Journal of Biogeography, **29**, 857–863

A comparison of δ^{13}C ratios of surface soils in savannas and forests in Amazonia

W. E. Magnusson[1]*, T. M. Sanaiotti[1], A. P. Lima[1], L. A. Martinelli[2], R. L. Victoria[2], M. C de Araújo[1] and A. L. Albernaz[1] [1]*Instituto Nacional de Pesquisas da Amazônia, Coordenação de Pesquisas em Ecologia, CP 478, 69011–970, Manaus AM, Brazil, and* [2]*Centro de Energia Nuclear na Agricultura, Av. Centenário 303, 13416–000 Piracicaba SP, Brazil*

Abstract

Aim To determine the relationship between stable carbon isotope ratios in surface soils and the present vegetation in Amazonian savannas.

Location Areas in and around savannas in the Brazilian Amazonian States of Amazonas, Pará, Amapá, Roraima, Mato Grosso and Maranhão.

Methods δ^{13}C ratios were measured from surface (0–5 cm depth) soils in fifty-two plots in savanna plots with different covers of trees, shrubs, and grasses, and in ten adjacent areas covered by forest.

Results Soil δ^{13}C ratios varied widely (–24.9 to –15.2‰) among and within savannas, but were distinguishable from δ^{13}C ratios under forest (–30.3 to –27.3‰). One site close to forest with 38% tree cover, 44% shrub cover and 45% grass cover was distinguishable from both forest and savanna on Landsat TM5 images, and had a δ^{13}C ratio of –26.7‰. Tree density (TD), basal area (BA) and cover differed strongly between savanna and forest areas. However, most savanna areas had soil organic matter with δ^{13}C ratios closer to those of forest trees than C_4 grasses.

Main conclusions In Amazonia, soil δ^{13}C values >–25‰ can be unequivocally attributed to savannas irrespective of depth. However, there is no precise relationship between tree or grass cover in savannas and surface-soil δ^{13}C values. This is partly because shrubs, as well as trees and grasses, contribute significantly to soil organic matter δ^{13}C ratios, and partly because there is a stronger negative relationship between area of bare ground and cover of C_4 grasses than between area of bare ground and cover of trees or shrubs. This means that the ratio of C_3 to C_4 plants tends to increase with a decrease in total cover. Areas with large amounts of open ground, may have a small proportion of grass cover relative to tree and shrub cover. Although we did not encounter any such places in this study, very harsh conditions could lead to desert-like formations with little grass cover and soil organic-matter δ^{13}C ratios similar to forest areas.

Keywords
Amazonia, stable isotope, savanna, carbon, soil, tree, shrub, forest.

INTRODUCTION

Grasses in tropical savannas usually use C_4 photosynthetic pathways and have more positive δ^{13}C ratios than tropical trees, which generally use C_3 photosynthetic pathways (Smith & Epstein, 1971). Organic matter in surface soils reflects the δ^{13}C of the current vegetation (Balesdent *et al.*, 1987). As some fractions of organic matter are resistant to decomposition, the soil retains information on past vegetation formations, and this information combined with carbon dating and/or other means of dating soil strata, can be used to infer past vegetation structure (e.g. Galimov,

---

*Correspondence: Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia, CP 478, 69011–970 Manaus AM, Brazil. E-mail: bill@inpa.gov.br

1980; Schwartz *et al.*, 1986, 1996; Guillet *et al.*, 1988; Desjardins *et al.*, 1991, 1996; Mariotti & Peterschmitt, 1994; Martinelli *et al.*, 1996; Pessenda *et al.*, 1996, 1998a, 1998b; Gouveia *et al.*, 1997; Boutton *et al.*, 1998; Freitas *et al.*, 2001).

Nevertheless, there remain several poorly understood factors that could affect interpretation of information from soil cores. Animals and deeply rooted plants can redistribute carbon among strata (Veldkamp, 1994; Trumbore *et al.*, 1995; Boutton *et al.*, 1998). Values of δ^{13}C under forest tend to become more positive with depth (Volkoff & Cerri, 1987; Balesdent *et al.*, 1993; Trumbore *et al.*, 1995; Desjardins *et al.*, 1996; Martinelli *et al.*, 1996; Gouveia *et al.*, 1997), stabilizing at about -25 to -24‰, which is the expected equilibrium value for soil (Veldkamp, 1994). Deep cores under Amazonian savannas indicate that, over long periods, these soils also tend to equilibrate at this value (Sanaiotti, 1996; Sanaiotti *et al.*, in press), but it is unknown to what extent this indicates past forest cover and to what extent it might reflect turnover in soil carbon and equilibration at the expected soil values of -24 to -25‰. Some C_3 plants have δ^{13}C values as positive as -23‰ (Smith & Epstein, 1971), but it has not been established which values of δ^{13}C in Amazonian surface soils are associated with savanna vegetation.

