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The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures

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shows that ice of age 130–140 kyr by the EGT chronology (corresponding to the coldest part of marine isotope stage 6) is therefore missing from GISP2, at least as sampled at 2–4 m depth increments. We also note that interglacial ice below 2,800 m in the GISP2 core consistently has  $\delta^{18}\text{O}_{\text{atm}} = -0.25 \pm 0.10\%$ ,  $[\text{Ca}] \sim 5$  p.p.b. and  $\delta^{18}\text{O}_{\text{ice}} = -32 \pm 0.5\%$ . We speculate that such ice samples may all have the same age, perhaps Eemian (corresponding to marine isotope substage 5e). It is possible that most ice in the GISP2 core below 2,850 m depth is largely from the latter part of Termination 2 (the penultimate deglaciation,  $\sim 128$ –140 kyr BP) and substages 5e and 5d. Finally, comparison of our data with Vostok suggests that the ice is disturbed below 2,790 m but may largely be in correct stratigraphic order to 2,850 m depth. Thus, it may be that ice between 2,790 and 2,850 m depth corresponds to the latter part of the Eemian (substage 5e) and the subsequent cooling (5e/5d transition).

One of the most intriguing results to emerge from the recent study of the GRIP ice core was the rapid  $\delta^{18}\text{O}_{\text{ice}}$  variations within the Eemian, which were interpreted as rapid changes to colder climates<sup>1</sup>. This conclusion has been questioned by Taylor *et al.*<sup>41</sup> on the grounds that the GRIP core, like GISP2, may be disturbed below 2,750 m (110 kyr BP). The GRIP core, drilled over the current ice divide, might have been subjected to less disturbance than GISP2 if the divide had remained at its present position. On the other hand, if the divide migrated, and Anandakrishnan *et al.*<sup>44</sup> have in fact argued that such migration is likely, then flow could have disturbed the GRIP stratigraphy just as we have observed at GISP2. The question of continuity of the “Eemian” and deeper sections of the GRIP ice core remains unresolved. However, this work demonstrates that continuity of the GRIP ice core below 2,750 m depth could be conclusively established by showing that  $\delta^{18}\text{O}_{\text{atm}}$  varies as it does at Vostok. □

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## The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures

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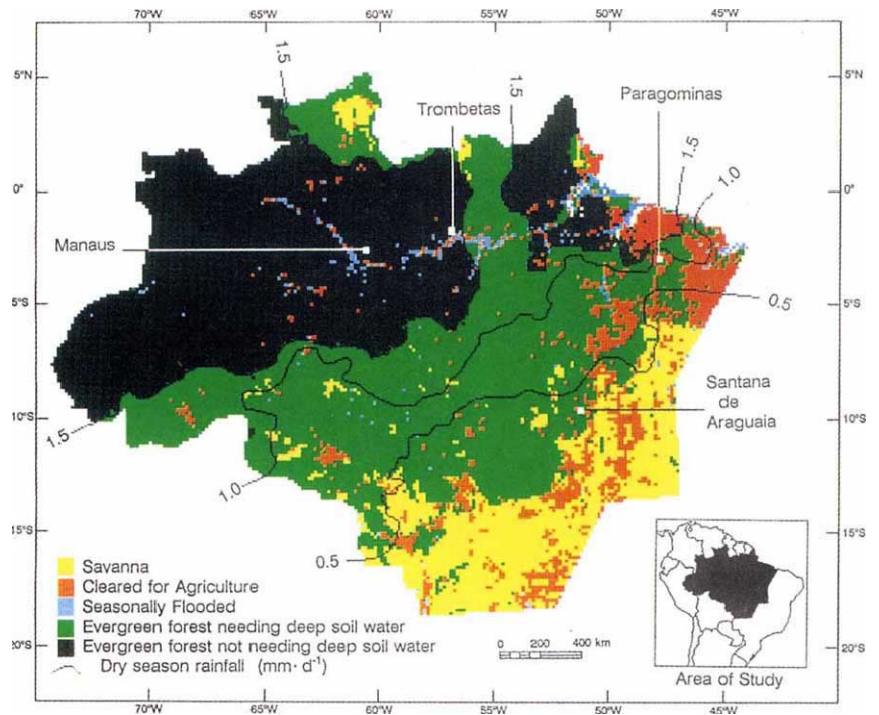
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DEFORESTATION and logging transform more forest in eastern and southern Amazonia than in any other region of the world<sup>1–3</sup>. This forest alteration affects regional hydrology<sup>4–11</sup> and the global carbon cycle<sup>12–14</sup>, but current analyses of these effects neglect an important deep-soil link between the water and carbon cycles. Using rainfall data, satellite imagery and field studies, we estimate here that half of the closed forests of Brazilian Amazonia depend on deep root systems to maintain green canopies during the dry season. Evergreen forests in northeastern Pará state maintain evapotranspiration during five-month dry periods by absorbing water from the soil to depths of more than 8 m. In contrast, although the degraded pastures of this region also contain deep-rooted woody plants, most pasture plants substantially reduce their leaf canopy in response to seasonal drought, thus reducing dry-season evapotranspiration and increasing potential subsurface runoff relative to the forests they replace. Deep roots that extract water also provide carbon to the soil. The forest soil below 1 m depth contains more carbon than does above-ground biomass, and as much as 15% of this deep-soil carbon turns over on annual or decadal timescales. Thus, forest alteration that affects depth distributions of carbon inputs from roots may also affect net carbon storage in the soil.

