems' carbon storage?** NPP is just the first, but necessary, step in addressing longer-term ecosystem carbon cycling questions. A critical uncertainty is how increased NPP is allocated to different plant and soil pools. The response of root production and turnover to elevated CO_2 in tropical forests is completely unknown, yet root responses have many important interaction points with an ecosystem's carbon, water, and nutrient budgets.
- **Will eCO_2 alter forest responses to drought?** Seasonal and episodic droughts are one of the most significant environmental factors affecting tropical forests, and drought is projected to be increasingly important in the future. Because eCO_2 has a strong potential for ameliorating drought responses, predictions of tropical forest responses to future drought scenarios will be unreliable unless the effects of eCO_2 are considered.
- **Will eCO_2 alter community composition?** Tropical forests are dynamic and diverse. Establishment of a new forest—whether in a forest gap created by a tree fall, after a large-scale disturbance (e.g., wind or fire), on abandoned land previous managed for crops or pasture, or at the forest-savannah border—can entail intense competition among species with differing resource requirements. Because tree seedlings in an exponential growth phase can respond much more strongly to eCO_2 than trees in a closed forest, eCO_2 has the potential to alter competitive outcomes and influence the trajectory of forest development (Souza et al. 2010). This in turn has long-term consequences for carbon cycling and climate feedbacks. Although there are some indications of differential responses to eCO_2 among tropical plant species or functional types, the effects of eCO_2 on forest establishment are undetermined and a modeling framework for incorporating such effects does not yet exist.

Addressing These Uncertainties

Unlike other aspects of global change, there is no possibility of substituting space for time or taking advantage of interannual variation to better understand the response of the Tropics to rising CO_2. Hence, intact tropical ecosystems are considered to

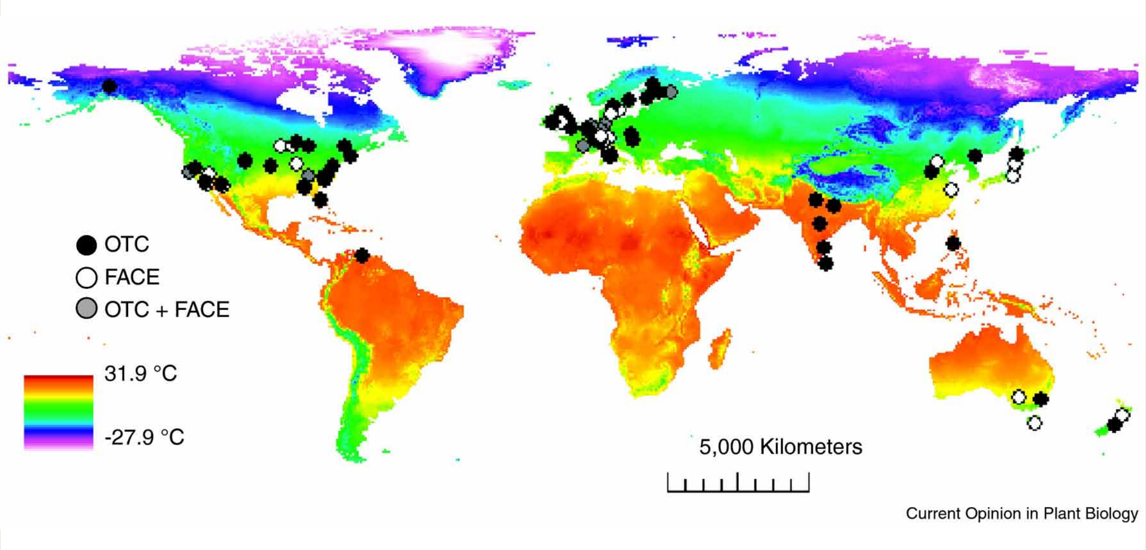


Fig. 3.3. Global Distribution of Elevated [CO_2] Experiments in Open-Top Chamber (OTC) and Free-Air CO_2 Enrichment (FACE) Facilities Where Plants Have Been Rooted in Soil. [Reprinted with permission by Elsevier from Leakey, A. D. B., K. A. Bishop, and E. A. Ainsworth. © 2012. "A Multi-Biome Gap in Understanding of Crop and Ecosystem Responses to Elevated CO_2," *Current Opinion in Plant Biology* **15**(3), 228–36.]

be high-priority targets for a next-generation FACE experiment (Calfapietra et al. 2010). In temperate ecosystems, open-top chamber (OTC) and FACE studies enabled significant advances in mechanistic understanding and constrained estimates of the response of temperate plants and ecosystems to rising CO_2 (Norby and Zak 2011). Results from temperate FACE experiments can be used to highlight critical uncertainties and guide hypotheses about possible tropical responses, but the inference space from these studies does not extend to tropical forests. CO_2 manipulation experiments have been strikingly absent in the Tropics (see Fig. 3.3, this page), and new FACE or OTC studies certainly would be highly informative. Current understanding of the CO_2 response in tropical systems is based on only a few experiments in which plants were rooted in soil and none in which the artifacts associated with enclosures were absent. FACE or OTC studies will be required to gain the process-level understanding, model algorithms, and scaling rules needed for integrating physiological processes with complex, whole-plant, and ecosystem feedbacks. These feedbacks are unique to the Tropics and undoubtedly will shape the response of tropical systems to rising CO_2. Critical resource interactions (e.g., drought and nutrient limitations) can be part of a long-term experimental campaign on eCO_2 by incorporating natural variability in precipitation, imposing extreme droughts, relieving nutrient limitations after baseline responses are established, or establishing experimental sites across resource gradients.

Clearly, no experiment or small set of experiments can ever represent the full diversity of the tropical biome. Furthermore, many of the critical questions about the role of tropical forests in global carbon cycling are inherently long term (e.g., 50 to 100 years). Models well informed and constrained by experimental observations offer an opportunity to extrapolate through space and time. Hence, an important strategy for designing experiments that will provide the most useful and needed data and process understanding is to engage a modeling perspective from the start. Existing ecosystem models as described in this chapter can identify the most critical uncertainties that can be addressed in models and also define specific hypotheses to guide the experimental approach.

CHAPTER 4

Temperature Effects on Tropical Plant, Soil, and Ecosystem Processes

Temperature Effects on Tropical Plant, Soil, and Ecosystem Processes

Overview

Earth system models (ESMs) predict temperature increases of 2 to 5°C in tropical regions by 2100 (IPCC 2007 A1B scenario; Christensen et al. 2007), and more recent work suggests tropical forests could be facing a sustained and significant shift toward a novel temperature regime within the next two decades (Anderson 2011; Diffenbaugh and Scherer 2011). Because lowland tropical forests typically maintain low seasonal and interannual variability in temperature, the majority of temperature research has focused on higher-latitude ecosystems where temperature changes are more apparent. The primary nonanthropogenic drivers of ecosystem change in tropical forests, however, often are thought to be carbon dioxide (CO_2) fertilization, shifts in precipitation, and stronger storms with a warming climate (Davidson, Ishida, and Nepstad 2004; Lewis, Malhi, and Phillips 2004; da Costa et al. 2010; Elmendorf et al. 2012; Emanuel 2005; Negrón-Juárez et al. 2010). Recent studies have challenged this view, suggesting that tropical forests could respond markedly to small increases in temperature (Clark et al. 2003; Lewis et al. 2009b). However, predicting the effects of increased temperature on the carbon balance in tropical forests is complicated by wide forest diversity (see Chapter 2, Regional Differences in Tropical Forest Response to Climate Change, p. 7). Given that most tropical forests are already quite warm [88% experience mean annual temperatures ≥ 20°C (FAO 2010)] and are responsible for cycling vast amounts of carbon, improving the ability to accurately predict their response to increased temperature is imperative (Booth et al. 2012). Presented in this chapter is an overview of the current understanding of temperature effects on key ecosystem processes and associated uncertainties. For more in-depth discussion of these topics see Wood, Cavaleri, and Reed (2012); Corlett (2011); and Reed, Wood, and Cavaleri (2012).

Temperature Effects on Plant Processes

Photosynthesis and Stomatal Conductance

Leaf-level photosynthesis experiments have shown that photosynthetic uptake rates increase with temperature until a thermal optimum is reached, beyond which rates begin to decline (Berry and Bjorkman 1980). Whether tropical forests are at or near a temperature threshold—leading to an overall decline in photosynthetic rates in the near future—is subject to debate (Doughty and Goulden 2008a; Lloyd and Farquhar 2008). At the leaf level, thermal optimums for photosynthesis of tropical tree species are between ~33 and 40°C, while eddy flux studies of tropical forests show overall declines in canopy-level photosynthesis at significantly lower temperatures (~20 to 27°C; Wood, Cavaleri, and Reed 2012). Photosynthesizing leaves in tropical forests exist in two states: cool and light-limited vs. warm and light-exposed. Research indicates that the warm, illuminated leaves—which are most responsible for photosynthesis—are at the upper limit of the photosynthetic temperature optimum. This observation implies a strong possibility for reduced photosynthesis with warming (Doughty and Goulden 2008a). The disconnect between leaf- and canopy-level photosynthetic response to temperature, while crucial for accurately representing tropical forest carbon flux, is not well represented in current models.

Warming temperatures have both direct physiological effects on photosynthetic machinery and indirect stomatal effects, with increased temperature associated with decreased relative humidity and higher vapor pressure deficit (VPD) and thus reduced stomatal exchange (Sage and Kubien 2007; Lloyd and Farquhar 2008). Direct physiological effects of warming under expected elevated CO_2 scenarios (>380 parts per million) include a decline in electron transport (J_{max}) and irreversible denaturation of enzymes associated with photosynthesis (especially RuBisCO activase; Sage and Kubien

2007). However, interactions between increased CO_2 concentrations and increased temperature may attenuate much of this reduction (Taub, Seemann, and Coleman 2000). Many models represent the temperature sensitivity of J_{max}, and whether indirect stomatal effects (Lloyd and Farquhar 2008) or direct effects of temperature on photosynthetic machinery (Doughty 2011) will dominate in tropical forests with increased temperatures is subject to debate. Data on either direct or indirect effects of temperature on tropical tree photosynthesis are quite sparse, and only a handful of potted seedling or branch- and leaf-warming studies are available from which to glean model parameters for tropical forests (Cunningham and Read 2002; Cunningham and Read 2003a; Cunningham 2005; Doughty 2011; Tribuzy 2005).

Climate-induced warming is likely to be associated with constant relative humidity due to increased evaporation from higher surface temperatures (Held and Soden 2006). However, on diurnal timescales, absolute humidity is more constant so that relative humidity decreases with increasing temperature (Lloyd and Farquhar 2008). The resulting "midday depression" of photosynthesis that has been measured in tropical forest canopies (Koch, Amthor, and Goulden 1994) may or may not hold true with longer-term warming. Furthermore, recent evidence suggests that tropical plants are unable to acclimate under longer-term warming conditions (Cunningham and Read 2003b; Doughty 2011). While these studies are limited to seedlings and branch-warming experiments, they suggest that tropical trees may not have the plasticity to respond to increasing temperatures because these plants develop under lower diurnal, seasonal, and interannual temperature variation. If photosynthesis is unable to thermally acclimate in the long term, tropical species may be more sensitive to climate change than temperate ones, potentially leading to an overall decrease in the strength of the carbon sink in tropical forests. Most models currently do not represent photosynthetic acclimation, and data on the thermal acclimation potential of tropical tree species are very limited because no *in situ* warming studies have been conducted in any tropical forest.

Autotrophic Respiration

The rates of autotrophic respiration (CO_2 respired by stems, leaves, and roots) increase with temperature over the short term in a roughly exponential relationship. For tropical rainforest trees, mean foliar and woody respiration Q_{10} values (the proportional change in rate with a 10°C rise in temperature) range from 1.8 to 2.3 (Ryan et al. 1994; Meir, Grace, and Miranda 2001; Cavaleri, Oberbauer, and Ryan 2008). To our knowledge, no studies have investigated Q_{10} values of tropical tree roots despite the fact that root respiration is estimated to account for 24 to 38% of total soil respiration in some tropical forests (Silver et al. 2005a; Sayer and Tanner 2010). Accounting for this dynamic response of autotrophic respiration to temperature is now recognized as essential for properly quantifying ecosystem respiration on a diurnal basis (Wythers et al. 2005), and with all else held constant, future warming might be expected to increase autotrophic respiratory losses of CO_2 to the atmosphere (Wythers et al. 2005; Atkin et al. 2008).

The temperature sensitivity of respiration is not constant with temperature (Tjoelker, Oleksyn, and Reich 2001; Atkin and Tjoelker 2003), and short-term respiration-temperature responses are not necessarily applicable to predicting long-term change with warming because acclimation to sustained changes in temperature is typically observed (Atkin and Tjoelker 2003). Respiratory thermal acclimation of leaves, wood, or roots (decreasing Q_{10} with increasing growth temperatures) can result from limited substrate availability or changes in enzyme activity (Atkin and Tjoelker 2003). As production shifts in response to changing climate, the potential for respiration ultimately may be limited by carbon supply. If substrate (photosynthate) availability is the primary driving force behind respiratory thermal acclimation of plants, then the acclimation potential of photosynthesis becomes the ultimate driver of the response of tropical forests to a warmer world. However, there have been only limited studies on the short-term respiration-temperature responses of tropical plants and no investigations of the long-term thermal acclimation of foliar, wood, or root respiration of tropical trees. This lack of research makes determining or predicting respiratory acclimation difficult.

Volatile Organic Carbon Emission

In addition to respiratory losses, 30 to 50% of all tropical trees emit volatile organic carbon compounds (VOCs), especially isoprene (Lerdau and Keller 1997; Harley et al. 2004), which has been suggested to be the single largest global source of photochemically reactive compounds in the atmosphere (Lerdau and Keller 1997). Isoprene emissions typically are observed to increase with increasing temperature (Guenther et al. 2006) and at high temperatures may be important both for the net carbon balance of forests and for atmospheric chemistry and secondary organic aerosol formation (Clark 2004; Harley et al. 2004). While isoprene helps plants tolerate high temperatures in the short term, it may not be helpful under long-term sustained warming because production may be limited by substrate supply (Sharkey, Wiberley, and Donohue 2008). These processes are beginning to be included in ESMs, though with great uncertainty (see Chapter 8, Biosphere-Atmosphere Interactions: Greenhouse Gases, Reactive Chemicals, and Aerosols, p. 55).

Plant Water Use

Warming may have indirect effects on tropical forest water balance. For example, certain species with better-adapted hydraulic architecture may outcompete more poorly adapted species, or increased temperatures may affect whole-plant water use via changes in water supply or evaporative demand. Evidence from a Costa Rican lowland tropical forest shows that transpiration may be more responsive to air temperature than to precipitation when soils are saturated (O'Brien, Oberbauer, and Clark 2004). In a more seasonal tropical rainforest in Brazil, however, transpiration was primarily driven by soil and root hydraulic resistance (Williams et al. 1998). Whole-canopy transpiration depends on the resistance of both stomata and the canopy boundary layer (Meinzer et al. 1997). While warming may greatly influence stomatal behavior, it will have little effect on boundary layer thickness (unless wind speed is affected indirectly). Some studies suggest that boundary layer conductance is actually a more important driver of canopy transpiration in tropical forests (Meinzer et al. 1997), but the opposite also may be true. The relative influence of boundary layer vs. stomatal conductance on whole-canopy transpiration is difficult to determine in the field.

Species-specific hydraulic architecture may greatly influence whole-forest response to warming. Trees that either have deep roots or are able to hydraulically redistribute water within soil profiles (as has been found among Amazonian species) may have a competitive advantage over other trees (Oliveira et al. 2005; Stork et al. 2007). For shallow-rooted species, hydraulic redistribution may be a mechanism that helps buffer the detrimental effects of increased evaporative demand with warming. Xylem architecture variation can greatly affect competitive advantage, as well. Lianas are more vulnerable to cavitation (disruption of the xylem water column by air emboli caused by high tension during transpiration) but also are able to transpire more water than a given tree of the same diameter (Fisher and Ewers 1995). Given the increasing abundance of lianas in the Neotropics (Phillips et al. 2002; Schnitzer and Bongers 2011), their high transpiration rates may increase the susceptibility of forests as a whole to water stress caused by increased warming. Alternatively, liana cover may buffer the responses of host tree sap flow to extreme temperatures, as was observed in Costa Rica (O'Brien, Oberbauer, and Clark 2004). The diversity of root architecture, soil water partitioning, and hydraulic architecture is neither well explored in tropical forests nor well represented in modeling efforts. Nevertheless, including this type of data in models would be important for understanding how water balance may be affected by the increased evaporative demand resulting from warmer temperatures.

Individual Plant Growth and Carbon Allocation

Overall tree growth depends on the partitioning of assimilated carbon, but growth rates cannot always be predicted by photosynthesis rates. For example, tropical rainforest species in Australia had optimum growth under much higher temperatures than is ideal for photosynthesis, indicating that growth can continue to increase with rising temperatures even as photosynthesis declines (Cunningham and Read 2003a). The apparent disconnect between photosynthesis and growth showed that carbon source and sink activity could have more influence over a tree's growth rate than CO_2 exchange. In addition, achieving a mechanistic understanding of tropical tree growth response to warming requires investigating the effects of temperature on plant cell division and expansion (Ryan 2010). However, no such studies have yet been conducted for tropical species.

Few experiments have investigated warming effects on tropical tree growth or morphology, and no large-scale field warming manipulation study exists anywhere in the Tropics. A recent global meta-analysis found decreased root:shoot ratios and taller, thinner stems under increasing mean annual temperatures. However, the same study indicated that tree growth in tropical forests decreased overall with warming compared to boreal and temperate forests where growth increased (Way and Oren 2010). A study of tropical tree seedlings, on the other hand, showed increased biomass allocation to roots vs. leaves under warming treatments (Cunningham and Read 2003a). Accordingly, increased temperatures may affect not only growth rates but also tree morphology and above- vs. belowground allocation, both of which are largely missing from many modeling efforts. Nevertheless, understanding how temperature affects carbon allocation is critical to predicting how both carbon flux and storage respond to or change with warming in tropical forests.

Recognizing that forests may respond to warming differently over different timescales also is important. Plant acclimation to warming with respect to photosynthetic rates will vary over the lifetime of individual trees in addition to any adaptation that is expressed through the replacement of individuals and species with others that may be more competitive under a changed climate. Thus, ecosystem-level responses over longer timescales are likely to be quite different from individual responses. A further (theoretical but disputed) uncertainty is whether higher temperatures will lead to increased plant mortality as a result of metabolic limitation, a response (McDowell et al. 2011) that in turn could lead to changes in forest community structure and distribution of tree lifetimes.

Temperature Effects on Soil Processes

Tropical forest soils contain more carbon than any other terrestrial biome and about twice the amount found in the aboveground vegetation (Raich and Schlesinger 1992; Jobbágy and Jackson 2000). The capacity to predict and ameliorate the consequences of global warming thus depends, in part, on an improved understanding of the temperature sensitivity of processes controlling carbon cycling and storage in tropical forest soils. Although no *in situ* warming experiments have been conducted in tropical forest ecosystems, field warming studies in high-latitude ecosystems and tropical soil laboratory incubations (e.g., Holland et al. 2000) suggest that soil respiration will increase with warming in the short term (months to years) and ultimately acclimate over the longer term (2 to 15 years). Completely unknown, however, is the amount of time before thermal acclimation of soil respiration would occur and the amount of carbon that would be released to the atmosphere in that time frame. Various theories have been suggested to explain the observed thermal acclimation of soil respiration in higher-latitude ecosystems (Kirschbaum 2000; Davidson and Janssens 2006; Bradford et al. 2008; Kleber 2010), yet how these theories will apply to tropical forests remains highly uncertain. Described in detail below are the current understanding of and evidence for temperature effects on tropical forest soil processes.

Heterotrophic Respiration

There are two types of respiration in soils: heterotrophic (CO_2 respired by microbes) and autotrophic (CO_2 respired by plant roots). Incubations of tropical forest soils would suggest that soil microbes respond positively to short-term exposure to elevated temperatures, with notably high soil respiration rates observed at temperatures as warm as 55°C when substrate is not limiting (Holland et al. 2000; Balser and Wixon 2009). Although the longer-term responses of soil heterotrophic communities to elevated temperature remain uncertain, potential effects could include a shift in community composition, biochemical acclimation of respiration, and changes in carbon-use efficiency. Each result would significantly alter the trajectory of

the temperature response of soil respiration in tropical forests (Balser and Wixon 2009; Allison, Wallenstein, and Bradford 2010; Bradford, Watts, and Davies 2010). The role of the chemical complexity of soil carbon represents another challenge to quantifying the effect of temperature on soil heterotrophic respiration. Soil respiration responses to temperature are, in part, regulated by the quality of carbon the heterotrophs consume (Davidson and Janssens 2006). If elevated temperature alters soil organic carbon inputs or stocks, both soil respiration rates and responses to continued temperature change could be affected. However, the importance of different carbon chemical pools in regulating soil microbial respiration responses to changing temperature remains a topic of significant debate (Giardina and Ryan 2000; Fang et al. 2005; Conant et al. 2008; Kleber 2010). High variability among tropical forests in the size of the easily accessible labile carbon pool and in the depth profiles adds an additional layer of complexity (Jobbágy and Jackson 2000). Finally, plant photosynthesis and soil respiration are tightly linked (Högberg et al. 2008; Kuzyakov and Gavrichkova 2010). Not only is root respiration an important component of tropical soil CO_2 efflux (see Autotrophic Respiration section, this page), but carbon allocated by plants to soils (via root exudates) also could supply key substrate for heterotrophic soil respiration. Thus, if warming reduced photosynthesis and carbon exudation belowground, it also could dramatically affect soil respiration rates (see the Plant-Soil Feedbacks section, this page). Research exploring soil microbial responses to increased temperature across a diversity of tropical soil types would be essential for accurately predicting the fate of tropical soil carbon in a warmer world. Because soil heterotrophic CO_2 fluxes to the atmosphere are very large, determining their response to elevated temperature also would be important at the global scale.

Autotrophic Respiration

Root respiration is estimated to account for as much as 24 to 38% of total soil respiration in some tropical forests (Silver et al. 2005a; Sayer and Tanner 2010). Studies that evaluate microbial responses alone thus exclude a significant component of soil respiration and consequently could lead to inaccurate representations of soil respiration in global models. Evidence from high-latitude systems suggests that temperature may influence root respiration via its effects on photosynthesis and allocation of photosynthate to roots. Changes in plant carbon allocation to roots and in the distribution of roots within the soil profile could further alter soil respiration rates (Davidson et al. 2000a; Sotta et al. 2006; Metcalfe et al. 2007). Little is known about either the temperature sensitivity of tropical root respiration or the influence of temperature on the mass and distribution of roots in the soil profile.

Plant-Soil Feedbacks

As highlighted above, soil and plant processes are intricately linked, and the temperature response of carbon cycling in tropical forest soils cannot be accurately predicted without considering how temperature affects a variety of aboveground processes. For example, increases in litter and root inputs have been shown to stimulate additional CO_2 loss from soils via a process known as "priming" (Sayer, Powers, and Tanner 2007; Kuzyakov 2010; Kuzyakov and Gavrichkova 2010). Priming occurs when soil heterotrophs respond to additional carbon inputs by respiring carbon well beyond the amount added. These litter and root inputs have primed the soil heterotrophic community to decompose soil organic carbon that otherwise would remain stabilized within the soil. Plants also may change belowground carbon allocation patterns under increasing temperature, potentially leading to differences in the amount and location of autotrophic respiration in the soil profile and also changes in soil heterotrophic respiration. Through these mechanisms, changes in the quality and quantity of litter and root inputs subsequently can determine the short- and long-term stability of that carbon in the soil profile (see Chapter 10, Belowground Processes: Roots and Soil Biogeochemistry, p. 69). The potential for plant temperature responses to have subsequent effects on soil processes is strong. High research priorities therefore include belowground studies investigating the effects of increased temperature on aboveground net primary productivity (NPP) and plant carbon allocation, as well as the linkage between photosynthesis and root respiration.

Nutrient Cycling

An exciting advance in recent modeling efforts is a focus on the significant role nutrient cycling could play

in net carbon flux responses to warming (Thornton et al. 2009; Wang and Houlton 2009; Bonan and Levis 2010). A robust inclusion of nutrient cycling could similarly improve tropical modeling efforts. The few tropical fertilization studies that exist support the conclusion that soil nutrient availability plays a large role in regulating carbon flux and storage in tropical forests (Vitousek and Farrington 1997; Tanner, Vitousek, and Cuevas 1998; Cleveland and Townsend 2006). Temperature can dramatically affect the rates of various nutrient cycling pathways that regulate nutrient availability and loss (e.g., nitrogen mineralization, phosphorus mineralization, and nitrification). Accordingly, temperature effects on nutrient cycling and subsequent feedbacks to carbon cycling pathways, such as aboveground NPP, represent major uncertainties in predicting how increased temperature will influence ecosystem processes in tropical forests.

Temperature Effects on Ecosystem Carbon Balance

Potential effects of warming on ecosystem carbon balance can be assessed using several approaches, such as elevation gradients, cross-site comparisons, eddy covariance, coupled carbon-climate models, and field warming experiments (Wood, Cavaleri, and Reed 2012). Cross-site comparisons and elevation gradient studies suggest that forest NPP will increase enough to offset any additional loss in soil carbon caused by warming, leading to no net change in ecosystem carbon balance (Raich et al. 2006). However, these results probably will have limited applicability to understanding future responses, given the likelihood that most tropical forests will experience novel temperature regimes within the next two decades (Wright, Muller-Landau, and Schipper 2009; Anderson 2011; Diffenbaugh and Scherer 2011). Results from eddy covariance and ESMs predict that tropical forests will become a net source of carbon, but eddy covariance results vary among studies depending on the duration (Grace et al. 1996; Loescher et al. 2003; Hutyra et al. 2007; Doughty and Goulden 2008a), and models disagree on what the primary drivers of increased carbon loss will be (White, Cannell, and Friend 2000; Cramer et al. 2001). Interannual variability also can be used to infer relationships between temperature and tropical forest productivity. For example, warmer El Niño years are associated with reduced growth at the site level, as well as reduced overall carbon uptake from tropical forests (Clark et al. 2003). However, the hydrologic cycle co-varies strongly with temperature on this timescale, so inferring a strict temperature response from these relationships is difficult. Furthermore, we know of no studies that evaluate long-term variability (>10 years) of the net ecosystem carbon balance of tropical forests (i.e., both above- and belowground responses). Resolving the potential effects of temperature on the net carbon balance in these ecosystems will require an improved understanding of temperature controls on the flow of carbon into and out of the system over multiple spatial and temporal scales. Using a variety of approaches in concert would allow research questions to span these scales and could offer the richest insight and predictive power into how tropical forest carbon balance will respond to increased temperatures.

Representation in Global Models

Aboveground Representation

Model representation of foliar respiration currently is based on the hypothesis that tissue nutrient concentration dictates basal maintenance respiration rates (Ryan et al. 1994). If plant respiration acclimates to increased temperature, modelers may have cause (at least for tropical forest vegetation) to more explicitly represent the influence of plant-scale source and sink relationships on tissue basal respiration rates and temperature responses. These changes would have important consequences for global-scale carbon-climate feedbacks, although speculating the magnitude of the effect at the global scale is not yet possible.

In ESMs, parameters describing carbon allocation are some of the most sensitive constraints on total growth and accumulation of vegetation and soil carbon stocks over time (White, Cannell, and Friend 2000). However, such parameters are poorly defined for tropical forests, so research investigating temperature effects on these processes would provide critical new constraints on model performance. In turn, these improvements likely would have important consequences for predicting global-scale carbon balance and changes under a warming climate. ESMs currently have limited dynamic range for their allocation parameterization,

partly because of a lack of both data and understanding of the fundamental processes guiding carbon allocation patterns in real ecosystems.

