Ecological Applications, 14(4) Supplement, 2004, pp. S3–S16

ECOLOGICAL RESEARCH IN THE LARGE-SCALE BIOSPHERE–ATMOSPHERE EXPERIMENT IN AMAZONIA: EARLY RESULTS

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Abstract. The Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA) is a multinational, interdisciplinary research program led by Brazil. Ecological studies in LBA focus on how tropical forest conversion, regrowth, and selective logging influence carbon storage, nutrient dynamics, trace gas fluxes, and the prospect for sustainable land use in the Amazon region. Early results from ecological studies within LBA emphasize the variability within the vast Amazon region and the profound effects that land-use and land-cover changes are having on that landscape. The predominant land cover of the Amazon region is evergreen forest; nonetheless, LBA studies have observed strong seasonal patterns in gross primary production, ecosystem respiration, and net ecosystem exchange, as well as phenology and tree growth. The seasonal patterns vary spatially and interannually and evidence suggests that these patterns are driven not only by variations in weather but also by innate biological rhythms of the forest species. Rapid rates of deforestation have marked the forests of the Amazon region over the past three decades. Evidence from ground-based surveys and remote sensing show that substantial areas of forest are being degraded by logging activities and through the collapse of forest edges. Because forest edges and logged forests are susceptible to fire, positive feedback cycles of forest degradation may be initiated by land-use-change events. LBA studies indicate that cleared lands in the Amazon, once released from cultivation or pasture usage, regenerate biomass rapidly. However, the pace of biomass accumulation is dependent upon past land use and the depletion of nutrients by unsustainable land-management practices. The challenge for ongoing research within LBA is to integrate the recognition of diverse patterns and processes into general models for prediction of regional ecosystem function.

Key words: Amazon; carbon; cerrado; land-use and land-cover change; LBA; nutrients; Oxisol; savanna; trace gases; tropical forest; Ultisol.

Manuscript received 12 May 2003; revised 17 June 2003; accepted 12 August 2003. Corresponding Editor: D. S. Schimel. For reprints of this Special Issue, see footnote 1, p. S1.
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Introduction

The Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA) is a multinational, interdisciplinary, research program led by Brazil. LBA is not formally an experiment; instead, it links many researchers whose goal is to understand how Amazonia functions as a regional entity in the Earth system. Research within LBA is guided by the recognition that Amazonia is changing rapidly through development. Therefore, LBA researchers seek to understand how changes in land use and climate will affect the biological, chemical, and physical functions of Amazonia, including the sustainability of development in the region and the influence of Amazonia on global climate. LBA scientific activities cover seven themes: (1) land-use and land-cover change, (2) physical climate, (3) carbon dynamics, (4) biogeochemistry, (5) atmospheric chemistry, (6) land-surface hydrology and aquatic chemistry, and (7) human dimensions.

Studies of the effects of land-use and land-cover changes on Amazonian ecosystems developed as a result of a deliberate planning process that engaged both Brazilian and international scientists. The key question guiding ecological studies within LBA was defined as: ''How do tropical forest conversion, regrowth, and selective logging influence carbon storage, nutrient dynamics, trace gas fluxes, and the prospect for sustainable land use in the Amazon region?'' (Cerri et al. 1995).

''Forest conversion'' refers to forest clearing and conversion to agricultural uses, especially cattle pasture, and ''forest regrowth'' refers to vegetation succession following the abandonment of agricultural lands. This question calls for an explicit consideration of the effects of these land-cover and land-use changes on terrestrial carbon and nutrient budgets, the fluxes of trace gases between the land and the atmosphere, and the exchange of materials between the land and river systems. Implicitly, the question also calls for an understanding of these budgets, fluxes, and exchanges in ''primary'' or predisturbance forest ecosystems. Scientists participating in ecological studies within LBA have elaborated on this initial question to develop a set of more detailed questions to guide our research in four thematic areas, land-use and land-cover change, carbon dynamics, nutrient dynamics and surface water chemistry, and trace gas and aerosol fluxes (Box 1).

In this paper, we briefly review the design of the LBA study with an emphasis on ecological research. Then we review the results from 22 studies in LBA in this issue that consider the science themes of physical climate, carbon dynamics, nutrient dynamics, trace gas fluxes, and land-use and land-cover change. These studies either deal with the Amazon region generally or were conducted at one or more of 13 sites that are listed in Table 1. Early results from LBA focusing mainly on physical climate and atmospheric chemistry have recently been collected in a special issue of the *Journal of Geophysical Research* (see Andreae et al. 2002, Avissar and Nobre 2002, Avissar et al. 2002, and Silva-Dias et al. 2002 for summaries). Recent work on land-cover and land-use change has been compiled for a special issue of *Remote Sensing of the Environment* (Roberts et al. 2003). The papers collected in this issue do not cover all current ecological work within LBA. In this summary paper, we attempt to compare the results presented in this volume and to place this work within the context of other recently published studies within LBA and within the broader scope of tropical ecosystem studies without attempting an exhaustive review. We conclude by identifying emerging trends and challenges for future ecological research in LBA.

Biophysical and Biogeochemical Characteristics of the Amazon Region

The Amazon Basin covers 5.8×10^6 km^2 and contains the world's largest river with a discharge of nearly 6×10^{12} m^3/yr (Salati and Vose 1984). The natural land cover of the Amazon Basin is mainly closed-canopy tropical forest, although a substantial portion is covered by savanna, known in Brazil as cerrado. The cerrado is itself an extensive biome (2×10^6 km^2) that lies mainly outside of the hydrographic basin of the Amazon (Oliveira and Marques 2002). Energy and moisture exchanges in the Amazon region play a significant role in global atmospheric circulation. From 1350 to 1570 mm/yr, equivalent to 63–73% of the annual rainfall, evaporates or transpires at the surface (Costa and Foley 1999, Marengo and Nobre 2001). Models indicate that extensive regional deforestation would lead to regional declines in precipitation and could have significant effects on global climate (Nobre et al. 1991, Marengo and Nobre 2001, Werth and Avissar 2002). In contrast to regional scale deforestation, deforestation on a mesoscale (<100 km) may lead to locally increased precipitation (Baidya Roy and Avissar 2002). This raises the hypothesis that there is a threshold of deforestation amount and distribution beyond which precipitation will decline (Avissar et al. 2002).

