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SEÇÃO V - GÊNESE, MORFOLOGIA E CLASSIFICAÇÃO DO SOLO

GEOECOLOGICAL DRIVERS OF CERRADO HETEROGENEITY AND ^{13}C NATURAL ABUNDANCE IN OXISOLS AFTER LAND-USE CHANGE⁽¹⁾

Henry Neufeldt⁽²⁾

SUMMARY

The ^{13}C natural abundance technique was applied to study C dynamics after land-use change from native savanna to *Brachiaria*, *Pinus*, and *Eucalyptus* in differently textured Cerrado Oxisols. But due to differences in the $\delta^{13}\text{C}$ signatures of subsoils under native savanna and under introduced species, C substitution could only be calculated based on results of cultivated soils nearby. It was estimated that after 20 years, *Pinus* C had replaced only 5 % of the native C in the 0–1.2 m layer, in which substitution was restricted to the top 0.4 m. Conversely, after 12 years, *Brachiaria* had replaced 21 % of Cerrado C to a depth of 1.2 m, where substitution decreased only slightly throughout the entire profile. The high $\delta^{13}\text{C}$ values in the subsoils of the cultivated sites led to the hypothesis that the natural vegetation there had been grassland rather than Cerrado *sensu stricto*, in spite of the comparable soil and site characteristics and the proximity of the studied sites. The hypothesis was tested using aerial photographs of 1964, which showed that the cultivated sites were located on a desiccated runoff head. The vegetation shift to a grass-dominated savanna formation might therefore have occurred in response to waterlogging and reduced soil aeration. A simple model was developed thereof, which ascribes the different Cerrado formations mainly to the plant-available water content and soil aeration. Soil fertility is considered of minor significance only, since at the studied native savanna sites tree density was independent of soil texture or nutrient status.

Index terms: Cerrado formations; ^{13}C natural abundance; waterlogging; Oxisol; soil fertility; land-use change.

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RESUMO: *FATORES GEOECOLÓGICOS DAS DIFERENTES FORMAÇÕES DE CERRADOS - UMA HIPÓTESE BASEADA EM ABUNDÂNCIA NATURAL DE ^{13}C E FOTOGRAFIA AÉREA*

A abundância natural de ^{13}C foi utilizada para estudar a dinâmica de carbono em latossolos de textura média e argilosa após plantação de pastagens (*Brachiaria decumbens*) e reflorestamentos (*Pinus caribaea* e *Eucalyptus citriodora*). Considerando as diferenças de $\delta^{13}\text{C}$ nos subsolos das savanas nativas e das espécies introduzidas, pôde-se calcular a substituição de carbono somente para os solos argilosos, baseando-se em resultados publicados de $\delta^{13}\text{C}$ em solos adjacentes. Estimou-se que somente 5 % do carbono nativo foram substituídos após 20 anos de plantação com pinus na camada de 0–1,2 m, ficando a substituição restrita aos primeiros 0,4 m do solo. Na pastagem de 12 anos, 21 % do carbono novo foram introduzidos na camada de 0–1,2 m, sendo a substituição diminuída gradativamente pelo perfil inteiro. De acordo com os altos valores de $\delta^{13}\text{C}$ nos subsolos das áreas cultivadas, levantou-se a hipótese de que a vegetação natural teria sido de campo limpo em vez de cerrado stricto sensu apesar da semelhança dos solos e da proximidade dos sítios estudados. A hipótese foi testada com fotos aéreas de 1964, mostrando que as áreas cultivadas encontravam-se numa cabeceira de escoamento ressecada. Portanto, a vegetação dominada por gramíneas pode ter sido induzida pela hidromorfia e pela baixa aeração do solo. Com base nessas observações, desenvolveu-se um modelo simplificado, atribuindo às diferentes formações de cerrados o acesso de água para as plantas e a aeração do solo. A fertilidade do solo foi considerada de menor importância porque a densidade arbórea das áreas de cerrados encontrava-se independente da textura ou do nível de nutrientes dos solos.

Termos de indexação: formações de cerrados; abundância natural de ^{13}C ; hidromorfia; Latossólos; fertilidade do solo; manejo do solo.

INTRODUCTION

The Cerrado region covers roughly two million square kilometers of Central Brazil, i.e. 20 % of the national territory, and is characterized by a seasonal climate, low-fertility soils, and a savanna-like vegetation (Adámoli et al., 1986). During the past four decades, the Cerrado region underwent severe changes as gradually more areas were cleared for cultivation. Today pastures cover around 400,000 km², and approximately 150,000 km² are cultivated with annual crops and tree plantations (Resck et al., 2000).

After land-use change, C derived from the introduced species (predominantly *Brachiaria* pastures, maize and soybean as annual crops, and *Pinus* or *Eucalyptus* in tree plantations) gradually replaces the original C. By the ^{13}C natural abundance technique (Balesdent & Mariotti, 1996) this alteration can be calculated based on the physiologically different CO₂ assimilation pathways between C-3 and C-4 plants. C-3 plants have $\delta^{13}\text{C}$ signatures ranging from -32 ‰ to -22 ‰ with an average of -27 ‰, and C-4 plants have values ranging from -16 to -9 ‰, with a mean of -13 ‰ (Balesdent & Mariotti, 1996).