Studies of surface soils under grasslands have revealed a wide range of δ^{13}C values (e.g. McPherson *et al.*, 1993; Boutton *et al.*, 1998). In some areas, this may be because of the presence of C_3 grasses (e.g. Tieszen *et al.*, 1997) or effects of altitude (e.g. Bird *et al.*, 1994). Lowland tropical savannas, which usually have few C_3 grasses (Tieszen *et al.*, 1979), may have a wide range of δ^{13}C values (Mondenesi *et al.*, 1986; Volkoff & Cerri, 1987; Martin *et al.*, 1990; Bird *et al.*, 1994; Trouve *et al.*, 1994; McClaran & McPherson, 1995). Victoria *et al.* (1995) recorded δ^{13}C values of less than -28‰ under arboreal savanna in the Brazilian Pantanal. Jenkinson *et al.* (1999) reported δ^{13}C values as high as -22‰ under dry woodland in Zambia, an association considered to be forest rather than savanna.

Savanna vegetation is not uniform. Definitions of savannas always include some cover of grasses and/or sedges, but savannas vary greatly in density of trees (Sanaiotti, 1996; Grainger, 1999). Savannas also vary in the cover of shrubs (C_3 species) and no study has evaluated the independent contributions of trees, shrubs and grasses to soil δ^{13}C values. Characteristics of soils vary widely over small areas and large samples may be necessary to characterize habitats (Hammer, 1998). Except for Jenkinson *et al.* (1999), values of δ^{13}C for superficial savanna soils have been based on point samples taken from the upper strata of soil cores and it is not known how well they represent large areas.

Phytosociological studies are often based on the density of trees with diameter at breast height (d.b.h) greater than the minimum value, on basal area (BA), or on an index derived from these measures. However, forests are generally recognized as having close to 100% canopy cover, and not by the stature or density of the trees. In this paper, we investigate the relationship between vegetation cover and surface soil δ^{13}C in Amazonian savannas and forests, and assess the value of different commonly used measures of vegetation structure to differentiate Amazonian savannas from adjacent forests.

MATERIALS AND METHODS

Our results were based on two independent studies of Brazilian Amazonian savannas. In study no. 1, T. Sanaiotti recorded phytosociology of trees and δ^{13}C values in soil cores in seven savanna areas in Amazonia (Sanaiotti, 1996; Sanaiotti *et al.*, in press). She also obtained δ^{13}C values from ten soil cores in forests adjacent to savannas. In study no. 2, W. Magnusson and A. Lima collected superficial soil samples (<5 cm depth) and estimated vegetation cover in forty plots in a savanna in Pará and in four plots in Roraima. Data on tree densities were also collected in nine forest plots near the Alter do Chão savannas.

Study areas

The savanna areas were selected because they appeared to be relatively undisturbed and had not been cleared for pasture. Common trees in the savannas included *Byrsonima crassifolia* H. B. K and *Anacardium occidentale* L. Common grasses included *Trachypogon plumosus* H. & B. and *Paspalum carinatum* Fluegge. Introduced grasses were rare in all areas and covered $<<1$% of the plots. Magnusson *et al.* (1999) listed most of the common plants found in the savannas of Alter do Chão, and Sanaiotti (1996) listed the common tree species of all the areas.

In study no. 1, data on vegetation and soils were collected at two sites in each of the savannas of Amapá and Roraima States, Humaitá (Amazonas State), Redenção and Alter do Chão (Pará State), and in one site in each of the savannas of Parecis (Mato Grosso State) and Carolina (Maranhão State) (Sanaiotti, 1996; Sanaiotti *et al.*, in press). These include all of the major Amazonian savannas. Forest soil samples came from two forest sites near each of the savannas of Alter do Chão, Amapá and Redenção, and one forest site near each of the savannas of Humaitá, Roraima, Parecis and Carolina (Sanaiotti, 1996; Sanaiotti *et al.*, in press).

In study no. 2, forty plots were distributed throughout the savannas in the region of Alter do Chão (Magnusson *et al.* 2001), and four in Roraima. Positions of the forty plots at Alter do Chão were decided a priori using a Landsat TM5 image that distinguished savanna from forest formations without regard to details of tree cover within savannas. As they were selected systematically, and covered all the savanna areas around Alter do Chão, we believe that they are representative of savannas in that area. Plot no. 3 at Alter do Chão was included because it had a high density of trees and bushes mixed with grasses. It appears similar to another heath-like formation identified on the Landsat TM5 image. This type of formation was rare in the area and might not be considered savanna by many researchers. However, we considered that it could reveal information about the characteristics of formations intermediate between forest and savanna.