The Amazon forest vegetation in Brazil alone contains $\sim 7 \times 10^{16}$ g of carbon (C), which amounts to between 10% and 15% of global biomass (Houghton et al. 2001). The biomass density of Amazon forests is poorly quantified, mainly because of the scarcity of plot-based data (Houghton et al. 2001, Keller et al. 2001). Forests in the Amazon region are mostly evergreen and highly productive. Deep rooting allows Amazon forests to maintain productivity through dry seasons that extend up to 5–6 mo (Fig. 1) (Nepstad et al. 1994). The productivity of the forests is sustained despite the infertility of the highly weathered soils common to the region (Irion 1978). Although ~70% of Amazon soils are dystrophic Oxisols and Ultisols, soils that are more fertile do cover substantial areas

TABLE 1. A list of LBA study sites highlighted in this special issue. This represents a subset of all LBA study sites.

Site name	Nearest city	South latitude	West longitude	Description
Biological Dynamics of Forest Fragments Project	Manaus, Amazonas	2.5	60	fragmented mature forest
Cuieras Reserve (C14)†	Manaus, Amazonas	2.5892	60.1149	mature forest
Cuieras Reserve (k34)†	Manaus, Amazonas	2.6091	60.2093	mature forest
EMBRAPA Cerrados	Brasilia, D.F.	15.65	47.75	pasture
Fazenda Cauaxi	Paragominas, Pará	3.75	48.3	logged forest
Fazenda Vitoria	Paragominas, Pará	2.97	47.41	pastures and secondary forest
Fazenda Maracai†	Sinop, Mato Grosso	11.4125	55.325	mature forest
Fazenda Nova Vida	Ariquemes, Rondônia	10.14	62.79	pasture
IBGE Reserve	Brasilia, D.F.	15.95	47.86	native *cerrado*
Jarú Biological Reserve†	Ji-Paraná, Rondônia	10.078	61.9331	mature forest
SUFRAMA Agricultural District	Manaus, Amazonas	2.45	60.05	secondary forests
Tapajós National Forest (km 83)†	Santarém, Pará	3.013	54.5815	mature forest (logged in 2001)
Tapajós National Forest (km 67)†	Santarém, Pará	2.8567	54.9589	mature forest tower

† Tower sites. These are geolocated with finer spatial resolution.

(Richter and Babbar 1991). Nutrients such as phosphorus (P) and base cations (K^+, Ca^{++}, and Mg^{++}) are relatively scarce or only slowly available in most heavily weathered Amazon soils, whereas, under mature upland forests, nitrogen is often abundant. The rapid cycling of nitrogen supports large emissions of the greenhouse gas nitrous oxide (N_2O). Emissions of N_2O from the forests of the Amazon Basin account for ~0.8–1.3 $\times 10^{12}$ g N/yr, or nearly 10–15%, of the global natural emissions of that gas (Melillo et al. 2001).

LAND-USE CHANGE AND DEVELOPMENT IN THE BRAZILIAN AMAZON FORESTS

Over the past three decades, the Amazon region has been undergoing a burst of development. This development takes place on a backdrop of forest that has recorded the imprint of human habitation and use extending back 10 000 years (Roosevelt et al. 1996). The region, particularly the populated river corridors, suffered depopulation following the influx of European explorers and settlers in the 16th century. The population enumerated by censuses in the Amazon region of Brazil grew from slightly more than 100 000 in 1840 to 1.2 million in 1912 (Weinstein 1983). Regional population then stagnated through 1940 (1.5 million) but grew exponentially thereafter, reaching nearly 18 million by 2000.[18] More than 50% of the population is urban, which is defined as living in towns and cities with at least 5000 inhabitants (Browder and Godfrey 1997).

Agricultural colonization and development schemes have a long history in the Amazon, beginning with the Jesuit missions. The history of recent agricultural exploitation began during the rubber boom. From 1875 to 1900, settlements were encouraged along a railroad line from Belém to Bragança in Pará; lands along the route were cleared to help feed the growing trading metropolis of Belém (Weinstein 1983). Forest clearance and agricultural development was catalyzed by the opening of the Belém-Brasilia Highway in the 1960s and accelerated enormously in the 1970s and 1980s with the construction of roads such as the Trans-Amazon Highway and BR-364 in Rondônia. Rates of forest clearance have averaged ~20 000 km²/yr during the past decade (Houghton et al. 2001; see also the deforestation estimates from Instituto Nacional de Pesquisas Espacias [INPE]).[19]

Recent trends in land use indicate consolidation of the old frontiers, a new phase of experimentation in land management, and a heightened level of governance (Carvalho et al. 2002). Whereas previous development depended largely on a mixture of logging, cattle ranching, and subsistence cropping, current trends suggest a move toward more intensive management including mechanized production of grains, dairy cattle, and agroforestry products (Carvalho et al. 2002). Logging continues to expand and most logging might still be considered predatory or timber mining where valuable species are removed and little or no attention is paid to future timber production. Canopy opening is one effect of logging that leaves normally nonflammable forests susceptible to fire (Nepstad et al. 1999). The potential for fire to spread from deforested areas into fragmented forests represents a threat to long-term ecosystem health and sustainability (Cochrane et al. 1999, Nepstad et al. 1999, Cochrane and Laurance 2002).

LBA STUDY DESIGN

Design and planning of LBA began in 1993 (Kirchhoff 1994, Wickland 1994, Wofsy et al. 1994, Avissar and Nobre 2002). LBA science and the selection of LBA study sites reflect the history of Brazilian-led research in the Amazon region. LBA owes a debt to the Anglo-Brazilian Climatic Observation Study (ABRA-

[18] ⟨http://www.ibge.gov.br⟩

[19] ⟨http://sputnik.dpi.inpe.br:1910/col/dpi.inpe.br/vagner/2000/05.18.16.34/doc/index.html⟩

BOX 1. Questions for Ecological Research within LBA

Land-use and -cover change

1) What are the rates and mechanisms of forest conversion to agricultural land uses, and what is the relative importance of these land uses?
2) At what rate are converted lands abandoned to secondary forests; what is the fate of these converted lands, and what are the overall dynamic patterns of land conversion and abandonment?
3) What is the area of forest that is affected by selective logging each year? How does the intensity of selective logging influence forest ecosystem function, thus altering forest regrowth and flammability?
4) What are plausible scenarios for future land-cover change in Amazônia?

Carbon dynamics

1) What is the (climatically driven) seasonal and interannual variability of the CO_2 flux between the atmosphere and different land-cover/land-use types?
2) How do biological processes such as mortality and recruitment or succession following land-use change influence the net annual C balance for different land-cover/land-use types?
3) What are the relative contributions of fluxes from natural and disturbed ecosystems to the net Amazonia-wide flux? This question can be approached through a number of subsidiary questions:
   a) How do pools and fluxes of C and nutrients (in soils) of pasture/cropland change over time and what factors determine C gain or loss?
   b) How does selective logging change the storage and cycling of C in forests?
   c) What factors (biologically mediated, land-use history, soil properties, etc.) control the rate of C sequestration in biomass and soils of regrowing forest?
   d) What portion of the Amazonia-wide C flux is from fire? How do ecosystems recover from fire? What are the relations between land management and fire occurrence/frequency?