Pastures are the most common type of vegetation on deforested land in Amazonia. They vary greatly in the ratio of grass to woody-plant cover, including managed pastures (from which woody vegetation is removed by heavy machinery) and the more common shrub- and tree-dominated “degraded” pastures<sup>15–17</sup>. We studied deep roots in a mature, evergreen forest and in adjacent pastures near the town of Paragominas, in the Brazilian state of Pará. The deeply weathered clay soils at the

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FIG. 1 Major forest types and dry-season rainfall of Brazilian Amazonia. Savannas and deciduous forests (14%) were separated from evergreen forests (75%) based on seasonal patterns of canopy greenness (as seen from satellites) and a vegetation map. Evergreen forests include areas that did not display a seasonal depression of the normalized difference vegetation index (NDVI)<sup>28,29</sup> during the dry seasons of 1986–88. To minimize the effects of clouds and smoke, only maximum monthly values of NDVI were used. Areas cleared for agriculture and seasonally flooded land (that is, pixels with the spectral signature of water) were adapted from Stone *et al.*<sup>23</sup>. Dry-season rainfall refers to the driest three-month period of the year averaged for each rainfall record<sup>30</sup>. Of the 212 weather stations used, 75% had more than eight years of rainfall data. Interpolation of rainfall data was conducted using a Geographic Information System software package (IDRISI; Clark Univ., Worcester, Massachusetts). Annual rainfall is 1,500 mm at Santana de Araguaia and daily rainfall is <0.5 mm during the driest three months. Annual rainfall at Manaus and Trombetas is 2,300 mm and daily rainfall is >1.5 mm during the driest three months. Evergreen forests in areas with <1.5 mm d<sup>-1</sup> during the driest three months of the year cover 36% of the region, and must depend on soil water extraction below 1 m depth, as described for the Paragominas study site (2° 59' S, 47° 31' W).



site are common in Amazonia<sup>18</sup>. Precipitation is highly seasonal with an average of 1,750 mm annually and <250 mm from July to November. This seasonality is typical of the eastern and southern portions of Amazonia where most deforestation is occurring (Fig. 1).

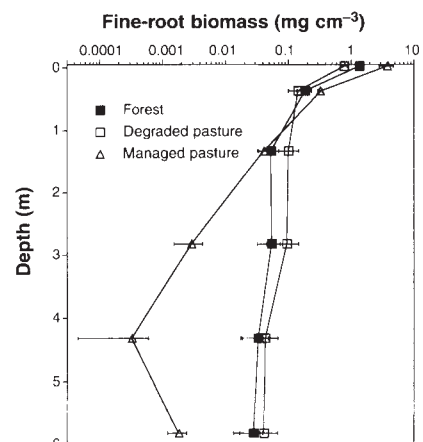
Roots were most abundant near the soil surface, as expected, but were found in deep shafts to depths of ~8 m in the managed pasture, ~12 m in the degraded pasture, and ~18 m in the forest. Fine-root biomass was lower in the top 10 cm of the degraded pasture soil than in the forest, but no differences occurred at greater depths. In the managed pasture, fine-root biomass was three times greater than in the forest near the soil surface and 15–100 times lower at depth (Fig. 2).

We assessed the hydrological role of deeply penetrating roots using a soil water-balance approach. During the severe 5.5-month dry season of 1992, when total rainfall was only 95 mm, plant-available soil water (PAW) from 2–8 m depth declined by 380 mm in the forest and 310 mm in the degraded pasture. In the upper 2 m of soil, the decline in PAW for this period was 130 mm and 100 mm, respectively (Fig. 3a, b). Hence PAW stored below 2 m in the soil provided >75% of the water

extracted from the soil in both ecosystems, and 100 mm more water was extracted from the forest soil. This is the case despite the fact that the deep forest soil began the 1992 dry season without being fully recharged (Fig. 3b) because of below-average rainfall in the wet season. More rainfall is needed to recharge the soil of the forest because it extracts more soil water during the dry season and because its canopy intercepts a larger portion of incoming rain.