Since Cerrado *sensu stricto* (s.s.) comprises both C-3 trees and shrubs and C-4 grasses, its $\delta^{13}\text{C}$ signature is between that of pure C-3 and C-4

vegetations. Roscoe et al. (2001) and Wilcke & Lilienfein (2004) used this feature to quantify the replacement of C derived from Cerrado vegetation after introduction of *Brachiaria* and *Pinus* on clayey Oxisols. Neufeldt (1998) applied the ^{13}C technique to differently textured Cerrado Oxisols, but was not able to calculate C replacement due to surprisingly high subsoil $\delta^{13}\text{C}$ values on the sites with the introduced crops.

Neufeldt (1998) hypothesized that slightly higher groundwater levels at the catchment scale had induced a higher natural C-4 grass abundance in the past. Accordingly, catchment scale variations of the moisture balance could explain the occurrence of Cerrado savannas of varied densities on the nearly flat terrain (< 2 % inclination). Similarly, Ker & Resende (1996) observed that the Cerrado on hilltops was tree-dominated and gradually changed into grass-dominated Cerrado formations towards the effluents. In studies of forest-savanna boundaries within the Cerrado region, Emmerich (1989) found that the soil moisture balance was the main determinant factor of vegetation formation, so that mesophytic forests developed where the moisture balance was more stable, whereas soil fertility had no marked influence.

However, this hypothesis disagrees with the common belief that, within the Cerrado biome, there is a relation between, the shift from grass to tree

dominated Cerrado formations⁽³⁾ and soil fertility (Lopes & Cox, 1977; Haridasan, 2000), water availability (Alvim, 1996), or soil acidity and aluminum toxicity (Goodland & Pollard, 1973; Goodland & Ferri, 1979). Furthermore, frequent burning strongly affects height and density of the Cerrado vegetation (Eiten & Sambuichi, 1996; Roscoe et al., 2000), but fires are nowadays seen as a predominantly anthropogenic factor of Cerrado degradation (Alvim, 1996). These contrasting hypotheses on the determining factors of Cerrado formations call for more in-depth research.

For this study, $\delta^{13}\text{C}$ of soils under Cerrado, *Brachiaria* pastures, and *Pinus* and *Eucalyptus* plantations were analyzed and aerial photographs were assessed to test the hypothesis of waterlogging as a key factor of the varied catchment-scale Cerrado formations.

MATERIALS AND METHODS

Site location and history

The study area lies between 19.10 ° to 19.20 ° S and 48.12 ° to 48.18 ° W, at a distance of approximately 25 km SSE from Uberlândia, Minas Gerais, Brazil. The mean annual temperature is 22 °C and average precipitation 1.650 mm, 90 % of which falls between October and April. Coarse-loamy, mixed, isohyperthermic Typic Haplustox and very fine, allitic, isohyperthermic Anionic Acrustox (Soil Survey Staff, 1997) were chosen for a regionally representative sampling (Neufeldt et al., 1999). According to the Brazilian taxonomy, the soils were classified as Latossolos vermelho-amarelos álicos A moderado textura média / muito argilosa fase cerrado (Camargo et al., 1986). On the clayey soil, a degraded *Brachiaria decumbens* pasture, a *Pinus caribaea* plantation and a Cerrado *s.s.* savanna were chosen, while on the coarse-loamy soil a degraded *Brachiaria decumbens* pasture, a *Eucalyptus citriodora* plantation and a Cerradão were selected. The sites were chosen for their longstanding management history and for being close to each other (< 2 km). The savanna sites differed in tree density, because no comparable sites could be identified within an acceptable distance. Detailed management histories as well as a discussion on the chemical and physical properties of the soils under study are provided in Neufeldt (1999). Table 1 gives an overview of site locations, management records, and soil properties.

Sampling and sample preparation

Soil samples were collected in March 1995, at the end of the rainy season, from each of the six sites. At five randomly selected points per site, samples were taken with an Edelman soil auger from the 0–0.1, 0.1–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, 0.8–1, and 1–1.2 m layers and pooled. The samples were dried in an air-forced oven at 40 °C and passed through a 2 mm sieve to remove roots. For the chemical analyses, sub-samples from each depth were ground for greater homogeneity. Litter samples were collected using a 0.25 × 0.25 m² frame. Thirty samples per treatment were randomly collected, pooled, and dried in an air-forced oven at 65 °C for at least 48 h. One litter sub-sample per treatment was finely ground for further analysis.