Nutrient dynamics and surface water chemistry

1) How do stocks, cycling rates, and budgets of carbon and important elements N, P, K, Ca, Mg, and Al change under different land covers and land uses?
2) Are nutrients major factors that control the rates of regrowth and carbon accumulation in abandoned pastures and regrowing secondary forests?
3) What are the processes and consequences of atmospheric horizontal transport of nutrients (wind) on the nutrient stocks and cycles of ecosystems within the Amazon basin at various spatial and temporal scales? (For example, Saharan dust inputs, losses and redistribution due to fire, and links between physical climate models and nutrient cycling.)
4) How do changes in land use and climate alter the stocks, processes, and fluxes of dissolved and particulate organic matter, nutrients, and trace gases from the uplands across the riparian zones and floodplains and down the channels of river corridors?
   a) How will the composition and quantity of nutrients and organic matter entering and being processed within streams be altered under different land-use change scenarios?
   b) Are there unique signatures that can be traced downstream?
   c) To what extent do intact riparian zones buffer streams against changes due to anthropogenic activities in surrounding uplands?
5) What is the importance of periodically wet environments (from moist soils to standing and flowing waters) for the land and atmospheric balances of nutrients, CO_2, trace gases, and water and energy on multiple scales?

Trace gas and aerosol flux

1) How are fluxes of trace gases and aerosols between ecosystems (both upland and wetland) and the atmosphere of Amazonia affected by land-cover and land-use change?
2) What is the (climatically driven) seasonal and interannual variability of trace gas and aerosol fluxes between the atmosphere and different land-use/land-cover types?
3) Are losses and gains of carbon from Amazonian ecosystems in forms other than CO_2 (e.g., CO, CH_4, VOC, organic aerosol) of sufficient magnitude to influence ecosystem carbon balance?

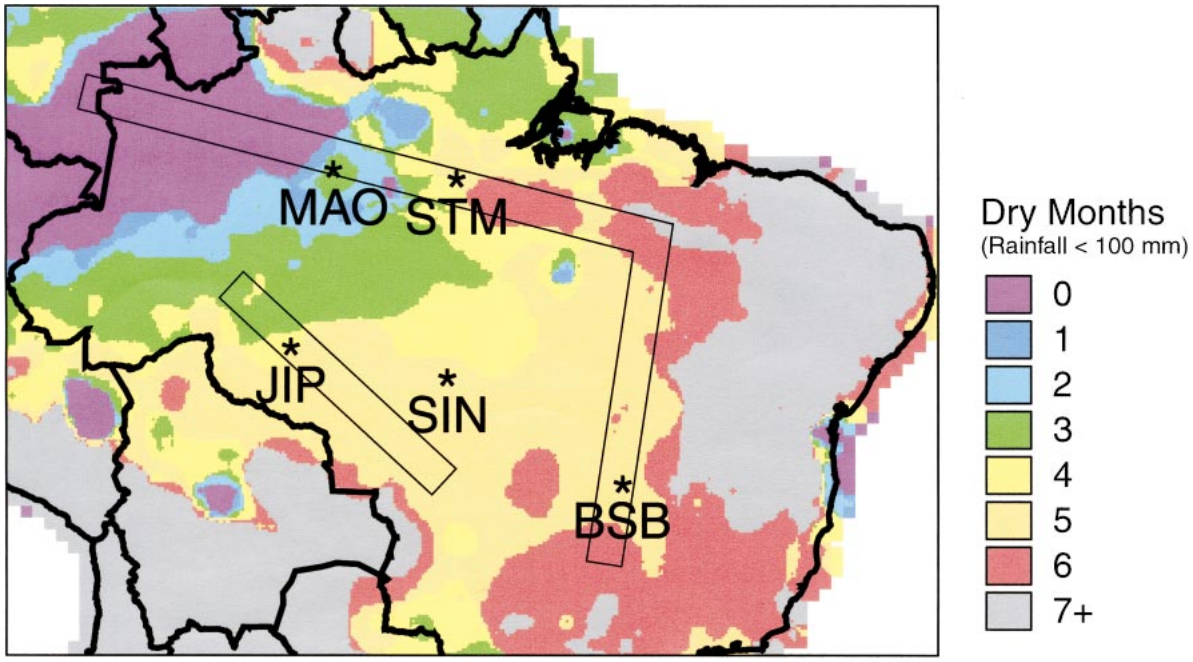

FIG. 1. Mean number of months with less than 100 mm rainfall based on a compilation by C. J. Wilmott and S. R. Webber. The LBA transects are shown along with research sites mentioned in this issue (BSB, IBGE Reserve, Brasilia; SIN, Fazenda Maracai, Sinop, Mato Grosso; JIP, Jarú Biological Reserve, Ji-Paraná, Rondônia; MAO, Cueiras Reserve Manaus, Amazonas; STM, Tapajós National Forest, Santarém, Pará).
Data were provided courtesy of LBA-HYDRONET, ⟨http://eos-webster.sr.unh.edu/⟩.

COS) (Gash et al. 1996) and the Amazon Boundary Layer Experiments (ABLE) sponsored by INPE and NASA (Harriss et al. 1988, 1990) in the 1980s and early 1990s. Planning for ecological studies within LBA was summarized in the Manaus Workshop Report led by Carlos Cerri and Jerry Melillo (Cerri et al. 1995). This report established a design including two transects to incorporate the main climatic variability within the Amazon region, especially total rainfall and dry season length (Fig. 1). The northern transect traverses more highly weathered and dystrophic soils compared to the southern transect. The two transects both cover a range in the extent, intensity, and character of land-use change.

Study-site selection was guided by the transect design. Prince and Steininger (1999) suggested a biophysical classification of the Amazon region to further guide the observational strategy. Practical considerations, especially site logistics and research history, also strongly influenced the selection of LBA study sites. For example, the long-term studies supported by Brazil's National Institute for Amazon Research (INPA), in the vicinity of Manaus, made that area a leading candidate for study. Specific opportunities to study land-use changes also influenced site selection. The presence of the only logging concession in the Amazon region managed by the Brazilian government in the Tapajós National Forest outside of Santarém led to the inclusion of sites there for the study of selective logging.