Belowground Representation

Current representation of soil carbon cycling in ecosystem-scale models does not effectively enable prediction of belowground tropical forest responses to climate change. Models parameterized with temperature functions developed for temperate systems are highly unlikely to adequately simulate tropical ecosystems, which harbor plants and microbes with specific carbon-use efficiencies and acclimation potentials (see Chapter 10, Belowground Processes: Roots and Soil Biogeochemistry, p. 69). Research that refines rate variables and temperature functions for key belowground processes in tropical forest soils (i.e., autotrophic and heterotrophic respiration) across diverse soil types is critical for accurately representing such processes in traditional and Tropic-specific soil carbon cycling models.

Few ESMs explicitly incorporate fundamental ecological interactions between carbon and nitrogen cycling in their land components. However, those that do suggest that nitrogen biogeochemistry can significantly affect the carbon cycle feedback in climate simulations (Randerson et al. 2009; Bonan and Levis 2010). Given that carbon cycling in lowland tropical forests is commonly considered phosphorus limited (Walker and Syers 1976; Vitousek 1984), phosphorus availability could constrain the response of organisms to changing temperature, and temperature-induced effects on this availability (e.g., via altered phosphorus mineralization rates) could affect carbon cycling in tropical ecosystems. Key research gaps include improved understanding of how soil nutrients regulate tropical carbon cycling, better insights into how temperature will affect soil nutrient availability, and effective incorporation of phosphorus cycling into ESMs.

Ecosystem Representation

Currently, the most widely used tropical simulations do not represent the full range of climate possibilities, nor do they account for the immense diversity of tropical forest ecosystems. These uncertainties are compounded by a general lack of understanding of the potential biological consequences of warming on tropical forest processes. Model experiments are needed that explore the range and variability of tropical forest responses to temperature change at multiple scales. Furthermore, multidimensional sensitivity analyses of models to variations in subcomponent temperature functions would help determine which pools, parameters, and processes can maintain subtle changes yet have large effects on carbon cycling and future climate.

Key Uncertainties and Research Opportunities

Research that simultaneously explores above- and belowground responses to temperature and the linkages between plants and soil is vital for accurately predicting the net response of tropical forests to increased temperature (Wood, Cavaleri, and Reed 2012). For some areas of tropical forest research, however, almost no field data on temperature responses are available. These areas include nutrient cycling, heterotrophic vs. autotrophic respiration, thermal acclimation vs. substrate limitation of plant and soil microbial communities, belowground carbon allocation, temperature effects on plant and microbial species composition, hydraulic architecture of roots, sensitivity of soil carbon loss to temperature, and temperature effects on abiotic soil properties. Because of fundamental differences between tropical forests and other biomes and the large diversity among tropical forests themselves, knowledge about temperate systems may reveal little about the potential effects of increased temperature on tropical forests. ESMs require new data to correctly represent the effects of increased temperatures on tropical forest carbon balance across diverse landscapes. Key research uncertainties and gaps are:

- **How will warming temperatures affect canopy gas exchange in tropical forests?** Investigations of tropical tree responses to increased temperature reveal large uncertainties in understanding how photosynthesis and autotrophic respiration will respond to warming. These uncertainties, which greatly constrain the ability to predict future global carbon cycling and feedbacks to climate, include the following: Will tropical plant photosynthesis acclimate to long-term warming?

If photosynthesis is reduced with warming, will plant respiration (leaf, wood, root) decline concomitantly via substrate limitation? Will the effects of warming on tropical plant photosynthesis be primarily stomatal or biochemical? How do long-term responses to increased temperature relate to those observed in the short term, and how does temporal variation in net photosynthetic responses drive overall carbon exchange between tropical forests and the atmosphere? How can canopy-level gas exchange best be modeled using leaf-level information? What are the long-term temperature responses (i.e., acclimation or substrate limitation) of volatile organic compounds in tropical forest canopies? How will increased temperature interact with other environmental stresses (e.g., drought) and ecosystem characteristics (e.g., phosphorus availability) to affect aboveground carbon cycling?

- **How will increasing temperature affect patterns of above- vs. belowground carbon allocation and overall morphology of tropical trees?** Changes to carbon allocation and source and sink relationships can greatly affect carbon storage, with direct implications for altering the net exchange of carbon between tropical forests and the atmosphere. Little is known about how increasing temperature will alter carbon allocation to above- vs. belowground pools (e.g., root biomass and exudation), and no research has been done to investigate the effects of increasing temperature on cell expansion and division of tropical plant species.

- **How will temperature effects on both above- and belowground processes regulate gross and net carbon fluxes?** Strong evidence suggests that above- and belowground processes will respond to changing climate in concert. However, no studies simultaneously investigate canopy and soil warming, and a whole-system perspective may be difficult to gather from studies that do not explore above- and belowground effects concurrently. For example, reduced photosynthesis can quickly result in reduced belowground respiration without any change to root biomass.

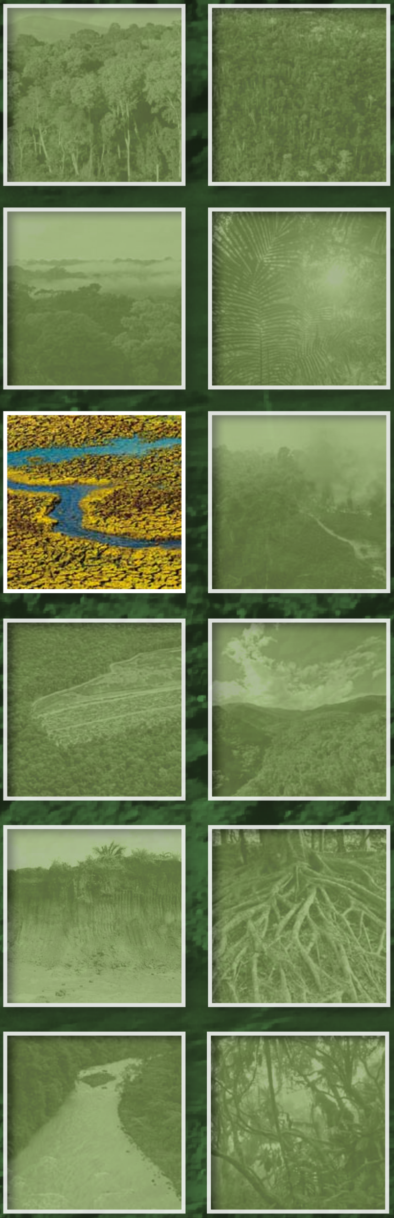
- **Will soil respiration (autotrophic and heterotrophic) acclimate to increased temperature?** No field warming experiments currently exist in the Tropics, but evidence from high-latitude experiments would suggest that soil respiration will acclimate to increased temperature. If so, what is the primary driver (e.g., substrate limitation, changes in microbial carbon-use efficiency) of this response? Over what timescales will this acclimation occur, and how will it vary among different tropical forests?

- **How will nutrient availability interact with increased temperature to regulate carbon cycling and storage?** Current model simulations suggest that temperature-nutrient interactions could strongly regulate carbon cycling and storage. For example, nutrient limitation to tree growth and soil respiration could help mediate forest responses to increased temperature. If so, temperature effects on soil nutrient availability (e.g., via changes to mineralization rates) could act as important indirect controls over tropical forest carbon exchange.

- **How will increased temperature affect whole-forest water use?** As temperature increases, so does vapor pressure deficit. Plants can respond to these changes through various mechanisms, each of which could differentially interact with other ecosystem processes related to carbon cycling and storage. Specific questions include: What is the relative importance of stomatal vs. boundary layer conductance in whole-forest water use? How does distribution of species-specific root architecture, xylem architecture, and hydraulic redistribution affect response to warming in tropical forests? Although characterized by relatively abundant rainfall, tropical forests depend greatly on the availability of water. Because of the tight coupling between water and carbon cycling, increased temperature has the potential to alter carbon cycling and storage via changes to water use.

CHAPTER 5

Drought and Drought-Induced Mortality in Tropical Forests



Drought and Drought-Induced Mortality in Tropical Forests

The vulnerability of tropical forest trees to drought and drought-induced mortality is a function of climate risk and vegetation sensitivity (Meir and Woodward 2010). Both historical evidence and model predictions indicate increasing exposure of tropical forests to drought. In recent decades, severe episodic droughts have affected tropical forests globally in association with El Niño incidence, especially during 1982–83 and 1997–98. Unrelated to El Niño, two exceptionally severe (e.g., "1-in-100 year") drought events occurred in Amazonia in 2005 and 2010 (see Fig. 5.1, this page; Cox et al. 2008; Marengo et al. 2008, 2010; Lewis et al. 2011) during a period of increased weather extremes in several areas of South America (Marengo et al. 2012). Modeled future climate scenarios (IPCC 2007) indicate overall warming over the tropical biome and spatially nonuniform changes in rainfall. Climate models vary with respect to their fidelity in predicting 20th century rainfall in Amazonia (the region for which the most intensive analyses have been performed) and with their predictions of 21st century drought (Jupp et al. 2010). However, in an ensemble analysis by Malhi et al. (2008), models agreed on the scenario of an increased likelihood of drying and warming, especially in eastern and southern Amazonia (IPCC 2007). Model analyses also indicate a likely increase in drought severity associated with increased deforestation and other land-use change (Werth and Avissar 2002; Soares-Filho 2006).

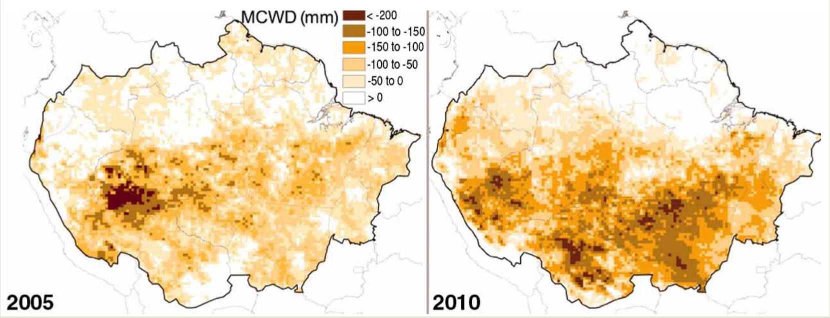
Nonlethal Effects of Moisture Stress

Overview

Nonlethal physiological effects of drought on forest ecosystems include changes in photosynthetic uptake, alterations in plant and soil respiration rates, and subsequent shifts in growth rates. Thus, even if drought thresholds are not reached, drought may still induce significant changes in forest carbon storage (Phillips et al. 2009). Physiological responses to drought are known to depend on a combination of (1) climate patterns (with respect to prevailing past variability), (2) subsurface moisture storage capacity (in soil, saprolite, and rock aquifers), (3) plant adaptations (particularly rooting behavior and stem construction), and (4) plant physiological strategies. The interactions among these factors may be complex and are examined at both plant and ecosystem scales.

Establishing how intact rainforests respond to anomalously low rainfall is difficult because natural droughts are rare in space and time, and the logistics of making detailed physiological measurements typically preclude intense observations during these unpredictable events (although simpler measurements may be deployable, given appropriate planning). Current understanding of the long-term effects of moisture stress on plant physiology, ecology, and vegetation-atmosphere interactions remains limited because few ecosystem-scale datasets exist for

Fig. 5.1. Drought Intensity and Tree Mortality in the Amazon. The difference in the 12-month (October to September) maximum cumulative water deficit (MCWD) from the decadal mean (excluding 2005 and 2010) is shown for the two most extensive droughts of the 21st century in Amazonia. This difference represents a measure of drought intensity that correlates with tree mortality. [From Lewis, S. L., et. al. 2011. "The 2010 Amazon Drought," *Science* **331**(6017), 554. Reprinted with permission from AAAS.]



periods of detectable moisture stress and such data have been collected only for relatively short periods (Malhi et al. 1998).

Although drought-related inventory data exist (e.g., Phillips et al. 2009, 2010), the main datasets available for constraining physiological responses to water stress in mature humid tropical forests derive from throughfall exclusion experiments. At large scales (e.g., 1 hectare), only two such studies have been implemented, both in eastern Amazonia, at Caxiuanã and Tapajós in Brazil (see Fig. 5.2, this page; Meir et al. 2008). A third, smaller-scale experiment has been implemented in Sulawesi in Southeast Asia (Schuldt et al. 2011; van Straaten, Veldkamp, and Corre 2011). Soil-only rainfall exclusion or irrigation experiments also have been performed at the scale of a few square meters (Vasconcelos et al. 2004; Cleveland et al. 2010; Wood and Silver 2012). These studies have the advantage of allowing more treatment replication, but the results are focused on soil biogeochemistry, considered in Chapter 10, Belowground Processes: Roots and Soil Biogeochemistry, p. 69. Some ecosystem flux measurements derived from eddy covariance are available for seasonally dry forests (Vourlitis et al. 2001, 2005). However, the vegetation in these ecosystems probably already possesses adaptive mechanisms for coping with reduced rainfall, and thus they are less useful for predicting the responses of intact rainforests to changes in climate regime.

Remote-sensing observations of the effect of both seasonal and episodic drought on forest reflectance properties (i.e., "greenness") also are potentially useful (Asner et al. 2004; Huete et al. 2006; Myneni et al. 2007; Doughty and Goulden 2008b). However, alternative interpretations of satellite-derived data streams during drought have indicated both increased and decreased greenness, for example, in response to the 2005 Amazonia drought (Saleska et al. 2007; Samanta et al. 2010; Samanta, Ganguly, and Myneni 2011). Anderson et al. (2010) determined a positive correlation between increasing enhanced vegetation index and ground-based mortality rates during the 2005 drought, suggesting that greenness *per se* is not indicative of resistance to drought events. Thus, a clear interpretation of changes in apparent greenness across Amazonia remains challenging (Samanta et al. 2012), and indeed Asner et al. (2010) have argued that improved satellite instrumentation is required to resolve this issue.

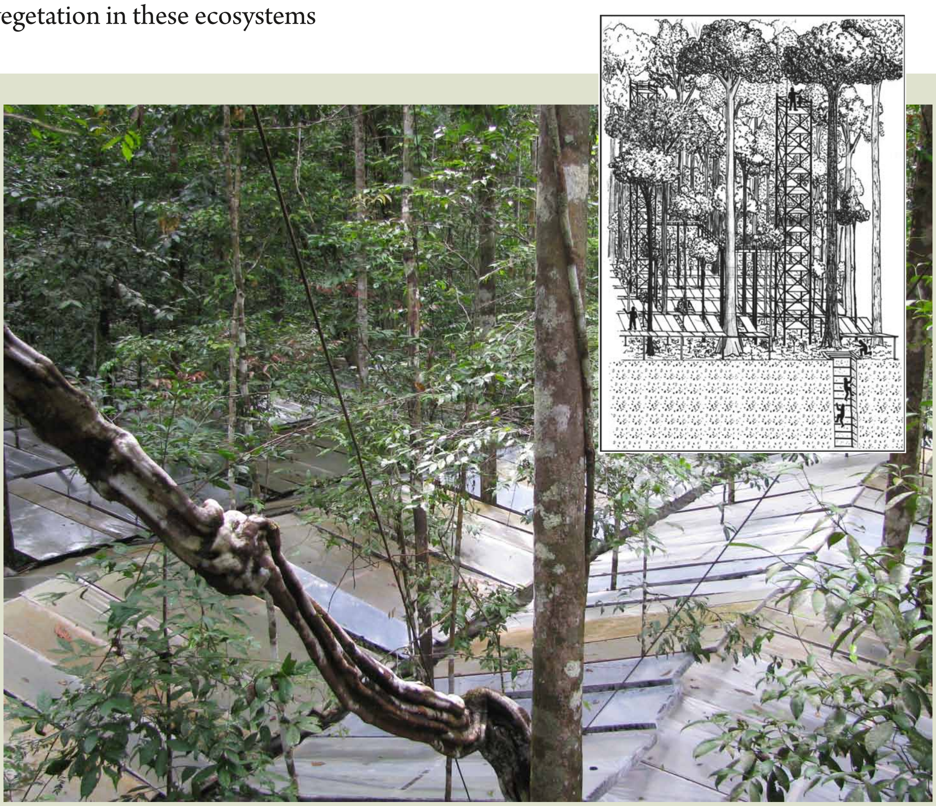


Fig. 5.2. Drought Experiment Infrastructure at Tapajós and Caxiuanã National Forests in Para, Brazil. [Drawing from Nepstad, D.C., et al. 2002. "The Effects of Partial Throughfall Exclusion on Canopy Processes, Aboveground Production, and Biogeochemistry of an Amazon Forest," *Journal of Geophysical Research* **107**, 8085. DOI: 10.1029/2001JD000360. Photo courtesy of P. Meir, University of Edinburgh.]

Representation of Physiological Effects of Water Stress in Land Surface Models

Water stress is represented as a simple and uniformly applied empirical function of either soil moisture content or soil water potential in every major land surface model. The "water stress" factor, applied directly to reduce either unstressed stomatal conductance or unstressed photosynthesis rates, is a function of soil moisture content relative to soil texture–specific "critical" and "wilting" points. Root depth (but not root quantity) typically influences water stress calculations via weighting of the water-stress factor by the fraction of root biomass in each vertical layer of soil.

Using flux tower data from the Large-Scale Biosphere-Atmosphere Experiment in Amazonia study (LBA), several researchers have assessed how well the water-stress functions in land surface models capture the seasonal dynamics of observed gas exchange. In recent years, multiple studies have concluded that, in their default state, land surface models predict large reductions in gas exchange in the dry season (Saleska et al. 2003; Werth and Avissar 2004; Baker et al. 2008; Verbeeck et al. 2011). This contradicts most tower observations, both in the Amazon and Borneo (e.g., Kumagai et al. 2004), that indicate largely constant evapotranspiration (or even slight increases) in the dry season and net ecosystem exchange between seasons. Many modeling groups subsequently have improved predictions by increasing the depth of soil available for water uptake by roots. This modification is consistent with evidence that, in the areas covered by the LBA project, trees typically have access to water from a soil profile more than 3 m deep (Markewitz et al. 2010; Tomasella and Hodnett 1997; R. A. Fisher et al. 2008) and draw moisture from underlying saprolite. Many models (e.g., Baker et al. 2008; Verbeeck et al. 2011) thus have now resolved the problems of excessive water stress on gas exchange.

Predicting the correct average seasonality of the transpiration and photosynthesis observed by flux towers, however, does not actually improve confidence in model capacities to predict responses to rainfall reductions. This is because most forests observed to date are not subject to significant (if any) moisture stress in "normal" dry seasons, and so calibrating model water storage to generate conditions of "no drought stress under ambient conditions" leaves open the possibility of the models having too much buffering capacity in the event of a major drought. Testing models under conditions of imposed drought therefore is informative about whether or not this is indeed the case.

Drought Experiment Modeling Studies

Of the three mentioned ecosystem-scale drought experiments, more model-based validations have been conducted for the Caxiuanã site and are presently in review, along with validations and comparisons of the other Amazonian site. At Caxiuanã, R. A. Fisher et al. (2006, 2007, 2008) parameterized and tested a hydrodynamic model that simulates explicit water transport and the resistance of water transfer from soils to leaves (see Fig. 5.3, this page). Given an investment in

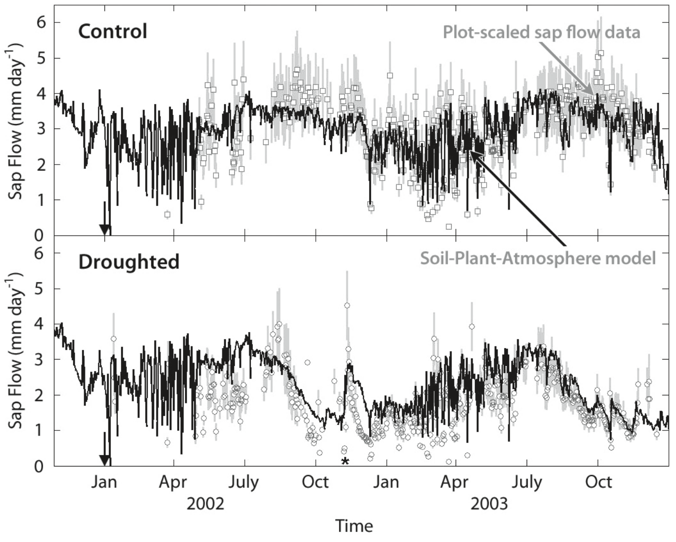


Fig. 5.3. Modeled and Observed Forest Water Use (Sap Flow) at the Caxiuanã National Forest. [From Fisher, R. A., et al. 2007. "The Response of an Eastern Amazonian Rain Forest to Drought Stress: Results and Modelling Analyses from a Throughfall Exclusion Experiment," *Global Change Biology* **13**(11), 2361–78.]

collecting data on the hydraulic and photosynthetic traits of soil and plants, the emergent properties of the Soil-Plant-Atmosphere model (Williams et al. 1996) were in good agreement with observed component- and ecosystem-scale fluxes of water and carbon. However, further studies currently in preparation indicate that traditional land surface models do not yet simulate stressed fluxes well. According to these studies, this difficulty may arise from the absence of adaptive capacity in the average depth of water uptake, among other model differences such as explicit simulation of water transport to leaves. At a diurnal timescale, water stored overnight by many tropical trees supports gas exchange in the morning. Consequently, the stomatal response to vapor pressure deficit (VPD) is much stronger as the day progresses (Meinzer et al. 2008). This diurnal change in stomatal behavior severely limits carbon uptake in the afternoon, particularly on sunny days when potential carbon gain is greatest but evapotranspiration and the loss of stored water also are greatest (Doughty and Goulden 2008a). Absence of explicit water transport models also precludes accurate simulation of this behavior.

Leaf Litterfall

Most litterfall studies in tropical forests have demonstrated a strong seasonality of leaf litterfall, with the peak at the end of the dry (or drier) season (Hopkins 1966; Klinge and Rodrigues 1968; Haines and Foster 1977; Kunkel-Westphal and Kunkel 1979; Herbohn and Congdon 1993; Swamy and Proctor 1994; Wieder and Wright 1995; Lawrence and Foster 2002). Periods of drought, therefore, might also be expected to drive temporary increases in leaf litter inputs.

Evidence suggests that both the quantity and quality of leaf litterfall affect a variety of ecosystem processes (Sayer, Powers, and Tanner 2007; Wood et al. 2009). Litter manipulation experiments demonstrate potential feedbacks of leaf litter quality and quantity on forest productivity (Wood et al. 2009), soil nutrient availability (Wieder, Cleveland, and Townsend 2011), and greenhouse gas emissions (Sayer, Powers, and Tanner 2007; Cleveland et al. 2010; Wieder, Cleveland, and Townsend 2011). As such, understanding how drought will affect the timing, quantity, and quality of leaf drop is vital. Interestingly, however, a dry season irrigation experiment in Panama did not result in significant changes in the timing of leaf litterfall (Wieder and Wright 1995), suggesting that the timing of leaf drop might be controlled by the canopy environment (e.g., light availability and VPD) rather than changes in soil moisture availability.

Drought-Induced Mortality in Tropical Forests

Overview

Drought and associated high temperatures are widely anticipated to be key drivers of tree mortality globally, and the reported frequency of such events has increased in recent decades (van Mantgem et al. 2009; McDowell et al. 2011; Allen et al. 2010). Large-scale increases in the mortality rate of tropical forests would have significant impacts on the terrestrial carbon cycle and land-atmosphere energy exchange, yet adequate predictions of the drought sensitivity of tropical tree mortality are not currently available (Meir, Cox, and Grace 2006; Friedlingstein et al. 2006; White, Cannell, and Friend 1999; Sitch et al. 2008; Delbart et al. 2010).

Observations from long-term forest-monitoring networks from Amazonia to Borneo suggest that extreme drought events can result in rates of mortality 100 to 1200% above background (Phillips et al. 2010), but the specific reasons for these increases, and particularly the differences among them, are not well understood (see Fig. 5.4, p. 38). Large-scale drought experiments in the same region have demonstrated soil drought-mortality response surfaces empirically similar to those obtained from the plot network study in Amazonia (Brando et al. 2008; da Costa et al. 2010). Where data have been combined globally, the sensitivity of rainforest tree mortality rates to soil moisture deficit appears to vary strongly by region, with the more perhumid rainforests of Southeast Asia showing substantially larger increases in mortality than those of Amazonia (Phillips et al. 2010). However, the data available for these analyses remain limited. An adequate representation of the similarities and differences in the climate sensitivity of tree mortality is needed if decadal to century drought responses in rainforest ecosystems are to be modeled convincingly in an Earth system context (Fisher et al. 2010).

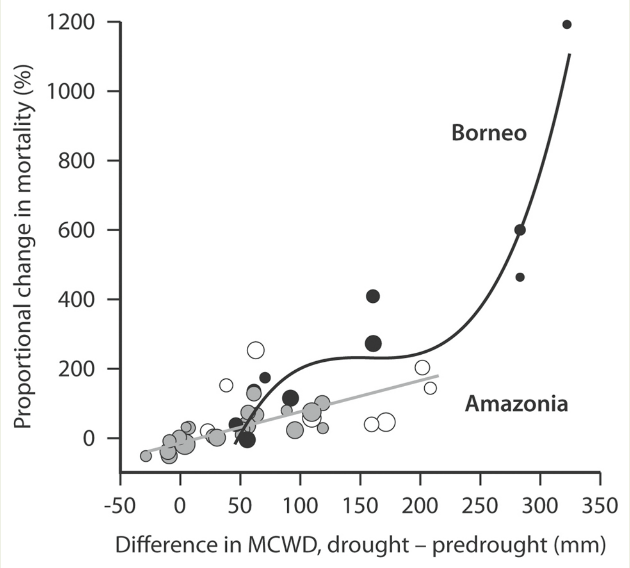


Fig. 5.4. Change in Mortality for Tropical Forests Under Varying Observed Soil Moisture Deficit. This change was determined by a simple bucket model (monthly cumulative water deficit, MCWD) assuming a transpiration rate of 100 mm per month. [From Phillips, O. L., et al. 2010. "Drought–Mortality Relationships for Tropical Forests," *New Phytologist* **187**(3), 631–46.]

Representation of Tropical Forest Mortality in Land Surface Models

Some "dieback" of the Amazon rainforest is a recurring feature of various land surface models driven with the output of climate simulations. Several modeling studies have highlighted the importance of the response of tropical forest mortality to drought in future predictions (Cox et al. 2000; Sitch et al. 2008; Delbart et al. 2010; Fisher et al. 2010; Galbraith et al. 2010). This modeled dieback response is ambiguous because of uncertainties in both climatic drivers and process representations in land surface models. The representations of mortality in these models were reviewed by McDowell et al. (2011) who found that most models included either no stress-induced mortality mechanisms or only very simple functions driven either by plant productivity or by the crossing of empirically defined climate thresholds.

Significant effort is being dedicated to developing improved algorithms for plant mortality. This development process reflects the general consensus, also expressed in McDowell et al. (2011), that a generic theory on the common causes of death in woody plants is not yet available. Emphasis has been placed on the need for gaining a greater understanding of preadaptations to drought (e.g., carbohydrate storage and hydraulic properties) and for representing the widely observed correlation among soil nutrient status, productivity, and turnover rates of tropical forests (Delbart et al. 2010). Multiple simultaneous laboratory studies are ongoing internationally, but so far none are concerned with tropical forest trees. Long-term field-scale manipulation studies likely will provide the best test of current understanding of tree mortality following environmental (i.e., climate) stress. However, none of the few such studies conducted thus far have included the detailed measurements required to investigate mortality physiology.

In addition, models also fail to represent known heterogeneity in contemporary mortality patterns because the drivers of these patterns, which are typically correlated with ecosystem productivity and soil nutrient status, are not understood (Delbart et al. 2010). Furthermore, there are known variations in the drought tolerance found among coexisting tropical tree species (Poorter and Kitajima 2007). Models that make no attempt to account for such variations in plant strategy are likely to predict exaggerated threshold behaviors.