Analytical methods

The analytical methods for the determination of soil properties are described in Neufeldt (1999). The signature of stable carbon isotopes was obtained after burning samples of 20–100 mg in the presence of CuO under a pure oxygen stream at 900 °C in a dry combustion furnace. In the resulting CO₂, ^{12}C and ^{13}C were determined with a mass spectrometer (Europa Scientific Roboprep Tracermass) and corrected for ^{17}O influence (Craig, 1957). All analyses were performed in triplicate and presented as mean ± standard error. The $\delta^{13}\text{C}$ value was calculated according to the international V-PDB standard and expressed in tenths of a percent (‰), according to the equation:

$$\delta^{13}\text{C} = \frac{(^{13}\text{C}/^{12}\text{C}_{\text{sample}} - ^{13}\text{C}/^{12}\text{C}_{\text{standard}})}{(^{13}\text{C}/^{12}\text{C}_{\text{standard}})} \times 1000 \quad (1)$$

Assessment of aerial photographs

Aerial photographs, taken long before any of the land-use systems were introduced, of flight VM AST-10 1370 PMW R-58, nr. 9298-9301, scale 1:50,000, from August 29, 1964, and of flight MG-103, nr. 100502-100507, nr. 100414-100417, and nr. 100525-100528, scale 1:15,000, from April 24, 1979, were analyzed visually. A stereoscope was used to assess natural differences between Cerrado formations as related to topography.

RESULTS

$\delta^{13}\text{C}$ signatures in the soil profile

Figure 1 shows the $\delta^{13}\text{C}$ signatures of the clayey and coarse-loamy Oxisols under different management systems in the 0–1.2 m soil layer. The $\delta^{13}\text{C}$ values of Cerrado litter on the clayey and coarse-loamy soil were -22.8 ‰ and -25.1 ‰, respectively, and therefore typical for Cerrados (Roscoe et al., 2000; Wilcke & Lilienfein, 2004). The standards of *Brachiaria*, *Pinus*,

⁽³⁾ According to Eiten (1972), tree component increases in the order Campo limpo (xeromorphic grassland), Campo sujo (xeromorphic shrub savanna), Campo cerrado (open xeromorphic arboreal savanna), Cerrado sensu strictu (dense xeromorphic arboreal savanna), and Cerradão (xeromorphic forest).

Table 1. Site characteristics and soil chemical and physical properties of clayey and coarse-loamy Cerrado Oxisols (adapted from Neufeldt, 1999)

Treatment, location Altitude, Inclination	Horizon	Depth	Sand	Silt	Clay	ρ ⁽¹⁾	C	C/N	pH _{H₂O}	P	CEC _e	CEC _p	BS ⁽²⁾
		cm	— g kg ⁻¹ —			g cm ⁻³	g kg ⁻¹			mg kg ⁻¹	— cmol _c kg ⁻¹ —		%
Very fine, allitic, isohyperthermic Anionic Acrustox													
Cerrado sensu stricto	A1	0–10	250	70	680	0.84	26.9	18	4.6	1.8	1.30	7.50	22
48.135°W 19.135°S	A2	-30	220	80	700	0.86	19.1	17	4.8	0.7	0.77	5.89	18
954 m, 0–1°	BoA	-48	220	80	720	0.89	14.8	17	5.0	0.5	0.40	3.91	20
	Bo11	-80	200	40	760	0.90	11.5	16	5.0	0.4	0.22	3.33	32
	Bo12	-140+	200	50	750	0.86	8.9	17	5.2	0.4	0.08	2.16	74
<i>Brachiaria decumbens</i>	Ap	0–20	190	140	670	0.87	24.8	18	5.3	0.9	2.46	5.63	96
48.113°W 19.160°S	A	-40	150	130	720	0.91	16.8	18	5.5	0.6	1.09	3.71	81
950 m, 0–1°	BoA	-63	150	110	740	0.89	13.3	19	5.2	0.5	0.35	2.67	60
Beginning: 1986	Bo11	-80	150	100	750	0.86	11.5	19	5.2	0.5	0.23	2.25	70
	Bo12	-140+	160	80	760	0.84	9.2	18	5.0	0.4	0.14	1.56	93
<i>Pinus caribaea</i>	AE	0-3	220	50	730	0.92	22.6	21	4.2	2.2	1.81	0.47	8
48.112°W 19.160°S	A1	-20	230	80	690	0.92	20.4	20	4.7	1.0	0.84	6.86	14
955 m, 0–1°	A2	-48	210	100	690	0.88	14.7	20	4.6	0.5	0.38	4.55	24
Beginning: 1975	Bo11	-90	190	80	730	0.85	11.8	20	4.5	0.4	0.08	2.91	75
	Bo12	-140+	190	60	750	0.82	9.0	20	4.5	0.3	0.05	1.31	100
Coarse-loamy, mixed, isohyperthermic Typic Haplustox													
Cerradão	A1	0–10	820	0	180	1.15	9.4	15	4.7	1.3	0.90	4.64	37
48.168°W 19.175°S	A2	-36	800	0	200	1.19	6.2	15	4.9	0.5	0.44	2.30	20
900 m, 1-2°	BoA	-65	790	0	210	1.22	5.2	16	4.9	0.4	0.26	1.67	23
	Bo11	-85	780	0	220	1.19	4.2	18	5.0	0.4	0.22	1.13	27
	Bo12	-140+	760	0	240	1.14	3.2	18	5.1	0.3	0.16	1.04	44
<i>Brachiaria decumbens</i>	Ap	0–18	810	0	190	1.23	7.7	17	5.4	1.0	1.29	4.18	91
48.157°W 19.182°S	A	-30	810	0	190	1.24	6.3	17	5.4	0.6	0.65	3.47	77
894 m, 1-2°	BoA	-55	800	0	200	1.28	5.4	18	5.3	0.5	0.44	2.58	50
Beginning: 1987	Bo11	-80	780	10	210	1.22	4.9	17	5.1	0.4	0.21	2.20	29
	Bo12	-135+	770	10	220	1.16	3.6	19	5.4	0.4	0.08	1.45	38
<i>Eucalyptus citriodora</i>	A	0-35	830	0	170	1.26	7.4	17	5.0	0.7	0.45	3.19	31
48.173°W 19.175°S	BoA	-53	820	0	180	1.20	5.0	18	5.1	0.4	0.21	2.04	33
890 m, 1-2°	Bo11	-86	820	0	180	1.17	4.3	19	5.1	0.3	0.18	1.41	39
Beginning: 1982	Bo12	-140+	800	0	200	1.15	3.4	21	5.2	0.3	0.08	0.89	63