PHYSICAL CLIMATE

LBA studies of physical climate extend from the global and continental scale to the microscale. The same range of scales is represented in this issue. Goncalves de Goncalves et al. (2004) discuss the importance of incorporating land-cover heterogeneity in weather prediction models for South America. Da Rocha et al. (2004) and Quesada et al. (2004) quantify water and energy budgets for a forested and a savanna site, respectively. The difference in the water budgets between the campo sujo savanna at the IBGE Reserve and the dense forest at the Tapajós National Forest are impressive. Dry season evapotranspiration in the savanna averaged 1.6 mm/d vs. 4.0 mm/d for the forest. Both ecosystems depend upon deep rooting to sustain evapotranspiration during the dry season. Da Rocha et al. (2004) also observed that hydraulic lift and/or capillary flow redistributed 0.3 mm/d of water to the top 60 cm of soil under the forest during the dry season. At Tapajós, the forest showed no signs of drought stress, allowing uniformly high carbon uptake throughout the dry season (July to December 2000) (da Rocha et al. 2004, Goulden et al. 2004). During the wet season, cloudiness greatly reduced incoming solar radia-

tion in the forest. Wet season evapotranspiration averaged only 3.2 mm/d.

Carbon Dynamics

Amazon forests are mainly evergreen, but results published in this special issue emphasize the seasonal variation of carbon fluxes from these forests. Patterns of seasonal variability are apparent in measurements of parts of the forest such as stem growth (Rice et al. 2004), litter fall (Goulden et al. 2004), and soil–atmosphere carbon dioxide flux (Chambers et al. 2004, Goulden et al. 2004). The seasonality of litterfall in evergreen Amazon forests is a well-known phenomenon (e.g., Luizão 1989) and litterfall generally peaks during the dry season. Leaf shedding may represent an adaptation to water stress, but the common pattern of dry season flushing of new leaves also suggests that leaf phenology has been strongly influenced by natural selection factors to avoid herbivory and nutrient leaching (Sarmiento et al. 1985, van Schaik et al. 1993). Innate seasonal rhythms may also account for the pulse of stem growth observed prior to the initiation of the wet season in Tapajós National Forest in 2001 (Goulden et al. 2004).

Soil atmosphere fluxes of carbon dioxide were highly seasonal although contrasting patterns were observed near Santarém and Manaus. Whereas Goulden et al. (2004) found that low moisture content in litter and soil constrained soil respiration in the Tapajós National Forest during the dry season, Chambers et al. (2004) found that excess moisture appeared to inhibit soil respiration in the Cueiras Reserve during the wet season. Differences in rainfall at the two sites (see Fig. 1) influence the pattern of litter and soil moisture. The region of Manaus tends to have shorter and less intense droughts. In addition, soil physical properties may explain the observed differences. For example, the Tapajós site is flat and well drained and the Cueiras site contains rolling topography with poorly drained valleys where soils are saturated during the wet season.

Whole-system eddy covariance measurements of net ecosystem exchange (NEE) are also distinctly seasonal (Goulden et al. 2004, Vourlitis et al. 2004). The first eddy covariance study in the Amazon region that included both wet season and dry season measurements noted differences in the NEE between the seasons (Grace et al. 1995). Working in the Jarú Biological Reserve near Ji-Paraná, Rondônia, Grace et al. (1995) measured NEE of -0.09 mol $C \cdot m^{-2} \cdot d^{-1}$ during 11 d in the dry season and -0.05 mol $C \cdot m^{-2} \cdot d^{-1}$ during 44 d in the wet season.

Contrasting patterns of NEE, ecosystem respiration (R_{eco}), and gross primary production (GPP) have been observed in different sites (Fig. 2). Most of these data cover only one year of measurements and so unobserved interannual variation may be as important as spatial variation for differences among the seasonal patterns. Nonetheless, these patterns raise some interesting questions. In two sites, Jarú Reserve and Fazenda Maracai, Mato Grosso, net carbon uptake (negative NEE) clearly occurred during the rainy season. At the Cueiras Reserve, NEE was nearly constant across the year while, in the Tapajós National Forest, NEE was most negative during the dry season. The latter pattern appears to be driven by the strong decrease in R_{eco} during the dry season at the Tapajós National Forest without a comparable decrease in GPP. Goulden et al. (2004) found that the vegetation did not show evidence of drought stress during the dry season.

In contrast to the Tapajós National Forest, the Cueiras Reserve, the Jarú Reserve and the Fazenda Maracai displayed greater GPP during the wet season as compared to the dry season. What controls seasonal differences in GPP across sites? The effect of the length of drought intervals as well as the degree of cloud cover remain to be investigated. Access to deep soil water or the efficiency of deep water extraction may vary across sites. Additionally, innate phenological controls may play an important role in the regulation of seasonal carbon uptake.

NEE is a relatively small quantity that represents the difference between two large quantities, GPP and R_{eco}. As the difference between large numbers and variable processes, NEE is difficult to measure and model accurately. The errors and biases related to the calculation of annual sums of NEE from eddy covariance data is a focus of two papers in this issue, Kruijt et al. (2004) and Miller et al. (2004). As noted previously by Araújo et al. (2002), both Kruijt et al. and Miller et al. conclude that interpretation of nocturnal fluxes is the largest single source of error for sites with strong nocturnal stability, a typical situation in tropical moist forests. Not all LBA sites appear to suffer equally from this problem. For example, Kruijt et al. present data from the Jarú Reserve that show no relation between measured nocturnal NEE and u^*, a measure of turbulence.

Difficulties in analyzing NEE from tropical forest sites reinforce the need to use complementary methods to constrain biological fluxes. As Kruijt et al. (2004) point out, biometric methods and eddy covariance methods provide independent approaches to measurements of NEE. Chambers et al. (2004), Rice et al. (2004), and Miller et al. (2004) make biometric measurements that can be compared to eddy covariance results. Rice et al. and Miller et al. measured aboveground biomass changes and concluded that stands studied at the Tapajós National Forest are either roughly in carbon balance or losing a moderate amount of carbon annually. Miller et al. found that these measurements of change in aboveground biomass were consistent with their own measurements of NEE using eddy covariance techniques. Chambers et al. made extensive measurements of four components of ecosystem respiration (leaf, stem, CWD, and soil) and scaled