Drought Effects on Soil Processes

Tropical forest soils are the largest natural source of both carbon dioxide (CO_2; Raich and Schlesinger 1992) and nitrous oxide (N_2O) globally (Matson and Vitousek 1990), and wet tropical soils are a globally important source of methane (CH_4) (Frankenberg et al. 2005; see also Chapter 8, Biosphere-Atmosphere Interactions, p. 55). Theory suggests that soil moisture is a key driver of biogeochemical processes in terrestrial ecosystems because of its effects on factors such as soil redox dynamics, diffusion, and soil carbon and nutrient pools (e.g., Conrad 1996; Vasconcelos et al. 2004; Holtgrieve, Jewett, and Matson 2006). As such, projected changes in precipitation for tropical regions probably will have significant effects

on key biogeochemical processes, including trace gas production and nutrient availability that, in turn, could feed back on future climate change. The potential effects of drought (i.e., reduced soil moisture) on key biogeochemical processes in tropical soils are discussed below.

Trace Gas Consumption and Production (CO_2, CH_4, N_2O)

Throughfall exclusion experiments investigating the effects of drought on trace gas emissions have been conducted in six tropical forests spanning a wide range of soil types and rainfall regimes. Results range from increased trace gas consumption to a net increase in emissions (see Table 5.1, p. 40). For CO_2, the variable responses have been attributed to several factors: soil texture that led to deeper rooting (Davidson et al. 2008; Davidson, Ishida, and Nepstad 2004); differential response of root, litter, and soil organic matter to drought (Sotta et al. 2007; Metcalfe et al. 2007; van Straaten, Veldkamp, and Corre 2011); increase in the concentration of dissolved organic carbon (Cleveland et al. 2010); and soil nutrient availability (Wood and Silver 2012). The diversity of CH_4 responses to drought has been attributed to a variety of factors, including an increase in termite activity (Cattânio et al. 2002); variability in soil texture, redox, and the soil microbial community (Teh, Silver, and Conrad 2005); and variability in nutrients or carbon with topography (Wood and Silver 2012).

Like CH_4, net N_2O released from soils reflects both N_2O production and consumption. Typically, N_2O consumption in soils occurs in anaerobic microsites under low NO_3^- conditions (Cleveland et al. 2010). Net consumption of N_2O in response to drought could occur as a result of net N_2O consumption in deeper, wet soil (Wood and Silver 2012). Net emissions of N_2O, in contrast, might result from increased concentrations of dissolved organic carbon (Wieder, Cleveland, and Townsend 2011).

Overall, the highly variable responses of trace gas fluxes to drought both within and among tropical forest sites reflect the high degree of spatial heterogeneity and complexity of biogeochemical cycling in tropical forest ecosystems. These diverse responses create significant uncertainty in the ability to accurately predict how changes in precipitation will influence trace gas emissions and ultimately their concentration in the atmosphere.

Soil Nutrient Availability

Changes in soil moisture resulting from alterations in the precipitation regime could significantly affect a variety of factors that regulate nutrient availability and loss (e.g., mineralization rates, leaching, soil redox, and diffusion). In tropical forest ecosystems, drought is likely to increase soil redox potential and thus favor aerobic processes such as nitrification and iron oxidation (Silver, Lugo, and Keller 1999; Schuur and Matson 2001). This, in turn, affects the availability of exchangeable phosphorus, as the binding of iron oxide compounds with phosphorus is affected by redox potential (Chacon et al. 2006; Liptzin and Silver 2009). In keeping with this theory, soil drying in a Puerto Rican forest led to a significant reduction in exchangeable phosphorus, although such a response was not seen at other sites with lower iron concentrations (Silver et al. 1994; Silver, Lugo, and Keller 1999; Chacon et al. 2006; Liptzin and Silver 2009). Evaluating the importance of iron-phosphorus dynamics may enable further insight into tropical soil responses to drought. Furthermore, competition between plants and microbes for nutrients is expected to be an important factor in understanding soil nutrient dynamics (Lodge, McDowell, and McSwiney 1994).

The effects of drought on nitrogen cycling also are poorly understood. Tropical forests on highly weathered soils tend to be nitrogen rich (Vitousek and Sanford 1986) and cycle nitrogen rapidly (Templer et al. 2008). Drought is likely to increase soil O_2 availability and thus decrease denitrification potential. However, drought also could increase nitrification rates, providing more substrate for denitrification during rainy periods. Experimental drought in Puerto Rico significantly increased NH_4^+ concentrations in the exclusion plots of the valley site, decreasing the ratio of NO_3^- to NH_4^+. Changes in the proportion of different soil nitrogen pools have been shown to affect a variety of ecosystem processes, such as decomposition rates, plant cover, and ultimately carbon cycling (Austin, Sala, and Jackson 2006).

Table 5.1. Comparison of Tropical Forest Throughfall Exclusion Experiments[a]

Forest Location	Annual Rainfall (mm)	Plot Size (No. Exp. Reps.)	Months of Exclusion	No. Years Repeated	CO_2 Response	CH_4 Response	N_2O Response	Citation
Fazenda Vitoria, Brazil	1800	100 m^2 (1)	12	4	−16%	171%	−25%	Cattânio et al. 2002
Tapajós National Forest, Brazil	2000	1 ha (1)	6	5	No effect	−206%	−33%	Davidson, Ishida, and Nepstad 2004; Davidson et al. 2008
Caxiuanã National Forest, Brazil	2300[b]	1 ha (1)	24[c]	1	−26%	NA	NA	Sotta et al. 2007
Caxiuanã National Forest, Brazil	2300[b]	1 ha (1)	48[c]	4	Weak effect[d]	NA	NA	Metcalfe et al. 2007
Central Sulawesi, Indonesia	2900	0.16 ha (3)	12[c]	2	−23%[e] −48%[f]	NA	NA	van Straaten, Veldkamp, and Corre 2011
LEF, Puerto Rico: Ridge	3500	1.54 m^2 (5)	3	1	−19%	No effect	−1788%	Wood and Silver 2012
LEF, Puerto Rico: Slope	3500	1.54 m^2 (5)	3	1	−26%	No effect	No effect	Wood and Silver 2012
LEF, Puerto Rico: Valley	3500	1.54 m^2 (5)	3	1	No effect	−480%	−108%	Wood and Silver 2012
Osa Peninsula, Costa Rica	5000	5.76 m^2 (10)	12[c]	1	25%	NA	35%	Cleveland et al. 2010; Wieder, Cleveland, and Townsend 2011

[Modified from Wood, T. E., and W. L. Silver. 2012. "Strong Spatial Variability in Trace Gas Dynamics Following Experimental Drought in a Humid Tropical Forest, *Global Biogeochemical Cycles* **26**, GB3005.]

[a] For comparison purposes, the responses reported in this table are the mean percent difference between control and exclusion plots over the entire study period (e.g., drought and nondrought).

[b] 2300 ± 200 mm.

[c] Partial throughfall exclusion experiment (e.g., 50%).

[d] When total soil respiration was partitioned, soil organic matter and litter respiration declined in response to drought and root respiration increased.

[e] 9 months of 50% exclusion.

[f] 15 months of 80% exclusion.

Key Uncertainties and Research Opportunities

In contrast to the simple empirical drought functions of existing land surface schemes, numerous ecosystem-scale models now explicitly simulate plant hydraulics, including the transport of water from soil to leaves, leaf water status, and associated control on stomatal conductance and gas exchange. Such models have been tested against observations from drought-stressed forests in temperate, Arctic, and subtropical ecosystems with encouraging results, but estimates of the ecosystem properties needed to properly specify them are only sparsely known at larger scales. Thus, predictions of tropical forest response to moisture stress could be improved by addressing the following critical gaps in knowledge of plant and soil traits:

- **How do soil, saprolite, and rock aquifer depths vary across tropical forests?** The potential size of the water store available to plants during the dry season is a function of soil depth and the presence of deep saprolite and rock aquifers below soils. As discussed, depths of porous media vary widely across the Tropics and can be

deep and challenging to observe. Currently, no reliable maps of these depths exist, either globally or across the Tropics.

- **How do the hydraulic properties of soil, saprolite, and rock aquifers vary below tropical forests?** Within deeper strata, the soil water and moisture available to plants vary by a factor of 4 to 5. The quantity of water available to plants depends on both water retention properties and how hydraulic conductivity varies with capillary potential. These combined datasets are very rare (n ~5) for the tropical rainforest biome.
- **How does root function vary among forests, and how does it affect drought tolerance?** Root biomass profiles are poorly understood despite the increasingly frequent finding that soil-to-root and within-root transport are critical bottlenecks in plant water supply (Sperry et al. 2002; Fisher et al. 2007; Williams et al. 2001; Plaut et al. 2012). The number of complete root profiles in tropical forests is very low (<10), and no published data exist that include possible taproots below trees in tropical rainforests.
- **How do plant hydraulic strategies with respect to drought vary across the Tropics?** Some evidence from Amazonia suggests that trees have conservative stomatal closure mechanisms. Other studies indicate less stomatal control of leaf water potential at sites where the climate is less seasonal (Kumagai et al. 2004, 2008; Kumagai and Porporato 2012). Alternative hydraulic strategies might be adaptive responses to hydraulic and competitive environments in different rainforests.
- **How does plant allocation of carbon and nutrients respond to drought stress?** Evidence from throughfall manipulation experiments suggests no short-term change in photosynthetic capacity with drought in tropical forests (Fisher et al. 2007). However, other studies from more persistently drought-affected nontropical ecosystems have indicated seasonal changes in photosynthetic capacity (Keenan et al. 2009). Over the longer term, there is evidence that leaf dark respiration increases under extended drought (Metcalfe et al. 2010), in contrast to the respiration reductions more frequently observed coincident with short-term drought (Atkin and Macherel 2009). This topic of carbon acquisition, use, and storage is poorly understood and may be critically important for modeling the ecosystem-scale outcomes of leaf-, stem-, or tree-level processes. Similarly, allocation to reproduction is highly variable; most plants forgo reproduction under unfavorable conditions and instead allocate resources to functions ensuring survival. Models failing to incorporate this well-known plant stress response will systematically predict forest-level responses to unfavorable conditions that are too strong.
- **What is the dominant mechanism of plant death under sporadic severe drought events?** Obtaining such knowledge would enable improved predictions of how this mechanism might or might not be affected by changes in climate and atmospheric composition. This challenge must incorporate knowledge of the existing functional diversity of plant responses to drought (Engelbrecht et al. 2007), how this diversity is related to specific plant traits, and how it affects the resistance and resilience of tropical forest communities to drought.
- **What are the mechanisms driving spatial and temporal variability in the production and emission of trace gases in response to reduced soil moisture?**
- **How does reduced soil moisture influence processes related to soil nutrient availability?** Studies are needed that explicitly evaluate specific mechanisms and potential controls across a diversity of forest types.

CHAPTER 6

Natural Disturbance and Recovery

Natural Disturbance and Recovery

One of the least understood aspects of climate change is its potential effect on natural disturbance regimes. This lack of understanding results in part from the unpredictable ways natural disturbance interacts with human land use (Drury and Nisbet 1973; Paine, Tagener, and Johnson 1998; Foster, Motzkin, and Slater 1998; Platt et al. 2002; Uriarte et al. 2009), yet individual disturbance events can dramatically affect carbon, water, and energy fluxes to the atmosphere. For instance, a strong, single storm can convert a large portion of forest carbon stocks to dead biomass (McNulty 2002; Chambers et al. 2007a; Negrón-Juárez et al. 2010). More importantly, these individual events add up to determine regional- to continental-scale disturbance regimes whose changes can affect mass and energy fluxes to the atmosphere, potentially resulting in important feedback processes (Frolking et al. 2009). Establishing regional baselines for these regimes is critical to evaluate potential shifts in disturbance with a warming climate.

Disturbance Effects on Tropical Tree Mortality and Climate Change

"Natural" disturbances are events not directly linked to human activities such as logging and deforestation. In tropical forests, these include drought, storms (e.g., wind, lightning, and flooding), fire, and other processes (e.g., pest and pathogen outbreaks and monocarpy). Each of these disturbances can lead to tree death and may respond differently to a changing climate. Thus, distinguishing among these mortality processes in field studies and developing improved disturbance algorithms for terrestrial models are important.

The death of an individual tropical tree can be a slow process resulting from a combination of factors. For example, a tree can be snapped midtrunk in a windstorm, yet many tropical tree species survive by sprouting, enabling more rapid access to a canopy position. Trees can regrow lost branches and repair damaged crowns within relatively short time periods (Walker 1991; Ostertag, Silver, and Lugo 2005). However, a damaged stem also can be colonized by pathogenic microbes and wood-boring organisms, resulting in a compromised tree potentially more vulnerable to other factors such as drought and windthrow. At the other extreme, high winds from tropical cyclones (Canham et al. 2010; Lugo 2008; Zimmerman et al.1994) or blowdowns in the Amazon (Negrón-Juárez et al. 2010, 2011) can lead to rapid mortality over large areas. In addition, cohorts of wind-damaged trees can experience elevated mortality for many years after the event (Lugo and Scatena 1996; Walker 1991; Uriarte et al. 2009).

Many types of natural disturbance including fires, cyclonic storms, and floods are expected to increase with climate change, and shifts in land use throughout the Tropics probably will exacerbate these effects (Allen et al. 2010; Frolking et al. 2009; Dale et al. 2001). Cyclonic storms (hurricanes, typhoons, and cyclones) represent the dominant natural disturbance in temperate and tropical forests in coastal regions of North, Central, and South America; the Indian subcontinent; localized parts of Southeast Asia and Africa; and northern Australia (Gray 1975; Boose, Foster, and Fluet 1994; Everham and Brokaw 1996; Mabry et al. 1998; Platt et al. 2002; McNab, Greenberg, and Berg 2004). In the past decade, the frequency and intensity of hurricanes in the North Atlantic have increased twofold and fourfold, respectively (Webster et al. 2005; Emanuel 2005; Goldenberg et al. 2001). Since hurricanes derive their energy from ocean heat, this increase in activity has generated much debate on the role that human-driven global climate change has played in recent storms. In addition to changes in tropical cyclones and similar to predictions for temperate regions, a general increase in storm intensity also is expected for the Tropics (Shepherd and Knutson 2007; IPCC 2007). Moreover, changes in storm intensity can interact with changes in the atmospheric aerosol environment caused by, for example, biomass burning in the Tropics. Such interactions could further intensify storm systems and alter precipitation patterns (Andreae et al. 2004; Li et al. 2011).

Increases in the frequency of extreme precipitation events coupled with deforestation also may amplify flood risk globally (Bradshaw et al. 2007; Bruijnzeel 1990, 2004). The anoxic conditions created by floods not only can kill trees but also increase emissions of trace gases, including methane, in flooded areas (Hess et al. 2003; Melack et al. 2004). A considerable body of literature is devoted to the development of complex, catchment-specific models to predict the temporal frequency of floods (Cameron, Beven, and Naden 2000; Arnaud and Lavabre 2002; Cunderlik and Burn 2002; Prudhomme, Reynard, and Crooks 2002). However, no attempts have been made to predict (1) flood frequency over broader spatial scales, (2) the influence of climate change on flood intensity and frequency, and (3) the effects of these changes on ecosystem fluxes and forest-atmosphere interactions.

Incorporating the vulnerability of tropical forests to shifts in disturbance regimes and the subsequent recovery of these ecosystems following disturbance requires the robust characterization of current disturbance regimes and a greater understanding of individual species responses. Tree species differ in their susceptibility to disturbance of varying intensities and in the nature of the damage they sustain from a given disturbance event. Their recovery also varies, at both the individual plant level through repair of damage and at the population level through reproduction, seedling establishment, and juvenile response to changes in resource conditions that typically follow disturbance events (Glitzenstein and Harcombe 1988; Peterson and Pickett 1991; You and Petty 1991; Walker 1991; Boucher et al. 1994; Zimmerman et al. 1994; Peterson and Rebertus 1997; Cooper-Ellis et al. 1999). For instance, hurricanes tend to damage larger, slower-growing trees, so short-term productivity may increase as a result (Sanford et al. 1991). However, higher-production ecosystems do not necessarily store more carbon, and the loss of massive trees can shift ecosystems to lower biomass states as dead trees decompose. In an Amazon forest, 50% of the aboveground biomass was contained in 3% of the trees (Brown et al. 1995), and large Amazon trees can live for many hundreds of years (Chambers, Higuchi, and Schimel 1998). Understanding the relative importance of these seemingly countervailing effects on long-term changes in forest composition and ecosystem fluxes requires the use of models. These models should be specifically designed to incorporate disturbance effects on the basic demographic processes (e.g., recruitment, growth, and mortality) that regulate forest community dynamics and the feedbacks between these changes and ecosystem processes.

Drought

The physiology of drought-induced mortality is described in more detail in Chapter 5, p. 33. To briefly summarize in the context of disturbance, little is known about the differential sensitivity of tropical forests to drought. In the Amazon, for example, forests span a broad range in precipitation seasonality, from those with a wet perhumid climate to others experiencing up to 4 to 5 months of drought (e.g., <100 mm/month) while maintaining a closed canopy and high biomass density (Sombroek 2001). Another important feature of forest sensitivity to drought is water table depth. Amazon forests on white sand soils can vary, ranging from tall, closed-canopy forests when the saturated zone is shallow to "campinaranas" ("caatinga" and "heath forests") when the water table occurs at depth (Anderson 1981; Jordan 1985). Tall forests on white sand soils with shallow water tables may be particularly vulnerable to intense droughts that substantially lower the depth of the saturation zone. Overall, more research is needed to determine regional variability and tree mortality patterns associated with drought.

Drought also interacts with other modes of disturbance. For example, increasing numbers of standing dead trees eventually will topple during a subsequent event such as a storm. Moreover, standing dead trees decay more slowly than downed trees (Chambers et al. 2000), so carbon fluxes to the atmosphere from drought-induced mortality may be delayed from mortality processes that transfer biomass to the forest floor. Standing dead trees represent a global process because they also are caused by insect outbreaks and drought in temperate forests and thus should be treated explicitly in terrestrial models that currently lack this mechanism.

Storms

Storm-induced mortality from wind, lightning, or flooding is one of the primary agents of disturbance

in tropical forests. Wind and lightning result in uprooted, snapped, and shattered trees that may survive by sprouting. However, a tree snapped below the diameter measurement height (generally 1.3 m or above buttresses) that sprouts is still considered part of the mortality flux, and this nonlethal damage also results in significant transfer of biomass from live to dead carbon pools. Thus for terrestrial and Earth system models (ESMs), the combined disturbance flux from both mortality and damage is important to quantify.

Some studies, including ones in the Amazon and Puerto Rico, partition mortality into different modes (e.g., standing, uprooted, and snapped), which can be valuable in assigning causal agents of death (Uriarte et al. 2009; Chambers et al. 2000; Chao et al. 2009; Toledo 2002; Fontes 2012). For example, wind disturbance causes uprooted and snapped trees, whereas drought generally results in standing dead trees that can subsequently topple or snap. Individual variation in mortality damage is a function of species identity, tree size, and storm severity (Uriarte et al. 2009). Overall, there are too few studies to draw generalizations useful for model development, and more field studies are needed on the agents and modes of mortality and their variation among tropical forests at a global scale. Downscaling natural disturbance in models to scales relevant to field observations of tree mortality also is a critical need.

Three studies of tree mortality in Central Amazon forests north of Manaus, Brazil, demonstrate some of these contrasting results. In 2011, a study from Brazil's National Institute for Amazonian Research (INPA) examined agents of mortality with detailed field studies in two 5-hectare (ha) permanent plots, alternating monthly for a year (Fontes 2012). This study included six mortality classes and recognized both direct storm effects (e.g., wind and lightning), which accounted for 49% of tree mortality, and indirect effects (e.g., wind-damaged trees that eventually succumbed and senescing weakened trees that were windthrown), which represented 19%. The remaining deaths were attributed to direct effects of stress (e.g., standing dead trees from drought, flooding, and competition), which accounted for 30% of mortality, and other factors (2%). In contrast to the short-duration, detailed studies of Fontes (2012), research by Toledo (2002) found standing death was the predominant mode of mortality (54%) followed by snapping (26%) and uprooting (14%) for 72 1-ha permanent plots recensused twice (from 2003 to 2005 and 2005 to 2008). Chambers et al. (2000) assessed 18 ha of permanent plots monitored over an ~6-year period and found that wind disturbance (snapped and uprooted) was the dominant mode (54%), followed by treefalls (33%) and standing dead (13%). These studies illustrate the difficulties in determining regional disturbance patterns and their variation from year to year in association with changing environmental factors. To develop causal relationships among climate change variables and tree mortality, additional detailed mortality studies with high temporal resolution (at intervals of 1 year or less) are needed for tropical forests and should be considered a research priority.

Distinguishing among mortality agents at regional scales also is difficult in tropical forests (see Fig. 6.1, this page). For example, Phillips et al. (2009) found an increase in Amazon mortality rates in

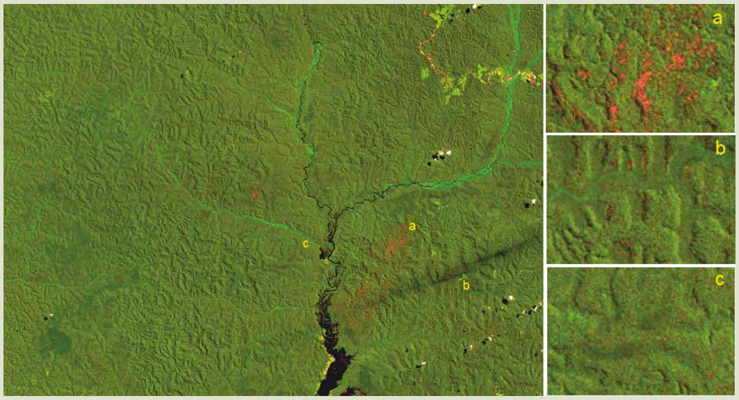


Fig. 6.1. Distribution of Intermediate-Size Tree Mortality Disturbance Events in Central Amazon North of Manaus, Brazil. [From Chambers, J. Q., et al. 2009. "Lack of Intermediate-Scale Disturbance Data Prevents Robust Extrapolation of Plot-Level Tree Mortality Rates for Old-Growth Tropical Forests," *Ecology Letters* **12**(12), E22–25.]

2005 associated with a large basin-wide drought. However, some Amazon sites such as Manaus did not experience severe drought during this period, and Negrón-Juárez et al. (2010) demonstrated that a powerful squall line in 2005 also caused basin-wide tree mortality that was particularly acute in the Manaus region. Detailed tree mortality studies would be useful for distinguishing among agents and would enable development of more mechanistic tree mortality algorithms for terrestrial ecosystem models. Additional measurements on modes and agents of mortality could be added to existing tropical plot networks to facilitate developing these disturbance baselines and could be coupled with remote sensing to scale from plots to regions.

Fire

Fire Disturbance and Tropical Forest Boundaries

Savanna and forest differ vastly in terms of biomass, flammability, and ecosystem fluxes, so climate-driven switches between these biomes have broad consequences for the Earth system. The structure, dynamics, and location of the savanna-forest boundary are emergent properties arising from the counteracting effects of fire and tree growth (Hoffmann et al. 2012), both of which are highly sensitive to climate. These opposing processes, combined with strong feedbacks between vegetation and flammability, result in complex dynamics (Beckage, Platt, and Gross 2009; Staver, Archibald, and Levin 2011) that pose an ultimate test of the ability of ESMs to integrate physics and biology.

The savanna-forest boundary represents the natural limit of distribution of tropical forests and therefore offers a unique opportunity to understand how these forests will respond to changing climate and disturbance regimes. Fire and acute drought, two primary factors that threaten tropical forests under climate change, have acted for millennia at natural savanna-forest boundaries. These factors can serve as model systems for obtaining a mechanistic understanding of climate change effects in tropical forests while allowing quantification of the long-term consequences of forest loss on ecosystem stocks and fluxes.

The extent of forest is particularly sensitive to any factor that influences ecosystem productivity (Lehmann et al. 2011) because of the importance of tree growth rates for determining ecosystem recovery between fires (Hoffmann et al. 2012). Post-fire recovery of resprouting trees is strongly sensitive to carbon dioxide (CO_2; Hoffmann et al. 2000; Kgope, Bond, and Midgley 2010), so forest margins should be more responsive to increasing CO_2 than intact forests (Bond and Midgley 2012; Higgins and Scheiter 2012).

Fires and Anthropogenic Disturbance

The incidence of fires in many tropical regions has increased steeply (Sanford et al. 1985; Hammond et al. 2007; Cochrane 2003). Research has focused on causal or exacerbating physical factors such as drought (Mueller-Dombois 1981; Woods 1989; Setzer and Pereira 1991; Nepstad et al. 2004), including "deforestation-induced drought" (Nepstad et al. 2007), and also has emphasized the increased flammability of forests due to timber extraction (Verissimo et al. 1995; Uhl and Kauffman 1990; Holdsworth and Uhl 1997; Cochrane 2003) and repeated burning (Cochrane et al.1999; Nepstad et al. 1999; Uhl and Kauffman 1990). Increased agricultural use, whether large or small in scale, often results in more frequent use of fire, the planting or invasion of more flammable vegetation including grasses, creation of more fire-susceptible forest fragments and edges, and increased quantities of highly flammable woody debris (Cochrane and Schulze 1999). The reduction of total regional rainfall, combined with large-scale deforestation and declines in evapotranspiration, also increases the probability of future drought. This effect suggests that positive feedbacks link deforestation, droughts, and fires with forest destruction, leading to decreased rainfall, increased probability of escaped fires, and yet more deforestation (Malhi et al. 2008; Baidya Roy and Avissar 2002; Oyama and Nobre 2003; Bala et al. 2007; Andreae et al. 2004; Nepstad et al. 2007; Laurance and Williamson 2001; Hoffmann, Schroeder, and Jackson 2002). Beyond Amazonia, the conflagration of severe El Niño–Southern Oscillation events, road building, changes in the types and scales of land use, and increasing landscape fragmentation is expected to lead to pantropical increases in fire activity (Nepstad et al. 2001; Cochrane 2003; Cochrane and Laurance 2008).

Disturbance and Landscape Carbon Balance

Landscape carbon balance is estimated by summing tree recruitment and growth in permanent forest plots and subtracting mortality from the total (Baker et al. 2004; Phillips et al. 1998). A number of potential complicating factors emerge in making this calculation (Davidson et al. 2012; J. I. Fisher et al. 2008; Wright 2005), and accounting for spatially and temporally aggregated mortality losses from disturbance events is particularly challenging (Körner 2003). Additional remote-sensing studies are needed to augment plot-based approaches that account for mortality events with return frequencies greater than ~50 years (Chambers et al. 2009). Comprehensive landscape-scale carbon balance studies will be particularly useful in addressing regional variability in net biomass accumulation and in providing improved estimates of tropical forest carbon sinks that may be driven by CO_2 fertilization.

Tropical forest plot-based studies aggregated at continental to global scales indicate an old-growth tropical forest carbon sink of ~0.5 Mg C ha^{-1} yr^{-1}, or a global sink of ~1.3 Pg C yr^{-1} (Lewis et al. 2009a). Using a similar approach, Chave et al. (2008) studied 10 larger globally distributed plots (16 to 52 ha each) and found a net sink of 0.24 Mg C ha^{-1} yr^{-1}, or about half of that estimated from a network of smaller plots. These studies were focused on quantifying continental- to global-scale sink estimates, and efforts to determine the magnitude of the net forest carbon sink at individual sites using plot-based approaches are lacking. Studies to determine the strength of the tropical forest carbon sink as a function of factors such as soil fertility are needed to develop improved terrestrial models.

Also important to consider is that a net increase in biomass can occur from an increase in both tree recruitment and growth rates. However, since the biomass of a new 10 cm tree is less than ~48 kg, shifts in recruitment rates must lead to changes in stem density and size structure to result in significant changes in biomass. To more directly address the issue of the CO_2 fertilization of productivity in tropical forests, increases in biomass caused by changes in recruitment and stand structure should be distinguished from biomass increases resulting from elevated growth rates. Feeley et al. (2007) examined tropical tree growth rates in two large (50-ha) forest dynamics plots in Panama and Malaysia and found that stem growth rates declined significantly for both forests, with growth rates negatively correlated with mean annual daily minimum temperature. Additional studies on tropical tree growth rates would help shed light on the CO_2 fertilization hypothesis for old-growth forests.

