

Carbon isotope discrimination in forest and pasture ecosystems of the Amazon Basin, Brazil

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Received 26 June 2001; revised 13 February 2002; accepted 8 May 2002; published 3 December 2002.

[1] Our objective was to measure the stable carbon isotope composition of leaf tissue and CO₂ released by respiration (δ_r), and to use this information as an estimate of changes in ecosystem isotopic discrimination that occur in response to seasonal and interannual changes in environmental conditions, and land-use change (forest-pasture conversion). We made measurements in primary forest and pastures in the Amazon Basin of Brazil. At the Santarém forest site, δ_r values showed a seasonal cycle varying from less than -29% to approximately -26% . The observed seasonal change in δ_r was correlated with variation in the observed monthly precipitation. In contrast, there was no significant seasonal variation in δ_r at the Manaus forest site (average δ_r approximately -28%), consistent with a narrower range of variation in monthly precipitation than occurred in Santarém. Despite substantial (9%) vertical variation in leaf $\delta^{13}\text{C}$, the average δ_r values observed for all forest sites were similar to the $\delta^{13}\text{C}$ values of the most exposed sun foliage of the dominant tree species. This suggested that the major portion of recently respired carbon dioxide in these forests was metabolized carbohydrate fixed by the sun leaves at the top of the forest canopy. There was no significant seasonal variation observed in the $\delta^{13}\text{C}$ values of leaf organic matter for the forest sites. We sampled in pastures dominated by the C₄ grass, *Brachiaria* spp., which is planted after forest vegetation has been cleared. The carbon isotope ratio of respired CO₂ in pastures was enriched in ¹³C by approximately 10% compared to forest ecosystems. A significant temporal change occurred in δ_r after the Manaus pasture was burned. Burning removed much of the encroaching C₃ shrub vegetation and so allowed an increased dominance of the C₄ pasture grass, which resulted in higher δ_r values. **INDEX TERMS:** 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1610 Global Change: Atmosphere (0315, 0325); 1615 Global Change: Biogeochemical processes (4805); 3309 Meteorology and Atmospheric Dynamics: Climatology (1620); **KEYWORDS:** carbon cycle, global change, tropical ecosystems, atmospheric carbon dioxide

Citation: Ometto, J. P. H. B., L. B. Flanagan, L. A. Martinelli, M. Z. Moreira, N. Higuchi, and J. R. Ehleringer, Carbon isotope discrimination in forest and pasture ecosystems of the Amazon Basin, Brazil, *Global Biogeochem. Cycles*, 16(4), 1109, doi:10.1029/2001GB001462, 2002.

1. Introduction

[2] There is substantial year-to-year variation in the annual increase of atmospheric carbon dioxide concentration [Conway *et al.*, 1994; Bousquet *et al.*, 2000; Fung, 2000]. For example, CO₂ concentration increased by over 3 ppm in 1998, while in other years the annual increase was

as low as 0.5 ppm. Interannual variation in the rise of atmospheric CO₂ occurs despite relatively constant anthropogenic emissions of carbon dioxide from fossil fuel burning [Marland *et al.*, 2001]. These observations have led to the hypothesis that variation in the uptake and release of carbon dioxide in terrestrial ecosystems, associated with changes in temperature and precipitation and their effects on carbon cycling processes, are largely responsible for the observed variation in the annual rate of atmospheric carbon dioxide increase [Fung, 2000; *Climate Monitoring and Diagnostics Laboratory*, 2000].

[3] El Niño/La Niña events are mechanisms that contribute substantially to yearly variation in temperature and precipitation, particularly in the Amazon Basin of Brazil [Marengo *et al.*, 1993; Marengo and Hastenrath, 1993; Nobre and Rennó, 1985]. Despite the evergreen nature of the primary forest vegetation in the Amazon Basin, there are

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indications that carbon cycling in these forests responds strongly to seasonal and interannual variation in environmental conditions [Tian *et al.*, 1998; Bousquet *et al.*, 2000]. In addition, disturbances caused by logging and forest conversion to cattle pastures are increasing, with potentially large effects on ecosystem function in this globally important biome [Nepstad *et al.*, 1999].

[4] Ecosystem carbon budgets are controlled by the balance between carbon uptake during photosynthesis and carbon loss during respiration [Malhi *et al.*, 1999]. Within an ecosystem, both photosynthesis and respiration occur in a range of different species and functional groups, so the environmental control of carbon exchange processes is quite different in these distinct ecosystem components. The study of individual components of the ecosystem carbon budget and their environmental control would improve our understanding of ecosystem function and the system's potential response to climate variation. However, because of high species diversity and large stature of tropical forests, it is not possible to combine measurements of all the component processes and species into analyses of ecosystem function because of the consequent complexity. Rather, it is necessary to focus on important synthetic properties or processes that are understood in a precise manner at one scale, but which can also be extended to larger spatial and temporal scales without loss of information [Field and Ehleringer, 1993].

[5] The measurement and analysis of carbon isotope ratios of leaf and atmospheric CO₂ samples can provide information that integrates important plant physiological characteristics spatially and temporally [Flanagan and Ehleringer, 1998]. For example, measurement of the carbon isotope ratio of leaf tissue provides an assimilation-weighted average of the ratio of intercellular (c_i) to ambient CO₂ concentration (c_a) [Farquhar *et al.*, 1982, 1989]. There are a number of important physiological characteristics such as water-use efficiency (ratio of net CO₂ assimilation and transpiration) [Farquhar *et al.*, 1989], stomatal limitation of photosynthesis [Farquhar and Sharkey, 1982; Jones, 1992], optimal stomatal behavior [Cowan and Farquhar, 1977], and leaf nitrogen-use efficiency (ratio of net CO₂ assimilation and leaf nitrogen content) [Field *et al.*, 1983] that are all directly related to the value of leaf c_i/c_a ratios. In addition, it is well documented that variation in environmental conditions causes change in the ratio of photosynthesis to stomatal conductance, and associated changes in leaf $\delta^{13}\text{C}$ values [Farquhar *et al.*, 1989; Ehleringer *et al.*, 1993]. Detailed mechanistic models have been developed that successfully explain the isotope effects that occur during photosynthetic gas exchange at the leaf level [Farquhar *et al.*, 1989; Ehleringer *et al.*, 1993]. It is possible to interpret variation in carbon isotope discrimination resulting from differences in plant photosynthetic pathway and environmental conditions [Farquhar *et al.*, 1989; Lloyd and Farquhar, 1994].