Few areas of savanna near Alter do Chão had close to zero tree cover, and all of the plots sampled were on sandy soils. Savannas with little tree cover and/or with clay soils occur in other Amazonian savannas (Sanaiotti, 1996). Therefore we sampled four plots in the savannas of Roraima to increase the range of tree densities and clay content of soils. The sampling techniques were the same as those at Alter do Chão. Samples for two sites at Alter do Chão and two sites in Roraima were close to or coincident with sites sampled in study no. 1.

Vegetation measurements

In study no. 1, the density and BA of trees at each site with d.b.h. > 5 cm were estimated by the Point Centred Quarter method in two 300 m transects using the program Fitopac 1995, public domain (written by G. Shepherd of UNICAMP-University of Campinas). This method of estimating densities is affected by the degree of clumping of the trees (Bullock, 1996), but we assume that differences caused by the degree of clumping are small in relation to the large variation in densities among sites because the trees were not strongly clumped at any of the sites.

In study no. 2, data were collected in 3.75 ha savanna plots which were traversed by four parallel 250 m long transects, spaced 50 m apart. Presence of cover of grasses-sedges and/or shrubs (principally dicotoledons < 2 m high) was recorded at intervals of 2 m along the transects, in 500 point quadrats (Bullock, 1996), using a 2-mm diameter metal rod. Presence of a tree was recorded if the point quadrat fell within the general outline of the tree canopy projected to ground level. The methods were similar to those of Magnusson *et al.* (1999, 2001).

The relative cover of plants < 2 m high can be determined with precision because the error is of the order of the diameter of the metal rod. However, the estimate of tree cover is much more subjective because the general outline of the canopy has to be estimated. Therefore, the data give only a relative index of tree cover and should of not be compared directly with the cover of shrubs and grass, which were measured on an absolute scale. Forests were considered to have 100% tree cover because the outlines of the canopies were contiguous.

Tree densities and BA were estimated for eight plots in continuous forest and one plot in a 31.5-ha forest fragment located around the savannas of Alter do Chão. The circumference of all trees with d.b.h. > 10 cm within 2 m of two 250 m transects in each plot was measured, and the data used to calculate densities and BAs.

Soil sampling and analysis

In study no. 1, a single soil core was taken from the centre of each site with a 5-cm diameter, 4 m auger, and the δ^{13}C values of various strata determined. In this study we analyse only the data for the upper 5 cm, excluding the litter layer. Soil cores were taken from forested areas adjacent to each savanna and analysed as for the savanna samples.

In study no. 2, soil cores 1 cm in diameter and 5 cm deep, excluding the litter layer, were taken at 10 m intervals along the four 250 m transects in each plot, and the resulting soil samples were thoroughly mixed to produce one composite soil sample based on 100 subsamples per plot.

Soil texture varied widely among sites (Sanaiotti, 1996). Alter do Chão and Carolina were the only sites with exclusively sandy soils (< 18% clay). Redenção and SE Humaitá had loamy to clay soils (18–35% clay); the highest variation among transects was found for Amapá and Roraima, which varied from sandy to clay soils (< 18–60% clay).

Soil samples from both studies were air dried, sieved (< 2 mm) to remove live roots, ground and sieved (< 220 μm) again and dispatched to the CENA/USP laboratories at Piracicaba. There, they were sealed in evacuated glass ampoules (break-seal tubing) with cupric oxide and burned in an oven at 900 °C for 12 h. The resulting CO_2 was purified in a vacuum line and injected into a Micromass 602 E mass spectrometer (Finnegan Mat, Bremer, Germany) fitted with double inlet and collector systems. Laboratory standards consisted of charcoal from corn ears and *Eucalyptus* wood with known relationships to the Peedee Belemnite (PDB) formation from South Carolina, USA. The results are expressed in δ^{13}C relative to the PDB standard in conventional δ per mil notation as the following:

$$\delta^{13}C = [(^{13}C/^{12}C)SA - (^{13}C/^{12}C)std - 1] \times 1000$$

where $^{13}C/^{12}C$ are the isotopic ratios of sample (SA) and PDB standard (std). The overall (sample preparation plus analysis) analytical precision was ± 0.2‰.

Statistical analyses

Statistical analyses were carried out with the program SYSTAT 8 (SPSS, 1998). When necessary, variables were transformed to meet the assumptions of linearity and homoscedasticity. Variables were included in regression analyses only when the tolerance was greater than 0.2.