⁽¹⁾ ρ : Bulk density. ⁽²⁾ BS: base saturation.

and *Eucalyptus* litter were -12.9 ‰, -26.9 ‰, and -28.1 ‰, respectively. The results are in line with the values obtained by Trouve et al. (1994), Roscoe et al. (2001), and Wilcke & Lilienfein (2004).

In the clayey soil under Cerrado *s.s.*, $\delta^{13}\text{C}$ was -20.0 ‰ in the 0–0.2 m layer and increased slightly with depth, reaching -18.7 ‰ at 0.8 m. Below that, the signal remained almost constant. Conversely, in

the coarse-loamy soil under Cerradão, $\delta^{13}\text{C}$ in the 0–0.1 m layer was -23.1 ‰, which reflects the higher tree component, and asymptotically approached -17.3 ‰ in the 1.0–1.2 m layer. Between 0.6 and 1.0 m the signals were erratic, which might reflect past vegetation shifts or distinct rooting distributions. According to Wedin et al. (1995), the frequently observed $\delta^{13}\text{C}$ increase at greater depths is related to

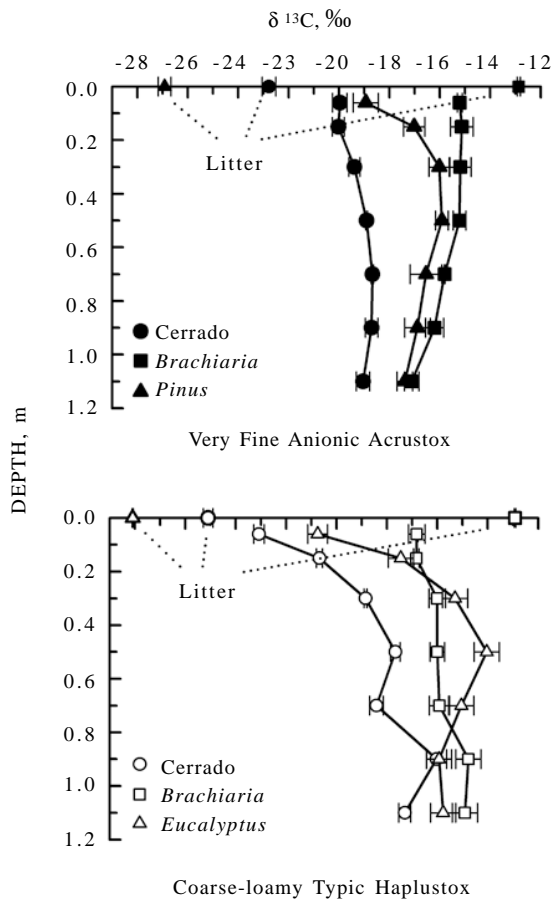


Figure 1. Distribution of $\delta^{13}\text{C}$ with depth in clayey (●) and coarse-loamy (○) Cerrado Oxisols subjected to different land use. Standard errors are given as error bars.

a gradual shift in the relative contributions of microbially-derived vs. plant-derived components, under the assumption that microbes show the same $\delta^{13}\text{C}$ signatures as the surrounding soil.

Despite lower $\delta^{13}\text{C}$ values of the litter, the soil signatures under *Pinus* and *Eucalyptus* clearly suggested enrichment of $\delta^{13}\text{C}$ throughout the profiles, in comparison to the respective Cerrado soils. There was a curvilinear signal increase in the upper 0.6 m ranging from -18.9 ‰ to -15.9 ‰ in the clayey soil and from -20.8 ‰ to -14.0 ‰ in the coarse-loamy soil, followed by a continuous decrease to -17.4 ‰ and -15.8 ‰ in the clayey and coarse-loamy soil, respectively. The signal range was therefore larger in the coarse-loamy soil.