[6] Spatially and temporally integrated values of ecosystem carbon isotope discrimination can be obtained from measurements of the isotope ratio of CO₂ respired by the entire ecosystem [Flanagan *et al.*, 1996; Buchmann *et al.*, 1998; Flanagan and Ehleringer, 1998]. A large fraction of

respired CO₂ comes from the metabolism of recently fixed carbohydrates [Malhi *et al.*, 1999; Ekblad and Hogberg, 2001]. The $^{13}\text{C}/^{12}\text{C}$ ratio of this carbohydrate records information about the plant physiological characteristics during the time it was fixed, assuming no significant fractionation occurs during respiration processes [Lin and Ehleringer, 1997]. A portion of respired carbon dioxide is the result of soil organic matter decomposition, but the carbon isotope ratio of this ecosystem component is not likely to change on timescales less than one year [Trumbore, 2000]. So we expect that measurements of the carbon isotope composition of CO₂ respired from the entire ecosystem will represent a spatially integrated measure of whole ecosystem discrimination [Flanagan *et al.*, 1996; Buchmann *et al.*, 1998; Flanagan and Ehleringer, 1998; Ekblad and Hogberg, 2001]. The temporal component of this integrated measurement depends on the magnitude of leaf and root respiration as well as that of respiration by rhizosphere organisms using carbon exudates from plant roots. Shifts in the carbon isotope composition of ecosystem respiration are likely to be dominated by fast-cycling carbon fixed from the atmosphere a few days prior to sample collection [Ekblad and Hogberg, 2001; Bowling *et al.*, 2002].

[7] Our objective in this study was to measure the stable carbon isotope composition of leaf tissue and CO₂ released by respiration, and to use this information as an estimate of changes in ecosystem isotopic discrimination that occur in response to seasonal and interannual changes in environmental conditions, and land-use change (forest-pasture conversion). We made measurements in primary forest and pastures in the Amazon Basin of Brazil. This research was part of a larger study, the Large Scale Biosphere Atmosphere Experiment in Amazonia that aims to improve our understanding of the interactions between the atmosphere and ecosystems of the Amazon Basin, a globally important biome.

2. Methods

2.1. Study Sites

[8] The forest and pasture study sites were located near Santarém, Manaus, and Ji-Paraná (Figure 1). The forests consisted of dense evergreen tropical vegetation, with mean canopy height of about 30–35 m, although some trees extended up to 45–50 m. High species diversity is a characteristic of these “terra firme” forests in Amazonia [Higuchi *et al.*, 1998; Alder and Silva, 2000]. The pastures were previously forested sites now planted with C₄ grasses (*Brachiaria brizantha*, and other *Brachiaria* spp.) cultivated widely in the Amazon region.

[9] The primary forest site near Santarém was located 67 km south of the city, in an area between the Tapajós River and the highway BR 163 (2.85°S; 54.05°W). The forest covers an area of approximately 600,000 ha and was established as National Forest in 1974 (FLONA Tapajós). The mean annual precipitation is 2207 mm, with a dry season (less than 100 mm precipitation per month) from July through November (Figure 2). The Santarém pasture site was located 77 km south of Santarém (3.02°S; 54.06°W). The Manaus forest site was located 70 km

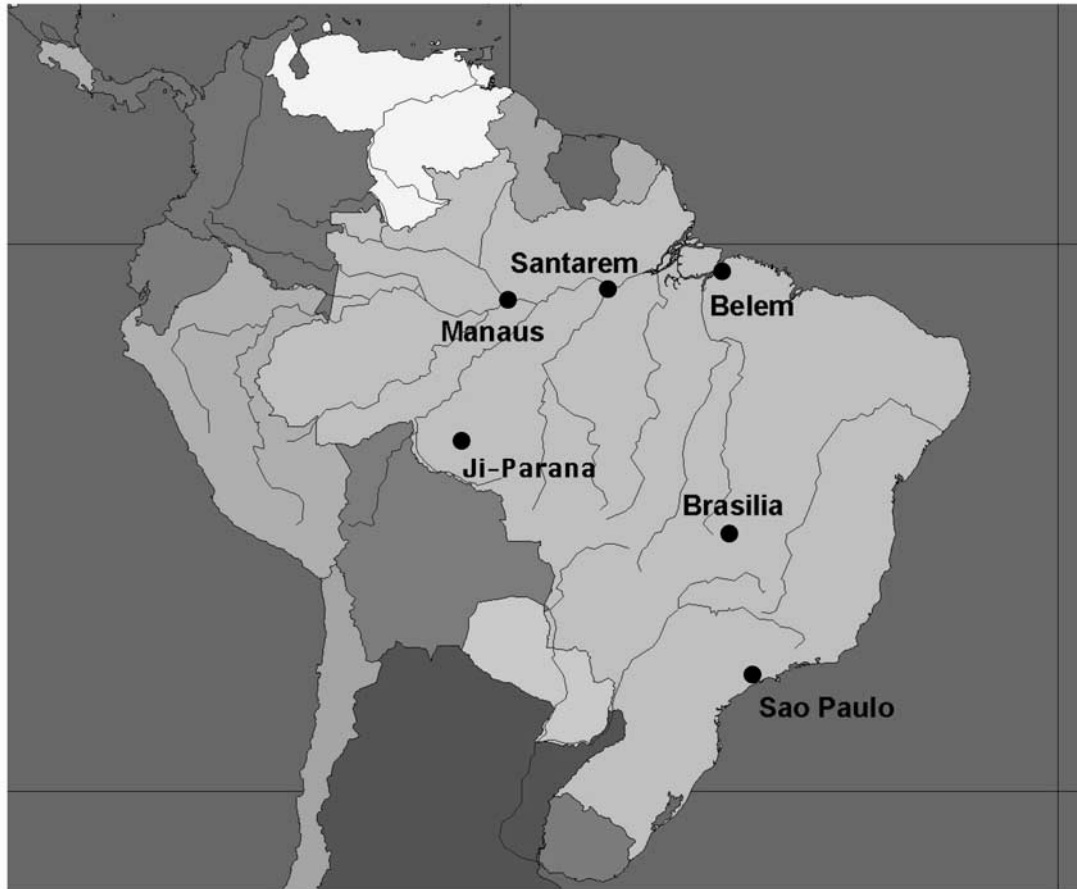


Figure 1. Map of Brazil and other countries in South America, with the locations of the cities (Santarém, Manaus, and Ji-Paraná) near the field sampling sites.

