

Expansion of gallery forests into central Brazilian savannas

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Abstract

Upland tropical forests have expanded and contracted in response to past climates, but it is not clear whether similar dynamics were exhibited by gallery (riparian) forests within savanna biomes. Because such forests generally have access to ample water, their extent may be buffered against changing climates. We tested the long-term stability of gallery forest boundaries by characterizing the border between gallery forests and savannas and tracing the presence of gallery forest through isotopic analysis of organic carbon in the soil profile. We measured leaf area index, grass vs. shrub or tree coverage, the organic carbon, phosphorus, nitrogen and calcium concentrations in soils and the carbon isotope ratios of soil organic matter in two transitions spanning gallery forests and savanna in a Cerrado ecosystem. Gallery forests without grasses typically show a greater leaf area index in contrast to savannas, which show dense grass coverage. Soils of gallery forests have significantly greater concentrations of organic carbon, phosphorus, nitrogen and calcium than those of savannas. Soil organic carbon of savannas is significantly more enriched in ^{13}C compared with that of gallery forests. This difference in enrichment is in part caused by the presence of C_4 grasses in savanna ecosystem and its absence in gallery forests. Using the ^{13}C abundance as a signature for savanna and gallery forest ecosystems in 1 m soil cores, we show that the borders of gallery forests have expanded into the savanna and that this process initiated at least 3000–4000 BP based on ^{14}C analysis. Gallery forests, however, may be still expanding as we found more recent transitions according to ^{14}C activity measurements. We discuss the possible mechanisms of gallery forest expansion and the means by which nutrients required for the expansion of gallery forest might accumulate.

Keywords: carbon isotope ratios, carbon sink, carbon stocks, climate change, gallery forest, leaf area index, nutrients, savanna, tropical ecosystems, vegetation dynamics

Received 17 December 2007; revised version received 11 February 2008 and accepted 23 February 2008

Introduction

The Cerrado biome of central Brazil encompasses open grassy fields (known as campo limpo), a savanna vegetation of variable structure (known as Cerrado *sensu lato*) and forest corridors along stream and river basins (known as gallery forests; Ribeiro & Walter, 1998). This biome covers a region of approximately 2 000 000 km²

(Ribeiro & Walter, 2001; Oliveira-Filho & Ratter, 2002), 5% of which is occupied by gallery forests. Gallery forests hold 1/3 of whole Cerrado plant diversity (Ribeiro & Walter, 2001) and represent the greatest biodiversity per area in the Cerrado biome (Mendonça *et al.*, 1998). Gallery forest soils typically have greater nutrient and water availability compared with the neighboring savanna (Furley, 1992; Haridasan, 1998) and boundaries between gallery forest and savanna tend to be sharp (Furley, 1992).

In other savanna regions, sharp forest–savanna boundaries are believed to arise primarily due to fires,

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which are common in savanna but do not typically penetrate into the forest (Biddulph & Kellman, 1998). To the extent that fire and climate govern the dynamics of gallery forest boundaries, their position may not be stable. The effect of fire in forest–savanna boundaries is particularly relevant in view of interest on future climate change. Projections by the Brazilian National Space Institute (INPE) indicate that global warming would cause a decrease in rainfall in the Cerrado biome of Brazil (Marengo, 2007). Because gallery forests are believed to have abundant access to ground water and runoff, it is not clear whether gallery forests will be as sensitive to this decrease in rainfall as other forest types. Of further interest is the hypothesis that the replacement of savannas with gallery forests having a greater biomass would represent an increase in carbon stocks. As gallery forests tend to follow streambeds, their perimeter-to-area ratios are large and a small incremental expansion of forests into savanna would mean a relatively large increase in forest area.

The boundary between gallery forests and savannas has often been suggested to be determined by edaphic characteristics of the landscape (Furley, 1992). Soil properties such as soil organic matter (SOM) concentration and exchangeable cations can be closely correlated with the vegetation physiognomy in the Cerrado biome of central Brazil (Furley, 1992). It is not known, however, if these characteristics are the cause or the effect of vegetation differences.

It is likely that the boundaries between savannas and gallery forests will remain fixed if the vegetation reacts passively to edaphic conditions. However, vegetation can profoundly affect the distribution and retention of nutrients in the soil profile and other soil characteristics (Chapin *et al.*, 1997; Jobbagy & Jackson, 2004). Likewise, the vegetation can influence regional and local climate (Hoffmann & Jackson, 2000; Sternberg, 2001; Oyama & Nobre, 2003). If such is the case, then it is likely that savanna–forest boundaries are dynamic with positive feedback loops driven by changes in climate and/or disturbances (Sternberg, 2001; Hoffmann *et al.*, 2002; Oyama & Nobre, 2003; Beerling & Osborne, 2006).

Here, we compare modern characteristics of gallery forests and savannas considering both vegetation structure (leaf area index of grasses and trees) and edaphic properties, including soil organic carbon, phosphorus (P), nitrogen (N) and calcium (Ca) concentrations and carbon isotope ratios of SOM. Phosphorus, nitrogen and calcium are considered the most important in limiting the aboveground biomass of central Brazilian savanna ecosystems (Haridasan, 1992, 2005). We then test whether the boundary between gallery forests and savannas in central Brazil has been stable. To do so, we rely on isotopic signatures to measure the relative