Another complicating factor in addressing the old-growth tropical forest carbon sink is the observed increase in forest turnover (average of recruitment and mortality) rates (Phillips et al. 2004; Phillips and Gentry 1994). An increase in mortality rates will drive forest biomass lower, so simultaneous increases in biomass and mortality rates must be compensated by an even greater increase in growth rates (Chambers et al. 2004a) or recruitment rates and forest structure. To elucidate these complex interactions and develop an improved mechanistic understanding of the underlying processes, recruitment rates should be studied independently of mortality rates.

Tree Mortality in Terrestrial Ecosystem Models

Representation of Fire Disturbance in ESMs

There has been a proliferation of fire models in ESMs in recent years, reflecting an increased interest in feedbacks to the climate system. However, many of these models have very similar theoretical bases and thus have converged on comparable operating principles. For example, ignition sources and moisture conditions determine the number of fires simulated by the models. The rate of spread and area of elliptically shaped fires are determined using algorithms based on fire-service statistics from either the United States (Rothermel 1972), in the case of the SPITFIRE family of models (Thonicke et al. 2010; Lehsten et al. 2009), or Canada (van Wagner and Pickett 1985), in the case of the CTEM-derived family of models (Arora and Boer 2005; Kloster et al. 2010, 2011; Li, Zeng, and Levis 2012). Litter quality, humidity, and wind speed are typically the drivers of fire size.

Neither of these baseline datasets is from the Tropics, so applicability to these ecosystems is seldom validated. One particular problem in these models is the assumption of homogeneous vegetated surfaces that include no element of landscape-level impedance to fire spread, which likely will be important both at natural forest boundaries and in deforestation-dominated frontiers.

To predict fire effects on natural vegetation, capturing the variability in fire tolerance of different vegetation types is highly important. Differences in plant functional type (PFT) tolerances are represented in some models such as SPITFIRE and a dynamic global vegetation model (DGVM; Scheiter et al. 2012), but the resolution of such representations remains low. This situation could be improved by modeling studies that include higher-resolution representations of observed functional trade-offs between, for example, growth rates and bark thickness or resprouting capacity (Hoffmann et al. 2012). In addition to this challenge, no ESMs take into account other types of disturbance such as windstorms, floods, or pest outbreaks, all of which may be critical to understanding ecosystem fluxes in the Tropics. However, work in these areas is ongoing.

Representation of Post-Disturbance Succession, Regrowth, and Competition in ESMs

Traditional DGVMs typically represent portions of the land surface as tiles of continuous PFTs (e.g., LPJ; Sitch et al. 2008). Although this approach can simulate recovery after disturbance (Shevliakova et al. 2009), representing shifts in community composition that arise from changing conditions across successional gradients is not possible using the traditional methodology. Second-generation DGVMs are being developed that can simulate horizontal heterogeneity in light availability using either the individual-based and stochastic "gap model" approach (Smith, Prentice, and Sykes 2001; Sato, Itoh, and Kohyama 2007; Scheiter and Higgins 2009) or a statistically aggregated approach, typified by the Ecosystem Demography model (Moorcroft, Hurtt, and Pacala 2001; Fisher et al. 2010). Both approaches enable the representation of succession, competition for light, multiple height classes, and potential coexistence of plant types at all phases of succession. Although an active area of research, many challenges remain, particularly in representing existing theories of vegetation competition, distribution, and coexistence in a quantitative manner. Clearly, the existing representation of tropical diversity in ESMs is insufficient and often consists of only one plant type to represent all tropical forest species. The next generation of models needs to represent at least the major axes of plant variation, especially with respect to plant responses to the major forcings discussed in this report. Empirically quantifying the basic trade-offs in plant form and function (e.g., Markesteijn et al. 2011; Baraloto et al. 2010; Paine et al. 2011) is particularly useful for generating hypotheses of vegetation distribution (which currently are mostly verbal arguments that have not been quantitatively tested) and should be considered a high priority for future efforts.

Disturbance Research Themes Relevant to ESMs

Four model developments are critical for representing disturbances in tropical landscapes and their influence on Earth system processes:

- **Robust characterization of disturbance regimes, differing agents and modes of tree mortality across the Tropics, and their interactions with climate change.** This will require understanding the frequency distribution of disturbance events of differing intensities (possibly using spatial extent as a proxy). Also needed is an understanding of return intervals for mortality events driven by different processes (e.g., drought, fire, and storms) and how these might shift with a changing atmosphere and warming climate.
- **Improved representation of the diversity of species' responses to disturbance.** The range of PFTs currently in models does not adequately capture this diversity. Tree species differ in their susceptibility to disturbance of different types and intensities, the nature of the damage they sustain from a given disturbance event, and community recovery from disturbance. Understanding the links between tree community assembly processes and the trajectory of ecosystem fluxes remains a challenge.

- **A better understanding of how landscape configuration (i.e., the distribution and size of different land cover types) influences the susceptibility of forests to fire and wind disturbance.** Increased agricultural use and fragmentation often result in more frequent disturbance, a greater abundance of invasive species, creation of more disturbance-susceptible forest fragments and edges (Cochrane and Schulze 1999; Laurance et al. 2002), and altered feedbacks to the atmosphere.

- **Greater insight into how disturbance intensity interacts with soil fertility, precipitation, and rising atmospheric CO_2 concentrations to influence succession rates, shifts in species composition, and biomass recovery** (Chazdon 2003; Zarin et al. 2005; Crk et al. 2009; Lawrence et al. 2010; Aide et al. 2012; Poorter and Navas 2003).

Key Uncertainties and Research Opportunities

Three key uncertainties in the response of natural disturbance to climate change in tropical forests are:

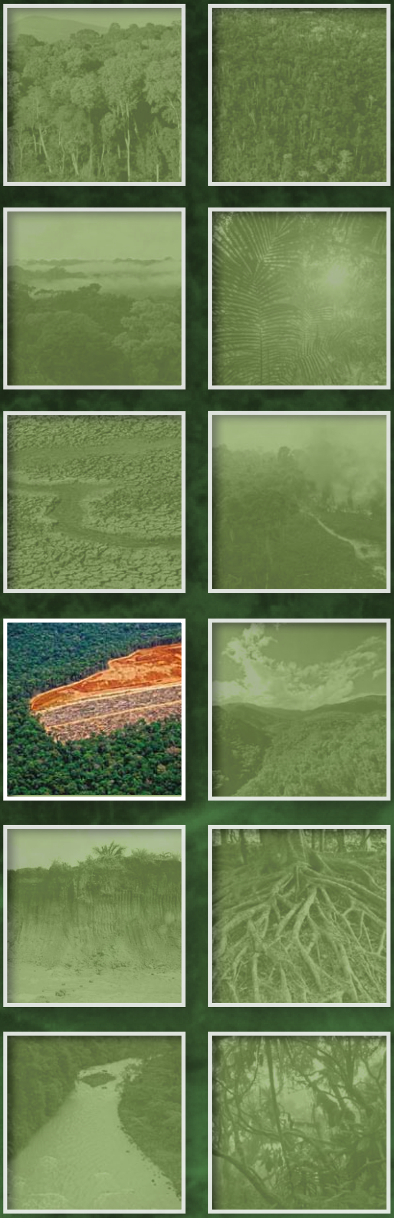
- **What are the biomass loss fluxes from tree mortality and damage?** Addressing this question is critical for generating robust landscape-scale carbon balance estimates and determining the magnitude of the terrestrial carbon sink attributed to old-growth tropical forests. These insights in turn will improve the understanding of how forest-atmosphere CO_2 exchange may shift with a warming climate.

- **How will natural disturbance processes change with a warming climate?** Climate change predictions for the Tropics include the potential for increased incidence of regional drought, intensification of storm systems, and elevated temperature effects on tree ecophysiology. Each of these can result in elevated disturbance regimes and higher tree mortality rates that in turn can affect the forest-atmosphere exchange of CO_2, moisture, and energy.

- **How will atmospheric and climate change affect the successional trajectory following tree mortality disturbance?** Biomass recovery rates and associated changes in species composition in tropical forests depend on the size and severity of disturbance, distribution of disturbed patches over the landscape, interval between subsequent disturbance events, and environmental constraints (Uriarte and Papaik 2007; Sousa 1984). The recovery pathway also will be influenced by competitive interactions among individual trees and how these interactions vary with increasing atmospheric CO_2, changing precipitation regimes, and elevated temperature from a warming climate.

CHAPTER 7

Anthropogenic Disturbance and Land Use



Anthropogenic Disturbance and Land Use

Human Land Use and Forest Regeneration

Human land use can have direct and indirect effects on nutrient and energy fluxes to the atmosphere. For example, deforestation is the second largest anthropogenic source of carbon dioxide emitted to the atmosphere, after fossil fuel combustion (van der Werf et al. 2009). This contribution is fairly well characterized, accounting for 12% of carbon emissions. Of these emissions, about half are attributed to forest fire, and the largest proportion come from the Tropics. Brazil alone accounts for an average annual release of 0.28 (0.17 to 0.49) Pg of carbon to the atmosphere, representing 24% of the world's carbon emissions from land cover change [1.15 (0.58 to 1.79) Pg of carbon per year; Aragão and Shimabukuro 2010].

Despite the strong focus of Earth systems research on emissions from deforestation and degradation of primary forests, most tropical landscapes are mosaics of forest, agricultural lands, and successional forest patches undergoing natural regeneration following abandonment from diverse land uses (Chazdon 2003; Grau et al. 2003; Asner et al. 2009). Primary or old-growth forests represent less than 25% of the total area of tropical forests worldwide (FAO 2010). A significant fraction of the tropical forest cover lies in areas recovering from logging or in secondary forests and land abandoned from agriculture. Much remains to be learned about the processes involved in forest regeneration, their response to global change, and their ability to mitigate species loss and carbon emissions resulting from deforestation. Global estimates of the cover of regenerating forests and of "committed forest regrowth" are inaccurate and imprecise (Asner et al. 2009). All three aspects of forest attributes—biodiversity, structure, and ecosystem functions—change during forest regeneration but at different rates. Changes in species composition, vegetation structure, and biomass accumulation following land abandonment or large-scale natural disturbances are intricately linked and govern the recovery of carbon and nutrient stocks above- and belowground during secondary succession. Structure and ecosystem functions appear to recover more quickly than species composition (Chazdon et al. 2007). Although these coordinated changes are poorly understood, current knowledge suggests a high degree of functional redundancy of tree species in tropical forests (Chazdon and Arroyo-Mora, in press). During forest regeneration, the number of species in different functional groups of trees changes, but the number of functional groups remains constant (Zhang, Zang, and Qi 2008; Chazdon et al. 2010). Links between species composition and ecosystem processes in regenerating tropical forests are poorly understood.

Despite the high degree of uncertainty in estimating carbon sinks and rates of deforestation (Ramankutty et al. 2007), regenerating forests in the Tropics unquestionably are major sinks for carbon (Yang, Richardson, and Jain 2010). The carbon sink in regrowth forests varies considerably across tropical regions. Since 1990, the greatest increase in carbon stocks has been in the Americas, followed by Asia, and then Africa (Pan et al. 2011). However, the high potential for carbon sequestration in regenerating forests is not even close to being achieved on a global scale for two major reasons. First, regrowth vegetation in the Tropics is being recleared at high rates (Chazdon et al. 2009). Second, intensification of land use, reduction of fallow cycles, and multiple cycles of forest clearing and burning can arrest succession because degraded soils cannot support vegetation without management interventions (Chazdon 2003; Zarin et al. 2005; Lawrence et al. 2010). These factors, should they become significant, could reduce future carbon storage in the Tropics. In addition to these anthropogenic disturbances, the effects of global climate change on tropical forests are major concerns. Growth and survival of trees in moist tropical second-growth forests are highly sensitive to seasonal drought conditions, particularly the severity of the relatively short dry season (Chazdon, Brenes, and Alvarado 2005). For example, severe drought in the Amazon in 2005 (Phillips et al. 2009) reduced the estimated decadal carbon sinks in the Tropics by 15% (Pan et al. 2011).

Biomass estimation (and thus estimation of carbon in vegetation) is an imprecise science because robust data on allometric relationships are available for only a few vegetation zones and assemblages. Biomass estimation of second-growth forests in Rondonia, Brazil (Alves et al. 1997), and northeastern Costa Rica (Letcher and Chazdon 2009) varied substantially when different allometric equations were used. Species differences in specific wood gravity, tree height:diameter allometry, and tree damage are significant sources of error that have not been carefully assessed in most tropical forests. Estimates of carbon accumulation rates during forest regrowth therefore should be scrutinized carefully because many of these sources of error can lead to inaccurate estimates (Kauffman, Hughes, and Heider 2009; Nelson et al. 1999).

Tropical forests amass much more than carbon as they regenerate. They also accumulate nitrogen, phosphorus, calcium, and other nutrients in foliage, stems, branches, and roots and recycle these nutrients in litter and dead plant matter. Aboveground pools of nutrients were restored rapidly during the first 14 years of regrowth on abandoned pastures in Central Amazonia, with the bulk of nutrients stored in wood tissue (Feldpausch et al. 2004). Increased soil organic matter enhances soil fertility and water-holding capacity. Regrowth forests also pump water from soils into the atmosphere, influencing local rainfall and regulating flows within watersheds. In addition, these forests increase in height and structural complexity, creating arrays of microenvironments in the understory and canopy. Many of these ecosystem processes occur in actively restored tropical forests (Paul et al. 2010). During forest regeneration, nutrient limitations may shift seasonally, spatially, and temporally (Townsend et al. 2011). For example, in Amazonian forests, decreasing foliar concentrations of phosphorus with increasing forest age suggest that phosphorus becomes more limiting later in succession (Feldpausch et al. 2004; Davidson et al. 2007), although luxury consumption (Chapin 1980; Attiwill and Leeper 1987) during early developmental stages may reduce soil nutrient requirements for mature trees.

Representation of Land-Use Processes in Earth System Models

The representation of land-use change in Earth system models (ESMs), such as the Community Land Model version 4 (CLM4), remains rather limited. For instance, CLM4 relies on harmonized land-use datasets (Hurtt et al. 2006) to divide land surface into different land uses. Transitions between the different classes depend on potential vegetation and current CLM land surface parameters. Vegetation is further subdivided into crop, pasture, primary vegetation, and secondary vegetation land units (Bonan and Levis 2006; Oleson et al. 2010). The current dataset is based on the methodology of Lawrence and Chase (2007) and uses a variety of satellite products to develop present-day plant functional type (PFT) distributions with matching leaf area index values. The dataset initially derives fractions of bare ground and forest land cover from the Moderate Resolution Imaging Spectroradiometer (MODIS) continuous vegetation fields (Hansen et al. 2003). To further distinguish tree types, the tree fraction is divided into broadleaf or needleleaf and evergreen or deciduous types based on the Advanced Very High Resolution Radiometer (AVHRR) continuous fields tree cover (DeFries, Hansen, and Townshend 2000). The Hurtt et al. (2006) dataset is the *de facto* standard for ESM historical simulations (e.g., Shevliakova et al. 2009), but future land-use trajectories depend on the output of integrated assessment modeling efforts (Lawrence et al. 2012) that are highly uncertain.

Key Uncertainties and Research Opportunities

Addressing three significant research gaps is particularly important for representing forest succession in tropical landscapes and effects on Earth system processes. First, the range of PFTs currently in models does not capture the successional diversity of tropical forests, especially among shade-tolerant species. Although important for characterizing successional dynamics, species differences are significant sources of error in estimates of ecosystem fluxes and have not been carefully assessed in most tropical forests. Secondly, succession at the landscape scale

occurs much faster in the Tropics than in temperate zones. Landscape configuration (i.e., the distribution and size of different land cover types) around individual landscape patches (i.e., cell grids) is an important predictor of succession rates (Crk et al. 2009; Galanes and Thomlinson 2009). Finally, the intensity of land use interacts with soil fertility and precipitation to influence the rates of succession and biomass recovery (Chazdon 2003; Zarin et al. 2005; Crk et al. 2009; Lawrence et al. 2010; Aide et al. 2012). Intensification of land use, reduction of fallow cycles, and multiple cycles of forest clearing and burning can prevent forest regeneration in degraded areas (Chazdon 2003; Zarin et al. 2005; Lawrence et al. 2010). Such factors thus will significantly reduce future carbon storage in the Tropics. Based on these three areas, key research gaps and uncertainties include:

- **How does functional diversity in species composition influence forest regeneration processes in the Tropics?** The ability to predict tropical forest and biomass recovery from natural disturbance and human land use will depend on plant functional type characterizations that accurately capture the successional diversity of tropical forests, especially among shade-tolerant species. Studies should examine species differences in specific wood gravity, tree height:diameter allometry, and hydraulic properties and focus on scaling up the effects of plant functional traits to the community and ecosystem levels.
- **What are the links between functional diversity through succession and important climate parameters such as vulnerability to drought?** Significant portions of tropical forests are recovering from some type of human activity. Understanding how species functional traits that determine vulnerability to drought change through succession is critical to predicting how recovering forests will respond to shifts in drought frequency and intensity.
- **How do landscape- and stand-level processes interact to affect succession rates?** The tempo and mode of stand-level successional dynamics are strongly affected by features of the surrounding landscape, including the composition and spatial configuration of habitat types and land-cover classes. Studies should examine how landscape characteristics influence rates of succession and biomass accumulation.
- **How does biomass recovery and carbon storage resulting from succession vary with land-use intensity?** Human land-use legacies greatly influence the ecosystem properties of successional forests. Carbon and nitrogen stocks, as well as the ability of successional forests to accumulate biomass, strongly decline as the duration, intensity, and frequency of prior agricultural land use increase. Understanding how these land-use legacies influence rates of succession processes and biomass accumulation is a critical research need.

CHAPTER 8

Biosphere-Atmosphere Interactions: Greenhouse Gases, Reactive Chemicals, and Aerosols

Biosphere-Atmosphere Interactions: Greenhouse Gases, Reactive Chemicals, and Aerosols

Overview

Exchanges of mass and energy between tropical forests and the atmosphere are critical to the control of the Earth system. Among these exchanges, water and carbon dioxide (CO_2) are the most significant and most studied. The release and uptake of greenhouse gases (GHGs), reactive chemical compounds, and particles also are critically important for Earth system models (ESMs) due to the strong direct and indirect effects of these species on atmospheric chemistry, atmospheric radiation budgets, cloud processes, and precipitation. Atmospheric composition and energy fluxes in turn regulate tropical forest metabolism, creating a closely coupled, strong feedback system. For example, clouds and aerosols modulate the fluxes and direct:diffuse ratio of radiation received by the ecosystem. Aerosols derived from both the forest and biomass fires help control cloud lifetimes, droplet numbers, and convection. Several studies have suggested that human-caused changes in aerosol amounts and chemical properties in Amazonia can affect dry season length, rainfall amounts, and convective properties of clouds, with climate effects on regional and global scales.

This chapter will identify some critical science questions concerning biosphere-atmosphere exchanges (see Fig. 8.1, this page, for key features). First, the fluxes of gaseous compounds between the forest and atmosphere are discussed, focusing on the most important non-CO_2 GHGs: nitrous oxide (N_2O) and methane (CH_4). Next examined are biogenic volatile organic compounds (BVOCs) and nitrogen oxide (NO_x) radicals that participate in chemical reactions regulating atmospheric oxidative capacity, controlling atmospheric ozone (O_3) concentration, and generating secondary organic aerosols (SOA). The forest not only is a source of changes, it is a recipient as well. For example, land-use change, industrialization, and urbanization lead to increasing production of O_3, whose negative effects on trees in temperate forests are well known but essentially unstudied in the Tropics. Also discussed in this chapter are atmospheric particles and aerosols, including both primary particles and SOA.

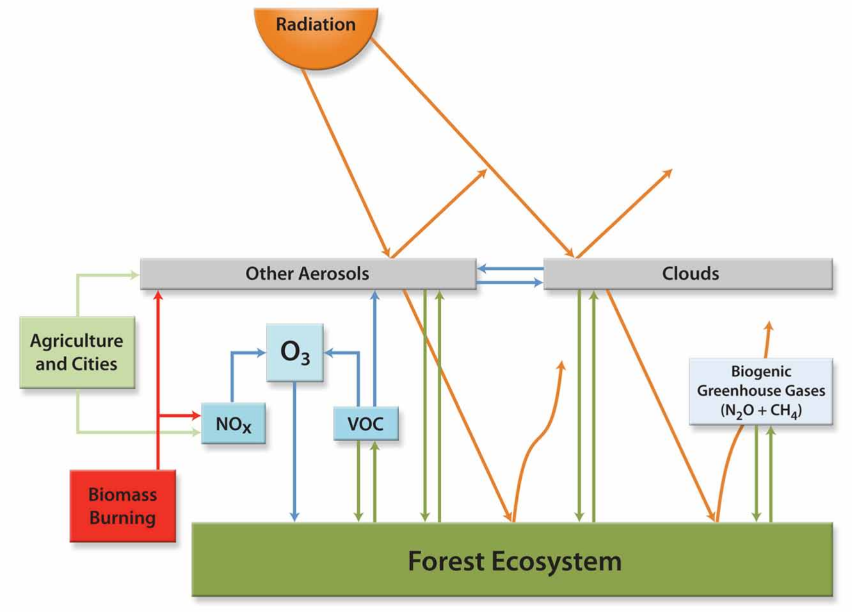


Fig. 8.1. Interactions Between Tropical Forest Ecosystems and the Global Atmosphere. This schematic emphasizes non-CO_2 greenhouse gases, reactive hydrocarbons, NO_x, O_3, and aerosols.

Exchange of Gaseous Compounds with Tropical Forests

> *"People look at a tree and they think that it comes out of the ground … but trees come out of the air."*
> *— Richard Feynman*

Tropical forests play a critical role in controlling the emission of two key GHGs: N_2O and CH_4. They also influence exchanges of organic compounds including isoprene, monoterpenes, sesquiterpenes, and a wide range of oxygenated compounds collectively known as BVOCs. These oxygenated compounds influence climate indirectly through atmospheric chemical reactions that can generate or remove O_3 or consume hydroxyl radical (OH). Hydroxyl is a main sink for CH_4, and its atmospheric distribution determines the lifetime, and thus potency, of this GHG. BVOCs also may condense or react to form SOA, as discussed in the aerosols section on p. 59.

Direct Exchange of Greenhouse Gases

Nitrogen Oxides

Globally, humid tropical forests are the largest sources of N_2O, a gas with strong radiative forcing (Zhuang, Lu, and Chen 2012; Bouwman et al. 1993). A recent estimate found that evergreen broadleaf forests and woody savannas emitted over 1.6 Tg of N_2O-N in 2000, the vast majority of which comes from the Tropics. This amount equals the sum of all other cover types combined (Zhuang, Lu, and Chen 2012). Warm and moist conditions, along with large ecosystem fluxes of organic and inorganic nitrogen, optimally position tropical forest soils to produce N_2O (Davidson et al. 2000b). In these humid environments, N_2O production occurs primarily via denitrification, a low redox process (Groffman and Tiedje 1989; Silver, Herman, and Firestone 2001; Silver et al. 2005b; Templer et al. 2008). Increases in the severity and frequency of rainfall events could lower soil redox potential (Silver, Liptzin, and Almaraz, in press) and increase the amount of N_2O emitted from tropical forests. Significant quantities of NO_x radicals also are emitted by tropical forest soils, providing a key ingredient for the highly reactive photochemical environment (Bakwin, Wofsy, and Fan 1990). In the future, if changing land use causes tropical forest areas to contract, natural N_2O and NO_x emissions might diminish, possibly to be replaced or exceeded by emissions associated with fertilized agriculture (Reiners et al. 2002) in the same areas. The natural sources could be enhanced by future increases in temperature and precipitation as well as deposition of pollution-derived fixed nitrogen (e.g., ammonia or nitric acid; Hietz et al. 2011; Matson et al. 1999; Matson, Lohse, and Hall 2002). Alternatively, these sources could be suppressed by increased aridity (Davidson et al. 2000b). The overall ecosystem response of tropical soil N_2O and NO_x emissions to global changes in climate and chemistry is thus very uncertain and a high priority for investigation.

Methane

Humid tropical forests and wetlands also are important sources of CH_4 emissions, which globally are dominated by anthropogenic sources such as fossil fuel extraction (coal and natural gas), rice agriculture, enteric fermentation, and the processing of human and animal wastes. As with N_2O, methanogenesis typically proceeds under low redox conditions. Research in Puerto Rico found that rates of CH_4 oxidation were more sensitive to redox than CH_4 production, largely because of the strong aggregation and aggregate stability of tropical soils, leading to an abundance of anaerobic microsites (Teh, Silver, and Conrad 2005) that facilitate methanogenesis even when bulk soil conditions are aerobic.

Prior to agricultural intensification and industrialization, wetland emissions likely accounted for most of the global CH_4 budgets, with strong contributions from Amazonia. Even now, natural wetland variability may control the interannual variability of CH_4 flux to the atmosphere (Gedney, Cox, and Huntingford 2004). Tropical wetlands, including areas of peat deposits with very high (and potentially vulnerable) carbon stocks, cover vast areas in tropical forest regions (Page, Rieley, and Banks 2011). Studies of wetland areas during the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) project revealed that about 20% (more at the end of the wet season) of the Amazon Basin has wetland character and may contribute 5% of global CH_4 emissions (Hess et al. 2003; Melack et al. 2004). Fluxes of CH_4 from Amazon Basin wetlands have been measured almost exclusively near the main

stem of the Amazon River, although other environments such as the interfluvial wetlands in the Upper Rio Negro Basin recently have been studied (Belger, Forsberg, and Melack 2011). Vast areas of seasonally flooded forests may be potent sources of CH_4 during particular phases of the cycle. These processes would be expected to shift markedly in response to an altered hydrograph resulting from changes in climate and land use.

Methane emissions from wetlands depend primarily on the availability of organic substrate and the extent of anaerobic environments. Thus, the extent and duration of flooding are the primary controls on CH_4 emissions (Walter and Heimann 2000). These factors change seasonally and interanually and can potentially shift with rainfall under climate change (Gedney, Cox, and Huntingford 2004). Temperature, availability of labile carbon, and route of CH_4 to the atmosphere (e.g., transport through plants, ebullition, or diffusion) also are important controls on CH_4 emissions. Measurements that can help improve representations of wetland areas and the temporal extent of flooding are critical for accurately modeling present and future wetland emissions.

Upland forest soils have long been known to consume CH_4 (Harriss and Sebacher 1981; Keller, Kaplan, and Wofsy 1986), representing a relatively small CH_4 sink. Hence, upland forests have been assumed to represent a net sink for CH_4. But atmospheric data from Amazon forest sites recently suggest that there is a net *source* of CH_4 in upland forests (Carmo et al. 2006). While this source is relatively small on a per-unit-area basis, it may be comparable to the wetland source if present throughout the Amazon forest area. Research in Ecuador suggests that tank bromeliads represent a potentially important source of CH_4 in tropical forest canopies (Martinson et al. 2010), along with termites (Jamali et al. 2011) and anaerobic aggregates in wet clay soils (Blagodatsky and Smith 2012). A recent paper by Covey et al. (2012) suggests that colonization of wood by archeae may produce significant aerobic CH_4.

Both N_2O and CH_4 fluxes have been studied in relatively few tropical forest locations, and most measurements have been made using chamber techniques subject to a variety of artifacts and challenging to scale up (Rochette and Eriksen-Hamel 2008). New measurement technologies using robust, portable laser-based sensors make wider-area measurements accessible even under relatively primitive conditions. Expanding GHG measurements to the ecosystem scale and larger in tropical forests is an important research priority.