Differences in water extraction between the forest and degraded pasture result in contrasting patterns of evapotranspiration. Evapotranspiration can be estimated for the dry season from the sum of rainfall and PAW depletion (surface runoff is insignificant in both ecosystems because of high soil infiltration rates<sup>19</sup>). During the dry season of 1992, average daily rainfall was 0.6 mm, and evapotranspiration in the forest and degraded pasture was 3.6 and 3.0 mm, respectively. Current vegetation-atmosphere models developed to predict the effect on climate of Amazonian deforestation assume rooting depths of only 1.3–2.0 m in forests and 0.6 m in pasture<sup>8–10</sup> and, therefore, would underestimate evapotranspiration by >60% in these Paragominas ecosystems during the 1992 dry season. Important

FIG. 2 Vertical profile of live fine-root biomass (diameter <1 mm) in adjacent mature forest and man-made pastures near Paragominas, eastern Amazonia. Points are means, and bars are one standard error of the mean from 1.5-kg soil samples taken at each sampling depth in 36 auger borings in the forest, 17 in the degraded pastures, and 6 in the managed pasture. Roots were cleaned by flotation sieving and sorted manually at 10× magnification. The forest was cleared at the pasture sites in 1969, planted with the grasses *Panicum maximum* and later *Brachiaria humidicola*, and was heavily grazed intermittently to the present. Woody shrubs and treelets now comprise 50% of live leaf area in the degraded pastures and they support little grazing. The managed pasture was disk-harrowed, fertilized and replanted with *Brachiaria brizantha* in 1988, and is virtually free of woody vegetation.



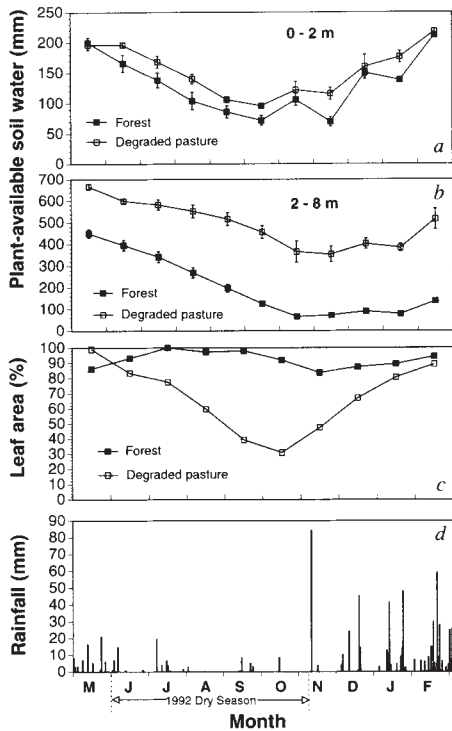


FIG. 3 Seasonal trends in soil water and leaf area in adjacent mature forest and degraded pasture, eastern Amazonia. Points are means, and bars are one standard error. *a*, Plant-available soil water (PAW) from 0–2 m depth. *b*, PAW from 2–8 m depth. *c*, Percentage of maximum leaf area of ten common species in the forest and degraded pasture, based on monthly observations of tagged branches ( $n=20$  branches per species). In degraded pasture, values were weighted by the relative abundance of grasses and non-grasses. *d*, Daily rainfall. PAW was calculated as the amount of soil water held at tensions between  $-0.01$  MPa (field capacity) and  $-1.5$  MPa, determined from soil moisture retention curves for intact soil samples taken at various depths. Biweekly measurements of volumetric soil water content were made using time domain reflectometry, with sensors (6–8 per depth) installed at the surface and 1.5 m horizontally into the shaft walls at 1-m depth intervals<sup>31,32</sup>.

hydrological processes, involving seasonal variation of deep water storage as high as 400 mm (Fig. 3*b*), are left out of models that ignore deep roots.

Evapotranspiration may have been reduced in the degraded pasture by a loss of green leaf area. The leaf area of degraded pasture vegetation declined 68% whereas average leaf area of forest plants declined only 16% during the 1992 dry season (Fig. 3*c*; the managed pasture lost 100% of its leaf area during this same period).