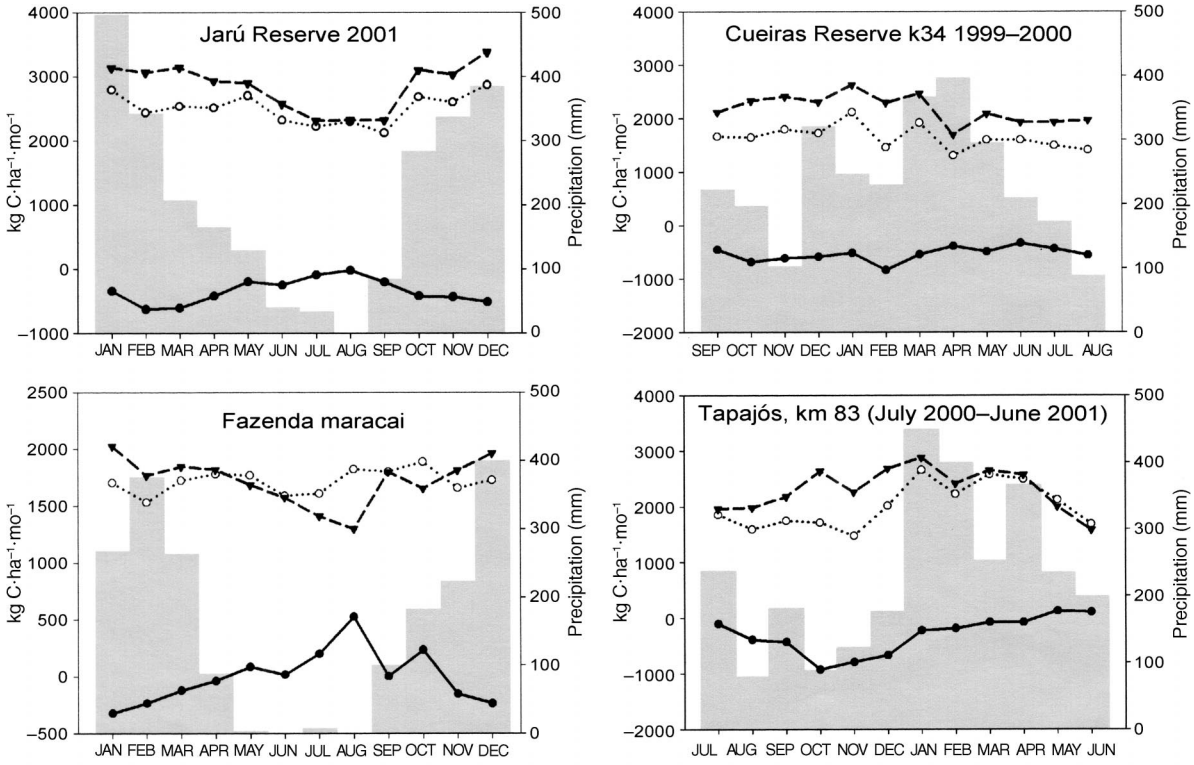

FIG. 2. Seasonal patterns of ecosystem–atmosphere carbon exchange from four forested LBA eddy covariance tower sites. Monthly net ecosystem exchange (NEE; solid line, filled circles) is shown using the atmospheric sign convention so that negative fluxes indicate ecosystem uptake of carbon from the atmosphere. Monthly gross primary production (GPP; dashed line, filled triangles) and monthly R_{eco} (dotted line, open circles) are shown as positive values. Total monthly precipitation is shown by gray bars (right-hand axes). Values for NEE, GPP, and R_{eco} for the Cueiras Reserve (k34), Jarú Biological Reserve, and Tapajós National Forest (kilometer 83) are based on data for which no u^* filter has been applied. Application of a u^* filter may cause absolute values to shift (see Miller et al. 2004, Kruijt et al. 2004) although seasonal patterns should be preserved. Estimates from Fazenda Maracai are based on a composite of three years of data and a simple model (Vourlitis et al. 2004). Data for Santarém are from Goulden et al. (2004), and data from the Reserva Jarú and Manaus are from Kruijt et al. (2004).

these measurements to annual values. They concluded that biometric and nocturnal eddy covariance results for sustained high turbulence conditions were indistinguishable within the errors of the methods. A challenge in both eddy covariance and biometric studies is to analyze and minimize those errors.

Biometric studies provide insights into controlling mechanisms that complement mechanistic inferences available from eddy covariance studies. For example, Chambers et al. (2004) conclude that the tropical moist forest at the Cueiras reserve has a low carbon-use efficiency (the ratio of NPP to GPP) compared to temperate forests but similar to other tropical forests. Rice et al. (2004) found that stand structure and the abundance of coarse woody debris (CWD) at their site in the Tapajós National Forest indicates that it suffered a recent disturbance that they attribute to severe ENSO related drought in the 1990s. The respiration fluxes from CWD are surprisingly large. Understanding this carbon pool and its site to site variation will be critical to accurate estimation of NEE. The CWD pool at the kilometer 67, Tapajós National Forest Site (4.8×10^7 g C/ha), is two to four times greater than the standing stock of CWD measured in forests near Manaus (Chambers et al. 2000, Nascimento and Laurance 2004). Similarly, estimates of the annual CWD respiration are 5.7×10^6 g C·ha^{-1}·yr^{-1} for the kilometer 67 site at Tapajós and a maximum of 1.8×10^6 g C·ha^{-1}·yr^{-1} for forest outside Manaus (Chambers et al. 2000, Rice et al. 2004).

Analysis of NEE from eddy covariance data spanning at least one year of measurements from Fazenda Maracai, the Tapajós National Forest, and the Cueiras Reserve (k34), as well as biometric data from the Tapajós National Forest, indicate that forest NEEs were relatively small 0 ± 2 Mg C·ha^{-1}·yr^{-1} (mean $\pm$ 1 SE; SE = standard error of the mean; Araújo et al. 2002, Miller et al. 2004, Rice et al. 2004, Vourlitis et al. 2004). Araújo et al. (2002) found a slightly greater uptake for the C14 tower in the Cueiras reserve even after filling nighttime fluxes for $u^* < 0.2$ m/s. Interestingly, net fluxes of magnitude of only 1×10^6 g

$C \cdot ha^{-1} \cdot yr^{-1}$ extrapolated over with the large extent of old-growth forest in the Amazon Basin ($\sim 5 \times 10^6$ km^2) lead to globally significant amounts of carbon (0.5×10^{15} g C/yr). Because of the locations of observing stations, even large fluxes are currently below the resolution of global atmospheric inversion models for the Amazon region (Rayner et al. 1999, Bousquet et al. 2000, Gurney et al. 2002) but not below the threshold for measurement using regional airborne sampling. Using a budget method, a reanalysis of CO_2 concentration data from the 1987 ABLE 2B flights showed that the central Amazon region had a near zero carbon flux (-0.03 ± 0.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$; mean $\pm$ 1 SE) during the wet season (Chou et al. 2002).