contribution of trees and grasses to SOM through the soil profile along two transects spanning forests and savannas. The feasibility of this technique is based on two assumptions. First, SOM through the soil profile in part represents a chronological sequence of the vegetation signature, with past vegetation recorded at deeper levels of the soil profile compared with present day vegetation (Victoria *et al.*, 1995; Boutton *et al.*, 1998). However, SOM at lower depths in the soil profile, in addition to having carbon from the previous vegetation also has carbon from root exudates or mobile organic carbon from the present vegetation (Krull *et al.*, 2002). Second, the difference in the mean carbon isotopic ratios between biomass of savannas and forests leads to different signatures in their respective SOM. This difference, in part, is based on the abundance of C₄ grasses in savannas compared to gallery forests (Klink & Joly, 1989; Victoria *et al.*, 1995; Martinelli *et al.*, 1996; Beerling & Osborne, 2006). C₄ plants discriminate less against ¹³C compared with C₃ plants (Smith & Epstein, 1971). So, we expect that total savanna biomass and SOM will be more enriched in ¹³C compared with forests having only C₃ plants. There are several processes that can modify the isotopic signature of SOM relative to that of the standing vegetation biomass (Ehleringer *et al.*, 2000). Even with these isotopic modifications, however, this method has been used successfully in the interpretation of past vegetation changes in wetlands and savannas of Brazil (Victoria *et al.*, 1995; Martinelli *et al.*, 1996; Sanaiotti *et al.*, 2002), Africa (Giresse *et al.*, 1994), United States (Boutton *et al.*, 1998) and Australia (Bowman *et al.*, 2004). Our study represents the first analysis of trends along a transition covering gallery forests and savannas. We estimate the date of changes in vegetation by ¹⁴C analysis of SOM and consider possible mechanisms causing ecotonal shifts.

Materials and methods

Site description

Measurements were done at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (RECOR-IBGE) located near the city of Brasilia (Federal District, Brazil) at 15°56'41"S and 47°56'07"W and at an elevation of 1100 m a.s.l. The average annual rainfall at this site is 1426 mm (1993–2002), having a distinct 5-month dry season (May–September) and an average annual temperature of 22.5 °C. This area (1300 ha) was designated as a conservation area in 1975 and protected against fire for approximately 30 years. The reserve is a patchwork of several different vegetation physiognomies of the Cerrado biome, having abundant stands of gallery forest associated with several streams (Fig. 1).

Transects

Transects were placed in two gallery forests boundaries along the Taquara and the Pitoco streams (Fig. 1). We sampled only two forest–savanna borders to allow a more intensive study of the transition and a better understanding of the processes involved in gallery forest shifts. The Taquara gallery forest, located at the southeastern limit of RECOR-IBGE, has calcium-rich patches downstream of the transect where the streambed becomes broad and shallow and prone to seasonal flooding. The Pitoco gallery forest lies in the northeast portion of RECOR-IBGE, and most of its area occurs over well-drained, nutrient-poor Cambisols. It is wider at the stream head and narrows downstream, where the forest is concentrated in a short toposequence. The savanna vegetation of both transects was similar and described previously (Ribeiro & Walter, 2001).

Each 100 m transect was perpendicular to the vegetation boundary and consisted of sampling points 10 m apart. The central point of the transect was chosen (designated as 0) at the savanna–forest border based

on visual observations and later confirmed by leaf area index (LAI) measurements. From this central point, the transect was extended 50 m in opposite directions into each vegetation.

Transect measurements

Leaf area index. LAI was measured every 10 m along each transect with a CI110 plant canopy imager (CID Inc., Camas, WA, USA) during March 2007 when all trees, including deciduous trees, had full foliage. This instrument estimates canopy LAI indirectly based on a digital hemispherical image of the vegetation overhead. To partition total LAI into grasses in the ground layer and tree + shrub components, separate images were taken at a height of 1 m and at the soil surface (after removal of herbaceous dicots). LAI values obtained at a height of 1 m are considered here to represent tree + shrub LAI. Grass LAI, in turn, was calculated by subtracting the tree + shrub LAI from total LAI (minus herbaceous dicots), as measured