Deposition fluxes of nitrogen oxides (NO_x, nitric acid) and O_3 to forest canopies can significantly affect both the ecosystem and atmosphere. Foliar uptake of fixed nitrogen is an efficient way to deliver fertilizer to the forest, leading to stimulation, and potentially overstimulation, of growth (Bryan et al. 2009). Ozone uptake is efficient and damaging to the photosynthetic organs of the plant (Lindroth 2010). Conversely, uptake of these species by tropical forests lowers concentrations available for photochemistry (Wu et al. 2011). Few observations of these processes have been made at the ecosystem scale, limiting guidance for their representation in ESMs.

Biogenic Volatile Organic Compounds

BVOCs include a very diverse set of molecules, hundreds of which have been identified and thousands that have yet to be. The most important by mass are relatively low-molecular-weight compounds such as isoprene, monoterpenes, methanol, acetone, acetaldehyde, formaldehyde, and formic and acetic acids (Lathiere et al. 2006). Isoprene accounts for about 40% of this flux by mass (Guenther et al. 2006) and provides the dominant chemical reactivity. BVOCs drive chemical reactions that lead to a sink for atmospheric hydroxyl radical (OH). This regulation of atmospheric oxidative capacity can affect the lifetime of CH_4, which primarily is consumed by reactions with OH (Wuebbles et al. 1989). Under conditions in which the NO_x concentration is sufficiently high (>5 to 30 ppt), as is typical in tropical forests due to endogenous biogenic emissions (Jacob and Wofsy 1988; Wu et al. 2011), BVOC oxidation contributes to the production of O_3, a GHG and potent toxin for plants (Lombardozzi et al. 2012). Another critical role of BVOCs is the formation of SOA when organic compounds react or condense to form aerosol particles as discussed in the following section.

Most global models that simulate BVOCs adopt some variation of G95, the Guenther algorithm (Guenther et al. 1995, 2006; Rinne et al. 2002;

Greenberg et al. 2004). This algorithm is based on empirical equations parameterized in terms of temperature, sunlight, leaf age, and plant functional type using data from studies of midlatitude plants. Translation of G95 to ESMs requires that parameters be assigned to plants in completely different environments with very diverse chemistry and life histories. Relevant information is known for only a few species and thus is approximated very crudely in current models (e.g., Lathiere et al. 2006).

Leaf temperature is a critical variable because BVOC emissions increase exponentially with temperature (Guenther et al. 1995). A key research need is to improve modeling of both leaf temperature distributions in complex tropical forest canopies and the covariance of temperature with physiological and metabolic parameters. Better simulation of leaf temperatures not only will improve estimates of BVOC emissions, but also will be important for modeling photosynthesis and the mortality of leaves that may exceed a critical temperature threshold under water stress (Doughty 2011). This is a high-priority issue for ESMs in the near term, requiring data on short- and longwave absorption, reflection, and emissions in a three-dimensional canopy, plus determination of the sensible and latent heat fluxes and water limitation affecting leaf elements in the same domain.

Recent research has questioned the basic framework of the G95 approach because it employs a "basal emission factor (E_s)" that is an emergent property of an ecosystem, divorced from basic leaf- or plant-level biophysics. E_s may vary seasonally, by species, by leaf age, with CO_2 concentration, and with previous light and temperature environments (Niinemets et al. 2010a). G95 provides an empirical fit such that the model responds only to instantaneous physical inputs of light and temperature. Recent reviews suggest that future models should more closely simulate the biological and biochemical controls on BVOC production, storage, and emission (Monson et al. 2007; Niinemets et al. 2010b), possibly including circadian control of isoprene emissions (Wilkinson et al. 2009; Loivamäki et al. 2007). Understanding how the inferred circadian control of these emissions functions (whether it is general to all isoprene emitters) is a strong research need, along with determining how this control should be accounted for in leaf-, ecosystem-, and global-scale models.

In the future, BVOC emissions may increase with temperature and decrease with CO_2, as appears to be the case for isoprene. To understand the future emissions from tropical forests, quantifying these trade-offs for tropical plants and the associated ecosystems is critical. Moreover, BVOC emissions are species specific, and hence large-scale changes in community composition will affect fluxes in the future.

Aerosol Particles and Tropical Forests

With the exception of some urbanized areas and transportation corridors, aerosol sources located within the Amazon Basin are dominated by natural and anthropogenic (fire-related) emissions from the biosphere (Martin et al. 2010). Sources include (1) low but consistent production of primary and secondary biological aerosol particles and components (Pöschl et al. 2010) and (2) high but intermittent natural and anthropogenic emissions from biomass burning (Andreae et al. 2004; see Fig. 8.2, p. 60). Primary biological aerosols (PBA) are produced both deliberately by flora (e.g., through the release of pollen and fungal spores) and incidentally (e.g., in leaf and soil debris or as suspended microbes; see Fig. 8.3, p. 60; Elbert et al. 2007) and are especially relevant as ice nuclei in the Amazon Basin (Prenni et al. 2009). Substantial production of secondary aerosols occurs by the atmospheric oxidation of trace gases to low-volatility compounds (Chen et al. 2009). These products can deposit on pre-existing particles or possibly nucleate new particles. This particle mode dominates the spectrum of cloud condensation nuclei (CCN).

Once in the atmosphere, particles undergo continuous transformations. Processes include photochemical reactions occurring within particles, reactions involving the gas phase such as the condensation of low-volatility compounds, and reactions with highly reactive gaseous species like the OH radical. Clouds are ubiquitous in the Amazon Basin, and aerosol particles may undergo several cycles of cloud processing during their residence in the region. Cloud processing can modify particle properties by chemical reactions in the liquid phase and by interactions among droplets (e.g., collision and coagulation). Aerosols in turn can modify clouds by changing, for example, droplet number and single scattering albedo. Particles leave the Amazonian atmosphere by dry deposition to the vegetation surface, cloud scavenging and precipitation, and advection out of the region.

During the wet season, the Amazon is one of the few continental regions where atmospheric aerosol particles and their effects on climate are not dominated by anthropogenic sources. During this period, particles are removed relatively quickly by wet deposition, and anthropogenic sources such as biomass burning are weak throughout the basin. Because of this combination of circumstances, natural processes (including contributions from marine and African sources)

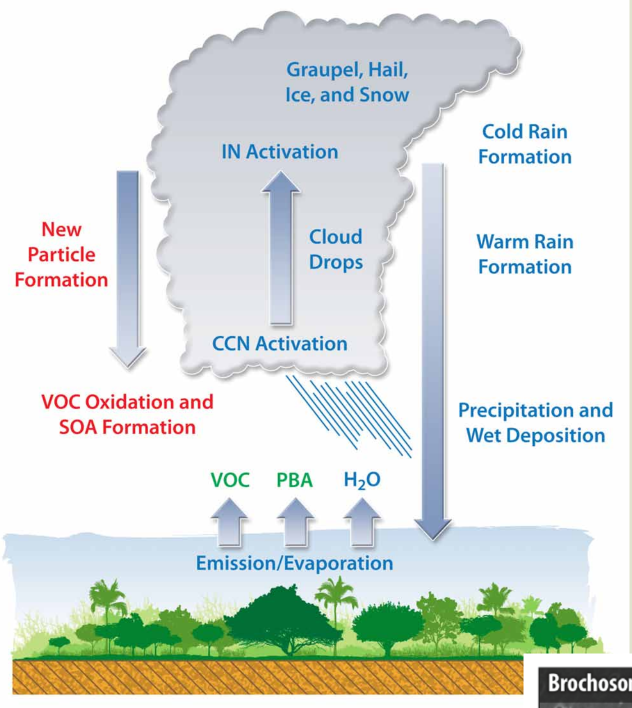


Fig. 8.2. Aerosol and Water Cycling over a Pristine Rainforest. Secondary organic aerosols (SOA) formed by photo-oxidation of volatile organic compounds (VOCs) and primary biological aerosols (PBA) emitted from plants and microbes in rainforests serve as biogenic nuclei for cloud condensation nuclei (CCN) and ice nuclei (IN). These nuclei induce warm or cold rain formation, precipitation, and wet deposition of gases and particles. [Adapted from Pöschl, U., et al. 2010. "Rainforest Aerosols as Biogenic Nuclei of Clouds and Precipitation in the Amazon," *Science* **329**(5998), 1513–16. Reprinted with permission from AAAS.]

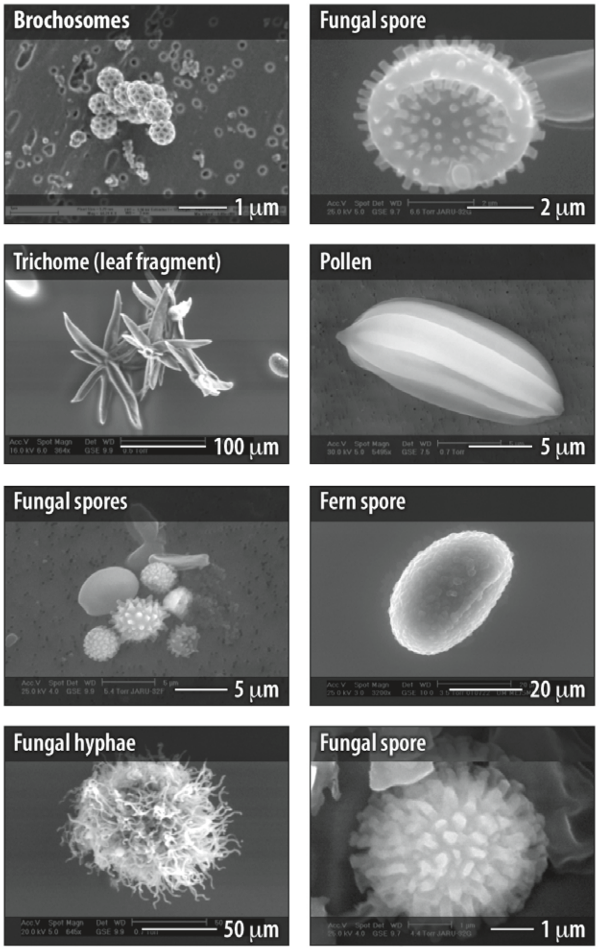


Fig. 8.3. Scanning Electron Micrographs of Primary Biological Particles Collected in the Amazon Basin. [Adapted from Martin, S. T., et al. 2010. "Sources and Properties of Amazonian Aerosol Particles," *Reviews of Geophysics* **48**, RG2002.]

become the dominant contributors to ambient particle populations over large expanses of the Amazon Basin during a significant part of the year. Particle concentrations measured during these conditions are among the lowest found on any continent and are similar to those over remote oceans (Andreae 2009). Consequently, the Amazon Basin has been dubbed the "green ocean" because of the similarities in particle concentrations and cloud microphysics between it and these remote oceanic regions (Williams et al. 2002). This may be the only region on the tropical continents where populations of nearly pristine aerosol particles free of direct anthropogenic influences can still be found at times.

In stark contrast to the green-ocean conditions of the wet season are those associated with the dry season for large areas of the Amazon Basin. Vast numbers of deforestation fires burn during the dry season, especially along the peripheries of the forest, and large parts of the region become among the most polluted places on Earth (Artaxo et al. 2002). Consequently, the regional energy balance is changed because high particle concentrations affect the amount and location of solar radiation absorbed by the planet. Simulations using regional climate models show that the changes in energy delivery significantly influence regional patterns of atmospheric circulation and meteorology. The high particle concentrations change cloud microphysics and rainfall, significantly influencing the overall water cycle (Rosenfeld et al. 2008). They also affect air quality by degrading visibility and affecting human health.

Aerosol Measurement and Modeling Needs

The current generation of land-atmosphere models does not adequately capture important aerosol particle dynamics, specifically in the Amazon region. To improve the representation of PBA emissions in modeling efforts, a number of important research gaps must be overcome. Specifically needed are investigation and implementation of models at the scale necessary to capture how vegetative heterogeneity within the rainforest canopy affects BVOC and PBA particle emissions. Modeling advances also should include all BVOC emissions (at the level of compounds or families) that contribute to the secondary components of particles. Another major research gap is model incorporation of new BVOC chemistry—such as the reactions of isoprene in the chemical regimes prevailing in the Amazon Basin (e.g., pristine, low NO_x)—and, more generally, of organic peroxy radicals. Finally, models (validated by measurements) need to represent how efficiently particles (e.g., over the Amazon Basin) are removed by precipitation and how this sink term is affected by the processing and alteration of particles during their residence in the atmosphere.

Despite many technological advances in the past 10 years for characterizing aerosol particles globally, many of the new instruments have yet to be deployed in the Amazon Basin. Logistical difficulties have constrained measurements temporally, spatially, and technically to levels insufficient for obtaining fully accurate descriptions of Amazonian aerosol particles and the processes affecting them. New instruments should be deployed to provide information on aerosol properties, especially related to particle chemical composition. Chemical information can be employed, in conjunction with models, to understand mechanisms of particle formation and subsequent aging processes.

The ideal field program for understanding particles, ecosystems, and climate would span several dry and wet seasons in the Amazon Basin. It would involve *in situ* and remote-sensing measurements from multiple ground-based and airborne platforms and be complemented by satellite observations from which particle and trace gas properties are derived.

In summary, the Amazon Basin can be pictured as a biogeochemical reactor that uses a feedstock of plant and microbial emissions in an environment with high water vapor, solar radiation, and photooxidant levels to produce SOA and PBA (Pöschl et al. 2010). Biogenic aerosol particles serve as nuclei for clouds and precipitation, sustaining the hydrological cycle and biological reproduction in the ecosystem. Aerosol-chemistry-ecosystem interactions are important in the Amazonian rainforest and also may be generally relevant for the evolution of ecosystems and climate on global scales and in Earth's history.

Key Uncertainties and Research Opportunities

Important research gaps for studying the exchange of GHGs, reactive chemical compounds, and atmospheric particles in tropical forests and for

understanding their connections with ecosystems and climate are summarized below.

- **What are the controls of GHG emissions from tropical forests, and how can they be better represented in ESMs?** Many studies have examined the magnitude of current emissions of biogenic GHGs (N_2O and CH_4) and precursors (e.g., NO_x and BVOCs) at the ecosystem scale in tropical forests. However, large uncertainties remain regarding which components of the ecosystem produce these gases. For example, a significant upland source for CH_4 has been identified, but there are only hints of the underlying sources (e.g., tank bromeliads and arboreal termites) and their potential response to climate change. Because most measurements have been made using small chambers focused on soil emissions, information that can be used to validate models at ecosystem and regional scales still is lacking. Chamber studies have been valuable for understanding physical and some chemical controls on GHG emissions, but more research is needed to elucidate the underlying biological and biochemical pathways. To test and enhance ESMs, future studies need to combine both improved quantification of ecosystem exchanges and better understanding of biological controls. A motivating question is, "How will future changes in temperature, precipitation, and nitrogen deposition affect N_2O, NO_x, and CH_4 fluxes from tropical forests?"

- **How will the effects of changing climate and hydrology affect the future emissions of CH_4 from wetlands?** Flooding conditions (e.g., extent, duration, and oxidation status of floodwaters) are the key controls on CH_4 emissions in tropical forested wetlands. Wetland extent and flooding duration will change under future climates in tropical forest regions.

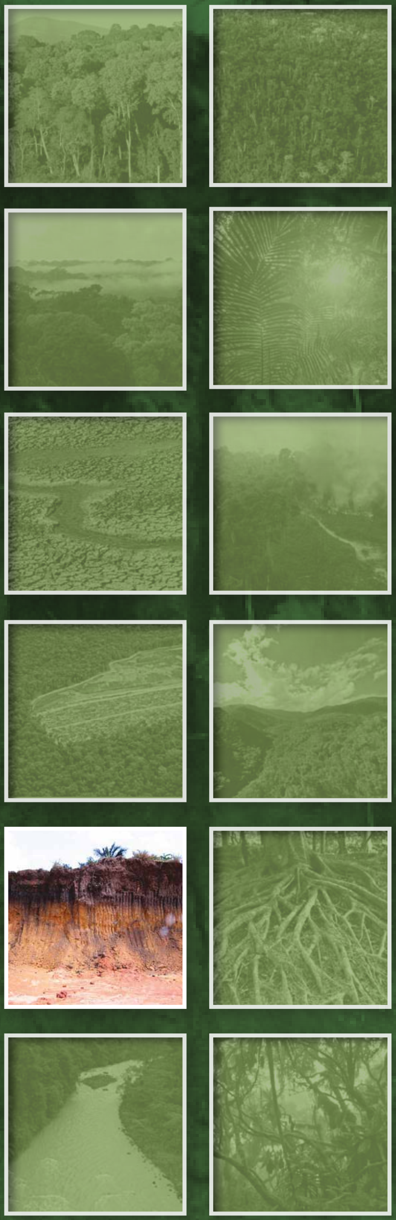
- **How do the deposition fluxes of NO_x, HNO_3, and O_3 affect tropical forests?** These fluxes are poorly quantified, demanding research to determine the origin of these gases and their effects on tropical forest ecosystems. Deposition of atmospheric nutrients and oxidants represents a possibly strong, human-mediated factor in changing the structure, composition, and function of tropical forests. How might this factor change in the future, and how should deposition processes be represented in ESMs?

- **What are the underlying biological and biochemical controls on BVOC production, storage, and emissions, and how should these be represented in ESMs?** Tropical vegetation diversity and the multiple biochemical pathways controlling BVOC production and emissions present formidable challenges to scaling the underlying mechanisms from the cellular to the leaf, canopy, ecosystem, and global levels. Nonetheless, recent studies have shown many new insights into biochemical and cellular-level controls. Two decades of studies have mapped current emission distributions globally. How can the mapping of basal emission factors to plant functional types be tested to determine if ecosystem emissions are adequately represented in ESMs? How will the competing effects of increasing temperature and elevated CO_2 affect isoprene emissions in tropical forest communities? Canopy temperature is a key control on BVOC emissions and therefore must be carefully measured to enable future ESMs to simulate the nonlinear effects of temperature on BVOC emissions.

- **How might plausible future changes (e.g., large-scale forest loss, anthropogenic pollution, and changes to land cover) influence the large-scale characteristics of Amazonian aerosol particles?** How might aerosols, in turn, affect aerosol-cloud-climate interactions in the Amazon Basin, providing a feedback to rainfall, vegetation, and climate change, all of which constrain and force ecosystem development? If large-scale vegetation change occurs in the Amazon Basin, the concentrations and properties of particles and their links to meteorology, cloud type, and rainfall intensity might change greatly. To what extent can these possible changes be predicted beforehand and thus be available for planning scenarios, including economic assessments? To what degree will increasing future anthropogenic pollution in the Amazon Basin enhance oxidant levels and thereby alter prevailing BVOC oxidation pathways, including the fraction of low-volatility products formed (i.e., those that eventually become particle components)? To what extent do past and anticipated future changes in land cover influence the abundance and properties of PBA particles and components?

CHAPTER 9

Nutrient Limitations



Nutrient Limitations

Over the coming century, tropical forest ecosystems will, with very high certainty, be subjected to anthropogenically forced increases in atmospheric carbon dioxide (CO_2) concentration. There is consensus in the climate modeling community that this change in atmospheric composition will drive global-scale increases in near-surface air temperature, including significant temperature increases over tropical forests in Central and South America, Central Africa, and Southeast Asia. Climate models agree that relative humidity remains stable as temperatures increase under radiative forcing, including over tropical forest regions (Soden et al. 2005). Compared to predictions of current temperature and future temperature change, models have lower fidelity in reproducing current distributions of precipitation over tropical forest, and there is less agreement among model projections regarding future changes in precipitation patterns.

Role of Nutrient Dynamics in Predicting Terrestrial Carbon Sink

The terrestrial biosphere is estimated to act as a sink for carbon released to the atmosphere from fossil fuel combustion, and models consistently show that a significant fraction of the current sink is occurring as increased carbon stocks in tropical forests, although direct observations do not consistently support this model result. Future predictions of the magnitude and spatial distribution of the terrestrial sink for fossil fuel carbon emissions differ widely among models, with estimates at the century scale varying by at least a factor of three among multiple models (Thornton et al. 2007). A robust pattern emerging from the current generation of models is that predicted sink strength is related to the models' representation of nutrient dynamics. Models that include coupled carbon-nutrient dynamics as a component of the land biosphere predict a weaker land sink than those that do not (Zaehle et al. 2010). The mechanism responsible for this difference in model behavior is limitation on plant growth imposed by the availability of nutrients, which constrains the response of the carbon-nutrient models to CO_2 fertilization. There is some experimental evidence for this mechanism, with declining CO_2 fertilization associated with signs of increasing nutrient limitation in a temperate forest (Norby et al. 2010). Nutrient limitation in the same forest has been demonstrated experimentally through significant response of net primary production to nitrogen fertilization (Iversen and Norby 2008). However, nutrient addition experiments (using various combinations of nitrogen, phosphorus, and potassium) in tropical forests demonstrate contrasting results, with varying responses of root allocation, tree growth, and litter production among studies and no clear process-level understanding of what drives the differences (Wright et al. 2011).

Although changes in CO_2 and climate co-occur in nature, models can be used to estimate the independent effects of CO_2, temperature, humidity, precipitation, and other dimensions of climate change. Evaluating the influence of radiatively forced climate change (in the absence of the physiological effects of higher CO_2 concentration), models generally agree that global land carbon stocks are reduced, although there is little agreement on the magnitude of the reduction (Friedlingstein et al. 2006; Thornton et al. 2009). One general prediction of these models is that inclusion of carbon-nutrient interactions may result in a smaller climate-driven reduction in carbon stocks (Bonan and Levis 2010). The mechanism hypothesized to cause these differences is increased mineralization of nutrients from litter and soil organic matter under warmer soil conditions, with important spatial variability introduced through changes in soil moisture status. Warming-induced increases in nutrient mineralization are maximized over tropical forest regions, as are associated increases in gross primary production. Temperature and substrate-induced increases in autotrophic respiration lead to a complex spatial pattern of increased and decreased vegetation carbon stocks over tropical forests. Soil organic matter stocks are predicted to be uniformly depleted by radiatively forced climate change over the tropical forest region.

Representation of carbon-nutrient dynamics in the current generation of Earth system models is incomplete and lacking in many mechanistic details. However, results summarized here suggest that improved predictive capability for future CO_2 concentrations and associated climate change depends in part on realistically representing carbon-nutrient interactions, with tropical forests significantly contributing to the globally integrated dynamics.

Improving Model Representation of Nutrient Limitation

An important deficiency in the current generation of nutrient-enabled models, particularly pertinent to tropical forests, is that only nitrogen and carbon-nitrogen coupling have been included. Plant growth probably is limited more by phosphorus than nitrogen in many tropical forests, and recent empirical (Domingues et al. 2010) and modeling studies (Mercado et al. 2011) have underlined the likely importance of phosphorus availability. Moreover, phosphorus-nitrogen co-limitation also appears to be common (Elser et al. 2007; LeBauer and Treseder 2008). By including only nitrogen as a limiting nutrient, current models have defined, at best, an upper envelope for current and future growth responses. In other words, introducing phosphorus as a further limiting nutrient can only reduce modeled estimates of current and future growth fertilization by CO_2 or future growth stimulation from increased mineralization under warming (Thornton et al. 2009) unless mechanisms are introduced in the models whereby current phosphorus limitation is alleviated under future conditions. For example, under elevated CO_2, phosphorus mineralization and availability could be stimulated through increased carbohydrate supply, exudation, and rhizosphere activity (Norby, O'Neill, and Luxmoore 1986; Lloyd and Farquhar 1996). Other nutrients also have been demonstrated to limit growth in some places, and with each new limitation introduced in the models, a further constraint on predicted CO_2 fertilization and predicted warming responses through mineralization would be expected. Therefore, although current nutrient-enabled models are incomplete, they have provided a compelling case for additional efforts to incorporate better mechanistic understanding and more comprehensive process representations.

Another important target for model improvement is representing disturbance processes and their effects on biogeochemical cycles, including interactions with nutrient limitation and carbon-nutrient-climate feedbacks. Chronosequence studies have demonstrated the importance of including "time since disturbance" and disturbance type as constraints on predicted net fluxes of carbon and carbon allocation patterns (Malhi et al. 2009a). Such studies also have highlighted the interactions of these disturbance and disturbance recovery dynamics with other forcings like increased CO_2 and climate trends (Law et al. 2001; Thornton et al. 2002). Model experiments suggest that nutrient limitation plays a critical role in disturbance recovery dynamics. The availability of nutrients for new growth is higher immediately after a stand-replacing disturbance because overall plant demand is low. As a new stand is established, nutrient availability becomes more limiting, partly resulting from both increased demand and from diminished labile litter and soil organic matter stocks reduced over the period of low vegetation inputs. Models predict that the responses of vegetation growth to CO_2 fertilization and climate change are sensitive to disturbance history, with nutrient dynamics and varying nutrient limitation playing important roles. To the extent that disturbance processes are affecting large areas in the Tropics—or are increasing or decreasing in prominence over time—inclusion of more mechanistic representations of disturbance and recovery in nutrient-enabled models should lead to improved model predictions of CO_2 and associated climate change. The rapid decomposition of fresh litter in tropical forests could make accurate model representation of time since disturbance even more critical in these forests than in the temperate zone.

Yet another deficiency in the structure of current nutrient-enabled models is the simplistic representation of soil heterotrophs and microbial community processes. Base rates for decomposition and respiration fractions are specified as global constants and are based on multiple exponential decay representations that ignore the influence of soil structure and microbe-mineral associations. Carbon-to-nitrogen ratios for microbes and microbial byproducts also are specified as global-scale constants. Several models represent nitrification and denitrification with some level of mechanistic detail, but none currently include

explicit representations of the microbial communities responsible for these processes. Insects are known to contribute significantly to litter decomposition rates in tropical forests, but no global-scale model incorporates this process. Current knowledge is adequate to support model improvements in these areas, but additional research is needed to quantify differences across the tropical forest biome.

The expression of plant and microbial demand for nutrients as well as their competition for available nutrient resources are poorly understood and very simply represented in current models. Plant demand and nutrient uptake are closely related to allocation, another critical area identified for model improvement in several previous analyses. For example, plant nutrient demand depends in part on fractional allocation among tissues with higher nutrient concentrations (e.g., leaves, fine roots, and phloem) and lower concentrations (e.g., stems and coarse roots). Plant nutrient uptake and competition with microbes depend on the structure and function of fine-root systems. Current understanding of the mechanistic controls on allocation and functional relationships among rooting distribution, root function, and nutrient uptake in tropical forests is not adequate to constrain models at the global or pantropical scale.

Interactions among nutrient availability, heterotrophic activity, and plant physiology in experimental manipulations can provide multidimensional constraints to test and improve model performance. For example, greater availability of both nitrogen and phosphorus has been shown to increase soil respiration in a lowland tropical forest (Cleveland and Townsend 2006). This research indicates that increased phosphorus affects soil respiration through heterotrophic activity, while the influence of increased nitrogen on soil respiration seems to be related to more production of fine roots. However, sites vary significantly in responses to experimental nutrient additions among tropical forests (Wright et al. 2011). Current models predict the influence of nutrient availability on heterotrophic activity (e.g., Thornton and Rosenbloom 2005), but combined laboratory, field, and modeling experiments at additional sites could lead to improved model prediction of these complex interactions.