The accuracy of global atmospheric transport model inversions could be greatly improved if high precision CO_2 concentration data from the Amazon region were to become available (Rayner et al. 1999). Weekly sampling of tropospheric air to 3 km is planned for coastal and interior sites in LBA. Even so, interpretation of the net fluxes derived from these models will remain ambiguous until we accurately quantify both the seasonality of biological exchanges and the magnitude of emissions caused by extensive annual burning (Langenfelds et al. 2002, Potter et al. 2002, Alencar et al. 2004).

Nutrient Dynamics

Efficient nutrient conservation mechanisms allow mature tropical forests to thrive even on dystrophic, acid soils. Base cations (e.g., K^+, Ca^{++}, and Mg^{++}) and phosphorus (P) are tightly cycled in tropical forests and thus they often are considered limiting factors for forest productivity (Vitousek and Sanford 1986). In this issue, Markewitz et al. (2004) confirmed prior studies showing significant losses of carbon (C), nitrogen (N), and P from cleared and burned sites (McGrath et al. 2001). Markewitz et al. showed through a budget analysis that base cations derived from forest clearing and burning are tightly retained in the surface soils of ''secondary lands'' (secondary forest, degraded pasture, and active pasture) at their Fazenda Vitoria study site after more than 20 yr following the land-clearing fires. It is generally accepted that C and N are lost from the ecosystem to the atmosphere during such fires and through subsequent mineralization of organic matter. Unlike C and N, P does not have a long-lived volatile phase in the atmosphere (Schlesinger 1997). The selective loss of P as opposed to other nonvolatile elements, such as K, Ca, and Mg, remains unexplained.

Conversion of forest to pasture was the most common land-use change in the exploitation of the Amazon region during the 1970s and 1980s. Pasture is still the most common land use in deforested areas although considerable areas of pasture have been abandoned to secondary vegetation (Schneider et al. 2002, Alves et al. 2003). The intensity of prior land use, the distance to seed sources, and the presence or absence of fire are all important factors regulating the pace of secondary succession in abandoned pastures (Uhl et al. 1982, Nepstad et al. 1996). In this issue, Davidson et al. (2004), Feldpausch et al. (2004), and Markewitz et al. (2004) each argue that the scarcity of key nutrients may limit the pace of secondary succession. Davidson et al. conducted a fertilization experiment in a 6-yr-old secondary forest at Fazenda Vitoria. They found that additions of N, or N together with P, increased the rate of aboveground biomass increment by woody vegetation. In contrast, additions of P only favored the growth of herbs and grasses. Davidson et al. concluded that forest biomass increment was limited by N at their site. Markewitz et al., who also worked at Fazenda Vitoria, came to a similar conclusion by inference from the relative rates of accumulation of N and P. The secondary forest they studied had only accumulated 33.5×10^6 g C/ha above ground over 19 yr (accumulation rate of $\sim 1.8 \times 10^6$ g $C \cdot ha^{-1} \cdot yr^{-1}$). In contrast, working in secondary forests growing on land formerly covered by pastures in the SUFRAMA Agricultural District north of Manaus, Feldpausch et al. observed an aboveground biomass accumulation rate of 5.5×10^6 g $C \cdot ha^{-1} \cdot yr^{-1}$ for a chronosequence of secondary forests (up to 14 yr old) developed on abandoned pastures. They found that surface soil to 45 cm depth was accruing N and while being depleted of extractable (Mehlich I) P. They concluded that it was likely that P or possibly Ca might limit growth and that these nutrients were actively extracted from the subsoil towards the surface layers.

Rates of biomass accumulation in secondary forests are highly variable and models that successfully capture regional behavior of secondary forest regrowth are based on soil texture (a proxy for water and nutrient availability) and growing season limitations (wet vs. dry months; Johnson et al. 2000). But, there are other important sources of variability. Fig. 3 shows the range of carbon-to-nutrient ratios encountered in two studies in this issue. It is not surprising that differences in nutrient availability appear to influence the rate of succession. Factors affecting nutrient stocks include the history of land use and management, particularly the use of fire, a practice that impoverishes system N stocks. As shown by Davidson et al. 2004, secondary succession on pastures that have been repeatedly burned can be nitrogen limited. Secondary vegetation on pastures that were grazed heavily and burned frequently may accumulate biomass more slowly compared to vegetation in areas that suffered a less intensive use. Therefore, future models of secondary forest regrowth should consider prior land management, especially the frequency of fire, in order to accurately predict biomass accumulation.

The importance of fire as a control of biogeochemical dynamics in Amazon ecosystems is difficult to overstate. The Brazilian cerrado (savanna) is highly diverse

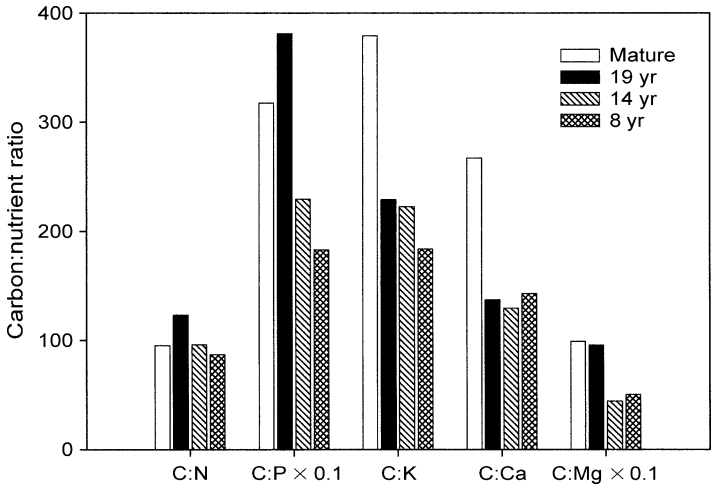

FIG. 3. Carbon-to-nutrient ratios in aboveground biomass for a mature forest and a 19-yr-old secondary forest at Fazenda Vitoria (Markewitz et al. 2004) and 14- and 8-yr-old secondary forests in the SUFRAMA Agricultural District (Feldpausch et al. 2004). Note that ratios for P and Mg have been multiplied by 0.1.

(Eiten 1972) and currently undergoing far greater relative rates of land-use change than the forests of the Amazon (Nepstad et al. 1997, Klink and Moreira 2002). The cerrado receives annual rainfall from ~1 to 2 m/yr, of which 90% falls in the ~6-mo rainy season. The cerrado is marked by a strong dry season, and fire is frequent. The return time for fire in the cerrado is 2–40 yr while it appears to be hundreds of years or more in the Amazon forests (Sanford et al. 1985, Coutinho 1990, Vicentini 1999). Analysis of ^{15}N:^{14}N ratios in cerrado vegetation shows that this vegetation shares wide ranges in these ratios characteristic of N-limited ecosystems. Additionally, ^{15}N contents reflected fire frequency even among different vegetation formations within the cerrado (Bustamante et al. 2004) with the most fire-prone and nitrogen-poor systems showing the greatest enrichment in ^{15}N. As predicted by Schimel et al. (1996), frequent fire causes chronic N limitation in dry tropical ecosystems so that they produce less carbon for the same amount of water vs. systems not dominated by fire.