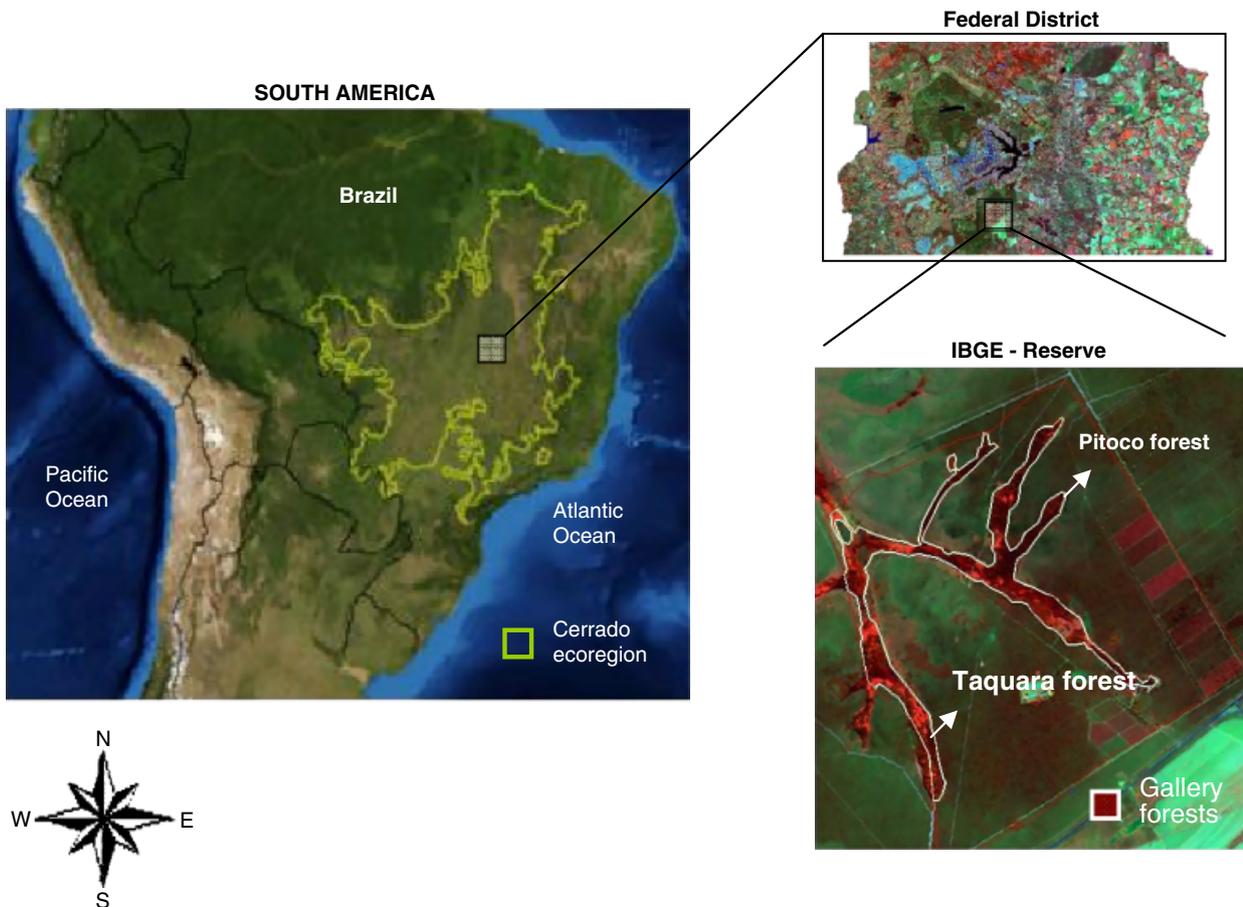


Fig. 1 The Ecological Cerrado Reserve (RECOR-IBGE) in central Brazil. The gallery forests are surrounded by savannas of variable tree density, which are depicted in green. The approximate locations of the Pitoco and Taquara transects are included.

from the soil surface. The values obtained in this manner are a measure of total vegetation area index, and as such are meant to quantify vegetation density rather than green leaf area *per se*. For trees, our values of LAI include stem area, as well as leaf area. For grasses, LAI comprise both living and dead leaf area.

Soil core analyses

Soil cores were taken every 10 m along each transect to the depth of 1 m, and soil samples were collected every 10 cm of depth. Soil samples were acquired by pressing 100 cm³ tubes into each layer of sequentially dug soil pits. Tubes were inserted so that pressure was only exerted in the tube walls, thereby preventing soil compaction and overestimation of soil density. Soil samples were dried at room temperature after which the fine roots were separated by sieving through a 0.8 mm mesh. We analyzed the soil samples for density using the mass of soil dried at 70 °C for 2 days. Available phosphorus concentration was determined by the method of Mehlich (1953). Exchangeable calcium was extracted by a 1 M KCl solution and its concentration determined by atomic absorption, while total nitrogen was determined by the Kjeldhal method (Bremner & Mulvaney, 1982). Organic carbon content was analyzed by wet oxidation (Walkley & Black, 1934). Soil organic carbon was always analyzed with two standard soils showing contrasting carbon percentages having the analytical error of $< \pm 5\%$ of the soil carbon content. We calculated the organic carbon stock (T ha⁻¹) of the soil by multiplying carbon concentration by total soil mass per hectare using bulk density measurements and thickness of the sampled layer. The total soil organic carbon stock (T ha⁻¹) to a depth of 1 m was summed using the organic carbon stocks at each 10 cm depth interval. We tested for a significant difference in soil organic carbon content between forests and savanna at each level of the soil profile using a one-way ANOVA with replication. We considered the cores within each ecosystem as replicates. Because this involved 10 different tests for each transect, we corrected for the experiment-wise error rate by making the significance level more stringent with the Dunn-Šidák method (Sokal & Rohlf, 1995). We tested for differences in total carbon per hectare between forests, savannas and border using a one-way ANOVA.

Carbon isotope ratios of soil samples were determined at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (LSIETE) at the University of Miami. Soil samples (10 mg) were loaded in tin cups (3 mm diameter and 8 mm height; Elemental Microanalysis, Milan, Italy), which were placed in an automated elemental analyzer (Euro-EA-Elemental Analyzer, Eurovector, Milan, Italy) connected to a

continuous flow isotope ratio mass spectrometer (Isoprime, GV, Manchester, UK). Soil samples were not pretreated with acid to remove carbonates because soil in this area is acidic (pH 4.5–5.5) and unlikely to have inorganic carbon. Carbon-13 abundances are expressed as $\delta^{13}\text{C}$ values:

$$\delta^{13}\text{C}(\text{‰}) = [(R_{\text{sample}}/R_{\text{PDB}}) - 1] \times 1000,$$

in which R_{sample} and R_{PDB} represent the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and PeeDee standard, respectively. The precision of analysis was $\pm 0.1\%$ ($\pm \sigma$).

We analyzed ^{14}C activity of carbon in SOM from depths in the soil profiles which showed major shifts from savanna to forest, which were: Taquara border at 20–30 cm depth, Pitoco border at 80–90 cm depth and one 50 m in the Pitoco forest at 40–50 cm depth. Carbon-14 activity of SOM was analyzed by accelerator mass spectrometry (AMS) and converted to mean age of SOM at Beta Analytic Radiocarbon Dating Laboratory (Miami, USA).

Results

LAI of trees and shrubs shows a transition from high values of 2.8 to 4.2 inside the gallery forest to low values of < 1 within 10 m of the forest–savanna boundary (Fig. 2). In contrast, the LAI of grasses was higher within the savanna ranging from 1.5 to 2.5 and quickly declining to 0 inside the forest (Fig. 2).