RESULTS

In study no. 1, both TD and BA were significantly associated with soil δ^{13}C in savannas but neither could explain more than 50% of the variance in δ^{13}C ($\delta^{13}C = -16.82 - 0.015$ TD, $r^2 = 0.45$, $n = 13$, $P = 0.012$; $\delta^{13}C = -17.88 - 0.747$BA, $r^2 = 0.40$, $n = 13$, $P = 0.021$). Soil δ^{13}C values in study no. 1 were based on point samples in the centre of the large area sampled for vegetation. However, the variability in the relationships probably does not result from imprecise sampling of soil δ^{13}C. Soil sampling was much more precise in study no. 2 (100 subsamples per plot) and there was a very strong relationship between the δ^{13}C values obtained in the four plots that were measured in both studies ($r = 0.97$, $P = 0.029$).

Amazonian savannas were distinct from forests in both BA (Fig. 1a) and TD (Fig. 1b). The highest TD in a savanna area was 398 stems per hectare and the lowest TD in forest near

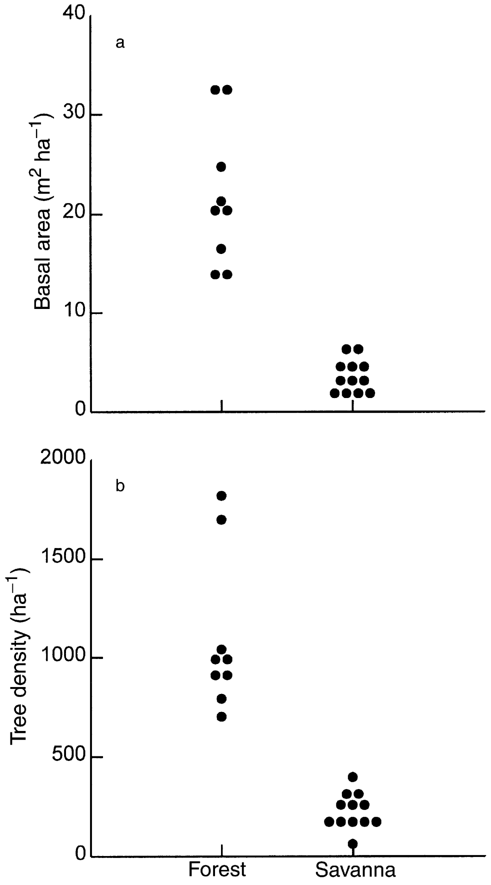

Figure 1 Basal area (a) and tree density (b) in seven Amazonian savannas, and nine forest plots near Alter do Chão.

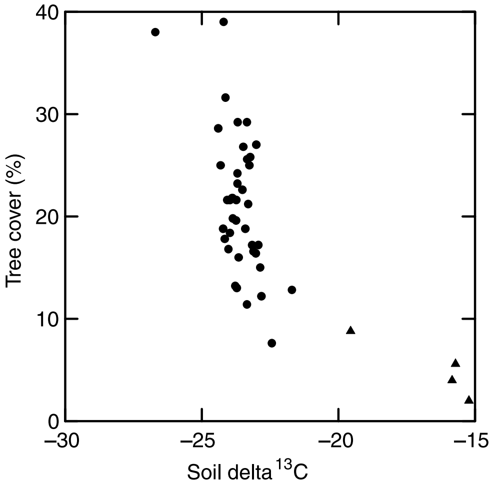

Figure 2 Relationship between tree cover and $\delta^{13}C$ values in surface soils of Amazonian savannas near Alter do Chão (circles) and savannas in Roraima (triangles).

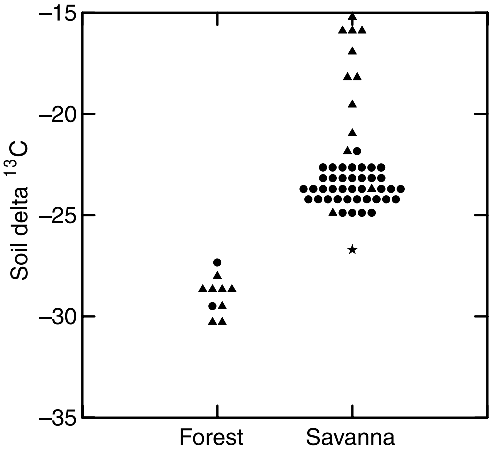

Figure 3 Values of $\delta^{13}C$ in Amazonian surface soils. Circles represent sites near Alter do Chão, triangles represent sites in or near other Amazonian savannas, and the asterisk represents site no. 3 at Alter do Chão that appeared to be intermediate between forest and savanna.

Alter do Chão was 700 stems per hectare. The highest BA in a savanna area was 6.8 m^2 ha^{-1} and the lowest BA in forest near Alter do Chão was 13.9 m^2 ha^{-1}. All forest areas shown in Fig. 1 are from the region of Alter do Chão and savanna plots are from a variety of Amazonian savannas sampled in study no. 1.