TRACE GAS FLUXES

Estimation of trace gas fluxes from the Amazon ecosystems to the atmosphere for both long- and short-lived trace gases is an essential component of LBA. This issue includes four examples of studies of gas fluxes for both long-lived radiatively important gases such as nitrous oxide (N_2O), methane (CH_4), and carbon dioxide (CO_2) (Davidson et al. 2004, Garcia-Montiel et al. 2004, Guild et al. 2004, Varella et al. 2004) or medium and short-lived gases such as carbon monoxide (CO) (Guild et al. 2004), nitric oxide (NO) (Davidson et al. 2004, Varella et al. 2004), and volatile organic compounds (Guild et al. 2004, Rottenberger et al. 2004).

Garcia-Montiel et al. (2004) present a new approach for regional estimation of N_2O emissions based on field investigations in Rondônia. In their analysis, soil N_2O emission is scaled linearly to the soil emission of CO_2; the latter is estimated based upon the TEM model (McGuire et al. 1992). This approach parallels a previous effort by Garcia-Montiel and her colleagues (Melillo et al. 2001) whereby regional N_2O emission was estimated from modeled N-mineralization using TEM.

Tropical forests release substantial quantities of volatile organic compounds (VOCs) to the atmosphere (Guenther et al. 1995). VOCs regulate the production and destruction of atmospheric oxidants and may be important to the ecosystem carbon balance (Crutzen et al. 1999). However, as Rottenberger et al. (2004) found in their study of small-chain aldehydes, vegetation can be a sink as well as a source of VOC. A full accounting of the influence of VOC on ecosystem carbon budgets must consider both sources and sinks for these compounds and the reaction products of VOC including atmospheric particulates.

Guild et al. (2004) quantified the emission of carbon compounds (CO_2, CO, CH_4, and several VOCs) from fires in a 94 000-ha area surrounding Jamari, Rondônia for the period 1984–1992. For estimation of burned area, they used a novel approach linking fire to land use rather than mapping active fires or fire scars. While they found that the initial forest clearing fires emitted the majority of the CO and CH_4, frequent pasture burning (0.3–0.5/y) could account for 15 to 20% of the CO emissions and 11 to 15% of the CH_4 emissions by fire from the study region. Frequent pasture burning is an important source of carbon trace gases.

LAND-USE AND LAND-COVER CHANGE

Current trends in land use in the Amazon region have caused significant fragmentation of the forest (Skole and Tucker 1993). Increasing fragmentation leads to an increasing length of forest edge and area of edge habitat. Living on the edge, whether for people or for trees, has its drawbacks. Nascimento and Laurance

(2004) quantify the biomass and necromass in forest edges and interior forests. They found that large tree mortality was accelerated in edge habitats compared to forest interiors.

As noted in the sections on nutrients and trace gases, land-use change has significant effects on biogeochemical cycles. Bernardes et al. (2004) showed that conversion of forest to pasture in Rondônia changes the quality of organic matter in rivers of the Ji-Paraná River Basin. Understanding the organic signals in rivers offers the prospect of tracing the signal of deforestation from low order streams through to larger river systems.

The acceleration of fire risk on the Amazon landscape has the potential to greatly alter ecosystem structure and function (Cochrane et al. 1999, Nepstad et al. 1999). Cochrane and Laurance (2002) recently demonstrated that fire risk is greatest within 2–3 km of existing forest edges. However, distance to the forest edge is not always a strong predictor of fire vulnerability. Alencar et al. (2004) demonstrated that the probability of fire in the region of Paragominas, Pará was related to forest degradation, settlement patterns, infrastructure, and economic activities such as charcoal manufacture. Their work showed radically greater probabilities of fire in El Niño vs. non-El Niño years. Forest degradation through logging or fire strongly predicted fire occurrence. Alencar et al. (2004) supplemented remote sensing interpretation with six months of field interviews to classify degraded forest. New approaches, such as the automated Monte-Carlo unmixing developed by Asner et al. (2004) used with Landsat 7 imagery show great promise for quantitative measurement of forest degradation. Combining their remote sensing techniques with a large-scale, detailed set of field studies, Asner et al. precisely measured canopy opening using remote sensing data for forests that were recently logged and forests recovering from logging. This measurement is valuable because canopy opening is associated with increased fuel loads in logging gaps and altered microclimates that make the forests more susceptible to fire. Measurements of forest degradation therefore can be used to predict future fire susceptibility (Alencar et al. 2004).

Fig. 4 highlights two important findings using Landsat and field observations during LBA. On the left, the Alencar et al. (2004) multitemporal analysis of Landsat fire areas in the eastern Amazon revealed a complex mosaic of fire patches spanning several years and land-cover types. Fire occurs in a spatially explicit patchwork driven by land use, and a single-year fire analysis does not depict the fire dynamics of a region. Distinct areas burned in different years while others burned multiple times. To the right side of Fig. 4, the technique presented by Asner et al. (2004) was applied to the same region, revealing a great deal of spatial variability in the proportions of three biophysical surface constituents, photosynthetic vegetation (PV), nonphotosynthetic vegetation (NPV), and bare soil in this region. Fire and postfire recovery processes generate complex mosaics of surface properties. Understanding the variability of surface properties bears on our ability to simulate the environmental impacts of land use and fire on regional carbon and nutrient cycles.

LBA research is contributing to understanding the processes governing land use and land cover change and to predicting the future course of land management in the Amazon. This is a tremendously complex task. Walker et al. (2004) consider the case of agricultural colonists. They present a theoretical model of household economy wherein smallholder families maximize utility (as opposed to profits) constrained by the productivity of the resource base and the availability of family labor. While Walker and colleagues have not implemented the full model, they produced a convincing simulation of the spatial pattern of clearing based on control variables for the farming rotation period and the deforestation event magnitude.

Future Challenges for Ecological Studies in LBA

Studies in LBA are advancing our understanding of the functions of managed and unmanaged ecosystems in the Amazon. The overall challenge for ecological research in LBA is the unification of the results of site-based studies into a regional synthetic framework. Better understanding of the region will require further emphasis on wetland areas to complement ongoing studies of the uplands. Results presented in this issue raise many questions and indicate some directions forward.