The carbon stock at each depth of the soil profile was significantly higher in the two forests compared to the savanna at all soil depths with the exception of the carbon stock at 10–20 cm at the Pitoco transect ($P < 0.005$; Fig. 3a). Carbon stocks ranged between 60 and 120 T ha⁻¹ for Taquara forest which was much greater than the observed 30 and 50 T ha⁻¹ for Pitoco forest. Savanna soil carbon stocks were < 30 T ha⁻¹,

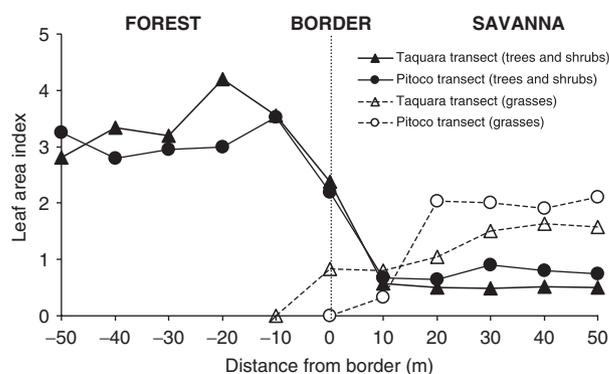


Fig. 2 Leaf area index for trees/shrubs and grasses along the Taquara and the Pitoco transects encompassing gallery forests and savanna.

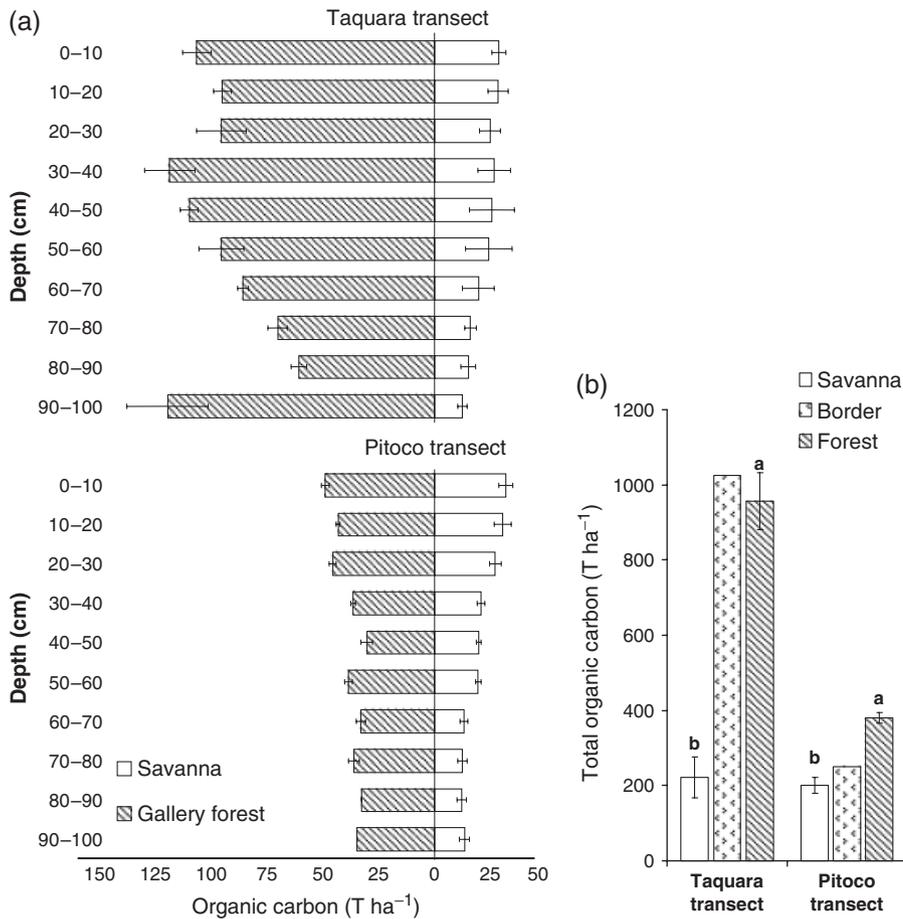


Fig. 3 Average organic carbon stocks ($\pm \sigma$, $n = 5$) of gallery forests and savanna areas at each depth in a 1 m soil profile (a). The average total organic carbon stocks ($\pm \sigma$, $n = 5$ for forests and savannas; $n = 1$ for border) in the top meter of the soil profile for savanna, border and forest for each transect (b). Different letters in part (b) represent statistical difference between means.

even near the surface. Carbon stocks integrated to 1 m depth and 1 ha at the Taquara and Pitoco forest (~ 1000 and 400 T ha^{-1} , respectively) are significantly greater than carbon stocks of approximately 200 T ha^{-1} found in the savanna ($F = 102$ and 36 respectively, $P < 0.01$ for both transects; Fig. 3b).

The tree/shrub and grass leaf area indices were highly correlated with the $\delta^{13}\text{C}$ value of the soil organic carbon at the surface for both transects (Fig. 4). These high correlations are consistent with an increase of grass LAI causing an increase in the $\delta^{13}\text{C}$ value of SOM and an increase of tree/shrub LAI causing a decrease in the $\delta^{13}\text{C}$ value of surface SOM (Fig. 4).