Tree cover may be a better index of the presence of forest because values of tree cover close to 100% unambiguously indicate forest. However, the relationship between the logarithm of tree cover (TC) and soil $\delta^{13}C$ in study no. 2 was only marginally better than the relationships between BA, TD, and soil $\delta^{13}C$ in study no. 1 ($\delta^{13}C = -7.73 - 3.41TC$, $r^2 = 0.75$, $n = 44$, $P < 0.001$). The logarithm of tree cover was used for the regression because the relationship was curvilinear (Fig. 2). Soil $\delta^{13}C$ values close to −25‰ were obtained from savannas with tree cover ranging from about 10 to 40%. The only soil $\delta^{13}C$ value < −25‰ from a nonforest area in either study was from plot no. 3 (Fig. 3 asterisk), which was in a marginal area that could not be unambiguously ascribed to the savanna category. It had 38% tree cover, 44% shrub cover and 45% grass cover, and was distinguishable from both forest and savanna on a Landsat image. The $\delta^{13}C$ ratio in surface soil in that plot was −26.7‰. Despite the fact that we tried to sample the range of savanna tree cover present, especially in study no. 2, nonforest areas with tree cover >40% were not encountered.

Soil $\delta^{13}C$ values do not only depend on input from trees. Trees (TR), shrubs (SH) and grasses (GR) provide carbon to the soil, and soil $\delta^{13}C$ values should reflect the relative proportions of these three sources. Multiple regression relating the percentage cover of these sources to soil $\delta^{13}C$ values ($\delta^{13}C = -23.48 - 0.092TR + 0.079GR - 0.095SH$) indicated that trees ($P = 0.005$), grasses ($P < 0.001$) and shrubs ($P = 0.010$) contributed significantly to the model. However, this model ($R^2 = 0.75$) did not explain more of the variance in soil $\delta^{13}C$ values than the logarithm of tree cover

($R^2 = 0.75$). Plot no. 3 had high leverage, but the results were qualitatively similar with plot no. 3 excluded ($\delta^{13}C = -23.05 - 0.084TR + 0.076GR - 0.142SH$, $R^2 = 0.74$, $P_{TR} = 0.011$, $P_{SH} < 0.001$, $P_{GR} = 0.01$).

One reason that the vegetation cover models cannot explain more of the variance in soil $\delta^{13}C$ values is that $\delta^{13}C$ is a ratio and depends not only on the amounts of the different vegetation sources, but also on their ratios. The proportion of bare ground was significantly negatively associated with tree cover [$r = -0.32$, $P = 0.046$ ($r = -0.17$ excluding plot no. 3)] and shrub cover [$r = -0.60$, $P < 0.001$ ($r = -0.44$ excluding plot no. 3)] but the negative correlation with grasses was much stronger [$r = -0.88$, $P < 0.001$ ($r = -0.95$ excluding plot no. 3)].

DISCUSSION

Estimates of $\delta^{13}C$ values in surface soils have generally been based on point samples deliberately placed only in grassy areas within the savanna, and point estimates of soil characteristics are generally imprecise (Hammer, 1998). However, our limited number of observations indicated a very strong relationship between point samples and compound samples based on 100 subsamples collected over an area of 3.75 ha. Soil $\delta^{13}C$ values generally equilibrate quickly (< 100 year) to the overlying vegetation (Balesdent *et al.*, 1987; Martin *et al.*, 1990). Therefore, soil $\delta^{13}C$ values reflecting the general vegetation of the savanna, rather than the vegetation directly above the sample, indicate that the vegetation at any point in the savanna is highly labile, or that there is strong lateral movement of carbon within the savanna. These aspects deserve further study.

In this study, tree densities and BAs in forests near Alter do Chão were distinct from tree densities and BAs in the savannas. No savanna area, including one site that could be considered intermediate, had tree cover >40%. Forests at Alter do Chão have similar densities of trees with d.b.h. >10 cm (533 ± 96.6 stems per ha – this study) to nine other Amazonian forests (586 ± 117 stems per ha – Oliveira & Nelson, 2001).

We have sampled all seven of the major Amazonian savannas and have qualitative observations on all of them. The sampling regime at Alter do Chão was designed to sample the savanna vegetation systematically, and this confirmed our qualitative observations that there were no heavily wooded (tree cover >40%) areas in the savannas surrounding Alter do Chão. Although, there are no detailed measurements for most of this vast area, our observations lead us to believe that areas with vegetation structure intermediate between forests and savannas are rare in Amazonia. This is consistent with the view that savanna-forest boundaries are generally easily recognizable on a scale of hundreds of meters (Furley *et al.*, 1992).