from the city (2.69°S ; 60.11°W), in a forest reserve controlled by the Instituto Nacional de Pesquisas Amazonicas. The mean annual precipitation is 2251 mm and the dry season extends from July through September (Figure 2). The Manaus pasture site was located about 60 km from the forest site, along a secondary road (ZF-3). The grass at this site had less vigorous growth than the Santarém pasture grass. The soils at the Manaus and Santarém sites were deeply weathered oxisols (Hapludox) with high clay content (60–80%), low pH (4.0–4.3), and low nutrient content. The Ji-Paraná primary forest site (Rebio Jaru, 10.08°S ; 61.92°W) was a reserve controlled by the Brazilian Environment Protection Agency, located north of Ji-Paraná (about 80 km), by the Machado river (120 m above sea level). The mean annual precipitation is 2040 mm, with a dry season from May through September (Figure 2). The pasture site (Fazenda Nossa Senhora da Aparecida; 10.75°S ; 62.37°W) was a cattle ranch 50 km north-east from Ji-Paraná. The soil in both Ji-Paraná sites has been classified by *Hodnett et al.* [1996] as an orthic Acrisol, with 85% or more, of sand at the surface layer. All sites, except the Manaus pasture, were official LBA-Ecology study areas. Field measurements were made during six field campaigns from March 1999 to September 2000 at the Manaus and Santarém sites. Less frequent

sampling occurred in Ji-Paraná, with only two field campaigns, February and September 2000.

2.2. Air Sample Collection

[10] At each site we collected samples of air at intervals during a 1–2 day period. Sample lines (Dekoron tubing, 6 mm outer diameter) were located at different heights in the canopy (31, 21, 7, and 0.2 m at forest sites; 0.7 and 0.2 m at pasture sites) by attachment to a scaffold tower (forest) or wooden pole (pasture). A small filter was placed over the inlet to prevent the entry of insects. Air was pulled down through the tubing, through a desiccant tube containing magnesium perchlorate, into glass flasks (100 ml) by a battery-operated pump (Capex V2X, Charles Austin, West Byfleet, Surrey, United Kingdom). Air was passed through the flasks for approximately 7–10 min before the high vacuum stopcocks on the flask were closed. The flask was then returned to the laboratory for stable isotope analyses and CO_2 concentration measurement.

[11] During September 2000, at the Santarém forest site only we also collected CO_2 respired from the soil surface for stable isotope analysis following a procedure similar to that described by *Flanagan et al.* [1999]. A darkened plexiglass chamber was placed on the soil surface. An

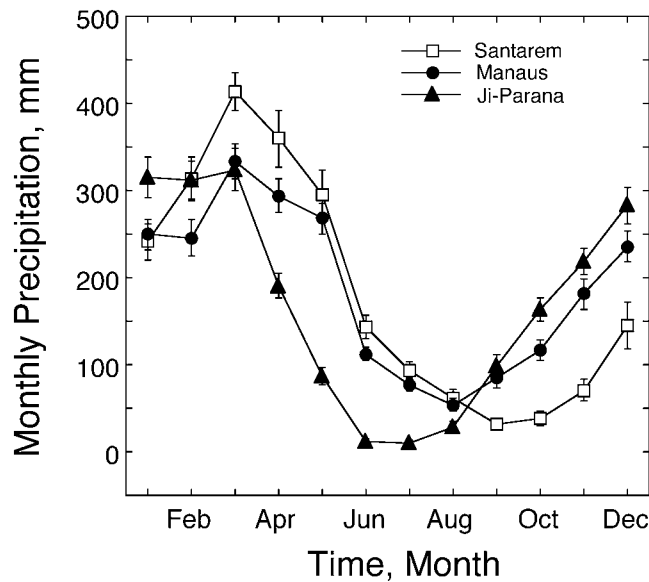


Figure 2. Seasonal variation in total monthly precipitation in Santarém, Manaus, and Ji-Paraná, Brazil. The Santarém data represent averages (\pm SE, standard error) for 1968–1998. The Manaus data represent averages (\pm SE) for 1961–1990. The Ji-Paraná data represent averages (\pm SE) for 1977–1997.

evacuated flask was connected to the chamber via a port with an Ultra-Torr (Cajon, Swagelok, Salt Lake Valve and Fitting, Utah) connector. At intervals during the rise in CO_2 concentration inside the chamber, samples of chamber air were collected by opening the high-vacuum stopcock on the glass flask. Air passing into the flask first passed through a small tube of magnesium perchlorate. After sample collection, the flasks were returned to the laboratory for stable isotope analyses and CO_2 concentration measurement, as described subsequently.

[12] Stable isotope ratios of CO_2 in flask samples were analyzed using a gas isotope ratio mass spectrometer (Model 252, Finnigan MAT, Bremen, Germany) operating in continuous flow mode. After removal of a subsample of air from the flask, a helium carrier gas moved the sample through a gas chromatograph (Model 3400, Varian, Walnut Creek, California) to separate CO_2 and N_2O before introducing the CO_2 into the mass spectrometer. The gas chromatograph was arranged such that its effluent was sent to the mass spectrometer through a 1:2 fixed post column split interface via a capillary. The gas chromatograph had a 25 m POROPLLOT column operated at 25°C. An analysis of the accuracy and precision of this method for determining stable isotope ratios of atmospheric CO_2 is presented by Ehleringer and Cook [1998]. The precision of the technique was estimated to be 0.13‰ for ^{13}C .

[13] The remaining air left in the flask, after stable isotope analysis, was used to measure CO_2 concentration using a system described by Bowling *et al.* [2001]. Briefly, the flask was attached to a stainless steel vacuum line connected to a variable volume bellows. Gas from the flask was released into the evacuated line and bellows. The bellows was

compressed to push the gas through the analysis cell of an infrared gas analyzer (LI-6262, LiCor, Lincoln, Nebraska). The analysis cell of the gas analyzer was flushed with a working standard gas before an unknown sample gas was measured. The gas analyzer was calibrated with gases obtained from the NOAA CMDL laboratory in Boulder, Colorado. The precision and accuracy of the technique were 0.2 and 0.3 ppm, respectively.