Soil total nitrogen, available phosphorus and exchangeable calcium concentrations averaged over the 1 m soil profile or at the soil surface (0–10 cm) were higher in the gallery forests compared with the savannas (Fig. 5). Total nitrogen and available phosphorus concentration along the savanna–gallery forest transect

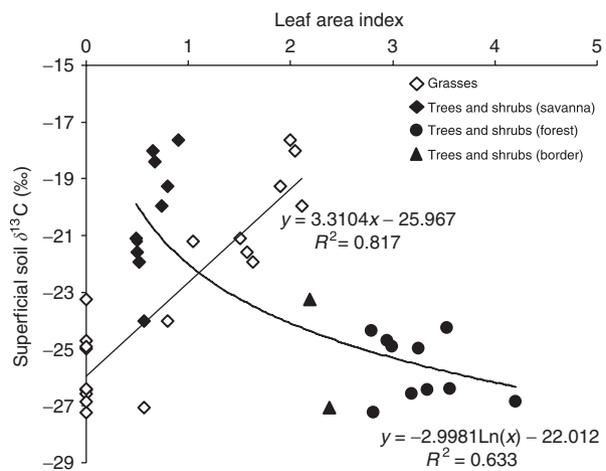


Fig. 4 The $\delta^{13}\text{C}$ values of the superficial soil organic matter (0–10 cm) along the transects as a function of grass and trees/shrub coverage.

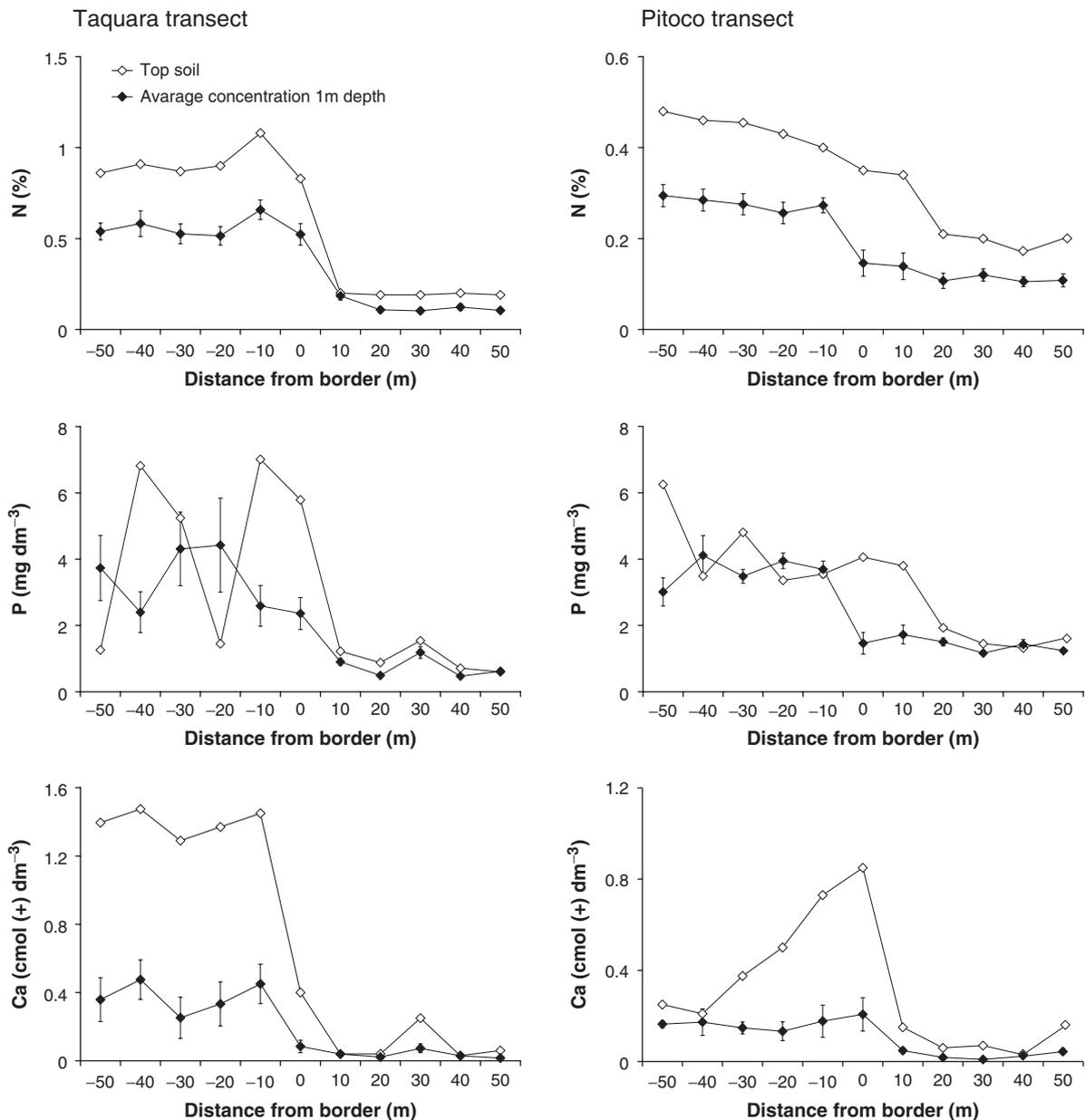


Fig. 5 Variation of the average soil concentrations of total N, available P and exchangeable Ca in the surface (0–10 cm) and in the top 1 m from gallery forest (left) to savanna (right) for the two transects.

changed sharply at the border of the Taquara forest transect, whereas changes in concentration of both elements along the savanna–gallery forest transect at Pitoco were more gradual. Changes at the border in the calcium concentration across both transects were sharp.