Less depletion of PAW in the degraded pasture signifies that this ecosystem can store less rainfall than the forest, and may therefore produce far more seepage to the groundwater aquifer or subsurface runoff to streams during the wet season. At the end of the 1992 dry season, the forest could store an additional

770 mm of water in the upper 8 m of soil, compared to 400 mm in the pasture (Fig. 3*a, b*).

We assessed the role of root distributions in the soil carbon cycle by assessing soil C stocks and by analysing the isotopic composition of soil CO<sub>2</sub> and soil organic matter. The degraded pasture soil has lost 1.6 kg C m<sup>-2</sup> in the top 1 m of soil relative to the forest (Fig. 4*a*); this loss is coincident with lower fine-root mass (and presumably lower C inputs) in the surface soil of the degraded pasture (Fig. 2). Changes in soil C stocks at depth are more difficult to determine reliably because small differences in C concentrations that are near detection limits must be extrapolated over large soil volumes. Soil C inventories and models of soil C processes seldom include analyses below 1 m, and the C present in deep soils is often assumed to be

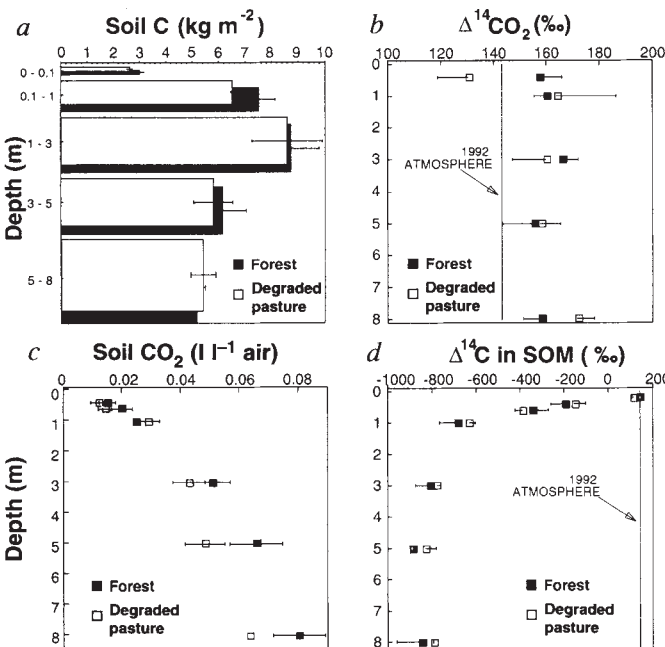


FIG. 4 Vertical profiles of soil C properties; points are means and bars are one standard error of the mean of three soil shafts per ecosystem. *a*, Soil C stocks (not including root C). *b*,  $\Delta^{14}\text{C}_{\text{CO}_2}$  of the soil atmosphere. *c*, Concentration of CO<sub>2</sub> in the soil atmosphere. *d*,  $\Delta^{14}\text{C}$  of soil organic matter (SOM) excluding root C. Soil gases were sampled through stainless-steel tubes (1.8 m long, 0.32 cm diameter) inserted horizontally into the sides of the soil shafts. Analysis of radon activities showed that the effect of gas exchange through the shaft wall was negligible. CO<sub>2</sub> concentrations were analysed in the field using a LiCor (Logan, Utah) infrared gas analyser. Gas samples were also stored in 0.5-l stainless-steel canisters for later analysis of <sup>14</sup>CO<sub>2</sub> by accelerator mass spectrometry. Reported as  $\Delta^{14}\text{C}$  (the <sup>14</sup>C/<sup>12</sup>C ratio in parts per thousand corrected for variations in <sup>13</sup>C/<sup>12</sup>C and compared to an absolute standard of oxalic acid in 1950), zero represents the 1950 atmospheric <sup>14</sup>CO<sub>2</sub> content, positive values reflect the influence of <sup>14</sup>C derived from above-ground thermonuclear weapons testing, and negative values indicate that significant portions of the C have been isolated from exchange with atmospheric CO<sub>2</sub> long enough for the <sup>14</sup>C to decay (half-life, 5,730 years)<sup>22</sup>.