The $\delta^{13}\text{C}$ signals in clayey soils under *Brachiaria* were constant at around -15.2 ‰ to a depth of 0.6 m and subsequently decreased to -17.1 ‰ in the deeper subsoil. Conversely, in the coarse-loamy soil under *Brachiaria*, signals increased stepwise from -16.8 ‰ in the 0–0.1 m layer to -14.9 ‰ in the 1.0–1.2 m layer.

Interpretation of aerial photographs

Figure 2 shows a section of an aerial photograph of 1964. Very clayey soils occur on the unconsolidated fine-textured Tertiary sediments of the tableland, to the right of the FEPASA railroad tracks at around 950 m altitude. Left hand of the tracks, the clay content of the soils continuously decreases as the sandstones of the Marília formation (Eocretaceous) are exposed (Nishiyama, 1989), reaching an altitude of approximately 900 m at the BR 050 interstate highway (then under construction). Hence, the sites with clayey soils were located near the railroad tracks, whereas the sites with coarse-loamy soils were close to the road (site locations encircled).

Savanna dominates the natural vegetation between the effluents and is generally denser on hilltops (Figure 2). The other natural vegetation forms are closely associated to the drainage system. Mata de galeria (gallery forest) grows where inclination gives the runoff a downhill direction. Veredas, which are palm groves characterized by the Buriti palm (*Mauritia flexuosa*), are found in shallow valleys with diffuse runoff and high groundwater levels throughout the whole year. Murundus are convex microstructures (probably termite mounds) of up to 1.5 m height and 20 m diameter within flat depressions or runoff heads with very low inclination (Ribeiro & Walter, 1998). The vegetation of the runoff heads is predominantly grassy with few or no woody components. In the study area, Murundus only occur on the fine-textured sediments of the tableland (Schneider, 1996). Figure 3 shows these structures more clearly, together with former runoff heads, later dried out, so that *Pinus* was planted on them in 1979.

DISCUSSION

Replacement of Cerrado C after land-use change

Since the cultivated soils and the adjacent Cerrado sites did not show similar subsoil $\delta^{13}\text{C}$ signatures, the Cerrado soils being depleted in $\delta^{13}\text{C}$ compared to the soil under introduced species, and hence lacking a common baseline, a direct calculation of C substitution after land-use change was not possible (Figure 1). On the clayey soils this was probably caused by a higher C-4 grass component in the past due to their proximity to an ancient runoff head (Figure 3). On the coarse-loamy soils, the Cerrado site seems to have been exceptionally dense, suggesting that the grass component had again been higher on the *Eucalyptus* and *Brachiaria* sites prior to cultivation (Figure 2).

An estimation of the C proportion derived from *Pinus* and *Brachiaria* in the clayey soils however seems possible, based on results of Wilcke & Lilienfein (2004) of comparable soils nearby. For the loamy soils,