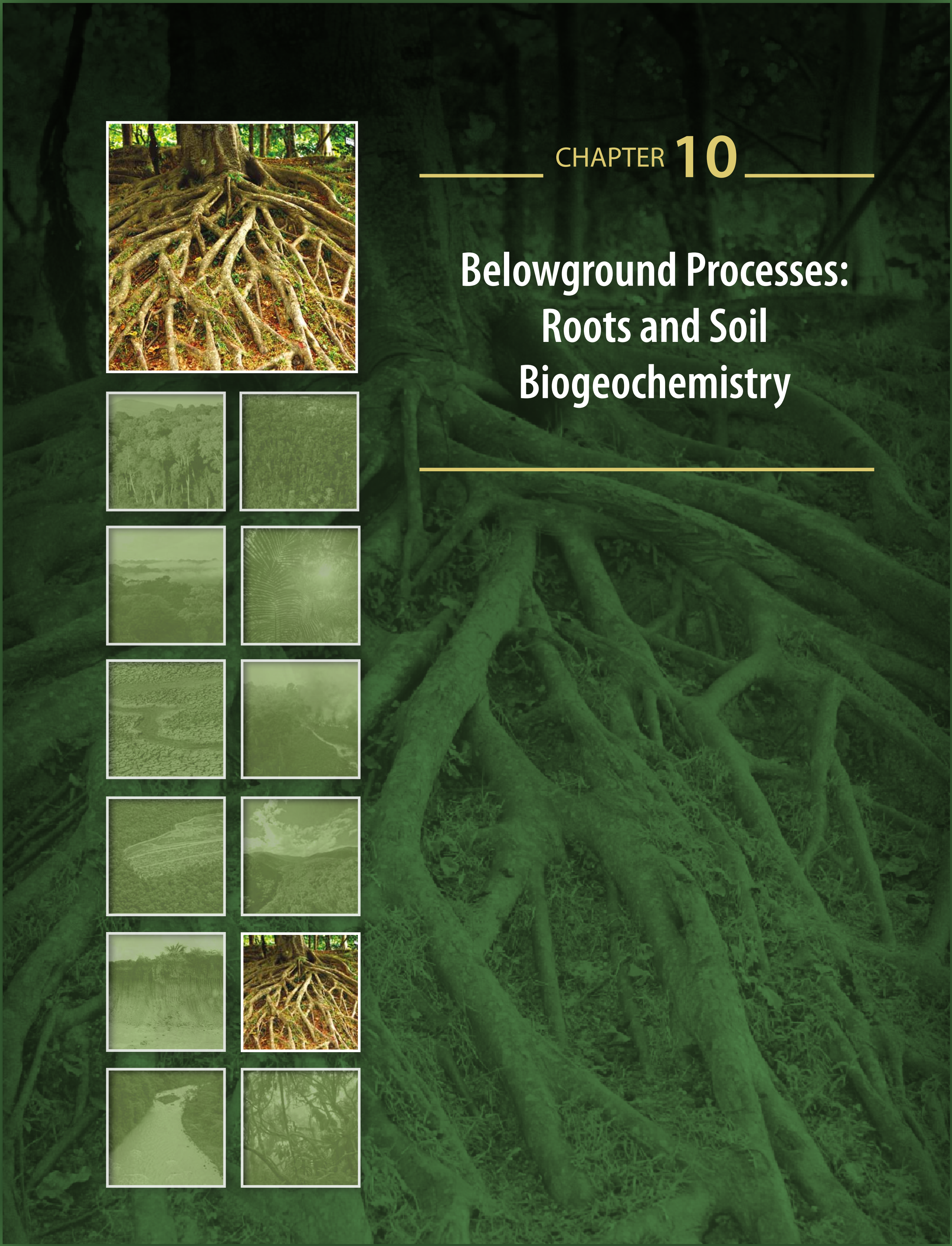
Key Uncertainties and Research Opportunities

Nutrient dynamics in tropical forest ecosystems are important points of interaction among radiatively forced climate change, rising CO_2 concentrations, anthropogenic and natural disturbance, and plant and microbial community ecology. Current knowledge of these interactions still is quite limited, lacking both empirical and theoretical understanding. The following uncertainties and research gaps help frame the key opportunities related to these interactions:

- **Will radiatively forced warming induce changes in tropical forest nutrient dynamics that influence carbon-climate feedbacks?** Warming experiments in the temperate zone and global-scale modeling studies suggest that warming of soil can accelerate organic matter decomposition and increase rates of nutrient mineralization. Shifting nutrient dynamics could influence net greenhouse gas fluxes, thereby driving carbon-climate feedbacks. Interactions with the hydrologic cycle through changes in precipitation and humidity also are likely to play a critical role in these feedbacks. These mechanisms could be explored through a variety of *in situ* and laboratory warming and environmental modification experiments, accompanied by modeling explorations.
- **Will the fertilization effect of rising atmospheric CO_2 concentration interact with nutrient dynamics in tropical forests in ways that modify the net land sink for anthropogenic carbon emissions?** Both field experiments and modeling studies strongly indicate that nitrogen availability and rising CO_2 interact to regulate the CO_2 fertilization feedback in temperate systems. Empirical knowledge of these interactions in tropical systems is limited, but modeling studies suggest the importance of both nitrogen and phosphorus as limiting nutrients that could interact strongly with rising CO_2 to affect net land uptake of anthropogenic CO_2 emissions. New field experiments in tropical forest systems could begin to explore these interactions.

- **Will disturbances associated with anthropogenic land use and changes in land cover interact with nutrient dynamics in a way that modifies the post-disturbance trajectories of net greenhouse gas emissions in tropical forests?** Land-use history, including disturbance type and time since disturbance, has been observed to play a significant role in determining net greenhouse gas fluxes, with important interactions between disturbance history and response of forests to changing climate and rising CO_2. Modeling studies suggest that these interactions are regulated in part by the influence of land-use disturbance on nutrient dynamics. Additional empirical studies in tropical systems are needed to establish the relevant timescales and interaction effects.

- **Are plant and microbial community dynamics influenced by the availability of nutrients in ways that affect climate system feedbacks?** Current theoretical understanding of soil microbial dynamics presents the interaction of microbial communities and nutrient dynamics as a dichotomy between (1) nutrient immobilization in the early stages of plant matter decomposition and (2) nutrient mineralization in the later stages of decay and in turnover of older soil organic matter. The theoretical outcome of these interactions depends strongly on assumptions about plasticity in microbial community stoichiometry and carbon-use efficiency and also on assumed dynamics for mechanisms linking the nitrogen and phosphorus cycles. Creating the potential for complex interactions are competition between plants and microbes for available nutrients and feedbacks between plant supply of fresh litter input (fueling microbial growth) and microbial supply of mineralized nutrients (fueling both plant and microbial growth). Laboratory and field studies are needed in tropical forest ecosystems to resolve these interactions and perhaps may best be accomplished with labeled tracer studies.



CHAPTER 10

Belowground Processes: Roots and Soil Biogeochemistry

Belowground Processes: Roots and Soil Biogeochemistry

Importance of Belowground Biogeochemical Cycling

Much research in tropical forests has concentrated on the easily accessible aboveground vegetation and its diversity, standing biomass, and productivity. However, factors such as nutrient and water availability that shape aboveground characteristics are inextricably linked to belowground biogeochemical cycling. Across a range of spatial scales, variation in soil depth, age, mineralogy, and indigenous microbial and faunal communities provides critical constraints on productivity and diversity in the aboveground components of ecosystems.

Belowground biogeochemical cycling is driven primarily by the delivery of organic matter (ranging from detritus to root exudates) to the soil decomposer community. The breakdown of organic matter provides the major source of energy to soil microorganisms, fueling large fluxes of carbon dioxide (CO_2) and causing soils to serve as sources or sinks of important non-CO_2 trace gases such as methane (CH_4), nitrogen oxides, and carbon monoxide. Except for the initial stages, understanding of the decomposition cascade and how it reflects local physical, chemical, and biological conditions is limited. The belowground biodiversity and biogeography of soil organisms also are still poorly explored, particularly in the Tropics.

Physicochemical interactions of decomposition products with minerals and recycling through belowground food webs result in the persistence of some organic compounds in the soil structure over periods of centuries to millennia. These insufficiently understood stabilization mechanisms are represented in models using empirical correlations with properties like soil texture rather than process understanding. Because soil organic matter controls key soil properties—particularly those associated with overall nutrient availability, water holding capacity, redox, fertility, and trace gas balance—its importance extends far beyond its role in the global carbon cycle.

Future changes in climate, CO_2, nitrogen deposition, and community composition will affect soils in several ways. Changes in productivity, allocation, and disturbance will alter the fluxes of detrital components (wood, leaf, and root litter) to the forest floor and soil. Changes in soil climate conditions and the rate or timing of substrate supply in turn will affect the cascade of processes involved in decomposition of detrital material. Roots and microbes interact to recycle limiting nutrients such as nitrogen, phosphorus, potassium, and other base cations. Therefore, changes in decomposition will feed back to further alter the aboveground portion of the ecosystem. In addition, nitrogen deposition is increasing in tropical regions (Matson et al. 1999) and can alter patterns in carbon storage and turnover times (Cusack et al. 2010). Even in the absence of climate change, Earth system models (ESMs) that do not incorporate nitrogen deposition and plant nutrient limitations due to soil processes may inaccurately predict net primary productivity (NPP), carbon storage, and atmospheric CO_2 concentrations.

Soils underlying tropical forests vary widely, but their responses to changes in climate, CO_2, or nitrogen deposition are uncertain because little has been done to synthesize belowground-aboveground interactions in a way that will aid prediction of such responses. Also unclear is how the responses of these different systems will feed back to atmospheric concentrations of greenhouse gases and aerosols. Given these uncertainties and the influence of belowground processes on ecosystem dynamics, investigation of subsurface biogeochemistry must be a strong component of any future experiments simulating future climate or vegetation change.

Root Productivity, Dynamics, and Function

The factors controlling tropical root biomass, productivity, lifetimes, and decomposition rates—all the components of the root carbon cycle—are poorly understood. Detailed studies of root dynamics in tropical forests are few, though the importance of roots in redistributing water vertically in soil profiles and enhancing nutrient availability to plants is unquestioned (Trumbore et al. 2006; Silver et al. 2005a; Silver and Vogt 1993). For example, forests growing in the deeply weathered, nutrient-poor soils of the eastern Amazon extend roots deep into soils to access water sufficient for maintaining a transpiring canopy during the dry season (Nepstad et al. 1994). The role of deeper roots has been demonstrated in central and eastern Amazon forests, where about 20% of water uptake (Markewitz et al. 2010) and 10 to 20% of soil respiration (Davidson and Trumbore 1995) occur at depths greater than normally measured in soil studies. Including this access to water sources extending deeper than a meter improved climate models (Kleidon and Heimann 2000). However, exactly how the deep rooting system offers advantages to emergent versus subcanopy trees remains unclear. Also uncertain is how forests in shallower or inundated soils differ from the terra firme Ultisols and Oxisols where deep rooting has been found. Root distributions and strategies for maintaining water availability during the dry season obviously will vary in tropical forests with different patterns of nutrient and water availability. The lack of basic understanding of plant allocation patterns belowground in the Tropics and of factors controlling the balance between root and heterotrophic respiration severely limits the ability to model whole-ecosystem carbon and nitrogen dynamics.

Soil Carbon Storage, Nutrient Bioavailability, and NPP

Stabilization mechanisms for soil organic matter vary, but the amount and age of stabilized carbon can be partly predicted from the mineralogy of the soil (Torn et al. 1997; Masiello et al. 2004). Approximately 70% of tropical soils are Ultisols and Oxisols (see Fig. 10.1, this page) with variable-charge iron- and aluminum-(hydr)oxide and 1:1 clay (e.g., kaolinite) minerals (Oades et al. 1989). These minerals have minimal capacity for chemical protection via sorption (Feller and Beare 1997) and shorter residence times. Tropical Andisols, in contrast, tend to weather initially into highly reactive

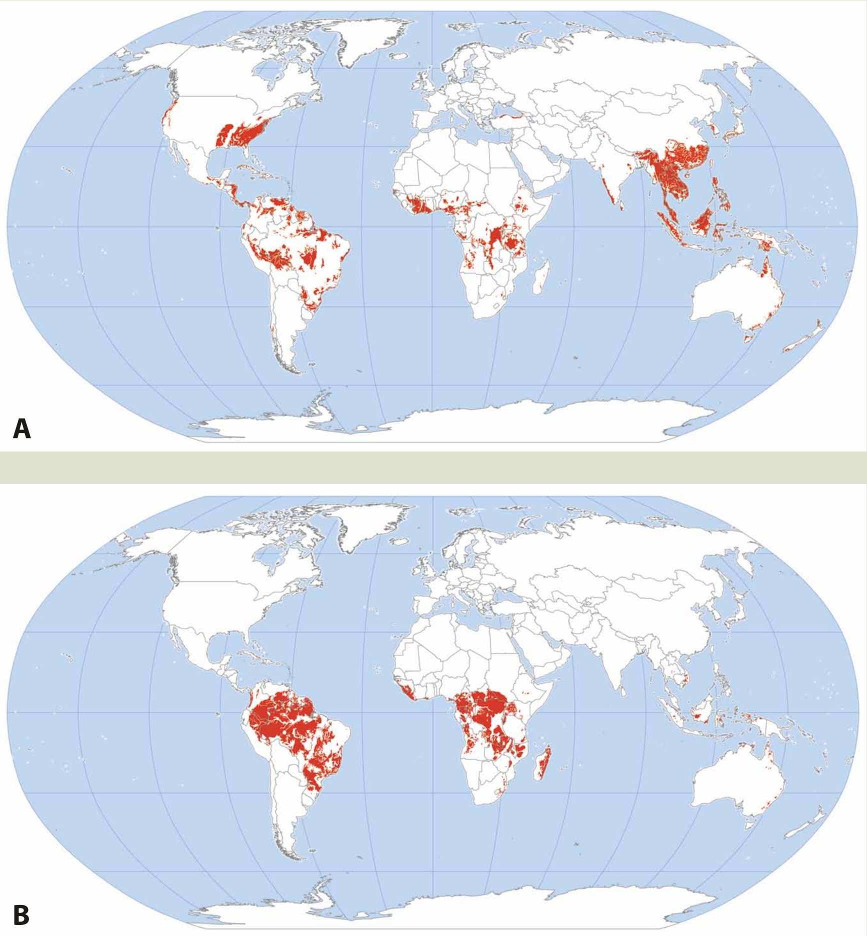


Fig. 10.1 Global Distributions of Ultisols (A) and Oxisols (B). [U.S. Department of Agriculture's Natural Resources Conservation Service.]

short-range-order minerals with a much higher capacity to stabilize carbon over long periods of time.

Tropical Ultisols and Oxisols together contain around one-fifth of the phosphorus present in temperate soils, and of that amount, "organic" phosphorus makes up a much larger proportion (60 to 80%; Duxbury et al. 1989). Orthophosphate forms extremely strong bonds and insoluble precipitates with amorphous iron and aluminum oxides, soil minerals that thus exert a major limitation on phosphorus bioavailability (Duxbury et al. 1989; Yang and Post 2011). Phosphorus limitation, therefore, is typical of tropical systems, although it may be masked during periods of extreme nitrogen limitation. Pulses of low redox conditions may temporarily liberate iron-bound phosphorus (Chacon et al. 2006) and are likely to play a critical role in nutrient availability in tropical forests (Liptzin and Silver 2009). Mycorrhizae (root-fungus associations) also can strongly affect plant access to soil phosphorus, but little is known about the importance and functioning of these associations in tropical systems. In addition, production of the microbial enzyme phosphatase can offset phosphorus limitations by independently releasing the element from organic matter, but enzyme production also depends on nitrogen availability. Although not often considered, potassium can be a co-limiting nutrient as well, so both soil pH status and cation exchange capacity are important aspects of soil fertility.

Rates and Stoichiometry of Nutrient Decomposition and Competition Between Soil Biota and Plants

Large-scale comparisons of common litter decomposition (e.g., the Long-Term Inter-site Decomposition Experiment Team, or LIDET) and cross-site comparisons show that decomposition rates for fresh plant litter and dead trees (i.e., coarse woody debris) in tropical forests are among the highest known (Parton et al. 2007; Cusack et al. 2010; Chambers et al. 2000). Many tropical forests experience only small variations in site temperature, so litter moisture and quality (especially nutrient content) often are used to explain local differences in decomposition rates of fresh surface litter. Cross-site comparisons demonstrate temperature effects along gradients, but these may not be applicable for estimating short-term warming effects, especially since overall soil conditions are likely to vary along elevation gradients. To date, no soil or ecosystem experimental warming study has been performed in tropical forests. Soil organic matter incubation experiments—though often confounded by substrate limitation in long-term studies—have demonstrated that short-term heterotrophic respiration rates increase with temperature, even up to 55°C (Holland et al. 2000). The short-term character of these studies, however, likely misses evolutionary adaptation of microbial communities to changing temperature, which would modulate the response of decomposition rates to temperature change.

Because of the large amounts of carbon in detrital layers and the faster-cycling organic matter pools that support heterotrophic respiration, the response of these pools (both production and decomposition) to future change is critical for carbon balance in the next decades. In the short term, increasing temperatures may be expected to increase carbon and nutrient mineralization, as they do in incubation studies. However, considerable uncertainty remains about the fate of released nutrients, particularly regarding whether plants will outcompete microbial communities or even leaching losses for those nutrients. In the longer term, microbial communities (and their allocation patterns) also can shift in response to changing temperatures, with concomitant alterations in decomposition rates or soil conditions (e.g., pH and oxygen solubility). Current ESMs that couple nitrogen, phosphorus, and carbon cycling disagree on the future trajectory of productivity and carbon storage because they implement nutrient dynamics differently, emphasizing the importance of understanding ecosystem stoichiometry for microbes and plants.

Saturated Soils and Wetlands

The Tropics contain about half of the world's wetland area and an estimated 250 GT of organic carbon (Neue et al. 1997). Tropical wetlands also are globally important sources of CH_4. Drainage and fire in Indonesia's large peat complexes have been implicated in episodic, substantial, and net additions of CO_2 to the atmosphere, especially in the El Niño–Southern Oscillation year of 1998 (Tosca et al. 2011). Recently, new information has demonstrated the existence of extensive peatlands in the Neotropics in subsiding basins in lowland Peru and the Orinoco delta (Lahteenoja et al. 2012). Large amounts of carbon are sequestered in Histosols and Spodosols in these and other areas subject to periodic or seasonal inundation. Figure 10.2, this page, demonstrates that the area of inundation in the Amazon Basin varies tremendously on both a seasonal and interannual basis. The spatial extent of saturated soils probably is highly variable as well and will be critical for understanding how future changes in the hydrologic regimes of different tropical forest regions may alter belowground biogeochemical cycling. Over the past decade, the Amazon Basin already has experienced the lowest (2005) and highest (2012) recorded levels of the Amazon River at Manaus.

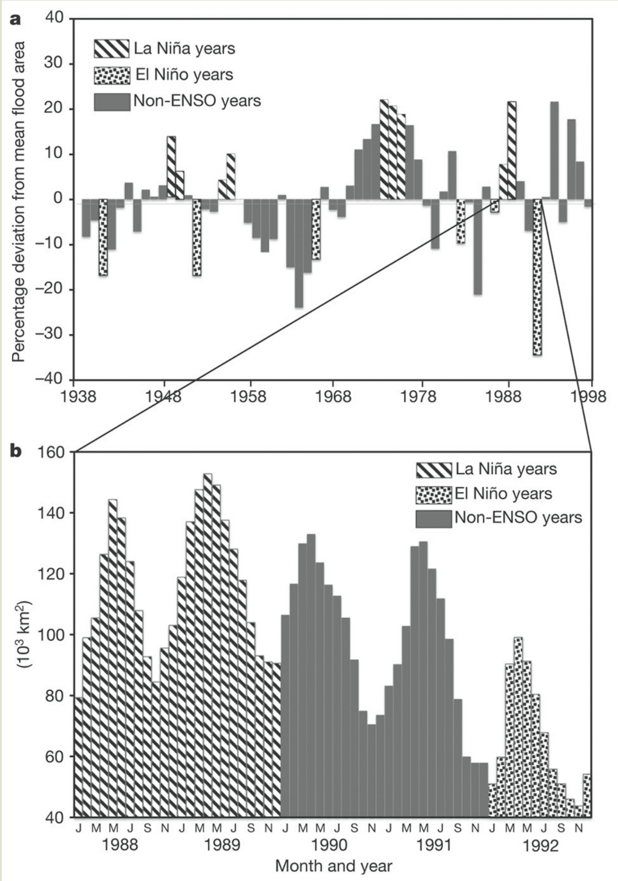


Fig. 10.2. Interannual and Seasonal Variation in Flooded Areas in the Amazon Basin. [Reprinted by permission from Macmillan Publishers Ltd. from Davidson, E. A., et al. 2012. "The Amazon Basin in Transition," *Nature* **481**, 321–28. DOI: 10.1038/nature10717.]

Saturation of soils can play a pivotal role in terms of nutrient availability because formerly stabilized nitrogen, phosphorus, and carbon can be released during seasonal waterlogging common to wet tropical forests. Growth rates decline in high rainfall years (da Silva et al. 2002), though whether this is due to limitation of light or saturation in soils is unclear. In saturated soils, or even in microsites in upland soils, oxygen can be depleted because it is consumed faster than it can be replaced by diffusion from the overlying air. Oxygen depletion leads to reduction of minerals including iron, which frees the associated nutrients for use and yields electrons for microbial mediation of reductive processes (Liptzin, Silver, and Detto 2011; Chacon et al. 2006; Silver, Lugo, and Keller 1999). Released nutrients may be incorporated by plants, leached into deep groundwaters and surface waters, or re-adsorbed to soil mineral surfaces. Even partly saturated soils can switch from net consumption to net production of CH_4 and can become large sources of nitrogen oxide gases (including N_2O). The fate of mobilized nutrients, leaching, plant uptake, microbial respiration, or adsorption may depend on several factors. These include the timescale of oxygen limitation, spatial configuration of roots, age of vegetation, location of microbial biomass and exo-enzymes, availability of mineral surfaces for re-adsorption, and soil hydrologic properties.

Thus, carbon cycle feedbacks in tropical forests are sensitive to the combined mechanisms of the entire integrated ecosystem including, specifically, the intense competition for nutrients by soil minerals, plants, transport advection, and the microbial community. No current models represent key aspects of microbes, enzymes, vegetation, redox, and soil minerals or the role of hydrology in nutrient removal via leaching. Consequently, predicting the effects of shifts in soil moisture content resulting from climate change in the Tropics poses a major challenge.

Current Models and Their Limitations

Coupled land-atmosphere ESMs use extremely simplified processes for the soil carbon cycle, yet the process understanding needed to improve models still is lacking. For example, soil carbon cycling appears to be much faster in the Tropics versus temperate climates, partly because of high temperatures and high microbial biomass (Dubinsky, Silver, and Firestone 2010). Significant and *ad hoc* modifications to rate variables are required for traditional and detailed soil carbon cycling models (e.g., CENTURY and ROTHC; Parton et al. 1989; Diels et al. 2004). This suggests that the models or model parameters developed for temperate systems are not adequate to simulate tropical ecosystems. Some of these soil carbon cycling models are much more detailed than those used in ESMs. Regardless, research now indicates that these detailed models inaccurately or inadequately represent a number of relevant processes, including (1) preservation of labile carbon (Sollins et al. 2009), (2) sorption of dissolved carbon (Conant et al. 2011), (3) the nature of biochemical recalcitrance (Kleber et al. 2010), (4) enzyme-facilitated degradation (Sinsabaugh, Antibus, and Linkins 1991; Allison, Wallenstein, and Bradford 2010), and (5) functional pools of soil carbon (Schmidt et al. 2011). One example of an area of uncertainty involves enzymes that catalyze the depolymerization of inputs, which produces small soluble oligomers and monomers as bioavailable substrates for microbial metabolism. Key factors controlling enzymatic degradation of organic matter and the subsequent release of bioavailable nutrients are largely unknown, limiting the ability to model ecosystem processes under current and future climates (Wallenstein et al. 2011). Additionally, changes in moisture and redox regimes may impart significant shifts in microbial community structure and function (Lawrence, Neff, and Schimel 2009) and in nutrient flow and transport through the subsurface. However, neither process is included in current soil carbon models at either the plot or ESM scales.

The absence in models of most key interactions among microbes, plants, and soil minerals that control dissolved carbon, nitrogen, and phosphorus dynamics seriously undermines realistic rendition of response to change. An important contribution would be determining how to tractably include into larger-scale climate models the key controllers of process-level nutrient interactions, including deterministic aspects of microbial community function. Key soil functional traits that can be successfully scaled in space and time must be identified.

Oversimplification in models can give very misleading results. For example, Falloon et al. (2007) predicted a large net loss of carbon in the Amazon Basin with climate change alone because drying reduced carbon gained in forest productivity to less than that of carbon lost through organic matter decomposition. However, the magnitude of their estimated carbon loss (a decline from 45 to 23 Pg between 2000 and 2100 in the Amazon Basin) is too large to be credible given that >70% of the carbon in the 0- to 30-cm soil layer is in soil organic matter fractions with turnover times longer than centuries (Telles et al. 2003). The prediction of large losses likely results from using a single pool model for soil carbon that overpredicts carbon changes in the short term (Knorr et al. 2005). With more realistic models of carbon dynamics that have been highly parameterized for local conditions, losses from soils are small to minimal compared to changes in aboveground biomass that occur with deforestation and reforestation (Cerri et al. 2007). Far more important is the fate of nutrients like nitrogen, phosphorus, and potassium that rely on recycling through decomposition to be sustained.

There is a growing consensus that model structures using empirically defined "pools" of carbon with different intrinsic decomposition rates are not adequate to describe carbon and nutrient cycling in soils (Schmidt et al. 2011). However, improved formulations, which might be specific for different soil types, have yet to be developed and tested. Within the next several years, though, modeling approaches that include biological processes more explicitly are expected. As part of a coordinated research effort in the Tropics, a belowground experimental component could supply critical tests for this new generation of models that include soil biology more explicitly.

Detailed data for tropical forest soils, while increasing rapidly, are concentrated in only a few soil types and regions. Key tests for the new models will be their ability to make predictions across a range of soil types in the Tropics, which will require collecting new types of data at diverse field sites.

Key Uncertainties and Research Opportunities

Gaining better insights into belowground processes in the Tropics is an important component of strengthening model predictions of tropical forest response to climate change. Workshop participants identified several research gaps, including improved process understanding and model representation of how soil biogeochemistry interacts with vegetation to determine overall ecosystem response to disturbance (e.g., moisture, temperature, CO_2 increase, and vegetation loss). Also needed is a better understanding of how root and mycorrhizal production (including rates and controls), vertical distribution, turnover, and function affect the uptake and redistribution of water and nutrients in different tropical forests and under disturbance. The significance of soil redox and pH as critical elements in biogeochemical cycling needs to be quantified, as well. This includes understanding the spatial and temporal importance of low redox and its relationship to (1) ecosystem productivity, (2) soil and wetland carbon storage, (3) phosphorus and nitrogen cycling, and (4) microbial mediation of atmospherically important gases. Indigenous microbial communities across the range of tropical soils should be investigated, along with how shifts in community function or allocation patterns (enzymes vs. growth) could modulate system response to changing conditions. Finally, the cross-disciplinary interactions necessary to identify and scale key belowground characteristics should be fostered. Research gaps and uncertainties in belowground processes include:

- **What controls spatial and temporal patterns of root production, and how will root production shift with changes in climate and atmospheric inputs?** Understanding gained from temperate systems cannot be directly extrapolated to the Tropics because of substantial differences in plant communities, soil characteristics, climate, and soil biology. What factors (e.g., nutrient availability and soil hydrology, redox, pH, texture, depth, and biology) control spatial and temporal patterns in root productivity? What traits are important for modeling root function, and are they predictable from aboveground plant traits or soil characteristics? How will root allocation depend on or reflect changes in soil fauna and microbial communities?