2.3. Leaf and Litter Sample Collection

[14] Leaf samples were collected from plants along a height profile through the canopy at all sites during each study period. Three samples of leaf litter were randomly collected from each study site during each sample trip. Live and dead foliage was dried at 65°C and ground to a fine powder with a tissue grinder or a mortar and pestle. The organic tissue samples were prepared for measurements of carbon isotopic composition by combustion. A 1–2 mg subsample of ground organic material was sealed in a tin capsule and loaded into an elemental analyzer for combustion (Carla Erba). The carbon dioxide generated from the combustion was purified in a gas chromatographic column and passed directly to the inlet of a gas isotope ratio mass spectrometer (Delta Plus, Finnigan Mat, San Jose, California).

2.4. Isotopic Analysis

[15] Stable isotope ratios were expressed in delta notation, where the international standard for atmospheric CO_2 samples and leaf organic samples is CO_2 from Peedee belemnite limestone [Ehleringer and Osmond, 1989]. The δ values are conveniently presented in parts per thousand (‰).

[16] We used a simple mixing model developed by Keeling [1958, 1961] to calculate the isotope ratio of CO_2 respired (δ_r) by an entire ecosystem and that released from the soil surface. Estimates for δ_r were obtained from the y -intercept of a geometric mean linear regression [Sokal and Rohlf, 1995] between $\delta^{13}\text{C}$ and $1/[\text{CO}_2]$ values measured on air samples collected at different heights within a vegetation canopy during the night when photosynthesis was not active [Keeling, 1958, 1961]. This analysis was also applied to the air samples collected from the soil chamber. The geometric mean regression is a model II regression that should be implemented when both variables used in the regression have a measurement error associated with them, and are not controlled by the investigator [Sokal and Rohlf, 1995].

3. Results

3.1. Forest Height Profile for Leaf $\delta^{13}\text{C}$ Values

[17] There was a strong vertical gradient for leaf $\delta^{13}\text{C}$ values at all three of the primary forest sites (Figure 3a). Leaves at the top of the canopy had high leaf $\delta^{13}\text{C}$ values, while leaves at the bottom of the canopy had lower leaf $\delta^{13}\text{C}$ values. There was a strong linear relationship between leaf $\delta^{13}\text{C}$ and height, and the slope and intercept of this relationship were similar for both Manaus and Santarém sites, with slightly lower slopes observed in Ji-Paraná (Table 1). Both mature leaves and newly produced immature leaves showed identical linear gradients for leaf $\delta^{13}\text{C}$ with height (Figure 3b). The strong linear relationship between leaf $\delta^{13}\text{C}$ values and height contrasted with the

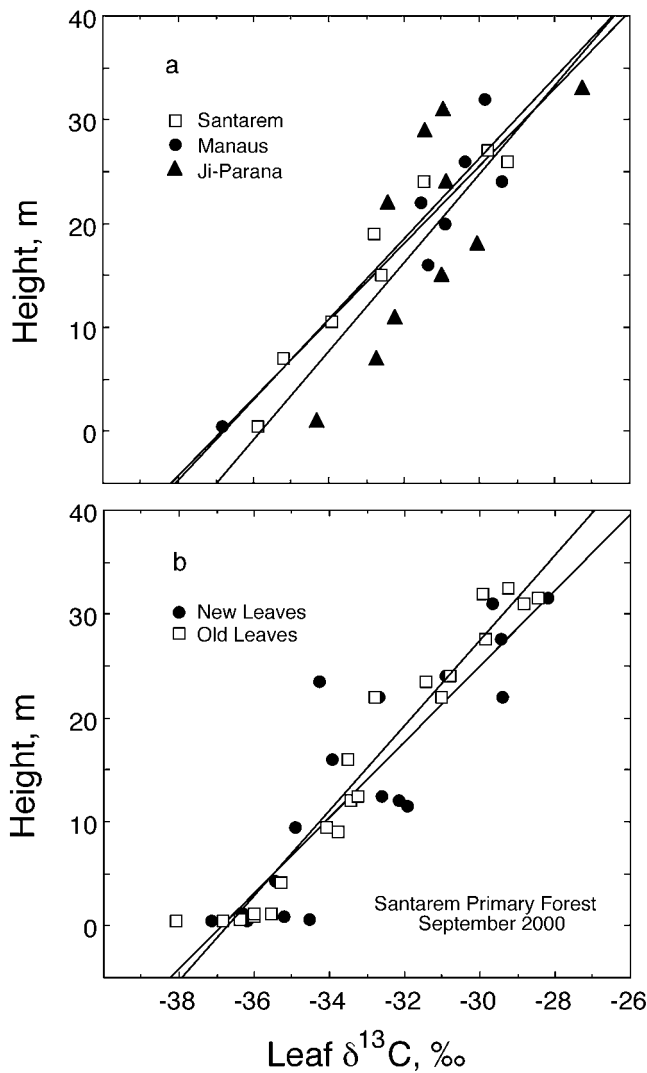


Figure 3. (a) Composite height profile for leaf $\delta^{13}\text{C}$ values in evergreen tropical forests near Santarém, Manaus, and Ji-Paraná, Brazil. See Table 1 for details of the linear regression statistics for samples collected on specific sampling dates. (b) Relationship between leaf height and leaf $\delta^{13}\text{C}$ value for young and mature leaves in an evergreen tropical forest near Santarém, Brazil, during September 2000.

pattern of change in the $\delta^{13}\text{C}$ values of atmospheric CO_2 along a canopy height profile (Figure 4). At any given sampling time during the daylight hours (6 am to 6 pm), the $\delta^{13}\text{C}$ values of atmospheric CO_2 and CO_2 concentration remained relatively constant between the top of the canopy (~30 m) and 7 m above ground. Only in the lowest levels of the forest understory was the concentration of atmospheric CO_2 elevated above ambient levels, with $\delta^{13}\text{C}$ values lower than ambient values (Figure 4). This suggests that the linear relationship between leaf $\delta^{13}\text{C}$ values and height was not primarily caused by differences in the isotopic composition of source CO_2 along a height profile through the canopy. Some of the vertical pattern in leaf $\delta^{13}\text{C}$ values was certainly a result of source CO_2 being depleted in ^{13}C in the lower layers of the forest. However, other factors such as

light and humidity gradients within the forest will also affect the ratio of leaf photosynthetic capacity and stomatal conductance, and therefore have a significant effect on leaf $\delta^{13}\text{C}$ values [Farquhar et al., 1989]. At night (after 8 pm) the entire forest canopy space can have elevated atmospheric CO_2 concentrations and CO_2 with very depleted $\delta^{13}\text{C}$ values (Figure 4).