Carbon isotope ratios of SOM changed both spatially along the two transect and with depth (Fig. 6). Carbon of surface SOM from soil cores 20 m and further into the savanna had an average $\delta^{13}\text{C}$ values of $-18.7 \pm 1.0\%$ and $-21.4 \pm 0.4\%$ for the Taquara and the Pitoco trans-

ect, respectively (Fig. 6). These values are similar to a previous report on a forest–savanna transition (Pessenda *et al.*, 1998). The $\delta^{13}\text{C}$ values of surface SOM in the Taquara forest were depleted, and typical of forests having only C_3 plants ($-24.6 \pm 0.14\%$), but SOM $\delta^{13}\text{C}$ values increased rapidly at lower depths of the soil profile. In contrast, $\delta^{13}\text{C}$ values of the Pitoco forest remained low ($-26.8 \pm 0.24\%$) to a depth of 50 cm below the soil surface and increased abruptly for two cores at deeper levels (Fig. 6). The increase in the $\delta^{13}\text{C}$

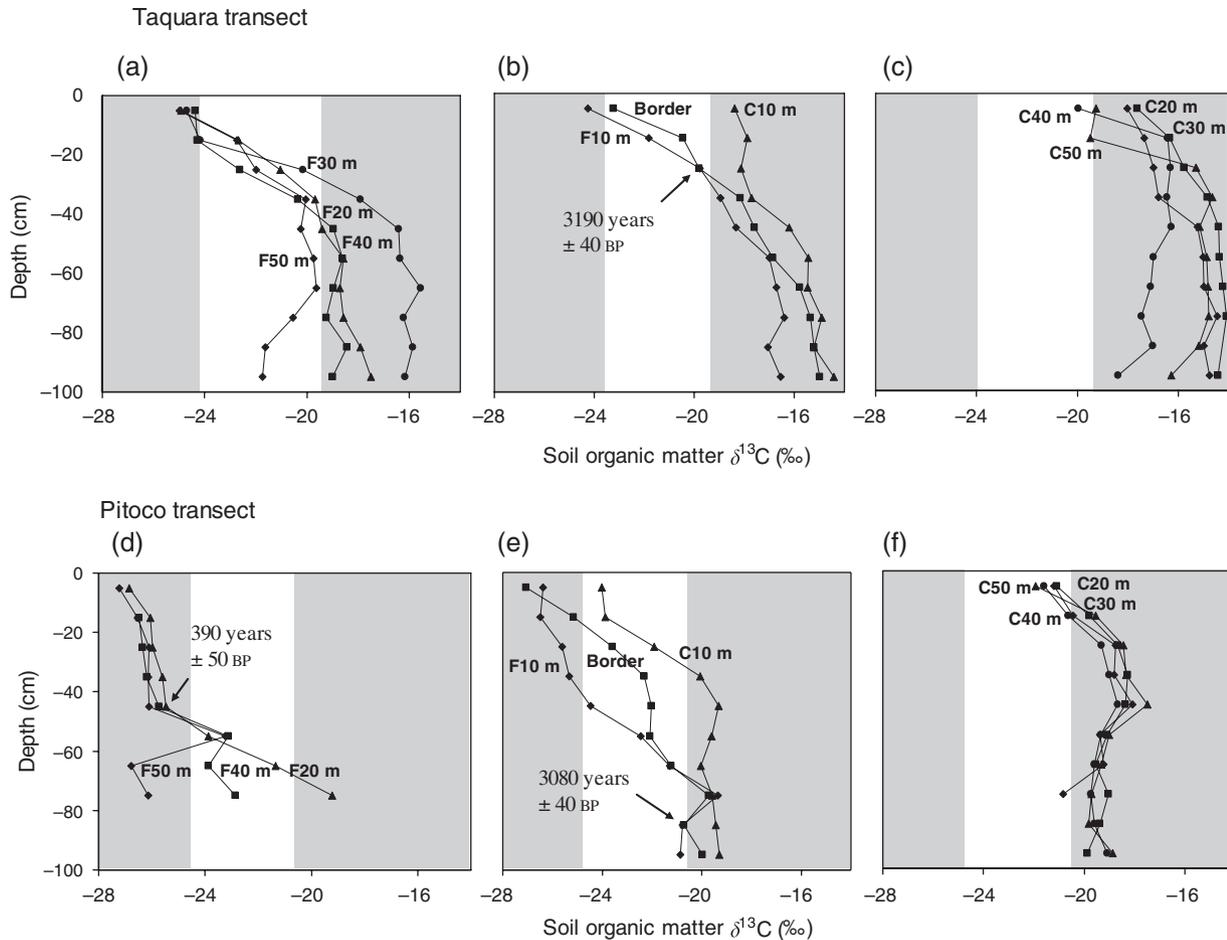


Fig. 6 The $\delta^{13}\text{C}$ values of SOM for the profiles within the gallery forests [20 m or further from the border, (a) and (d)], at the border of the gallery forests [(b) and (e), respectively] and within the savanna [20 m or further from the border, (c) and (f), respectively] for the Taquara and Pitoco transects. Gray areas represent the range of $\delta^{13}\text{C}$ values of SOM from savanna vegetation (right area) and for the gallery forest (left area).

values of soil organic carbon with depth was much greater in the Taquara forest compared with the Pitoco forest (Fig. 6). Soil cores from the transition zones (border and 10 m into each ecosystem) for the Taquara and Pitoco transects showed similar patterns with an increase in $\delta^{13}\text{C}$ at depths below 30 and 40 cm, respectively, from values typical of forests or savanna–forest mixtures to those observed for cores taken within the savanna (Fig. 6).

Carbon-14 activity of SOM at transition depths indicates that the shifts in vegetation at edge of the Taquara forest (30–40 cm depth) and the Pitoco forest (80–90 cm depth) occurred approximately at the same time, having the SOM mean age of 3190 ± 40 BP and 3080 ± 40 BP, respectively (Fig. 6). Carbon-14 activity of SOM 50 m inside Pitoco gallery forest also shows that in some locations transitions may have occurred recently with a SOM mean age of 390 ± 50 BP (Fig. 6).