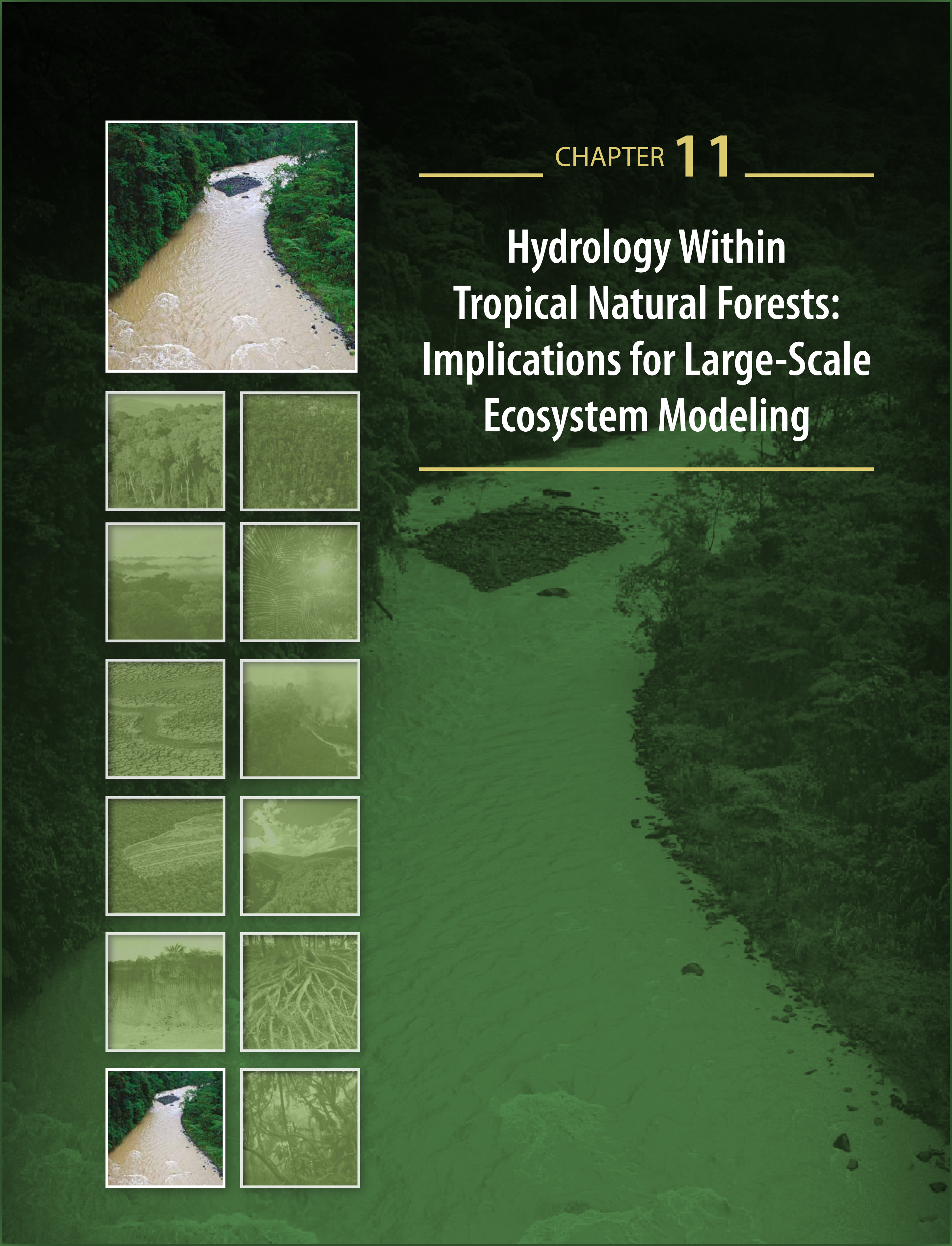
- **How will changes in root inputs alter belowground biogeochemistry and carbon stabilization?** Improved understanding of the processes involved in the transformation of root carbon to stabilized soil carbon is the focus of intense interest. A high priority is investigating microbial and mineralogical mediation of carbon stabilization in tropical soils and the ways that root inputs alter these processes. Also important are efforts to identify and distinguish factors critical for stabilizing soil organic matter on short (decades or less) and long (decades to centuries) timescales. The soils near roots are important zones of carbon, nitrogen, iron, and phosphorus (hydrolysis) transformation. Changes in the inputs of root carbon likely will alter the transformation and resulting availability of these nutrients.

- **How will components of a changing climate alter critical soil characteristics?** More information is needed on the extent of tropical Histosols (peatlands) and their vulnerability to drying, land-use change, and fire. Changing patterns of leaching, soil redox, and soil organic carbon will alter the rates of release and recycling of potentially limiting nutrients (e.g., nitrogen, phosphorus, and potassium).

- **To what degree will changes in microbial community composition and function alter nutrient availability (e.g., mycorrhizae and mineralization), trace gas production (e.g., of CH_4, nitric and nitrous oxide, and CO_2), and carbon stabilization?** Current understanding of the response of soil microbial communities to climate change is derived largely from studies of Arctic and, to some extent, temperate systems. The marked differences in tropical soils, plants, and climate make extrapolations from these studies tenuous at best. A number of important aspects of soil biology are poorly understood in tropical systems, including the role of biological nitrogen

fixation in different tropical forests (disturbed and undisturbed) and the importance of mycorrhizae in phosphorus-limited tropical forests.

- **How can the biological controls of belowground biogeochemistry best be represented in models?** In temperate systems, basing decomposition models on enzyme parameters has been a topic of interest, but how can models most accurately represent control of decomposition in tropical systems? In the next decade, a wealth of information will emerge from molecular characterizations of soil communities. Are there components of these huge datasets that will be useful in large-scale models? Are there indices of microbial community function that can be scaled up in time and space in tractable and robust ways?



CHAPTER 11

Hydrology Within Tropical Natural Forests: Implications for Large-Scale Ecosystem Modeling

Hydrology Within Tropical Natural Forests: Implications for Large-Scale Ecosystem Modeling

The discipline of hydrology when focused on issues pertinent to tropical natural forests (sometimes described as "tropical forest hydrology"; Bonell 1999) may be divided into the study of (1) canopy hydrology and (2) hydrologic or "runoff" pathways (Bonell, Callaghan, and Connor 2004; Wohl et al. 2012).

Canopy Hydrology: Water Interactions Among the Atmosphere, Forest Canopy, and Land

Two central concerns for studying canopy hydrology within forests are (1) the effect of the vegetation canopy on the magnitude and distribution of rainfall reaching the ground surface and (2) the flux of water to the atmosphere by evapotranspiration mechanisms, also described as "latent heat flux" or simply "evaporation" (Penman and Schofield 1951).

Rainfall received by the canopy of a tropical natural forest is a fundamental component of the regional (and global) water cycle and is the key driver for:

- The rate of wet-canopy evaporation (a component of evapotranspiration).
- Rates and locations of water flows on and below the ground surface.
- Rates of nutrient and carbon mobilization and transport within watersheds.
- River behavior (including nutrient and carbon losses).

When compared to temperate biomes, the higher rainfall intensities characteristic of tropical forests can have a disproportionate effect (due to nonlinearities in the hydrological system) on the dynamics of wet-canopy evaporation (Calder 1996) and the preferential pathways of water, nutrients, and particles (mineral or organic) toward tropical rivers (Chappell 2010; Walsh et al. 2011; Zimmermann, Francke, and Elsenbeer 2012). This is particularly the case in natural forest areas beneath tropical cyclone tracks—including the Caribbean, Queensland (Australia), Madagascar, and the Philippines—given their even greater rainfall intensities (Bonell, Callaghan, and Connor 2004; Howard et al. 2010; Chappell et al. 2012). Because of the impact of these regional differences in rainfall characteristics, large-scale ecosystem models must be able to capture how nonlinearities affect the hydrologic pathways and associated subsurface nutrient and carbon flows within small, low-order watersheds that contribute most riverflow and hence aquatic (chemical and particulate) flux within tropical natural forests.

Evapotranspiration is the summation of flux by wet-canopy evaporation (sometimes ambiguously called "interception loss"), transpiration, soil evaporation, and open-water evaporation. Recent advances in the direct measurement of evapotranspiration over subminute to interannual timescales using the eddy covariance (EC) method give observations over areas up to a few square kilometers that can assist parameterization and evaluation of regional or global ecosystem models (Mueller et al. 2011). Synchronous measurement of latent heat, sensible heat, and carbon dioxide (CO_2) fluxes with EC systems allows study of the interactions among key variables of the global water and carbon budgets. This is an essential aspect of intrinsically interdisciplinary ecosystem models, such as Community Land Model version 4 (CLM4) (Barron-Gafford et al. 2012). Though the number of tower-based EC systems is increasing within tropical natural forests (Fisher et al. 2009), it is only a fraction of the number of published studies on basin water balance across this biome (Bruijnzeel 1990).

A key uncertainty arising from the extensive basin studies within forested and adjacent land uses—whether in the Humid Tropics or across all global biomes—is the large variability in change to evapotranspiration with forest cutting or establishment. With the same proportion of forest being cut, observed evapotranspiration changes lie within a huge range of values, whether expressed as a depth of evaporation (mm) or a proportion of rainfall

(Andréssian 2004; Brown et al. 2005). This variability makes it difficult to generalize how regional evapotranspiration is affected by various intensities of tropical natural forest cutting. The Zhang et al. (2001) generalization (so-called "Zhang curves") is based on 250 global studies, including 35 basin studies from tropical latitudes. It indicates that forests have significantly higher evaporation rates compared to grasslands where annual precipitation is high (>2000 mm per year), but the rates are comparable in low rainfall areas (<500 mm per year). Important to note is that some of the variability in the evapotranspiration difference between forests and herbaceous vegetation arises from errors in basin water-balance studies. Many studies use basins that are too small (<0.5 km^2) to discount the effects of deep seepage (so-called "basin leakage"), resulting in overestimation of evapotranspiration totals from annual rainfall minus river discharge balances (Bruijnzeel 1996). In addition, many reforestation studies are not monitored long enough to show peak (or average) water-use effects (Vertessy, Zhang, and Dawes 2003), and studies monitoring the effects of forest cutting for only a few years emphasize maximum rather than longer-term differences between forests and herbaceous vegetation (Kuczera 1987; Andréssian 2004).

Earlier general circulation model (GCM) studies indicated that severe droughts within the Amazon produced by anthropogenically forced climate change could so deplete the subsurface moisture available to tropical natural forests that extensive tree mortality could occur (Cox et al. 2004). More recent studies, however, have demonstrated that Amazonian rainforests can maintain high transpiration rates during severe droughts, a finding that suggests tree roots are much deeper than specified in earlier GCM simulations (Canadell et al. 1996; Fisher et al. 2007). This, in turn, indicates that the subsurface moisture stores (accessible to deep tap roots) are often much deeper than the few meters specified in many GCM simulations. Consequently, an understanding of the subsurface hydrology and associated hydrologic pathways is fundamental for accurately simulating moisture availability in the dry season to support transpiration and associated tree hydraulic functions.

Hydrologic Pathways: Regulating Moisture Availability and Nutrient-Carbon Migration

The hydrologic (or water) pathways within watersheds of tropical natural forests can be defined the most unambiguously as the lateral flow routes toward a stream or river. These routes comprise:

- Lateral flow on slopes by infiltration- or saturation-excess overland flow mechanisms, both including lateral flow within the litter layer (Hewlett 1982).
- Lateral flow within the solum (i.e., A and B soil horizons).
- Lateral flow within deep saprolite (sometimes called the C soil horizon including, for example, deep granite saprolite).
- Lateral flow within rock aquifers (or localized rock fractures).

All these terms have precise definitions within the discipline of scientific hydrology (Kirkby 1978), and much ambiguity and misinterpretation arise when used incorrectly.

The magnitude of water flow within these paths and the moisture states along them (e.g., soil moisture content, soil-water potential, and water-table depth) govern (1) the availability of moisture for consumptive use by trees within the rooting zone (including deep tap roots), (2) rates of soil organic matter decomposition, (3) rates of nutrient release and transformation, (4) weathering rates, and (5) transport of nutrients and carbon from the land system to rivers and oceans (Anderson and Spencer 1991; Proctor 2004; Buss et al. 2010; Shanley, McDowell, and Stallard 2011; Eaton et al. 2012). All these hydrologically mediated processes will need to be simulated within the next generation of regional (or global) ecosystem models.

Observations of the difference between mean annual rates of rainfall and evapotranspiration are insufficient to judge the accuracy and role of hydrologic (and hence associated nutrient) pathways represented within regional ecosystem models. Observations of the flows in each of the four lateral pathways (where present locally) through sequences of storm events are

needed for robust validation. While infiltration- and saturation-excess overland flows can be directly measured relatively easily (at least at very small, subhectare scales), quantifying the proportion of infiltrated water that travels laterally within the solum, saprolite, and rock aquifer is extremely difficult to do without introducing artificial and very unrealistic boundary conditions (Knapp 1970; McDonnell 2003).

Particulate, carbon, nitrogen, and phosphorus fluxes within both overland or subsurface flows and then small, low-order streams of tropical natural forests are equally dynamic through individual storm events, though they are imperfectly correlated with water flow (Wilcke et al. 2009; Walsh et al. 2011). This is partly because of the highly dynamic nature of water flows within shallow hydrologic pathways (over subhourly time intervals). Flux associated with particulate transport is particularly episodic, being dominated by extreme (rare) storm events (Douglas et al. 1999). Thus, ecosystem model simulations of observed time series of nutrients and aquatic carbon must be based on very high frequency sampling (often subhourly) of concentration and flow within the low-order tropical watersheds where most of the load is sourced. Although there are significantly fewer river gauging stations within tropical forests compared to temperate biomes, those with frequently sampled water-quality data are extremely sparse. Hence, observed evidence of linkages between locally dominant hydrologic pathways and resultant physicochemical flux (even integrated at the small watershed scale via stream-based observations) is very limited within tropical forest systems (Wohl et al. 2012).

In terms of observational knowledge of the hydrologic pathways across tropical natural forests, detailed hillslope and microbasin studies have been conducted throughout the region and summarized within several publications, notably Bonell et al. (2004). However, there is no real consensus on how the presence of particular pathways can be identified at large scales relevant to global climate models or on their volumetric significance when present. This is partly because few studies have been conducted within the Tropics and the volumetric significance of each pathway at specific sites in any climatic region is debated (McDonnell 2003). Some conclusions, however, can be drawn from available experimental evidence.

Widely believed outside the tropical hydrological community is that infiltration-excess overland flow—also called Hortonian overland flow (HOF)—generates a significant proportion of flow within rivers. HOF is defined precisely as surface flow (including flow in the litter layer) generated outside channels and produced by rainfall intensities (in units of millimeters per hour) greater than the saturated hydraulic conductivity of the ground surface (also in millimeters per hour). Contrary to popular view, experimental studies show that, except for a few isolated examples (e.g., Zimmermann, Franke, and Elsenbeer 2012), HOF per unit basin area is only a few percent of the riverflow per unit basin area (Norcliff, Thornes, and Waylen 1979; Chappell et al. 2006). The popular misconception partly arises from misinterpreting the results of inclined-line, hydrograph separation into "stormflow" or "quickflow" and "baseflow" (or "delayed flow"; Hewlett and Hibbert 1967). This method is very useful in deriving a single number (i.e., quickflow percent) that characterizes the flashiness of a river's response (Hewlett 1982). However, this proportion should not be used to infer the percentage of the total hydrograph sourced from a particular hydrologic pathway (e.g., overland flow), as was originally envisaged by Robert Horton (Beven 1991, 2012). When such inferences are made, the volumetric importance of the (infiltration- or saturation-excess) overland flow pathway is grossly exaggerated. For example, quickflow is approximately 46% of the total hydrograph in the Danum basins within tropical natural forests in Borneo (Bidin and Greer 1997), but measured overland flow is only 4% of the total hydrograph (Chappell et al. 2006). The volumetric insignificance of this pathway does not mean that its role in transporting particulates (erosion) or nutrients from the organic surface horizons of tropical soils is unimportant. In fact, this small volume of water does much work redistributing particles (and organic solutes) across slopes to streams. Certain soil types found within the Humid Tropics typically have a lower ground-surface saturated hydraulic conductivity, K_s, (also called infiltration capacity), notably Gleysols and Vertisols (Chappell and Ternan 1992; Bonell et al. 2010). Consequently, these soils should have a greater propensity for generating overland flow (whether by HOF or saturation overland flow). However, studies that quantify

ground-surface K_s, overland flow per unit area, and riverflow per unit area are largely absent within the Humid Tropics.

With forest disturbance, soils can be affected by localized compaction from vehicles or by trampling from domesticated animals, causing ground-surface K_s to decrease locally (Bonell et al. 2010) and recover relatively slowly (Hassler et al. 2011). Within landscapes that remain forested, however, marked K_s reductions are highly localized and any HOF generated often reinfiltrates as it moves to less disturbed soils before reaching a river, an often unappreciated effect called the runoff–runon phenomenon (Bonell and Williams 1986). Even with better data on the proportion of rainfall generating HOF, an open question remains about how that process should be represented within finite element meshes of ecosystem models in which element size is so large (i.e., several square kilometers or larger) that overland flow cannot be separated from channel flow.

Given that almost all rainfall penetrating a tropical forest canopy infiltrates the ground, research into hydrologic pathways should be focused on subsurface pathways. Most streamflow-generation studies conducted within tropical natural forests have focused on examining the subsurface A and B soil horizons. However, few studies have been conducted on the role of deeper strata, notably saprolite and rock aquifers (Bonell, Callaghan, and Connor 2004). Underlying small experimental watersheds in, for example, northern Thailand (Kog Ma), Peninsular Malaysia (Bukit Tarek), Cambodia (O Toek Loork), and the central Amazon (Reserva Ducke) are many meters of deep saprolite (C soil horizon) with high saturated hydraulic conductivity. As a result, the lateral flow deep within the saprolite becomes a dominant pathway, subsequently damping the riverflow hydrograph (i.e., hydrograph recessions extending several days after a storm event; Lesack 1993). There are even fewer small experimental watersheds established on rock aquifers within tropical natural forests. Large areas of the central Amazon and Congo basins, however, are underlain by major rock aquifers (Struckmeier et al. 2006; www.whymap.org). Where percolation readily penetrates both the solum and saprolite to recharge deep rock aquifers ("deep groundwater"), then river hydrograph recessions extending over several months clearly demonstrate the dominance of lateral flow within rock aquifers (Ockenden and Chappell 2011). Capturing in new ecosystem models the subsurface strata having root-available moisture storage and the transport of dissolved nutrients or carbon (e.g., dissolved organic carbon and CO_2) within tropical natural forests will require identifying the presence and role of deep saprolite and rock aquifers at a pantropical scale; where present, hydraulic properties also will need to be characterized. Initially, this would serve as a basis for classifying tropical hydrologic systems into those with a deep rock aquifer (Type IV), a deep saprolite (Type III), a solum developed on impermeable bedrock and limited saprolite (Type II), and steep mountains only supporting an A soil horizon (Type I). Areas observed to be dominated by HOF (where infiltration is severally restricted) might be classified as shallow Type I systems also. In very simplistic terms, Type I to IV systems might be seen to have active hydrologic depths of 0.2 m, 2 m, 20 m, and 200 m, respectively, with corresponding hydrograph time constants. Such constants are based on the recession characteristics associated with the dominant hydrologic pathways (Box, Jenkins, and Reinsel 2008) of minutes, hours, days, and months, respectively (see Fig. 11.1, p. 82; Chappell et al. 2007).

Although this conceptual model exists, it does require pantropical mapping using a combination of existing soil and hydrogeological map data combined with hydrograph recession analyses (Peña-Arancibia et al. 2010), plus further evaluation against observations from experimental basins in the Humid Tropics (Bonell, Callaghan, and Connor 2004). Such work potentially would provide the necessary pantropical parameterization for next-generation ecosystem models that would simulate (1) locations where deep rooting in deeper subsurface hydrologic systems affect transpiration and resilience against tree mortality (Fisher et al. 2007) and (2) locations where deep hydrologic pathways regulate the biogeochemistry of tropical natural forests (Buss et al. 2010).

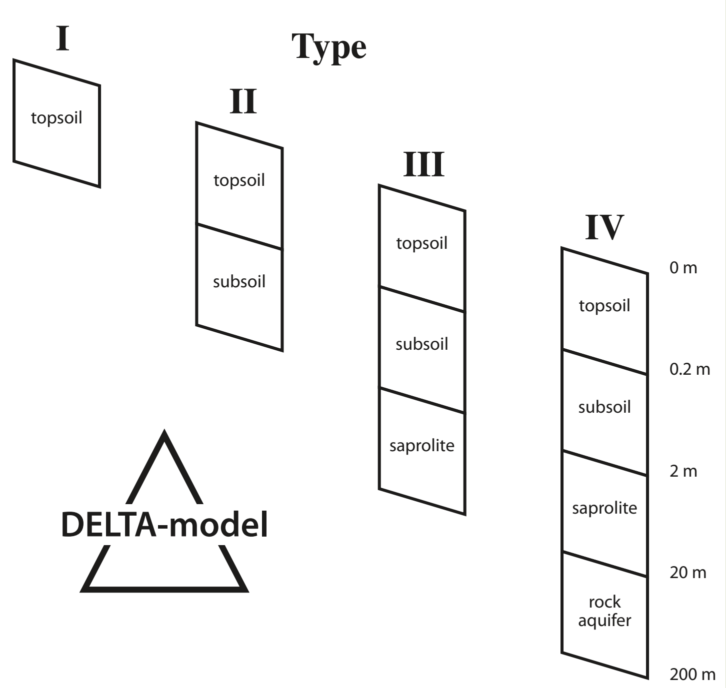


Fig. 11.1. Schematic Representation of Hydrologic Systems in Tropical Natural Forests. This figure indicates where different pathway systems dominate, including near-surface hydrologic pathways (Type I), lateral hydrologic pathways in the solum (A and B soil horizon; Type II), lateral hydrologic pathways in the saprolite (Type III), or lateral hydrologic pathways in a rock aquifer (Type IV). Example depths and the logarithmic depth scale are given. [Adapted with kind permission from Springer Science+Business Media: Chappell, N. A., et al. 2007. "Runoff Processes in Southeast Asia: Role of Soil, Regolith and Rock Type." In *Forest Environments in the Mekong River Basin*, 3–23. Eds. H. Sawada, M. Araki, N. A. Chappell, J. V. LaFrankie, and A. Shimizu, Springer Verlag, Tokyo. © 2007 Springer.]

Key Uncertainties and Research Opportunities

The preceding synthesis has highlighted several key research gaps and uncertainties related to both canopy hydrology and hydrologic pathways:

- **How can water budgets derived from eddy correlation and catchment balances be integrated to give a better understanding of the changes in forest evapotranspiration following disturbance and reforestation at tropical macroscales?** Understanding the evapotranspiration component of the tropical water cycle is of fundamental importance to ecosystem modeling. Although increasing, the number of locations with eddy flux observations above tropical forests still is limited. Consequently, most evapotranspiration estimates for tropical forests, in undisturbed and disturbed states, are derived from catchment water budgets (i.e., the difference between annual rainfall and annual stream flow per unit area) or the analysis of automatic weather station data (Zhang, Dawes, and Walker 2001; Roberts et al. 2005). All these methods are now known to be prone to considerable error (Drexler et al. 2004; Burba and Anderson 2010). Error analysis and method intercomparisons thus are necessary for all new observational studies and as integral parts of any new data assimilation studies. Such analyses enable confidence within the findings of new syntheses of long-term estimates of evapotranspiration or the effects of forest disturbance or reforestation on regional evapotranspiration.

- **What is the depth of the dominant hydrological path mapped at each 100 km^2 location across the Humid Tropics? What saturated hydraulic conductivity distribution can be associated with this dominant path for each mapped location?** The pathways of water over and below the land surface regulate which strata (soil horizons, saprolite, and solid rock) provide the water and chemical resources that support tropical forests and associated faunal communities (including microbiology) and how nutrients are leached to rivers. In steep mountain environments, the dominant hydrological path may extend only to decimeters below the ground surface, but, within areas underlain by rock aquifers, it may be hectometers deep. Although

maps of the soil types covering the Humid Tropics are available, the hydrological functioning of each soil type (e.g., whether the flow is predominantly vertical or horizontal) is much debated, and there is often much variability within each soil type (e.g., McDonnell 2003; Chappell and Sherlock 2005; Chappell et al. 2007). Maps showing the presence of rock aquifers across the Humid Tropics are available (www.whymap.org), but maps of the extent of shallow saprolite layers are incomplete. Physics-based models of catchment hydrology that can predict the dominant hydrological paths normally are most sensitive to the model parameter of the saturated hydraulic conductivity. Within the Humid Tropics, observations of the saturated hydraulic conductivity typically are available only for very small volumes of soil or saprolite. It is now known that the values needed to parameterize models with grid elements much larger than the measured volumes are not easily derived from direct observations (Brooks, Boll, and McDaniel 2004). Much research is needed to understand how saturated hydraulic conductivity values appropriate for the parameterization of regional or global ecosystem models can be derived for the mapped soil, saprolite, and rock types across the Humid Tropics.

- **Can hydrograph shape be used to help determine the dominant hydrological path, (i.e., a lateral path via the soil, a saprolite layer, fractured rock, or rock aquifer) at gauged locations throughout the Humid Tropics?** The recession of a river hydrograph is an area-integrated expression of the dominant hydrological path or paths within a watershed. Watersheds where the water movement is dominated by shallow water pathways through the soil have rapid hydrograph recessions (i.e., minutes to hours). In areas underlain by major rock aquifers, the hydrological pathways are much deeper and the hydrograph recessions much longer (i.e., months). In areas where saprolite pathways or shallow rock fractures dominate, then the intermediate duration recessions dominate (Ockenden and Chappell 2011). Analysis of recession constants for many watersheds across the Humid Tropics should be undertaken systematically (Peña-Arancibia et al. 2010), as these findings have the potential to help develop the pantropical map of the dominant hydrological paths.

CHAPTER 12

Summary of Key Uncertainties and Research Opportunities

Summary of Key Uncertainties and Research Opportunities

Research Gaps for Improving Representation of Tropical Forests

Large differences in Earth system model (ESM) prognoses of future climates are driven by land model variations in tropical forest response to temperature, precipitation, natural disturbances and associated tree mortality, carbon dioxide (CO_2) fertilization, shifts in species community composition, and land-use change. Given these large uncertainties, the current suite of models is able to suggest testable hypotheses that can help guide experimental design. As a major contributor to national climate change research, the U.S. Department of Energy is committed to enhancing these models to better determine the effects of climate change on tropical forests and the role of ecological change in feedbacks on the climate system. Identifying important research uncertainties for achieving this objective was the overarching goal of the Research Priorities for Tropical Ecosystems Under Climate Change Workshop. Research gaps and uncertainties discussed throughout this report were examined as independent forcings and responses. In reality, the individual themes and variables described herein likely will be interactive by nature. For example, temperature and precipitation forcings will be co-dependent, requiring a complex systems approach to understand the adaptive rates of ecosystems and their feedbacks. The following highlights from this workshop report summarize important research questions critical for improving the representation of tropical forest ecosystems in ESMs.

- **How will tropical ecosystems respond to increasing temperatures?** In the Intergovernmental Panel on Climate Change's (IPCC) Fourth Assessment Report A1B scenario, temperatures are predicted to increase by 2 to 5°C over the tropical region by 2100, representing a substantial warming (IPCC 2007; Christensen et al. 2007). The change in temperature relative to weather patterns in the 1900s is particularly important because tropical species have adapted to a very narrow thermal range. Because the current climate is at the upper end of this range, projected temperature increases during this century will increasingly expose tropical forest systems to conditions that are beyond their natural operating regime. Thus, there are no analogue environments with which to compare tropical climates in a warmer world. To improve ESM predictions of tropical ecological response to increasing temperatures, more research is required to address several uncertainties including:
  - – Are there temperature thresholds beyond which photosynthesis significantly decreases? If so, what are they?
  - – Will the temperature sensitivity of respiration change with warming, and to what extent can plant respiration acclimate to this warming?
  - – How will plant carbon allocation and related respiration patterns change with warming?
  - – Will warming lead to sustained increases in heterotrophic respiration, reductions in soil and litter carbon content, and changes to soil nutrient availability?
  - – What is the functional diversity among tree species in temperature responses, and how does it vary across tropical regions?
- **How will tropical ecosystems respond to changes in rainfall?** Atmospheric processes are among the best developed aspects of current models. Projections from these models indicate reduced precipitation patterns and regimes across large tropical regions (such as the southern and eastern Amazon) and increased rainfall seasonality, raising concerns over the vulnerability of tropical forests to drought-induced changes in ecosystem structure and functioning. These projections also show increased rainfall over other regions such as tropical Africa. To improve model representation of tropical forests, a better understanding is needed of the response of these systems to changes in water supply and, most importantly, the spatial and temporal drivers and

feedbacks of drought stress and tree mortality. Specific uncertainties include:

  - How do soil depth, structure, and hydraulic properties affect tropical ecosystem responses to moisture stress?
  - What roles do root structure (e.g., taproots) and soil profiles play in responding to drought?
  - What is the functional diversity in stomatal control strategies among tropical species that help prevent desiccation?
  - How does the response of plant resource allocation to drought stress vary among tropical species?
  - What role does deep subsurface hydrology play in the prevalence of deep rooting in tropical forests, and how does it vary among sites and regions?