While most of the Amazon region is covered by evergreen forest, strong seasonality in rainfall leaves its imprint on the cycling of carbon and nutrients, the fluxes of trace gases, and the patterns of land management. Understanding how seasonal patterns are driven by variations in weather as well as by innate seasonal rhythms will be critical for development of reliable models of ecosystem function.

Development in the Amazon region has been accompanied by increasing forest fragmentation and poorly managed logging activities. Both fragmentation and logging increase the likelihood of fire escaping from managed systems into forest, especially during dry years often associated with El Niño. Fire may represent the single greatest threat to the forest ecosystem, yet the extent of burned forest in the region is poorly quantified, and the conditions leading to forest fires are only beginning to be understood. The spatial extent and magnitude of forest degradation in the Amazon region has not been comprehensively quantified. Nonetheless, the combined use of newly developed remote sensing techniques coupled with intensive ground studies shows great promise for quantifying forest degradation and recovery over vast areas.

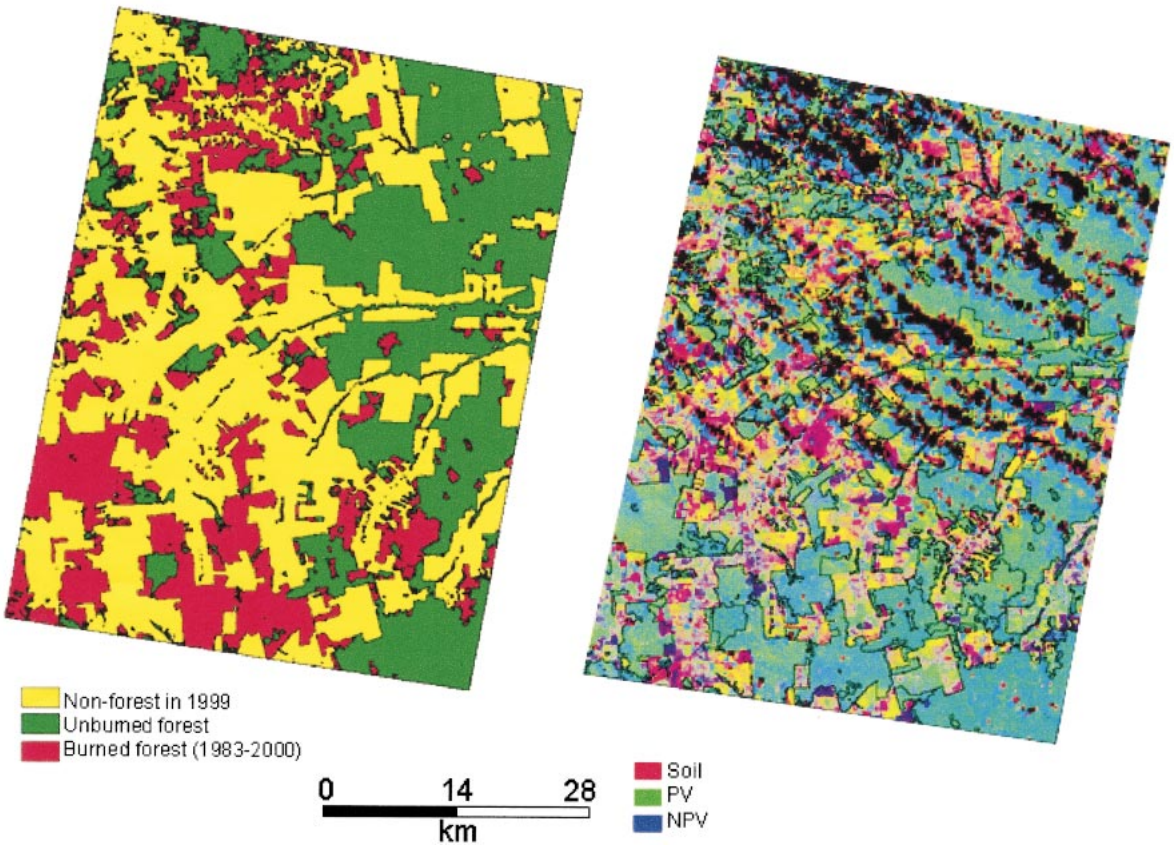

FIG. 4. Two interpretations of the same landscape around Paragominas, Pará. The left-hand diagram shows cleared areas, burned forest, and unburned forest based on interpretation of multitemporal Landsat images, interviews with land managers, and field visits (Alencar et al. 2004) while the right-hand image is an automated product of the Auto-MCU algorithm described by Asner et al. (2004) for a Landsat 7 ETM+ image from 2001. The black areas on the upper part of this image are clouds.

While recent development activities have led to extensive changes across the Amazon landscape, the ecosystems of the region, or at least their component species, show an ability to react to change. Secondary forest succession now covers extensive areas and secondary forests can rapidly achieve certain functions of primary forest such as the recycling of water in evapotranspiration (Brown and Lugo 1990, Nepstad et al. 1995, Hölscher 1997, Sommer 2002). On the other hand, the vigor of secondary succession may be limited by the shortage of plant available nutrients left behind as a legacy of past land-use practices such as overgrazing and repeated burning.

Geologists and other natural scientists depend on the uniformitarian principle of James Hutton that the present is the key to the past. Can ecologists and social scientists depend on the present and past as keys to the future of the Amazon? Frontier expansion in the Amazon region is confronting the modern world of instant communication and globalization. The population of the Amazon is urbanized and the economy no longer depends strictly on a mixture of extractive industries, extensive ranching, and subsistence agriculture. Will future land cover and land use continue to follow past patterns or will the future development of the Amazon region follow a different, and perhaps more sustainable, path? The answer to that question depends on choices made by the people of the Amazon region countries and the governments that they elect. We believe that LBA will offer new knowledge to decision makers to allow them to plan for a more sustainable future.

ACKNOWLEDGMENTS

We acknowledge Brazil's Ministry of Science and Technology (MCT) and its research institutions the Instituto Nacional de Pesquisas de Amazônia (INPA) and the Instituto Nacional de Pesquisas Espacias (INPE) for leadership of LBA. The U.S. National Aeronautics and Space Administration (NASA) and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) provided generous support for ecological research in LBA. Brazil's Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided many valuable fellowships to support students in LBA research. We are indebted to Drs. Diane Wickland, Tony Janetos, Jerry Melillo, and Carlos Cerri for their early vision of ecological research in LBA. We thank Drs. Darrel Williams and Peter Griffith for their comments and Michael Palace and Lorena Brewster for assistance in preparation of the paper. M. Keller is grateful for the patience, guidance, and material

support generously offered by Dr. Ariel Lugo of the USDA Forest Service, International Institute of Tropical Forestry.

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