An alternative explanation for the observed gradient in C4 plant tissues is that inland plants are exposed to the 13C-depleted biogenic CO2, which was previously described in the study area (Fig. 3) for most of the morning photoperiod than those near the ocean. The depletion of 13C in C4 was seen in Fig. 3 results from the trapping of biogenic CO2, which is reduced due to the formation of the overlying tropospheric boundary layer formed near-surface cooling of the atmosphere. The return of 13C in C4 and 13C concentration to values characteristic of the atmospheric CO2 takes place in the morning, when solar heating breaks up the boundary layer through thermal convection. The break up of the nocturnal boundary layer occurs, on average, later in the day in the western (upstream) part of the Amazon basin than in the east. Amazon trees take up proportionally more CO2 during the morning hours than during the afternoon. These two observations suggest that plants growing in the eastern portion of the basin would fix a higher proportion of nocturnally produced biogenic CO2, which would in turn result in their tissues being more depleted in 13C than those of plants in the east.

The change of the 13C values of CO2 grasses downriver was in the opposite direction to that of C3 plants. E. polystachya is a semiaquatic macrophyte, and its leaves are therefore close to the river surface. The Amazon river is supersaturated with CO2 by a factor of about 10 (refs 16, 17) with downriver water being 1.5-2.0 times more supersaturated than upstream. Consequently, the flux of CO2 from the river to the atmosphere could also increase downstream (Fig. 4). The CO2 supersaturation of the river results from respiratory input of biogenic CO2, which is depleted in 13C relative to the atmosphere. Immediately above the river surface, therefore, the dilution of atmospheric CO2 by light CO2 evading the river is greater downstream than upstream. This is probably the main cause of the decrease in 13C of CO2 grasses downstream.

The 13C of the CO2 evaporating from the (18O-2H)aq-aq also decreases downstream. Using the data of Quay et al.13 we calculated the isotopic composition of this CO2 (Fig. 4). The (18O-2H)aq-aq values decrease downriver by 1.5‰ during both the rising and the falling water cruises (Fig. 4). Consequently, aquatic grasses growing further downstream are bathed by increasingly greater fluxes of CO2, more depleted in 13C, from the river. Our results also show that gradients in carbon isotopic compositions expressed by vegetation over long distances can be generated by incremental change in physical processes affecting the extent of assimilation of locally derived biogenic CO2. Such gradients have previously been observed only in isolated forest stands, but not in aquatic environments. At an extreme upstream location, van der Meijden12,13 observed values of 20°C in higher values in organisms of a rain forest foodweb in the Orinoco River basin (northwest of Amazon). They attributed these to the depleted 13C of forest plants, caused in turn by the biogenic CO2 recycling mechanism discussed earlier. This depletion of 13C is of the same magnitude as our observed downstream gradient in C3 plant tissues. Consequently, in the upper Amazon one might expect a relatively negative 13C values for higher organisms, as was observed by van der Meijden12,13, but heavier (less negative) values downstream, in the lower Amazon.

Recently, Marino and McElroy reported a variation in 8°C of -1.1‰ for nitrate leaching from forest soils in the Amazon basin, cultivating between 1948 and 1986 in Iowa, USA. As the maize was all grown in the same fields, the authors attributed the variation to changes in the partial pressure of CO2 in the atmosphere. This explanation is probably correct for their data. Our data for E. polystachya show a similar variation of -1.5‰ and imply that the variability caused by assimilation of locally derived biogenic CO2 could produce an effect similar to that resulting from overall changes in the global atmospheric partial pressure of CO2. Caution should therefore be used when comparing and interpreting carbon isotopic compositions to deduce paleoatmospheric conditions, even when the same plant species are involved.

**Figure Legends**

FIG. 1. Study area. Sampling points are indicated by squares (C3 grasses) and by circles (C4 plants).

FIG. 2. Downriver variation of the carbon isotopic composition of CO2, C3 plant leaves, and tree leaves. C4 understory leaves. C3, C4 plant leaf samples.

FIG. 3. A variation of 8°C of the atmospheric CO2 (18O-2H)atm and its atmospheric CO2 concentration throughout the day, calculated using the following mass and isotopic balance equations: D1O + CO2 + A1K (equation 1), D13O + CO2 + A13K (equation 2), D18O + CO2 + A18K (equation 3), D16O + CO2 + A16K (equation 4), and D17O + CO2 + A17K (equation 5). The graph is constructed from data for different cruises presented in ref. 13. Note that there is a systematic daily variation although there is no apparent downstream trend.
Stable carbon isotope variation in C₃ and C₄ plants along the Amazon River

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All plants assimilate ¹³C in preference to ¹²C. As a result of this isotope fractionation, the tissues of subaerial plants have lower ¹²C/¹³C ratios than that of atmospheric CO₂. By contrast, plant respiration and tissue decomposition are accompanied by little, if any, fractionation and hence release ¹³C-depleted biogenic CO₂ back into the atmosphere. If this biogenic CO₂ is reasimilated before it is thoroughly mixed into the atmosphere, a further depletion of ¹³C in the plant tissue will result. This recycling effect has been found most often in vertical variations of stable isotope composition in tropical forests where plant tissues near the forest floor are more depleted in ¹³C (refs 1–5). Here we show that the intensity of biogenic CO₂ recycling in flood plain forests of the Amazon systematically increases inland, in the western Amazon basin. We also show that a similar recycling mechanism affects the ¹³C composition of semiaquatic grasses owing to evasion of biogenic CO₂ from the Amazon river. But in this case the degree of recycling is more pronounced in the eastern basin because the flux of ¹³C-CO₂ out of the river is smaller there. Our data indicate that significant spatial carbon isotope gradients can exist across the same general ecosystem, both between different species and also within a single species. Recycling effects therefore need to be taken into account in studies that try to relate plant carbon composition to animal and human diet, and in those attempting to determine the carbon isotope composition of the ancient atmosphere from preserved plant tissues.

Because of different pathways in photosynthetic biochemistry, C₃ and C₄ plants discriminate against the heavy carbon isotope (¹³C) (refs 6, 7). Consequently, tissues of C₃ plants such as trees have an average ¹³C value of −27% whereas C₄ plants, which are mainly grasses, average about −15% (ref. 8). Within both plant categories, genetic and environmental factors10–10 cause more subtle variability in the carbon isotope composition. The isotopic composition of the CO₂ source is one of the most important environmental factors. Here we show that there are clear trends in the ¹³C-CO₂ of C₃ and C₄ plants of the Amazon River flood plain (uáras), which result from the systematic variation in the biogenic CO₂ contribution to local atmospheric CO₂ composition on a regional scale (1,800 km).

Plant samples from the Amazon River uáras were collected along a 1,800-km west-to-east (upstream to downstream) transect between Vargem Grande (3°16' S, 67°55' W) and Obidos (3°55' S, 55°30' W), Brazil (Fig. 1). C₃ plants were collected during November and December 1988 from different uára sites. At each site, we sampled leaves from at least five different tree species and five different understory plant species. All tree leaves were collected in the forest 100–400 m from the river at a height of ~10 m, and the understory leaves were collected at a height less than 1 m. C₃ plant samples were restricted to Echinopsia pauciflora, a tropical semiaquatic grass with emergent leaves11. Grass leaf samples from 2–3 plants growing in flooded areas were collected as the water began to rise (October–November 1983) and as it began to fall (June–July

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