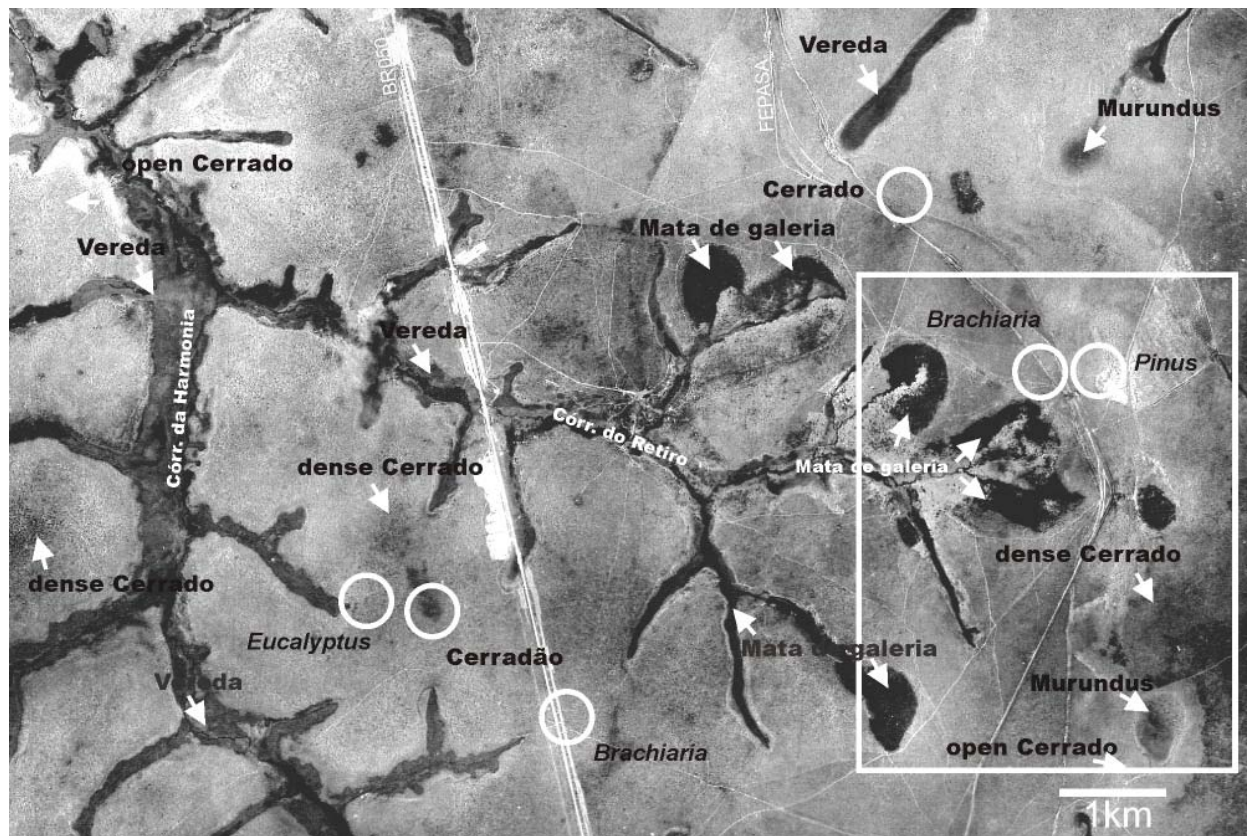


Figure 2. Aerial photograph of the study region from 1964. Circles highlight the study sites, which were under natural vegetation at the time. The different vegetation forms occurring in the region are marked with arrows. The frame shows the position of the aerial photograph from 1979.

the calculation of C replacement by introduced species was not undertaken, since neither reference studies were available to compare the measured values with nor a similar subsoil $\delta^{13}\text{C}$ distribution between Cerradão, *Eucalyptus*, and *Brachiaria* that could serve as baseline.

Wilcke & Lilienfein (2004) showed that 20 yr of *Pinus caribaea* plantation on a clayey soil only led to C replacement in the topsoil (0–0.3 m), whereas C in the subsoil (0.3–2 m) remained unaffected by the land-use change. Similar results were obtained by Trouve et al. (1994) for 30-year-old *Pinus caribaea* stands in Congo. Wilcke & Lilienfein (2004) further reported that *Brachiaria decumbens*-derived C replaced 5–31 % of the original in the 0–2 m layer after 12 yr of cultivation. Roscoe et al. (2001) described a similar C substitution throughout the whole soil profile after 23 yr under *Brachiaria* spp. pasture in Sete Lagoas, MG, Brazil. Hence, C substitution rates for *Pinus* and for *Brachiaria* were comparable at different locations in Brazil and elsewhere, and it therefore seems valid to assume a similar response to the introduction of *Pinus* and *Brachiaria* on the study sites as well.

C substitution after vegetation change to *Pinus* was calculated using the measured $\delta^{13}\text{C}$ values, and assuming that no C replacement occurred below 0.4 m under the studied *Pinus* plantation. It was estimated that C derived from *Pinus* replaced 27 % of the original C in the 0–0.1 m layer, 10 % in the 0.1–0.2 m layer, and 1 % in the 0.2–0.4 m layer. In the total layer (0–1.2 m), only 5 % C were *Pinus*-derived after 20 yr. The estimated values strongly agree with the results of Wilcke & Lilienfein (2004) and Trouve et al. (1994), and probably reflect the fact that the *Pinus* litter accumulates on the soil surface, forming a thick organic layer (5–20 cm) that is only slowly incorporated into the soil (Neufeldt et al., 2002), and a comparatively low rooting intensity in the subsoil.

C substitution by *Brachiaria* on the clayey soil was calculated by relating the $\delta^{13}\text{C}$ pasture values to those of the corresponding layer of the *Pinus* site, because both appeared to have had a similar grassland vegetation in the past due to the adjacent runoff head (Figure 1). C substitution under *Brachiaria* was estimated to be nearly constant at about 24 % to 0.6 m depth, and then decreased gradually to 6 % in the 1.0–1.2 m layer. In the total layer (0–1.2 m), 21 % C