Part of the reason for the weak relationship between tree cover and soil $\delta^{13}C$ values is that shrubs and other dicotoledons mixed with the grass contribute as much to soil $\delta^{13}C$ values as do trees. Many of the shrubs are juveniles or small reproductive individuals of the tree species. However, they appear as part of the field layer in photographs or Landsat images.

Although shrub cover complicates the interpretation of the relationship between tree cover and soil $\delta^{13}C$ values, incorporating tree, shrub and grass cover in the model did not increase its power of prediction. We believe that this is the result of the stronger negative relationship between grass cover and bare ground than between bare ground and shrub or tree cover. An area with little tree cover and no grass could have as negative soil $\delta^{13}C$ values as a forest. Extremely arid formations, such as deserts and caatinga, are often dominated by shrubs or cacti, and may have very little grass cover. Therefore, extreme climatic conditions may result in soil $\delta^{13}C$ values similar to those of forest.

Despite the lack of precision in estimation of tree cover in savannas, all savanna plots except no. 3 had soil $\delta^{3}C$ values $> -25‰$, and all forest samples had soil $\delta^{13}C$ values $< -27‰$. Plot no. 3 was in a transition area, does not appear as savanna on Landsat TM5 images and might not be considered savanna by many researchers because most of the area is not covered by grasses. Soil $\delta^{13}C$ values under forest equilibrate to about $-25‰$ with time (Desjardins *et al.*, 1991; Veldkamp, 1994; Sanaiotti *et al.*, in press). Therefore, it appears that, in Amazonia, soil $\delta^{13}C$ values $>-25‰$ can be unequivocally attributed to savannas, irrespective of depth.

These results might not apply in other regions. No savanna plot, including plot no. 3 had more than 40% tree cover, despite the fact that we tried to sample the full range of savanna tree cover. All of the commonly used measures of vegetation structure clearly separated the Amazonian savannas from forests. It appears that forests and savannas represent very distinct alternative states in Amazonia, and that savanna areas with greater than 40% tree cover are rare and/or ephemeral. Grasslands with more than 40% cover of trees are defined as 'bushland' on the UNESCO vegetation map of Africa, and areas with tree cover between 10 and 40% tree cover are considered to be 'wooded grasslands'. Wooded grasslands, the category that would include most Amazonian savannas, are not prominent on the UNESCO map of Africa. If savanna-like formations with more than 40% tree cover are common in other regions, they might be very difficult to distinguish from forest based on soil $\delta^{13}C$ values.

CONCLUSIONS

Soil $\delta^{13}C$ values generally differ between Amazonian savannas and forests, and it appears that soil $\delta^{13}C$ values $> -25‰$ can be unequivocally attributed to savannas in Amazonia, irrespective of depth. However, there was no precise relationship between tree or grass cover in savannas and surface-soil $\delta^{13}C$ values. None of the savannas we investigated had > 40% tree cover, except for limited areas around the borders of forests. While we know of no densely wooded grasslands in Amazonia, such habitats are reported to occur in Africa. We believe that it would be very difficult to differentiate forests from grasslands with > 40% tree cover, based on soil $\delta^{13}C$ values.

ACKNOWLEDGEMENTS

We thank the residents of Alter do Chão for their hospitality, and the Superintendência de Desenvolvimento da Amazônia (SUDAM) for accommodation and laboratory space at Alter do Chão. Financial support came from Auxílio a Pesquisa, Produtividade em Pesquisa and Projeto Integrado de Pesquisa grants from CNPq to W. Magnusson, grants from WWF-DF and Fundação Botânica Margaret Mee to T. Sanaiotti, as well as INPA PPI grants (2 – 3530 and 2 – 3540), and PPD/FINEP grant 64.00.0021.00.

REFERENCES

Balesdent, J., Girardin, C. & Mariotti, A. (1993) Site-related $\delta^{13}C$ of tree leaves and soil organic matter in a temperate forest. *Ecology*, **74**, 1713 – 1721.

Balesdent, J., Mariotti, A. & Guillet, B. (1987) Natural $\delta^{13}C$ abundance as a tracer for studies of soil organic matter dynamics. *Soil Biology and Biochemistry*, **19**, 25 – 30.

Bird, M.I., Haberle, S.G. & Chivas, A.R. (1994) Effect of altitude on the carbon-isotope composition of forest and grassland soils from Papua New Guinea. *Global Biogeochemical Cycles*, **8**, 13 – 22.

Boutton, T.W., Archer, S.R., Midwood, A.J., Zitzer, S.F. & Bol, R. (1998) $\delta^{13}C$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. *Geoderma*, **82**, 5 – 41.

Bullock, J. (1996) Plants. *Ecological census techniques: a handbook* (ed. W.J. Sutherland), pp. 111 – 138. Cambridge University Press, Cambridge.