inert<sup>20,21</sup>. But the soil C inventory below 1 m depth at Paragominas exceeds soil C above 1 m (Fig. 4a), as well as exceeding above-ground biomass (18 kg C m<sup>-2</sup>). Contrary to the assumption of inertness, our isotopic data indicate the presence of a significant fraction of modern C in deep soils. First, the  $\Delta^{14}\text{C}$  (see Fig. 4 legend for definition of this quantity) below 1 m depth remains at or above modern atmospheric levels (Fig. 4b), indicating that the high concentrations of CO<sub>2</sub> observed at depth (Fig. 4c) result from root respiration and from microbial decay of carbon fixed by plants within the past 30 years<sup>22</sup>. Second, the  $\Delta^{14}\text{C}$  of soil organic matter declines with depth, as expected, because the proportion of very old C increases with depth (Fig. 4d), but 10–15% of the soil C at 8 m depth may be modern (if the old C is essentially radiocarbon dead at a  $\Delta^{14}\text{C}$  value of -1,000‰, the remaining modern fraction at +143‰ to +200‰ would be ~13% of the total C present at 8 m depth:  $[( -850 + 1,000 ) / 1,000] / [1 + (143 / 1,000)] = 0.13$ ). This result suggests that up to 3 kg C m<sup>-2</sup> occurring below 1 m depth cycles on annual to decadal timescales, and that this C would be subject to change if root distributions were changed by land-use practices.

In the degraded pastures, woody plants have deep-root systems (Fig. 2) that may maintain the deep-soil C pool if fine-root turnover rates are similar to those in the forest. We have concentrated our studies of soil C dynamics on forests and degraded pastures, as these ecosystems are clearly the most abundant at present in eastern Amazonia. However, disk-harrowing and herd rotation can effectively exclude woody vegetation in more intensively managed pastures, and these practices are becoming more common<sup>16,17</sup>. Based on root distribution (Fig. 2), we would predict that these managed pastures would lose deep-soil C and possibly gain surface-soil C (a hypothesis which we now intend to test). Differences in pasture management that affect distributions of C inputs throughout the soil profile may help explain why some studies have shown increases while others have shown decreases in C inventories of the surface soil following conversion of forest to pasture<sup>23–25</sup>.

How common is deep rooting in the Amazon Basin? Roots have been inferred to 5 m depth in a forest of Surinam<sup>27</sup>. Our shaft excavations to 8 m depth at forest sites that are less seasonal (Trombetas, Manaus) and more seasonal (Santana de Araguaia) than Paragominas (Fig. 1) revealed root distributions very similar to that of the Paragominas forest. These initial field data indicate that deep rooting is common in Amazonia.

We estimated the geographical distribution of deeply rooting forests in Brazilian Amazonia by overlaying monthly estimates of canopy greenness from AVHRR satellite imagery with a Geographic Information Systems database of rainfall from 212 weather stations. Where forests are evergreen but seasonal drought is significant (<1.5 mm d<sup>-1</sup> during the driest three months) we deduce that the forest must rely on water uptake from deep soil. The forests meeting these criteria cover an area of  $\sim 1.8 \times 10^6$  km<sup>2</sup>, which is most of the eastern and southern half of the Amazonian closed-canopy forest (Fig. 1). Hence deep roots play an important role in maintaining dry-season canopy greenness and evapotranspiration in the regions where human activity is concentrated. Deep roots are not limited to seasonally dry regions and may also play a role in nutrient uptake.

Deep roots help explain why Amazonian evergreen forests extend well into a region characterized by a long dry season. Understanding the effect of human land-use practices on regional budgets of water and carbon will require knowledge of the basic processes involving deep roots and deep soils. □

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## Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala

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STUDIES in animals have shown that the amygdala receives highly processed visual input<sup>1,2</sup>, contains neurons that respond selectively to faces<sup>3</sup>, and that it participates in emotion<sup>4,5</sup> and social behaviour<sup>6</sup>. Although studies in epileptic patients support its role in emotion<sup>7</sup>, determination of the amygdala's function in humans has been hampered by the rarity of patients with selective amygdala lesions<sup>8</sup>. Here, with the help of one such rare patient, we report findings that suggest the human amygdala may be indispensable to: (1) recognize fear in facial expressions; (2) recognize multiple emotions in a single facial expression; but (3) is not required to recognize personal identity from faces. These results suggest that damage restricted to the amygdala causes very specific recognition impairments, and thus constrains the broad notion that the amygdala is involved in emotion.

We studied subject S.M., a 30-year old woman with normal IQ (low average; Wechsler Adult Intelligence Scale-Revised (WAIS-R) full scale = 86), a high-school education, and a neuropsychological profile remarkable for a history of defective personal and social decision making<sup>9,10</sup>. On all occasions of testing, her mood was stable and cheerful, with no indication of depression on either observation or formal assessment (Beck Depression Inventory, Minnesota Multiphasic Personality Inventory). Her visual-perceptual discrimination assessed using unfamiliar faces was normal<sup>10</sup>. S.M. suffers from Urbach-Wiethe disease<sup>11</sup>, a condition that caused a nearly complete bilateral destruction of the amygdala, while sparing hippocampus and all