3.2. Temporal Variation in the Carbon Isotope Ratio of Respired CO_2

[18] Strong linear relationships occurred between the inverse of CO_2 concentration and $\delta^{13}\text{C}$ values measured on air samples collected within a vegetation canopy at night (Figure 5). The values calculated for δ_r , using the linear regression between $1/[\text{CO}_2]$ and $\delta^{13}\text{C}$ were similar for CO_2 respired by an entire forest ecosystem and that released from the soil surface (Figure 5). At the Santarém forest site, δ_r showed a seasonal cycle varying from less than -29‰ to approximately -26‰ (Figure 6). The observed seasonal change in δ_r for the Santarém forest was correlated with variation in the total monthly precipitation recorded during the time when isotope sampling was conducted (Figure 7). The δ_r values became more enriched in ^{13}C as total monthly precipitation declined from 300 mm. In addition, during a month of higher than normal precipitation (February 2000, 463 mm), δ_r was enriched in ^{13}C (Figure 7). In contrast, there was no seasonal variation in δ_r at the Manaus forest site (average δ_r approximately -28‰), consistent with the narrower range of variation in monthly precipitation recorded in Manaus compared to that observed in Santarém (Figure 7).

[19] There was no significant seasonal variation observed in the $\delta^{13}\text{C}$ values of leaf organic matter for any of the forest sites during the course of this study (Table 2). The average δ_r values observed for all forest sites ($\sim 28\text{‰}$, Figure 8) were similar to the $\delta^{13}\text{C}$ values of the most exposed sun foliage of the dominant tree species (Figure 3). This suggests that the major portion of recently respired carbon dioxide in these forests was metabolized carbohydrate fixed by the sun leaves at the top of the forest canopy.

3.3. Comparison of $\delta^{13}\text{C}$ Values in Forest and Pasture Ecosystems

[20] In the Santarém, Manaus, and Ji-Paraná study areas, we collected samples in cattle pastures dominated by the C_4

Table 1. Linear Regression Statistics for the Relationship Between Canopy Height and Leaf $\delta^{13}\text{C}$ Value in Primary, Evergreen Tropical Forests Near Manaus, Santarém, and Ji-Paraná, Brazil

Site	Date	y-Intercept	Slope	r^2
Manaus	May 1999	-37.1	0.24	0.89
Manaus	Oct. 1999	-35.9	0.27	0.95
Manaus	Feb. 1999	-37.6	0.30	0.95
Santarém	May 1999	-36.9	0.23	0.90
Santarém	Oct. 1999	-35.8	0.23	0.79
Santarém	March 2000	-35.5	0.24	0.92
Santarém	June 2000	-35.5	0.21	0.93
Santarém	Feb. 2000	-35.8	0.20	0.74
Santarém	Sept. 2000	-36.5	0.23	0.95
Ji-Paraná	Feb. 2000	-35.0	0.16	0.62
Ji-Paraná	Sept. 2000	-33.6	0.14	0.61

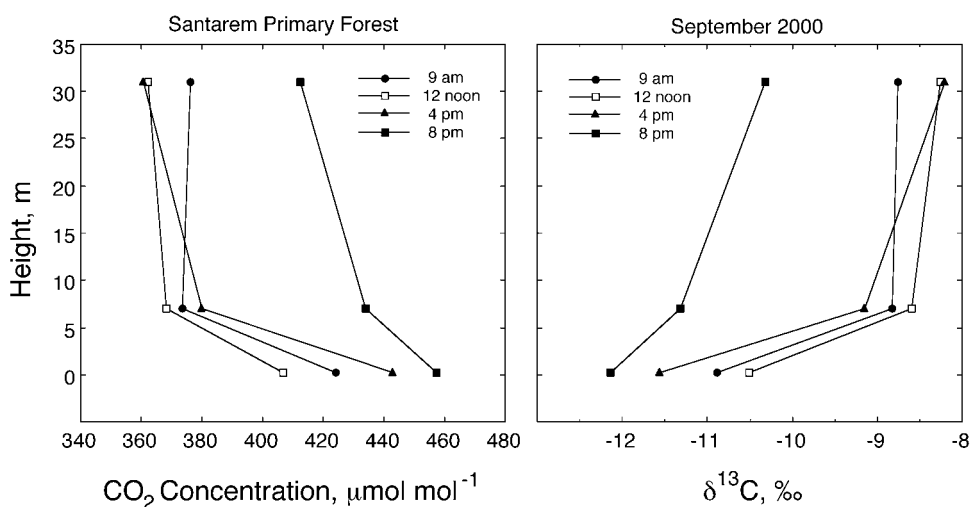


Figure 4. Vertical variation in the concentration and carbon isotope composition of CO_2 within an evergreen tropical forest near Santarém, Brazil, during diurnal sampling in September 2000.

grass, *Brachiaria* spp., which is planted on land after forest vegetation has been cleared [Smith *et al.*, 1995; Skole and Tucker, 1993; Brown and Lugo, 1990]. Because of the C_4 photosynthetic pathway, *Brachiaria* spp. has leaf $\delta^{13}\text{C}$ values significantly higher than the values for leaf tissue in forest ecosystems (Table 3 and Figure 3). In the pasture sites near Santarém and Manaus, there were also a few scattered C_3 shrub and small tree species, so leaf litter collected from the soil surface had slightly lower $\delta^{13}\text{C}$ values than the major pasture grass (Table 3). The carbon isotope ratio of respired CO_2 in pastures was enriched in ^{13}C by approximately 10‰ compared to forest ecosystems (Figure 8). The pasture in Ji-Paraná had slightly higher average δ_r than either of the Manaus or Santarém sites, indicating a smaller contribution from C_3 vegetation (Figure 8). We also observed a significant temporal change in the δ_r at the Manaus pasture site (Figure 9). This temporal change in stable isotope composition of respired CO_2 was associated with pasture burning before our sample trip in May 1999. The burning event removed much of the C_3 shrub vegetation that developed at the pasture since its establish-

ment, and so allowed an increased dominance of the C_4 pasture grass, which resulted in higher δ_r values (Figure 9).