Desjardins, T., Carneiro Filho, A., Mariotti, A., Chauvel, A. & Girardin, C. (1996) Changes of the forest – savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratios of soil organic matter. *Oecologia*, **108**, 749 – 756.

Desjardins, T., Volkoff, B., Andreux, F. & Cerri, C. (1991) Distribution du carbone total et de l'isotope $\delta^{13}C$ dans des sols ferralitiques due Brésil. *Science Du Sol*, **29**, 175 – 187.

Freitas, H.A., Pessenda, L.C.R., Aravena, R., Gouveia, S.E.M., Ribeiro, A.S. & Boulet, R. (2001) Late Quarternary vegetation dynamics in the southern Amazon Basin inferred from carbon isotopes in soil organic matter. *Quarternary Research*, **55**, 39 – 46.

Furley, P.A., Proctor, J. & Ratter, J.A. (1992) *Nature and Dynamics of Forest-Savanna Boundaries*. Chapman & Hall, London.

Galimov, E.M. (1980) C^{13}/C^{12} in kerogen. *Kerogen* (ed. B. Durand), pp. 291 – 299. Technip, Paris.

Gouveia, S.E.M., Pessenda, L.C.R., Aravena, R., Boulet, R., Roveratti, R. & Gomes, B.M. (1997) Dinâmica de vegetações durante o quarternário recente no sul do Amazonas, indicado pelos isótopos do carbono (^{12}C, ^{13}C, ^{14}C) do solo. *Geochimica Brasiliensis*, **11**, 355 – 367.

Grainger, A. (1999) Constraints on modelling the deforestation and degradation of tropical open woodlands. *Global Ecology and Biogeography*, **8**, 179 – 180.

Guillet, B., Faivre, P., Mariotti, A. & Khobzi, J. (1988) The ^{14}C dates and $^{13}C/^{12}C$ ratios of soils organic matter as a means of studying past vegetation in intertropical regions: examples from Colombia (South America). *Palaeogeography, Palaeoclimatology and Palaeoecology*, **65**, 51 – 58.

Hammer, R.D. (1998) Space and time in the soil landscape: the ill-defined ecological universe. *Ecological scale* (ed. D.L. Peterson and V.T. Parker), pp. 106 – 140. Colombia University Press, New York.

Jenkinson, D.S., Meredith, J., Kinyamario, J.I., Warren, G.P., Wong, M.T.F., Harkness, D.D., Bol, R. & Coleman, K. (1999) Estimating net primary production from measurements made on soil organic matter. *Ecology*, **80**, 2762 – 2773.

Magnusson, W.E., Lima, A.P., Faria, A.S., Victoria, R.L. & Martinelli, L.A. (2001) Effects of size on carbon acquisition in lizards from Amazonian savanna: evidence from isotope analysis. *Ecology*, **82**, 1772 – 1780.

Mariotti, A. & Peterschmitt, E. (1994) Forest savanna ecotone dynamics in India as revealed by carbon isotope ratios of soil organic matter. *Oecologia*, **97**, 475 – 480.

Martin, A., Mariotti, A., Balesdent, J., Lavelle, P. & Vuattoux, V. (1990) Estimate of organic matter turnover rate in savanna soil by $\delta^{13}C$ natural abundance measurements. *Soil Biology and Biochemistry*, **22**, 517 – 523.

Martinelli, L.A., Pessenda, L.C.R., Spinoza, E., Camargo, P.B., Telles, E.C., Cerri, C.C., Victoria, R.L., Aravena, R., Richey, J. & Trumbore, S. (1996) Carbon-13 variation with depth in soils of Brazil and climate change during the Quaternary. *Oecologia*, **106**, 376 – 381.

McClaran, M.P. & McPherson, G.R. (1995) Can soil organic carbon isotopes be used to describe grass-tree dynamics at a savanna-grassland ecotone and within a savanna? *Journal of Vegetation Science*, **6**, 857 – 862.

McPherson, G.R., Boutton, T.W. & Midwood, A.J. (1993) Stable isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. *Oecologia*, **93**, 95 – 101.

Mondenesi, M.C., Matsui, E. & Volkoff, B. (1986) Relação $^{13}C/^{12}C$ nos horizontes humíferos superficiais e nos horizontes escuros profundos dos solos de campo e mata da região de Campos de Jordão, São Paulo, Brasil. *Regional Colloquium on Soil Organic Matter Studies*, pp. 155 – 160. Centro de Energia Nuclear na Agricultura, Piracicaba.

Oliveira, A.A. & Nelson, B.W. (2001) Floristic relationships of terra firme forests in the Brazilian Amazon. *Forest Ecology and Management*, **146**, 169 – 179.