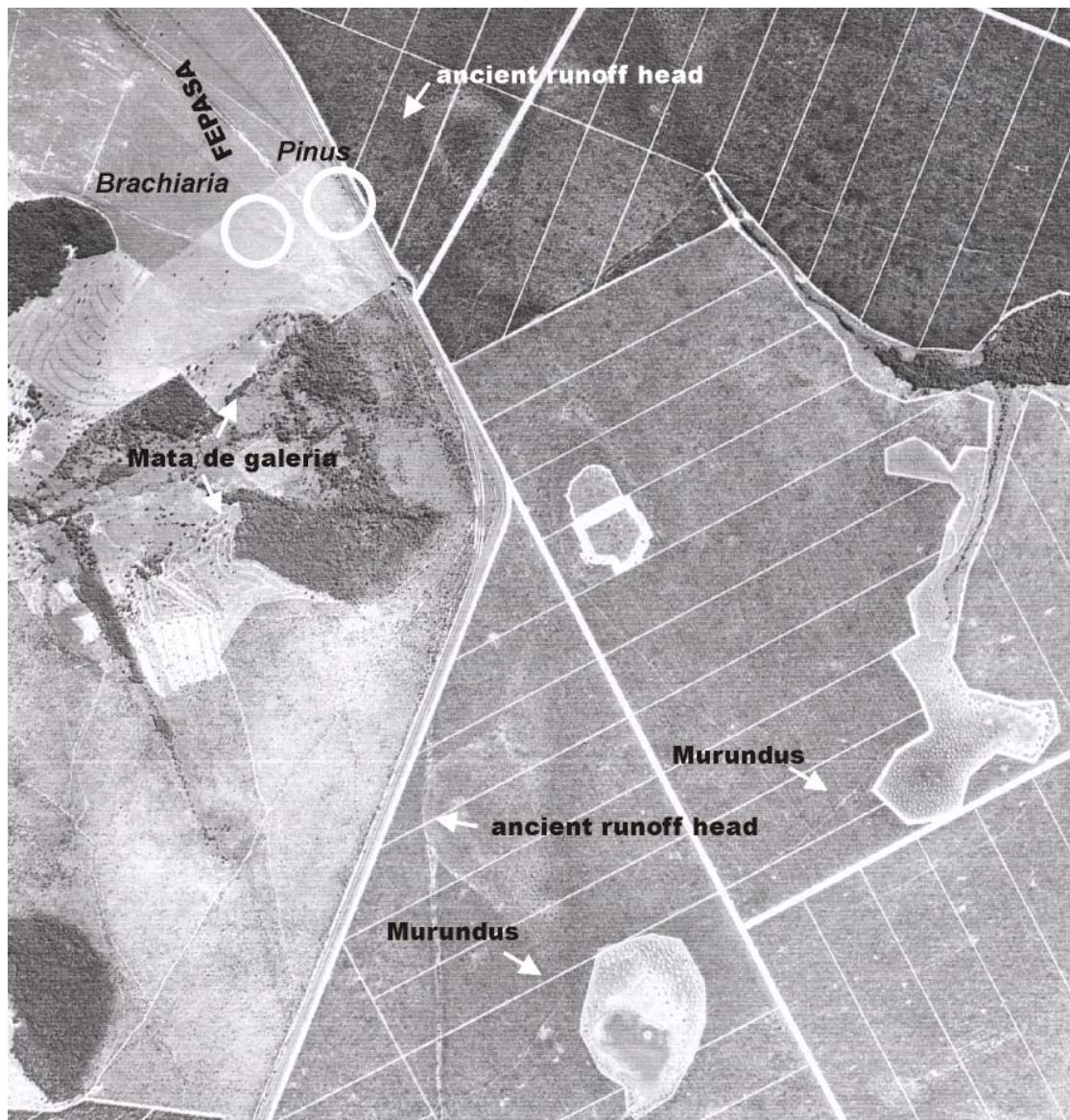


Figure 3. Aerial photograph from 1979, showing several Cerrado vegetation forms and ancient runoff heads which were already cultivated at the time.

were pasture-derived. Both the amounts of C replacement and their distribution in the profile are in close agreement with the results of Wilcke & Lilienfein (2004) and Roscoe et al. (2001). The high C substitution is a response to the profound and dense pasture rooting system and the relatively low recalcitrance of the soil organic matter despite high clay contents (Roscoe et al., 2001; Neufeldt et al., 2002).

Summing up, the underlying assumptions allowed the calculation of C replacements, which agree very well with published results. This suggests that the initial hypothesis, according to which the vegetation on the *Brachiaria* and *Pinus* sites had been dominated

by C-4 grasses in the past due to waterlogging, appears to be correct. Aerial photographs (Figures 1 and 2), which were taken into consideration thereupon, reinforced the premise. However, analyses of stable isotopes and soil moisture contents along natural Cerrado vegetation gradients are required to verify the hypothesis.

Cerrado formations in response to geoeological drivers

Aerial photographs (Figure 2) and ^{13}C natural abundance (Figure 1) indicated a strong heterogeneity of the studied savanna formations and suggest that high groundwater levels limit Cerrado tree growth in