- **How will natural disturbance events and tree mortality increase as a result of climate forcings?** Relatively small directional shifts in tree mortality rates (e.g., 1 to 1.5%) can significantly affect the global carbon cycle and net forest-atmosphere CO_2 exchanges. The potential for increased tree mortality from drought, fire, temperature, and windthrow is a primary concern. To improve model predictions of disturbance regimes, several research gaps must be addressed:

  - What are the dominant mechanisms of vegetation mortality in tropical forests, and how do they vary among tropical regions?
  - How does mortality risk from climate forcings vary as a function of geography and vegetation composition?
  - What is the relationship between atmospheric convection patterns and the distribution of forest blowdown events? How will this change through time?
  - What vegetation, soil, and climate characteristics define the current edges of the tropical forest biome, and how are they likely to shift with changes in climate regimes?
  - Under what conditions will intact tropical forests become susceptible to burning?
  - How will forest functional composition shift in response to altered disturbance regimes?

- **How will tropical ecosystems respond to increasing atmospheric CO_2 concentrations?** Although the increase in atmospheric CO_2 is unambiguous and short-term physiological responses are universal, the integrated response of forest ecosystems and the feedbacks to the atmosphere are harder to predict. Research is needed to understand the response of tropical forests to elevated CO_2, including the study of critical interactions among CO_2, water, and nutrient cycles. Large-scale biomass dynamics and belowground responses are also important for understanding the longer-term fate of carbon. ESMs cannot predict the response of tropical forests to elevated CO_2 without new data that address critical uncertainties, including:

  - How will increasing atmospheric CO_2 affect leaf-level gas exchange under tropical conditions?
  - How do nutrient limitations affect tropical forest response to elevated atmospheric CO_2, do these limitations vary spatially at present, and how will they change with predicted environmental forcings?
  - How will water-use efficiency and drought tolerance respond to rising atmospheric CO_2?
  - How will ecosystem allocation patterns change in response to increased CO_2?
  - Will elevated atmospheric CO_2 alter plant species composition?
  - How will belowground biogeochemical cycles respond to increasing CO_2 and affect the longer-term fate of carbon?
  - Will elevated atmospheric CO_2 ameliorate drought responses of tropical ecosystems and alter their plant community composition?

- **What are the interactions between climate change and aerosols, particulates, and other trace gas emissions from tropical forests?** Tropical forests are large sources of biological aerosols and trace gases such as methane, nitrous oxide, and biogenic volatile organic compounds

(BVOCs), which all have significant roles in the Earth system. Many unanswered questions about these compounds and their roles limit the understanding and representation of tropical ecosystems in ESMs. Key uncertainties include:

  - What are the physiological and climatic factors that control plant and soil methane, nitrous oxide, and BVOC emissions?
  - How does a changing aerosol environment affect forest ecosystem properties and processes, such as light quality, storm intensity, cloud-aerosol interactions, nutrient deposition, and ozone effects on plant physiology?
  - How does climate affect production of forest aerosols, including those derived from fungi?

- **How will tropical forest interactions with the Earth system shift as a result of anthropogenic disturbance and land-use change?** A significant fraction of the tropical forest cover lies in areas recovering from logging or in secondary forests and land abandoned from agriculture (FAO 2010). The consequences of this land-use change on ecosystem function remain uncertain. Addressing the following gaps would help improve model predictions:
  - What are the hydrological changes in sensible and latent heat fluxes associated with deforestation, logging, and the conversion of forest to agricultural activities?
  - How does land-use change affect soil biogeochemistry and the ability of forests to recover on abandoned agricultural land?
  - What are the spatial scales and magnitudes of feedbacks among land-use change, climate patterns, and forest fire frequency?
  - How will climate change affect aerosol and particulate emissions from biomass burning and the interactions among fire-derived aerosols and atmospheric processes?
  - How do secondary succession and biomass accumulation trajectories in abandoned agricultural areas vary with factors such as the intensity of land use or the proximity of seed sources for tree establishment?
  - What are the key differences in potential climate feedbacks between managed and unmanaged systems?

Geographical Considerations for a Large-Scale Project in the Tropics

Geographical constraints need to be considered when developing a large comprehensive scientific effort to address interactions between tropical forests and Earth's climate system. The high-biomass forests of the Amazon, Congo Basin, and Southeast Asia on Oxisol and Ultisol soils comprise the bulk of climate-relevant fluxes and potential feedbacks in the Tropics. The Amazon and portions of Southeast Asia take on added importance with the expectation of decreased precipitation, increased prevalence of widespread drought, and the potential for elevated tree mortality over large eastern and southern portions of the basin (Lewis et al. 2011; Marengo et al. 2011; IPCC 2007).

Another consideration is that key mechanisms ubiquitous across the tropical forest biome probably can be studied at a variety of sites. For example, although tropical forests in Hawaii are quite unique compared to others, numerous studies of ecosystem development there have shed light on important processes (Chadwick et al. 1999; Vitousek et al. 1997).

Logistical constraints and past research efforts also should be taken into account. Central America, the Caribbean, and the Brazilian Amazon offer well-established infrastructure and decades of outstanding tropical forest research activities. The Brazilian-led Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) project—which had substantial support from the National Aeronautics and Space Administration's Terrestrial Ecosystems program—carried out high-quality research relevant to ESMs at a variety of spatial and temporal scales (Davidson et al. 2012; Keller et al. 2004). Alternatively, there may be compelling reasons to focus new research efforts in less-studied regions for which there is a dearth of data.

Leveraging existing small-scale research networks and efforts also should be considered to maximize representation of all tropical regions. Ultimately, good hypothesis-driven science carried out anywhere in the Tropics will be valuable in informing models

about critical processes that can improve their predictive capacity. Several approaches could be used to address the research gaps and uncertainties described throughout this report, including:

- Experimental manipulations and detailed observational studies at intensive study sites.
- Extensive studies at sites spanning important functional gradients in collaboration with existing networks such as RAINFOR and the Center for Tropical Forest Science within the Smithsonian Tropical Research Institute (Condit 1995; Malhi et al. 2002).
- Extension of these studies using remote sensing and geographic information systems for extrapolating site-level results to regional and continental scales and ensuring adequate sampling of key ecosystem gradients (Asner et al. 2005; Chambers et al. 2007b; DeFries et al. 2002; Saatchi et al. 2011).

Need for Integrated Multidisciplinary Effort Examining Tropical Ecosystems

A changing climate has the potential to significantly affect the structure and function of tropical forests and the direct and indirect feedbacks they provide to the climate system. Efforts to predict these effects and thus inform future research, energy policy, and adaptation strategies are challenged by numerous uncertainties discussed throughout this report. Robust climate predictions therefore will require both a better understanding of how climate forcing factors influence critical ecosystem processes and improved representations of these processes in ESMs. Given their scope and complexity, addressing these knowledge gaps and model limitations demands a coordinated effort by scientists from many disciplines. This urgently needed effort will leverage existing resources and information and also integrate new data, experimental results, and process knowledge into fully coupled global climate models. These robust, fully coupled community models must incorporate diverse sources of information that describe the physical, chemical, and biological processes by which tropical ecosystems affect and are affected by climate. Coordination and stewardship of data from existing and future research activities also should be carefully considered as part of an integrated modeling-experimental approach to predictively understand the Tropics. Together, these needed improvements in both process and modeling research represent the broad goals of a concentrated multidisciplinary effort that closely integrates experimental approaches and modeling to maximize research investments in ecosystem science.

Appendices

Appendix 1

Next-Generation Ecosystem Experiment: Integrating Modeling and Experimentation

DOE Builds on Legacy in Ecosystem Science

The U.S. Department of Energy (DOE) is responsible for the nation's energy policy and energy futures, and DOE's Office of Science (SC) supports the fundamental scientific research needed to meet this responsibility. Within SC, the Office of Biological and Environmental Research (BER) includes the Climate and Environmental Sciences Division (CESD). This division seeks to advance a robust predictive understanding of Earth's climate and environmental systems and to inform development of sustainable solutions to U.S. energy and environmental challenges. In particular, CESD seeks to synthesize new process knowledge and innovative computational methods advancing next-generation integrated models of the human-Earth system. These models integrate the state of the science, help inform future research, and form the basis for decisions on energy policy.

CESD has a long history in the ecological sciences, including sponsoring a number of large-scale, long-term ecosystem experiments that manipulate critical environmental parameters including: precipitation (Oak Ridge Throughfall Displacement Experiment; tde.ornl.gov), temperature, carbon dioxide (public.ornl.gov/face/global_face.shtml), and combinations thereof. In 2007, as the most recent generation of these studies neared completion, BER began planning for the next generation of ecosystem experiments. The goal of this planning activity was to develop an approach that closely and iteratively connects modeling and process research. In this approach—aptly named Next-Generation Ecosystem Experiment, or NGEE—model structure and needs are considered in the development of process studies, and process outcomes are designed to directly inform and challenge models at appropriate scales. Planning for the NGEE activity involved a series of workshops ranging from large community meetings to small focused groups. Emerging from a large community workshop held in spring 2008 was the concept of focusing on systems that are globally (or regionally) important, climatically sensitive, and understudied or underrepresented in Earth system models (ESMs). Details of the workshop are summarized in the report *Ecosystem Experiments: Understanding Climate Change Impacts on Ecosystems and Feedbacks to the Physical Climate* (science.energy.gov/~/media/ber/pdf/ecosystem_experiments.pdf). Based on these scientific considerations and practical limitations, Arctic tundra was found to best meet the criteria for the first Next-Generation Ecosystem Experiment: NGEE Arctic.

NGEE Approach Bridges Process and Modeling Research

The field of climate science has been advanced from two important perspectives: process research and modeling research. For purposes of this discussion, process research involves experiments, observations, and measurements performed in the field or laboratory. Modeling research describes the development, evaluation, and exercising of computer models that, in this case, simulate these same processes.

In many areas of science, models have become powerful tools to capture, scale, and describe process understanding of complex systems. For climate science, models are critical mechanisms that consolidate current understanding of the many processes and their interactions that create "climate." Models enable testing of system understanding by conducting computerized experiments that in some cases would be impossible to reproduce in nature. The analysis of such experiments suggests needed model developments and identifies areas of process understanding that are insufficient (or missing altogether).

Models also can be used prognostically to project the outcome of future conditions like climate change. Such applications are extremely valuable for exploring potential future scenarios but are limited by the system knowledge underpinning the model.

Climate models must consider the myriad processes that drive the Earth system and its climate. These models are extremely complex and challenge the capabilities of the most advanced computer systems in the world. Such modeling is an exercise in compromise as decisions are made about which processes to include (and at what level of detail). Climate modeling has become a highly technical and specialized field, demanding specialists with advanced knowledge and capabilities in the science of modeling and high-performance computing. This specialization often leads to a separation between experts in the processes being modeled and the modelers themselves. This separation means that process research and climate modeling are often independent activities, even when they address the same topics. Process research is conducted and published in topical or discipline-specific journals. Modelers mine these journals for insights into pertinent processes and data to support parameterization or model validation. Significant time and effort are invested in consolidating and formatting disparate datasets and making them compatible with model needs. The process scientists who produced the original publications are often unaware that their research has been used, missing the opportunity to contribute to model development or gain insights from model representations of their processes.

This separation is inefficient for developing and validating models and improving the process science needed to support them. As a major contributor to the national climate change research activity, DOE has unique capabilities in the process understanding of clouds, aerosols, and terrestrial ecosystems; regional, global, and integrated assessment modeling; and the high-performance computing expertise and hardware needed to implement those models. NGEE, which leverages these capabilities, is designed as an integrated activity whereby the separation between modeling and process research is closed as models are exercised to evaluate the impacts of new parameterizations or representations and then the results are applied to inform further process research. This approach is implemented at both the program level as DOE program managers cooperate to design and initiate projects and at the project level where large efforts (such as NGEE Arctic) incorporate modeling and process research components.

The concept of model-experimental (ModEx) integration is now fundamental to NGEE. ModEx recognizes that improved collaboration between modeling and process scientists is needed to develop, test, and implement process representations in models of all scales. Strongly coupling modeling and process-science research ensures that models incorporate state-of-the-science knowledge about critical systems, reducing the steps between traditional process research and modeling as described above. Process studies can advance understanding in weak or unrepresented areas, and the resulting improved models can be used to guide field and laboratory research and to inform future decisions. This approach more efficiently meets DOE's goals of predictive understanding but also leverages its investments and national leadership in climate process and modeling science, scientific user facilities, and high-performance computing.

NGEE Goals, Mechanisms, and Implementation

Based on DOE's mission needs and unique capabilities, NGEE Arctic has been designed to deliver a "process-rich ecosystem model, extending from the bedrock to the top of the vegetative canopy, in which the evolution of target ecosystems in a changing climate can be modeled at the scale of a high-resolution ESM grid cell (i.e., 30 × 30 km grid size)." This concept is recognized as being applicable to any target system (ecosystem or otherwise) where close coupling of process and modeling research could benefit the system's representation in ESMs. BER envisions other possible NGEE projects focused on critical ecosystems (e.g., the Tropics), climate systems (e.g., precipitation and clouds), or processes such as water cycling.

The NGEE process is informed by community input, guided by the three criteria described previously (globally or regionally important, climatically sensitive, and understudied), and directed by BER

to best match the science direction with DOE mission needs. An NGEE project begins by interactions and discussions between process and modeling scientists to understand the needs and limitations of each side. Target models are then exercised and evaluated to identify obvious areas of weakness and poor or missing process representation. NGEE incorporates and considers processes and scales, recognizing that processes critical to one scale may be much less important at higher (or lower) scales. Myriad small processes shape the function of a larger-scale process. The scaling challenge in modeling is deciding which small-scale processes must be represented and how to include them. Models address this challenge through parameterization—describing complex, smaller-scale processes as simplified, mathematical representations in larger-scale models. Parameterization requires understanding both the systems in question and the target model. Observations and process understanding need to be developed at scales that correspond to the modeling goal (or parameterization). Close and improved collaboration between modeling and process scientists is needed to develop, test, and implement parameterizations.

Based on this goal, NGEE works carefully to facilitate collaborations between process and model scientists. For example, modelers work with process scientists to understand how state-of-the-art models represent various processes. Process scientists in turn work with modelers to capture the complexity of natural systems in ways feasible for model representation. These partnerships provide opportunities to identify and address omissions and insufficiencies in process or modeling science; understand the needs and constraints of large-scale, coupled models; and tailor process science to the needs of models, resulting in more robust process representations. Ultimately, NGEE evaluates a model, designs experiments and observations, confronts the model, and then iterates. The final goal is significant improvement in representing the NGEE topic of interest (e.g., Arctic permafrost in the case of NGEE Arctic) in coupled, community-based ESMs.

DOE national laboratories are uniquely qualified to design, implement, and manage large long-term research projects such as NGEE. NGEE efforts have broad input from the scientific community, including direct and indirect collaborations involving other national laboratories, universities, and private research entities as appropriate. NGEE projects also welcome collaborators from many institutions, providing opportunities for field research in established and characterized areas and serving as a resource for sample collection. For the initial geography-based NGEE projects, DOE anticipates a 10-year duration for field experiments and observations. This time frame balances the need for answering critical questions with the timescales necessary to examine change in terrestrial ecosystems.

Appendix 2

Workshop Agenda, Breakout Sessions, and Participants

Agenda

Hyatt Regency Bethesda, Bethesda, Maryland

Monday, June 4

7:00 a.m.	**Breakfast** (Lobby)		
8:00 a.m.	**Welcome and Introductory Comments** (Cabinet/Judiciary Room)		
	8:00 a.m.	Welcome	Workshop Organizers
	8:05 a.m.	Welcome and Workshop Charge	Dan Stover (DOE)
	8:15 a.m.	CESD Investments in the Tropics	Gary Geernaert (DOE)
	8:25 a.m.	BER and NGEE	Sharlene Weatherwax (DOE)
	8:35 a.m.	NGEE Philosophy	Mike Kuperberg (DOE)
8:45 a.m.	**Plenary Sessions** (Cabinet/Judiciary)		
	8:45 a.m.	Introductions and Workshop Discussion	Organizing Committee
	9:15 a.m.	Tropical Forests and Climate Change	Joe Wright (Smithsonian Tropical Research Institute)
	9:45 a.m.	Break	
	10:00 a.m.	Modeling Tropical Ecosystems	Peter Thornton (Oak Ridge National Laboratory) and Marcos Costa (Federal University of Viçosa)
	10:30 a.m.	Modeling Tropical Ecosystems	Rosie Fisher (National Center for Atmospheric Research) and Jeffrey Chambers (Lawrence Berkeley National Laboratory)
11:00 a.m.	**Breakout Session**		
	11:00 a.m.	Breakout logistics	Workshop Organizers
	11:05 a.m.	**Breakout Session 1: Tree Ecophysiology**	
		Group A (Cabinet/Judiciary)	Lead: Rosie Fisher
		Group B (Waterford)	Lead: Richard Norby (Oak Ridge National Laboratory)
		Group C (Congressional)	Lead: Jeffrey Chambers
12:30 p.m.	**Working Lunch** (Lobby)		
1:00 p.m.	**Breakout Session Outbrief** (Cabinet/Judiciary)		
1:45 p.m.	**Breakout Session 2: Soil Biogeochemistry and Hydrology**		
		Group A (Cabinet/Judiciary)	Lead: Jefferson Hall (Smithsonian Tropical Research Institute)
		Group B (Waterford)	Lead: Steven C. Wofsy (Harvard University)
		Group C (Congressional)	Lead: Sue Trumbore (Max Planck Institute for Biogeochemistry)
3:15 p.m.	**Breakout Session Outbrief** (Cabinet/Judiciary)		
3:45 p.m.	**Break**		
4:00 p.m.	**Plenary Session** (Cabinet/Judiciary)		
	4:00 p.m.	LBA and NGEE	Michael Keller (U.S. Forest Service)
4:30 p.m.	**Open Discussion** (Cabinet/Judiciary)		
4:50 p.m.	**Summary and Closing** (Cabinet/Judiciary)		
5:30 p.m.	**Writing Teams Collaborate**		

Tuesday, June 5

7:00 a.m.	**Breakfast** (Lobby)		
8:00 a.m.	**Welcome and Reconvening Comments** (Cabinet/Judiciary)		
8:30 a.m.	**Plenary Session** (Cabinet/Judiciary)		
	8:30 a.m.	Tropical Landscapes	Yadvinder Malhi (University of Oxford)
	9:00 a.m.	Drought Experiments, Ecophysiology	Patrick Meir (University of Edinburgh)
	9:20 a.m.	CO_2 and Tropical Forests	Lucas Cernusak (Australian National University)
	9:40 a.m.	Temperature Effects on Tropical Forests	Molly Cavaleri (Michigan Technological University)
	10:00 a.m.	Forest-Atmosphere Interactions	Paulo Artaxo (University of São Paulo)
10:30 a.m.	**Break**		
10:45 a.m.	**Breakout Session 3: Disturbance and Forest-Atmosphere Interactions**		
		Group A (Cabinet/Judiciary)	Lead: Maria Uriarte (Columbia University)
		Group B (Waterford)	Lead: Michael Keller
		Group C (Congressional)	Lead: Peter Thornton
12:15 p.m.	**Working Lunch** (Lobby)		
1:00 p.m.	**Breakout Session Outbrief** (Cabinet/Judiciary)		
1:30 p.m.	**Breakout Session 4: Brainstorming of Additional Topics**		
		Group A (Cabinet/Judiciary)	Lead: Charlie Koven (Lawrence Berkeley National Laboratory)
		Group B (Waterford)	Lead: Richard Norby
		Group C (Congressional)	Lead: Jeffrey Chambers
3:00 p.m.	**Breakout Session Outbrief** (Cabinet/Judiciary)		
3:30 p.m.	**Break**		
3:45 p.m.	**Open Discussion** (Cabinet/Judiciary)		
4:45 p.m.	**Synthesizing the Major Themes** (Cabinet/Judiciary)		
5:15 p.m.	**Summary and Closing** (Cabinet/Judiciary)		
6:00 p.m.	**Writing Teams Collaborate**		

Wednesday, June 6

7:00 a.m.	**Breakfast** (Lobby)
8:00 a.m.	**Writing and Finalization of Workshop Report** (Writing team)

Workshop Breakout Sessions

Monday, June 4

Breakout Session 1: Tree Ecophysiology

11:05 a.m. — What are the direct effects of CO_2 on leaf physiology and plant carbon metabolism?

11:20 a.m. — How does drought affect tree ecophysiology, and what are the drought-induced mortality thresholds?

11:40 a.m. — How will trees respond to rising atmospheric temperature with a changing climate?

12:00 p.m. — Open discussion on other key tree ecophysiology questions.

Breakout Session 2: Soil Biogeochemistry and Hydrology

1:45 p.m. — How will forests on different soils respond to the same climate change drivers?

2:05 p.m. — How do differences in soil properties and hydrology influence tree susceptibility to drought-induced mortality?

2:25 p.m. — How will soil nutrient availability respond to rising temperature and changes in precipitation?

2:45 p.m. — Open discussion on other key soil biogeochemistry and hydrology questions.

Tuesday, June 5

Breakout Session 3: Disturbance (Natural and Anthropogenic) and Forest-Atmosphere Interactions

10:45 a.m. — How does land use and land-use change affect mass and energy fluxes to the atmosphere?

11:05 a.m. — How does fire interact with other environmental factors to affect closed-canopy forests and transitions to other states?

11:25 a.m. — What are other major natural disturbances, and how will they change with climate?

11:45 a.m. — Open discussion on other key disturbance questions.

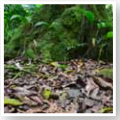
Breakout Session 4: Brainstorming of Additional Topics

1:30 p.m. — Diversity and demography.

1:50 p.m. — Forest-atmosphere interactions (e.g., biogenic volatile organic compounds and convection).

2:10 p.m. — Remote sensing and landscape-, regional-, and continental-scale questions.

2:30 p.m. — Open discussion.



Workshop Participants

Organizing Committee

Jeffrey Chambers
Lawrence Berkeley National Laboratory

Rosie Fisher
National Center for Atmospheric Research

Jefferson Hall
Smithsonian Tropical Research Institute

Richard J. Norby
Oak Ridge National Laboratory

Steven C. Wofsy
Harvard University

Participants

Ane Alencar
Amazon Institute of Environmental Studies

Paulo Artaxo
University of São Paulo

Patrick Baker
Monash University

Joseph Berry
Stanford University

Molly Cavaleri
Michigan Technological University

Lucas Cernusak
Australian National University

Nick Chappell
Lancaster University

Michael Coe
Woods Hole Research Center

Marcos Costa
Federal University of Viçosa

Stuart Davies
Smithsonian Tropical Research Institute

Mary Firestone
University of California, Berkeley

Guillermo Goldstein
University of Miami

Michael Goulden
University of California, Irvine

Lars Hedin
Princeton University

David Hilbert
Commonwealth Scientific and Industrial Research Organisation

Forrest Hoffman
Oak Ridge National Laboratory

William Hoffmann
North Carolina State University

Valeriy Ivanov
University of Michigan

Michael Keller
U.S. Forest Service

Charlie Koven
Lawrence Berkeley National Laboratory

Tomo'omi Kumagai
Nagoya University

Ariel Lugo
U.S. Forest Service

Yadvinder Malhi
University of Oxford

Antonio Manzi
National Institute of Amazonian Research

Nate McDowell
Los Alamos National Laboratory

Patrick Meir
University of Edinburgh

Lina Mercado
University of Exeter

Paul Moorcroft
Harvard University

Akira Osawa
Kyoto University

Sasha Reed
U.S. Geological Survey

Alistair Rogers
Brookhaven National Laboratory

Scott Saleska
University of Arizona

Whendee Silver
University of California, Berkeley

Peter Thornton
Oak Ridge National Laboratory

Sue Trumbore
Max Planck Institute for Biogeochemistry

Maria Uriarte
Columbia University

Joe Wright
Smithsonian Tropical Research Institute

Soenke Zaehle
Max Planck Institute for Biogeochemistry

U.S. Department of Energy

Office of Biological and Environmental Research

Sharlene Weatherwax
Associate Director of Science

Gary Geernaert
Director, Climate and Environmental Sciences Division

Paul Bayer
Program manager, Climate and Environmental Sciences Division

Patrick Horan
Science assistant, Climate and Environmental Sciences Division

Renu Joseph
Program manager, Climate and Environmental Sciences Division

Arthur Katz
Program manager, Biological Systems Science Division

Dorothy Koch
Program manager, Climate and Environmental Sciences Division

Mike Kuperberg
Program manager, Climate and Environmental Sciences Division

David Lesmes
Program manager, Climate and Environmental Sciences Division

Rick Petty
Program manager, Climate and Environmental Sciences Division

Daniel Stover
Program manager, Climate and Environmental Sciences Division

Bob Vallario
Program manager, Climate and Environmental Sciences Division

Observers

Robin Graham
Argonne National Laboratory

Tony Janetos
Pacific Northwest National Laboratory

Jennifer Pett-Ridge
Lawrence Livermore National Laboratory

Report Preparation

Biological and Environmental Research Information System, Oak Ridge National Laboratory

Kris Christen, LeJean Hardin, Holly Haun, Brett Hopwood, Betty Mansfield, Sheryl Martin, Marissa Mills, and Judy Wyrick

Appendix 3

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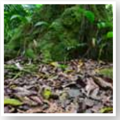

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Acronyms

AFR	Afrotropic
ANOVA	analysis of variance
AVHRR	Advanced Very High Resolution Radiometer
BER	Office of Biological and Environmental Research
Biome-BGC	Biome–BioGeochemical Cycles model
BVOC	biogenic volatile organic compound
C^4MIP	Coupled Climate–Carbon Cycle Model Intercomparison Project
CCN	cloud condensation nuclei
CESD	Climate and Environmental Sciences Division
CLM	Community Land Model
CPTEC-PVM2	Center for Weather Forecasts and Climate Studies—Potential Vegetation Model 2
DGVM	dynamic global vegetation model
DOE	U.S. Department of Energy
EC	eddy covariance
ENSO	El Niño–Southern Oscillation
ESM	Earth system model
FACE	free-air CO_2 enrichment
GCM	general circulation model
GHG	greenhouse gas
GPP	gross primary productivity
HOF	Hortonian overland flow
HyLand	Hyperspectral remote sensing for the assessment of crop and soil parameters in precision farming and yield estimation model
IMA	Indo-Malay-Australasia
IN	ice nuclei
INPA	Instituto Nacional de Pesquisas da Amazônia (National Institute for Amazonian Research)
IPCC	Intergovernmental Panel on Climate Change
LAI	leaf area index
LBA	Large-Scale Biosphere-Atmosphere Experiment in Amazonia
LIDET	Long-Term Inter-site Decomposition Experiment Team
LPJ	Lund-Potsdam-Jena dynamic global vegetation model
MCWD	monthly cumulative water deficit
MMD	multimodel data
ModEx	model-experimental
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	normalized difference vegetation index
NEO	Neotropic
NGEE	Next-Generation Ecosystem Experiment
NPP	net primary productivity
OTC	open-top chamber
PBA	primary biological aerosols
PFT	plant functional type
ROTHC	Rothamsted carbon model
SC	U.S. Department of Energy Office of Science
SOA	secondary organic aerosols
SRES	special report on emissions scenarios
TRIFFID	top-down representation of interactive foliage and flora including dynamics model
VOC	volatile organic compound
VPD	vapor pressure deficit
WUE	water-use efficiency