4. Discussion

[21] We observed a range of approximately 9–10‰ in leaf $\delta^{13}\text{C}$ values from the top of the forest canopy to ground level (Figure 3). This range was larger than the 4–5‰ vertical variation reported in several other studies in tropical forest ecosystems [Medina and Minchin, 1980; Ehleringer *et al.*, 1986; van der Merwe and Medina, 1989; Broadmeadow and Griffiths, 1993; Buchmann *et al.*, 1997; Martinelli *et al.*, 1998]. Berry *et al.* [1997] and Schleser [1990] have reported vertical variation in leaf $\delta^{13}\text{C}$ values of 6‰ in temperate forest ecosystems. The large height gradient for leaf $\delta^{13}\text{C}$ values was not associated with a major change in the carbon isotope composition of source CO_2 (Figure 4). We observed only about 3‰ variation in the $\delta^{13}\text{C}$ of atmospheric CO_2 from the top of the canopy to near ground level during daylight hours. These data were consistent with the results of the other studies conducted in

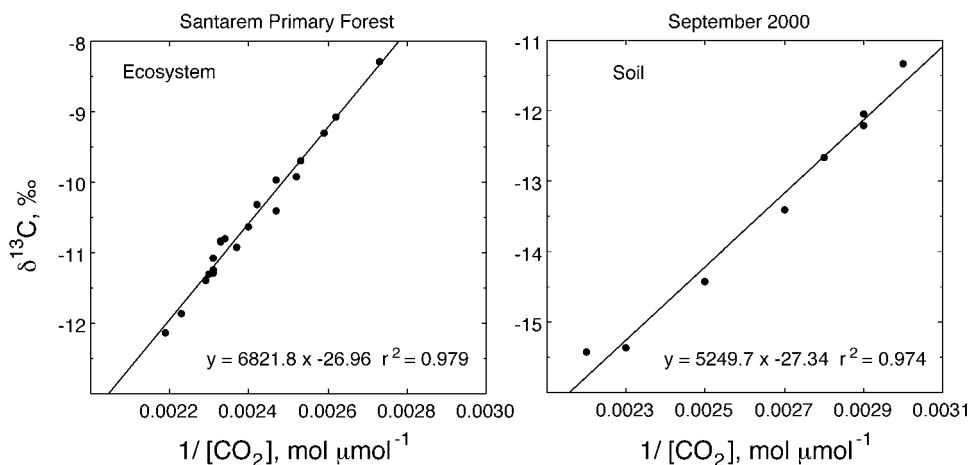


Figure 5. Relationship between $1/\text{CO}_2$ concentration and the carbon isotope ratio of CO_2 in air samples (Keeling plot) collected in an evergreen tropical forest near Santarém, Brazil, during September 2000.

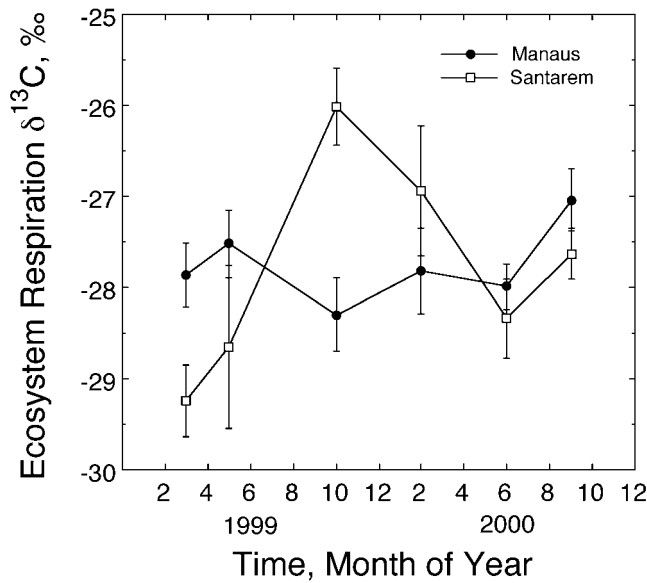


Figure 6. Seasonal variation in the carbon isotope composition of total ecosystem respiration at primary evergreen tropical forest sites near Santarém and Manaus, Brazil. The error bars represent the standard error of the δ_r measurement.

tropical ecosystems [Broadmeadow et al., 1992; van der Merwe and Medina, 1989; Lloyd et al., 1996; Kruijt et al., 1996]. For example, Quay et al. [1989] and Buchmann et al. [1997] observed variation of about 4 and 2–6‰, respectively, in source CO₂ $\delta^{13}C$ values between the upper canopy and ground level in other evergreen tropical forest canopies. Buchmann et al. calculated that only 20% of the observed variation in leaf $\delta^{13}C$ values could be explained by differences in source CO₂ effects. The primary cause of low leaf $\delta^{13}C$ values in the lower levels of the forest canopy was likely a reduction in light intensity, although canopy humidity gradients may also be important. The low light intensity and high humidity result in a high ratio of stomatal conductance to net photosynthesis and consequently higher intercellular CO₂/ambient CO₂ ratios. Carbon isotope discrimination varies linearly with changes in leaf intercellular CO₂/ambient CO₂ ratio [Farquhar et al., 1989]. There are ecological advantages of having high leaf intercellular CO₂ concentrations in low light environments [Percy, 1987]. First, quantum yield or light-use efficiency is improved with higher intercellular CO₂ [Ehleringer and Bjorkman, 1977]. Second, stomatal limitation of carbon gain during use of sunflecks is reduced with a high ratio of stomatal conductance to photosynthesis, and therefore higher intercellular CO₂/ambient CO₂ ratio [Percy, 1987; Percy and Pfitsch, 1991]. The relatively high stomatal conductance is not costly in terms of water loss under the humid conditions occurring in a tropical forest understory.