Discussion

Gallery forests and savanna present distinct above- and belowground characteristics

The LAI of gallery forests and the savanna were in the range of those reported by Hoffmann *et al.* (2005b) at the same ecological reserve. Likewise, the partition of total LAI into shrubs/trees and grasses conforms to the above study with gallery forest having little or no grasses and savannas having a mixture of trees/shrubs and grasses. The difference in the tree/shrub and grass coverage between gallery forests and savannas are the probable cause of the differences in the $\delta^{13}\text{C}$ values of surface SOM between forests and savannas (Fig. 4). Most tropical savanna grasses have the C_4 photosynthetic pathway (Klink & Joly, 1989) and, therefore, discriminate less against ^{13}C during photosynthesis in

contrast to the C₃ trees/shrubs. Typical $\delta^{13}\text{C}$ values for C₄ grasses range from -15% to -10% , while typical $\delta^{13}\text{C}$ values of trees and shrubs range from -30% to -24% (Smith & Epstein, 1971). The isotopic differences in the bulk photosynthate between these two ecosystems will be recorded in the SOM, as plant debris decays into recalcitrant carbon (Boutton *et al.*, 1998).

The carbon stocks (0–1 m) reported here, with the exception of the Taquara forest, are within the ranges reported for these respective biomes (Jobbagy & Jackson, 2000). There are distinct differences between carbon stocks and nutrients in the soil matrix of gallery forests and savannas. Soil organic carbon stocks are significantly greater in forests compared with savanna, with the Taquara forest having as much as five times more soil organic carbon than the savanna (Fig. 3). The much greater soil carbon stock in the Taquara forest and its border, compared with those of the Pitoco forest (Fig. 3), is probably due to the greater organic carbon preservation and accumulation under anoxic conditions of the periodically flooded Taquara forest. Another factor which may be responsible for the greater soil organic carbon stocks in the Taquara forest and its border is the likely greater productivity of this forest compared with the Pitoco forest, as indicated by its higher LAI. The greater productivity of the Taquara forest can be ascribed to a higher P, N and Ca concentrations in the soil compared with the Pitoco forest (Fig. 5).

Gallery forests are expanding

Changes in the $\delta^{13}\text{C}$ values of SOM along the soil profile could have been caused by several factors. These factors can be divided into post and preorganic matter deposition. The differential degradation of chemical compounds having different isotopic signatures (Benner *et al.*, 1987), fractionations associated with microbial degradation of organic substances (Balesdent *et al.*, 1993) and the heterotrophic fixation of CO₂ (Ehleringer *et al.*, 2000) are examples of postdepositional factors. Changes in the isotopic composition of atmospheric CO₂ through time (Marino *et al.*, 1992), the isotopic fractionations within C₃ and C₄ plants (Farquhar *et al.*, 1982; Buchmann *et al.*, 1996) and savanna to gallery forest vegetation (Giresse *et al.*, 1994; Victoria *et al.*, 1995; Martinelli *et al.*, 1996; Boutton *et al.*, 1998; Sanaiotti *et al.*, 2002; Bowman *et al.*, 2004) are examples of predepositional factors. Although it is difficult to distinguish between the various processes operating postdepositional, postdepositional changes in the $\delta^{13}\text{C}$ values of SOM through the soil profile is correlated with changes in the relative quantity of soil organic carbon (Balesdent *et al.*, 1993; Krull *et al.*, 2002). In a tropical region, it was observed that major postdepositional changes occurred

within the top 20 cm of the soil profile (Krull *et al.*, 2002). Changes in the $\delta^{13}\text{C}$ values of SOM in the transition zone observed here, however, occur up to a depth of 80 cm in the soil profile. Furthermore, we could not observe a significant correlation between $\delta^{13}\text{C}$ values of SOM and the concentration of carbon in the soil below 20 cm. We, therefore, reject the hypothesis that the isotopic changes deep in the soil profile observed here are caused by postdepositional effects, although some postdepositional changes could have occurred at the top 20 cm of the soil profile. We also reject the predepositional explanation of changes in the $\delta^{13}\text{C}$ values of atmospheric CO₂ through time and isotopic fractionation within C₃ and C₄ plants as an explanation for our observations. With the exclusion of modern CO₂ (1900 to present), differences in the $\delta^{13}\text{C}$ values of atmospheric CO₂ within the last 10 000 years have been small ($<1.0\%$; Marino *et al.*, 1992) and they would equally affect all profiles measured here, which was not observed. Although there could have been some changes in discrimination during photosynthesis through time, it is unlikely that changes in the range of 6% would not be accompanied by changes in vegetation as we propose here. We, therefore, conclude that shifts in the $\delta^{13}\text{C}$ values of SOM along the soil profiles in the forest-savanna border were caused by vegetation shifts from savanna to gallery forests. The shifts at the two sites, however, may represent shifts to gallery forest from two different savanna types. The higher $\delta^{13}\text{C}$ values of the deeper soil at the border of the Taquara forest compared with those of the Pitoco forest ($\sim -14\%$ vs. $\sim -18\%$, respectively) implies that the previous vegetation at the Taquara forest border had greater grass coverage and was more open than those of the Pitoco forest.