Pessenda, L.C.R., Gomes, B.M., Aravena, R., Ribeiro, A.S., Boulet, R. & Gouveia, S.M. (1998a) The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. *Holocene*, **8**, 599 – 603.

Pessenda, L.C.R., Gouveia, S.E.M., Gomes, M.B.M., Aravena, R., Boulet, R. & Ribeiro, A. (1998b) ^{14}C dating and stable isotope carbon isotopes of soil organic matter in forest – savanna boundary areas in the southern Brazilian Amazon region. *Radicarbon*, **40**, 1013 – 1022.

Pessenda, L.C.R., Valencia, E.P.E., Camargo, P.B., Martinelli, L.A., Teles, E.C.C. & Cerri, C.C. (1996) Natural radiocarbon measurements in Brazilian soils developed on basic rocks. *Radiocarbon*, **38**, 203 – 208.

Sanaiotti, T.M. (1996) *The woody flora and soils of seven Brazilian Amazonian dry savanna areas*. PhD Thesis. University of Stirling, Stirling, UK.

Sanaiotti, T.M., Martinelli, L.A., Victoria, R.L., Trumbore, S.E. & Camargo, P.B. (in press) Past vegetation changes in Amazon savannas by using carbon isotopes of soil organic matter. *Biotropica*.

Schwartz, D., de Foresta, H., Mariotti, A., Balesdent, J., Massimba, J.P. & Girardin, C. (1996) Present dynamics of the savanna–forest boundary in the Congolese Mayombe: a pedological, botanical and isotopic (^{13}C and ^{14}C) study. *Oecologia*, **106**, 516–524.

Schwartz, D., Mariotti, A., Lanfranchi, R. & Guillet, B. (1986) ^{13}C/^{12}C ratios of soil organic matter as indicators of vegetation change in the Congo. *Geoderma*, **39**, 97–103.

Smith, B.N. & Epstein, S. (1971) Two categories of ^{13}C/^{12}C ratios for higher plants. *Plant Physiology*, **47**, 380–384.

SPSS (1998) *SYSTAT 8.0: Statistics*. SPSS, Chicago, Illinois.

Tieszen, L.L., Reed, B.C., Bliss, N.B., Wylie, B.K. & DeJong, D.D. (1997) NDVI, and C_4 production, and distributions in Great Plains grassland and land cover classes. *Ecological Applications*, **7**, 59–78.

Tieszen, L.L., Senyimba, M.M., Imbamba, S.K. & Troughton, J.H. (1979) The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia*, **37**, 337–350.

Trouve, C., Mariotti, A., Schwartz, D. & Guillet, B. (1994) Soil organic carbon dynamics under *Eucalyptus* and *Pinus* planted on savannas in the Congo. *Soil Biology and Biochemistry*, **26**, 287–295.

Trumbore, S.E., Davidson, E.A., Camargo, P.B., Nepstad, D.C. & Martinelli, L.A. (1995) Below-ground cycling of carbon in forests and pastures of eastern Amazonia. *Global Biogeochemical Cycles*, **9**, 515–528.

Veldkamp, E. (1994) Organic carbon turnover in three tropical soils under pasture after deforestation. *Soil Science Society of America Journal*, **58**, 175–180.

Victoria, R.L., Fernandes, F., Martinelli, L.A., Picollo, M., Camargo, P.B. & Trumbore, S. (1995) Past vegetation changes in the Brazilian Pantanal arboreal-grassy savanna ecotone by using carbon isotopes in the soil organic matter. *Global Change Biology*, **1**, 165–171.

Volkoff, B. & Cerri, C.C. (1987) Carbon isotopic fractionation in subtropical Brazilian grassland soils. Comparison with tropical forest soil. *Plant Soil*, **102**, 27–31.

BIOSKETCHES

William E. Magnusson, **Tânia M. Sanaiotti** and **Albertina P. Lima** have been research scientists at the Instituto Nacional de Pesquisas da Amazônia (INPA) since 1979, 1987 and 1996 respectively. Their research interests include experimental design, savanna biogeography, vertebrate community structure and population dynamics and understanding the ecological impacts of land-use changes.

Luiz A. Martinelli and **Reynaldo L. Victoria** have been research scientists at the Universidade de São Paulo (USP-CENA) since 1985 and 1975, respectively. Their research interests include the use of stable isotopes as tracers in carbon, nitrogen and water cycles.

Maria Carmozina de Araújo has been a technician at INPA since 1988. Her research interests include behaviour of amphibians, invertebrate community surveys and systematics.

Ana L. Albernaz is an associate researcher at the Biological Dynamics of Forest Fragments Project (INPA/Smithsonian Institution). Her research interests include landscape ecology and conservation.