[22] The large vertical gradient in leaf $\delta^{13}C$ values in forest canopies complicates the use of leaf $\delta^{13}C$ values for studying the influence of precipitation and soil moisture changes on forest physiology in large stature tropical forests [Bonal et al., 2000]. We have attempted to use measurements of the carbon isotope ratio of CO₂ respired by the

entire ecosystem as an integrated measure of forest physiological characteristics. Our measurements of δ_r values ranged from approximately -26 to -29‰ for forests in the Santarém, Manaus, and Ji-Paraná study areas. Using an experimental approach similar to ours, Quay et al. [1989], Lloyd et al. [1996], and Buchmann et al. [1997] measured similar δ_r values (approximately -28, -27.1, and -27.7‰, respectively) for different primary forest sites in Amazonia. The Keeling plot approach (δ_r values) provided carbon isotope composition values for the whole forest that were close to, or even slightly more enriched in ¹³C than, the $\delta^{13}C$ values for the most exposed “sun” leaves at the top of the forest canopy (Figure 3). A similar pattern of δ_r values being slightly more enriched in ¹³C than leaf organic matter has also been observed in other tropical forests [Buchmann et al., 1997]. These data were also consistent with measurements made in boreal forests, where the moss and other

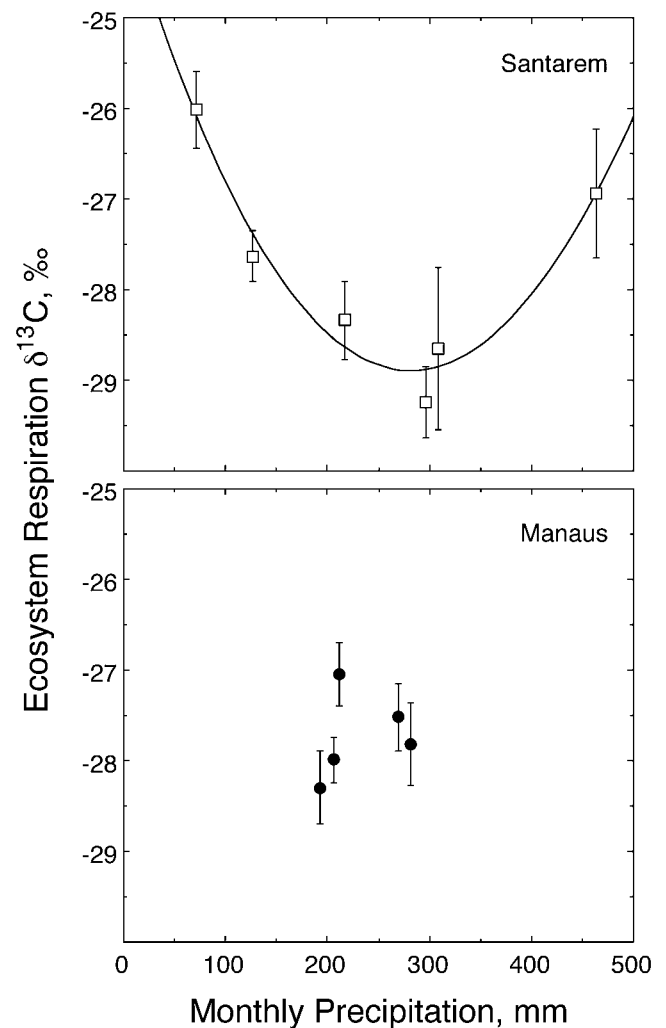


Figure 7. The influence of changes in monthly precipitation on the carbon isotope composition of total ecosystem respiration at primary evergreen tropical forest sites near Manaus and Santarém, Brazil. The error bars represent the standard error of the δ_r measurement. The precipitation values represent the amount of rain recorded at the location during the actual month of stable isotope sampling during 1999 and 2000.

Table 2. Carbon Isotope Ratio of Leaf Tissue ($\delta^{13}\text{C}$, ‰)^a

Date	Manaus	Santarém	Ji-Paraná
May 1999	-30.7 ± 0.7	-30.7 ± 0.8	no data
Oct. 1999	-29.4 ± 0.3	-29.7 ± 1.2	no data
Feb. 2000	-30.5 ± 0.3	-30.9 ± 1.0	-31.9 ± 0.5
June 2000	-30.4 ± 0.7	-29.0 ± 0.3	no data
Sept. 2000	-30.2 ± 0.5	-30.2 ± 0.5	-29.7 ± 1.2

^a Collected from the dominant tree species near the top of the canopy (greater than 20 m above ground) in primary, evergreen tropical forests near Manaus, Santarém, and Ji-Paraná, Brazil. Values are the mean \pm SE.

understory plants can be very depleted in ^{13}C , while δ_r values are similar to or slightly enriched in ^{13}C relative to leaf $\delta^{13}\text{C}$ values at the top of the dominant trees [Flanagan *et al.*, 1996, 1999]. This discrepancy between δ_r values and the carbon isotope ratio of leaf organic matter in forest ecosystems likely reflects the differences in temporal and spatial averaging for carbon metabolism that the two measurement approaches represent. The carbon isotope ratio of ecosystem respired CO_2 is likely dominated by labile, fast-cycling carbon that was primarily fixed by the leaves at the top of the dominant trees exposed to full sun during the previous few days [Ekblad and Hogberg, 2001; Bowling *et al.*, 2002]. In contrast, the $\delta^{13}\text{C}$ values of leaf organic matter represent a longer temporal integration of physiological activity (weeks to months), but provide a much more restricted spatial integration than the δ_r values.

[23] While the forest site near Manaus had relatively constant δ_r values, the forest site near Santarém showed significant seasonal variation in carbon isotope discrimination (Figure 6). The seasonal change in δ_r values at Santarém was consistent with observed seasonal variation in precipitation inputs (Figure 7) and expected changes to soil moisture. Lower precipitation likely reduced soil mois-

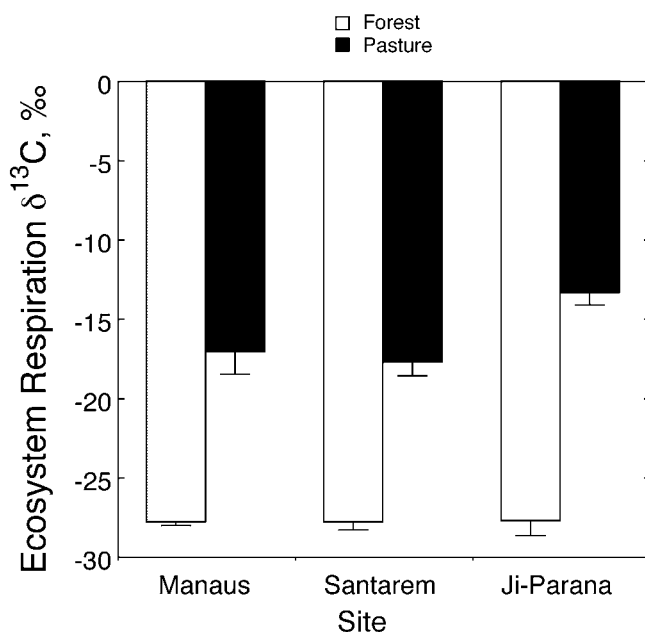


Figure 8. Comparison of the average (\pm SE) carbon isotope composition of total ecosystem respiration measured in forest and pasture sites in three locations in the Brazilian Amazon Basin.