At the border of both gallery forests, we recorded savanna signatures shifting to those of gallery forests at a soil depth having mean SOM ¹⁴C activity equivalent to 3190 and 3080 BP for the Taquara and Pitoco boundary, respectively (Fig. 6). Because roots from the modern day vegetation can exude additional ¹⁴C into the deeper soil matrix, the above ages probably represent the most recent of a range of possible ages of shifts from savanna to forests (Victoria *et al.*, 1995; Martinelli *et al.*, 1996; Trumbore, 2000). Our results are consistent with several other studies throughout Brazil, showing a general shift from savanna systems having a C₄ signature to forests having a high C₃ isotopic signature (Martinelli *et al.*, 1996). Palynological evidence shows that the greatest abundance of grass pollen, a proxy for dry periods, occurred in the range of 6000–4000 BP (Absy, 1980; Markgraf, 1989; Absy *et al.*, 1991; Ledru, 1992; Servant *et al.*, 1993). However, the shifts observed here and by Martinelli *et al.* (1996) did not happen all at once, and we document here shifts still occurring at the soil profile

with the SOM mean age of 390 BP (Fig. 6). Further evidence of continued shift from savanna to forest is provided by one core in the Pitoco transect 10 m inside the savanna showing SOM isotopic characteristics similar to gallery forests (Fig. 6).

Mechanism of gallery forest expansion

Gallery forest expansion initiated at least 3000–4000 years ago and continues to expand as recently as 390 BP (Fig. 6). The approximate average date of gallery forest expansion coincides with the expansion of other types of tropical forests reported by Martinelli *et al.* (1996) using the same techniques and of palynological studies (Absy, 1980; Markgraf, 1989; Absy *et al.*, 1991; Ledru, 1992; Servant *et al.*, 1993). This simultaneous expansion of woody vegetation throughout several regions in Brazil indicates that global climate change initiated gallery forest expansion at this site. There are several ways in which global climate change can bring about changes in gallery forest coverage. Interglacial periods associated with a higher atmospheric CO₂ concentration, for example, favors the growth of woody C₃ plants at the expense of the C₄ grasses (Ehleringer *et al.*, 1997). The decrease in C₄ grasses would lower fire frequency and allow for the expansion of forests (Bond *et al.*, 2003). Postglacial climate change also brought greater water availability. It is unlikely, however, that greater water availability is the only direct cause of forest expansion. It is well known that the standing biomass of savannas is not only limited by the lack of water (Sankaran *et al.*, 2005), but by lack of nutrients (Haridasan, 1992), drainage or high fire frequencies (Higgins *et al.*, 2007). Greater availability of water, for example, could indirectly facilitate forest expansion by decreasing fire frequency into the areas bordering gallery forests.

Concentrations of P, N and Ca are significantly greater in the gallery forest soils compared with savanna soils (Fig. 5), while soils at the border of the gallery forests and savannas have intermediate concentrations. These nutrients are the most limiting to woody vegetation growth in the central Brazilian savannas (Haridasan, 1992, 2005). The gradients in nutrient concentration differed markedly between the two gallery forest–savanna transects, with the Taquara transect showing a much sharper decline from forest to savanna compared with the Pitoco transect (Fig. 5). This difference in the profile between the two transects suggests that nutrient accumulation necessary for the expansion of gallery forests might have occurred by different mechanisms at each border. One possibility is that these nutrients were already present at the border, but gallery forest expansion was limited by other factors, such as

fire. This is a possible explanation for the expansion of the Pitoco forest where the differences in nutrient concentration across the transect was less distinct. The presence of forest species growing in the savanna but not the other way around (Hoffmann *et al.*, 2005a) suggests that gallery forests are poised to invade savannas given the right conditions. Gallery forest species at the Pitoco border, in the absence of fire, could certainly find savanna microhabitats containing sufficient nutrients to sustain their growth. However, the scenario described earlier is unlikely for the Taquara forest expansion because a sharp gradient in soil nutrients in transects crossing gallery and savanna ecosystems was observed. A second possibility, and a more likely scenario for the Taquara forest expansion, is that the expanding gallery forests received more nutrients via increased ground water flow from higher elevations during wetter periods. Ground water nutrients are an important component of nutrient input into gallery forests (Markewitz *et al.*, 2006). This would be a feasible scenario for the Taquara forest expansion because it is so close to the ground water and flooded periodically. Ground water flow over thousand of years may bring sufficient P, N and Ca to support gallery forest expansion, even though P and Ca have a low mobility.

Once gallery forests begin establishing in savannas, positive feedback effects may come into play and stabilize the expansion. Nutrient inputs through atmospheric deposition are known to be significant in this area (Lilienfein & Wilcke, 2004). Gallery forests, by the nature of their higher soil organic content and lower fire frequency, may retain nutrients in the soil to a greater degree than the savanna ecosystem. A more efficient retention of nutrients may also be maintained by higher transpiration of forests compared with savanna (Miranda *et al.*, 1996; Jipp *et al.*, 1998), which will prevent percolation of nutrients away from the rooting zone.

Conclusion

Gallery forests and savannas have significantly different aboveground and edaphic characteristics as has been shown elsewhere (Furley, 1992). We also show that the gallery forests expanded into savannas at a similar period of time as other tropical forests (Martinelli *et al.*, 1996), but expansion still occurred as recently as 390 BP. Our two transects, however, indicate that there may be more than one way in which climate change can provide the conditions necessary for gallery forest expansion. Our study suggests that climate change may initiate the expansion of gallery forest into savannas and consequently feedback effects such as nutrient accumulation and fire suppression may further the expansion of gallery forests into savannas.

Acknowledgements

We thank the staff of RECOR for the research infrastructure support. We also thank Dr José Carlos Sousa Silva at EMBRAPA Cerrados and Ricardo Flores Haidar for field assistance and valuable comments on this research. This research is based upon work supported by the National Science Foundation Grant No. DEB-0542912 (W. H.), AW Mellon Foundation (W. H.) and National Science Foundation Grant No. EAR-BE-332051 (L. S., M. H., F. M.-W., A. F.).

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