favor of grasses. This is confirmed by Eiten (1972), according to whom Cerrado trees are sensitive to waterlogging. Since the lateral extent of the groundwater influence is related to inclination, the affected zone may be very large on flat topographies. On the other hand, the coarse-loamy soils are clearly less fertile than clayey soils as indicated by their substantially lower cation exchange capacities (CEC) and C concentrations (Table 1). This does not seem to affect Cerrado physiognomy, as dense Cerrado *s.s.* and Cerradão frequently occur on the coarse-loamy soils derived from the Marília formation sandstones (Figure 1). Hence, on a catchment scale of several square kilometers, soil fertility does not seem to play such a prominent role for Cerrado density as frequently proposed (Goodland & Pollard, 1973; Lopes & Cox, 1977; Goodland & Ferri, 1979; Adámoli et al., 1986; Haridasan, 2000). This is consistent with Emmerich (1989) who showed that mainly the soil moisture balance determined the vegetation form along savanna-forest boundaries within the Cerrado region, whereas soil fertility played only a minor role. Recently, Ruggiero et al. (2002) studied the soil-vegetation relationships in Campo cerrado, Cerrado *s.s.*, and Cerradão, but found no similar trends in the Cerrado formations in terms of nutrient status, base saturation, Al saturation, and CEC. However, in contrast to Emmerich (1989), they could clearly distinguish the soil fertility of the Cerrado formations from the adjacent semideciduous forest. The forest plots presented higher clay contents and CEC and the Cerrado higher Al saturation in surface soils.

Based on these observations, a simple model is proposed in an attempt to integrate the distribution of Cerrado formations. The model centers around the plant-available water content and soil aeration, in view of the plants' water stress during the dry season (Alvim, 1996) and the sensitivity of the Cerrado trees

to waterlogging (Eiten, 1972), respectively. On the other hand, soil fertility is given a minor role only. The model is restricted to the catchment scale (up to several km²) and explicitly does not question the superordinate relevance of climate for the occurrence of the phytomorphological domains on the Brazilian territory. The Cerrado biome prevails where the amount and temporal distribution of precipitation is intermediate between the moist Amazonian and Atlantic forest biomes on the one hand and the dry Caatinga and Chaco biomes on the other (Ab'Sáber, 1971; Adámoli et al., 1986). The effects of fire on the Cerrado features are not discussed in this context either, since burning is seen as a predominantly anthropogenic cause of Cerrado degradation (Alvim, 1996; Eiten & Sambuichi, 1996).

Table 2 shows the different vegetation formations that occur naturally within the study region vs. different geocological drivers. With exception of the Vereda, which is characterized by the Burití palm tree, the vegetation formations are in the order of increasing canopy height and tree density (Goodland & Ferri, 1979). While the Vereda is flooded for most of the year, the grasses on the Murundu and Campo limpo or Campo sujo may temporarily suffer from drought during the dry season due to the restricted rooting depth, which limits the plant-available water content. While in the study area rooting depth is restricted by a high groundwater level in the vicinity of the effluents, solid bedrock may limit root penetration in other regions. According to Eiten (1972), Campo sujo and Campo limpo are frequently found on very shallow soils (e.g. steep slopes or rock outcrops) with good or poor drainage. Goodland & Ferri (1979) suggested that the few dwarf trees on the Campo sujo might reflect faults within a laterite crust or the bedrock. As rooting depth and thus the plant-available water content increases, the grass-

Table 2. Simplified relationship between vegetation formations and geocological drivers in the study region. Arrows represent a gradient

Geocological drivers	Vereda	Murundu	Campo limpo	Campo sujo	Campo cerrado	Cerrado <i>s.s.</i>	Cerradão	Mata de galeria
Plant available water	high	high	low	—————→				high
Rooting depth	shallow	shallow	shallow	—————→			deep	deep
Groundwater level	high	high	high	—————→			low	high
Drainage/soil aeration	poor	poor	poor	poor/good	good	good	good	good
Soil fertility	low	low	low	low	low	low	low	better
Topography	shallow valleys	depressions	depressions	slopes	slopes/planes	planes	planes/hilltops	steep valleys

dominated Cerrado formations are gradually replaced by tree-dominated Cerrado formations. This corresponds to the fact that some Cerrado trees are very deep-rooting (Eiten, 1972). Under otherwise comparable conditions, soil fertility should also play a role for the distribution of the vegetation forms and certainly has an influence on the phytosociological composition of the Cerrado (Goodland & Pollard, 1973; Alvim, 1996). In conclusion, tree density rises with increasing plant-available water content provided that good internal drainage conditions a well aerated solum which does not impose physical resistance (e.g. waterlogging, laterite, bedrock) to deep rooting. The Mata de galeria is restricted to the effluents with directed runoff and occurs on deep, well-drained, and possibly more fertile soils. Plants of the Mata de galeria, which floristically belong to the mesophytic Atlantic forest biome (Eiten, 1972), have access to water from the capillary fringe of the stream and are therefore less exposed to drought during the dry season. Apparently, Cerrado vegetation cannot compete with the gallery forest under these circumstances. Similarly, Emmerich (1989) reported that this feature can be observed on the intra-montane planes west of Brasília (Cerrado biome), where additional water (and possibly nutrients) from the surrounding slopes allows mesophytic forest to thrive. The centers of these planes, where the groundwater level reaches its minimum are, however, dominated by dense Cerrado.

Recapitulating, the presence of different Cerrado formations can mainly be ascribed to good internal drainage and the absence of waterlogging or other physical barriers to rooting. The soil nutrient status or Al saturation, frequently cited to explain the occurrence of different Cerrado formations, are seen as less important.

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