Table 3. Comparison of the Carbon Isotope Composition ($\delta^{13}\text{C}$, ‰) of Live and Dead Leaves (Litter)^a

Sample	Manaus	Santarém	Ji-Paraná
Pasture Grass (<i>Brachiaria</i> spp.)	-12.4 ± 0.1	-12.7 ± 0.1	-11.9 ± 0.1
Pasture Shrubs	-30.6 ± 0.3	-30.1 ± 0.4	not present
Litter	-15.5 ± 1.0	-15.1 ± 0.9	-12.0 ± 0.1

^a Collected in pasture sites near Manaus, Santarém, and Ji-Paraná, Brazil. Values are the mean \pm SE.

ture and led to an increase in the stomatal limitation of leaf photosynthesis. An increase in air temperature and vapor pressure deficit during the dry season would also contribute to an increase in the $\delta^{13}\text{C}$ values of carbohydrates synthesized during photosynthesis. Our sampling periods also coincided with a La Nina event and higher than average precipitation in the Amazon Basin of Brazil [Richey *et al.*, 1989; Marengo *et al.*, 1993]. The higher than normal precipitation at Santarém in February 2000 likely resulted in saturation of the soil and possible anaerobic stress effects on plants (Figure 7). Stomatal closure and reduced carbon isotope discrimination are general stress responses and have been demonstrated for plants exposed to flooding [Guy and Wample, 1984]. The 3‰ variation in δ_r observed in the Santarém forest suggests large variation in photosynthetic metabolism [Farquhar *et al.*, 1989]. The fact that no significant seasonal variation was observed in canopy leaf $\delta^{13}\text{C}$ values (Table 2) indicates that any adverse environmental conditions that caused shifts in the δ_r values were relatively short-term phenomenon. We did not observe seasonal variation in δ_r values at the Manaus forest site because of the small range of precipitation recorded during our sampling periods in Manaus (Figure 7).

[24] Conversion of primary forest to pastures in tropical areas results in changes to ecosystem carbon isotope dis-

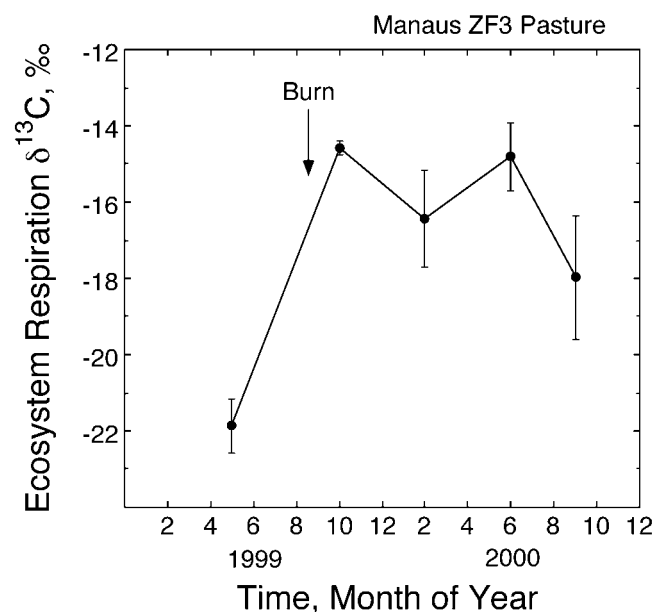


Figure 9. Temporal variation in the carbon isotope composition of total ecosystem respiration at a pasture site near Manaus, Brazil. The error bars represent the standard error of the δ_r measurement.

crimination because grasses with the C₄ photosynthetic pathway are used in establishing the pasture (Table 3). Our measurements of δ_r in forests and pasture ecosystems document these significant changes to ecosystem carbon isotope discrimination (Figure 8). Of greater interest was our observations of important differences in the δ_r values measured among different pasture systems (Figure 8), and those recorded within one pasture at different times (Figure 9). Pastures can also have some C₃ vegetation, primarily shrubs and palm trees, in addition to the dominant C₄ pasture grass. The amount of C₃ vegetation present depends on the time since establishment and on pasture management procedures. We observed approximately a 7‰ shift in the δ_r values after the Manaus pasture was burned to remove C₃ vegetation (Figure 9). This extent of variation in ecosystem carbon isotope discrimination in tropical areas can complicate some applications of carbon isotope techniques in global carbon cycling studies (see subsequently).

[25] Analysis of the net uptake of fossil fuel CO₂ emissions in ocean and terrestrial ecosystems, using stable isotope techniques, is dependent on the knowledge of carbon isotope discrimination during photosynthetic gas exchange in terrestrial ecosystems, and the isotope ratio of CO₂ released from ecosystem carbon pools [Ciais *et al.*, 1995; Fung *et al.*, 1997]. A major assumption in most global partitioning exercises is that isotopic discrimination that occurs during land photosynthesis remains constant on an annual basis. This assumption allows the global mass balance equations to be simplified by using net land and ocean fluxes, rather than the gross, one-way photosynthesis and respiration fluxes [Francey *et al.*, 1995]. It has been suggested that interannual changes in ecosystem photosynthesis and photosynthetic discrimination in tropical ecosystems could alter atmospheric ¹³C composition with significant effects on the ocean-land partitioning exercise [Randerson *et al.*, 2002]. Additional uncertainties in the ocean-land partitioning arise because of limited information on the magnitude and isotopic composition of the flux associated with deforestation and land-use change. In particular, the isotopic composition of the flux associated with land-use change can vary substantially in tropical regions because of the conversion of C₃ forest vegetation to C₄ pasture ecosystems. Our results illustrate significant seasonal and interannual variation in photosynthetic discrimination in tropical ecosystems. In addition, we have documented important temporal variation in the isotopic composition of respired CO₂ in pasture ecosystems, variation associated with woody vegetation encroachment, and the timing of pasture management practices (burning). Global models attempting the use of stable isotopes in partitioning ocean and land uptake of CO₂ must incorporate realistic, dynamic models of biosphere physiological processes to deal with this temporal variation in ecosystem isotopic discrimination [Ciais *et al.*, 1995; Fung *et al.*, 1997].

[26] **Acknowledgments.** This work was supported by a grant from NASA LBA-Ecology to J.R.E., L.B.F., and L.A.M. Shannon Kincaid analyzed the stable isotope ratios of atmospheric carbon dioxide.

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