

Spatial-temporal distribution of fire-protected savanna physiognomies in Southeastern Brazil

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ABSTRACT

The analysis of the influence of edaphic finer textures, as a facilitating factor for the expansion of forest formations in the absence of fire, was possible thanks to rare characteristics found in a savanna fragment located in the State of São Paulo, Brazil. The total suppression of fire for over four decades, and the occurrence of two savanna physiognomies, cerrado sensu stricto and cerradão, allowed the conduction of this study based on the hypothesis that cerradão, a physiognomy of forest aspect consisting of fire-sensitive tree and shrubs species, is favored by fire absence and higher soil hydric retention capacity. Edaphic samples were collected from a regular grid of 200 m² for the production of isopletic maps of the distribution of clay, fine sand, coarse sand and silt edaphic textures by the geostatistic method of ordinary kriging. Changes in the areas occupied by both savanna physiognomies, defined on the basis of aerial photographs taken over a period of 43 years, were assessed through mean variation rates. Besides corroborating the hypothesis of edaphic hydric retention as a facilitating factor for the expansion of forest physiognomies in savanna areas, we were able to infer the positive influence of higher precipitation on the increase in cerradão expansion rates.

Key words: cerrado, fire suppression, geostatistics, savanna dynamics.

INTRODUCTION

The characteristics of plant formations can be influenced by different abiotic factors, such as topography, soils, climate changes (Oliveira-Filho et al. 1994, Clark et al. 1998, Sollins 1998, Lindenmayer et al. 1999, Zeilhofer and Schessl 1999, Miyamoto et al. 2003, Guilherme et al. 2004) and fire (Kauffman et al. 1994, Moreira 2000, Roberts 2001, Ivanauskas et al. 2003). Fire in savannas has been the subject of several studies conducted worldwide (Greig-Smith 1991, Biddulph and Kellman 1998, Laclau et al. 2002, Fensham et al. 2003, Wilson and Witkowski 2003, Harcombe et al. 2004, Townsend and

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Douglas 2004, Barbosa and Fearnside 2005, Cardoso et al. 2008). However, the influence of the soil on the characteristics of savanna plant formations has also held the interest of investigators, such as Furley and Ratter (1988, 1990), Sankaran et al. (2005) and Banfai and Bowman (2007).

In Brazil, recent studies have demonstrated the importance of periodical fires in keeping the balance among the savanna physiognomies encompassed by *cerrado sensu lato*, by ensuring the permanence of these physiognomies, namely *campo limpo*, *campo sujo*, and *campo cerrado*, which are dominated by herbaceous plants and subshrubs, often fire-resistant (Coutinho 1990, 2002, Durigan et al. 1994, Hoffmann 1999). Other factors,

however, seem to play an equally critical role in determining the distribution, composition and structure of savanna forms, *e.g.*, edaphic hydric availability (Furley 1992, Haridasan 1992, Oliveira-Filho and Ratter 2002, Quesada et al. 2004, Marimon Júnior and Haridasan 2005), nearness to other remaining savanna or non-savanna areas (Ribeiro and Tabarelli 2002, Pinheiro and Monteiro 2006), besides the absence of fires (Moreira 2000, Henriques and Hay 2002, Durigan and Ratter 2006).

Incidentally, *campo limpo* is defined as a strictly gramineous physiognomy, commonly found on dystrophic soils. *Campo sujo* is a physiognomic form consisting of scattered shrubs, but dominated by herbaceous plants. *Campo cerrado* is the form where, despite taller shrubs, herbaceous plants still abound. *Cerrado senso stricto* (s.s.) is a physiognomy shared by trees, shrubs and herbaceous plants. *Cerradão* is the term used to describe the woodland where shrubs and trees prevail over herbaceous plants (Eiten 1977, Coutinho 1990, 2002, Ribeiro and Walter 1998). These physiognomies comprise the so-called *cerrado senso lato*, or just *cerrado* (Furley 1999).

The interaction among the above mentioned factors, especially fire, edaphic texture and rainfall variability, has been analyzed to investigate the temporal-spatial dynamics of the boundaries among different plant formations, particularly in Africa and Australia (Fensham and Holman 1999, Bowman et al. 2001, Roquest et al. 2001, Sankaran et al. 2005, Banfai and Bowman 2007). Furthermore, Durigan and Ratter (2006) studied density increase in the remaining areas of savanna vegetation found in the State of São Paulo, Brazil, through rapid successional change in the absence of anthropic pressures, *e.g.* fire.

Some works point out the importance of variation in edaphic hydric availability as an influencing factor in the definition of landscape occupation by plant formations (Jeltsch et al. 1998, Sankaran et al. 2005, Scanlon et al. 2005). Greater edaphic water availability would promote higher woody cover (Jeltsch et al. 1998, Sankaran et al. 2005, Banfai and Bowman 2007). However, fire should also be considered as a major determinant for the establishment of transition between forest and savanna formations (Favier et al. 2004).

In relation to the effects of fire absence on cerrado,

there are two distinct positions. On one hand, Rizzini (1997) advocates that, contrarily to other savanna formations, such as the Venezuelan *llanos*, fire-protected *cerra*dos show no tendency toward forest transition. Coutinho (1990), in turn, corroborated by other authors, as Bowman (2005) and Cardoso et al. 2008), considers that experiments involving long-term fire suppression induced the occurrence of forest transition where cerradão became the dominant vegetation. According to Haridasan (1992), the occupation of cerrado senso stricto by cerradão on dystrophic soils is determined not only by fire absence, but also by edaphic nutrient concentrations sufficient to increase plant biomass during ecological succession. Thus, dystrophic soils would represent a barrier to this mechanism unless sufficiently high soil nutrient concentrations were available at early succession (Haridasan 1992, Marimon Júnior and Haridasan 2005). Haridasan also points out the importance of higher soil hydric retention capacity as a facilitating factor during succession. Some studies, however, confirm that decrease in fire frequency is followed by increase in the density of savanna formations on dystrophic soils (Moreira 2000, Henriques and Hay 2002), indicating the effects of fire exclusion on the thickening of woody individuals and changes in the floristic composition and vegetational structure caused by the germination and growth of small fire-sensitive species (Coutinho 1990, Hoffmann and Moreira 2002).

Geostatistic methods are very helpful tools for the analysis of the spatial-temporal distribution pattern of plant formations (Robertson 1987). One of these techniques, kriging, has been used in surveys of the spatial distribution and characterization of the structure of plant populations and communities (Köhl and Gertner 1997, Grushecky and Fajvan 1999, Ushima et al. 2003, Nanos et al. 2004), studies of topographic influence on the rainfall variability of a given region (Diodato 2005), and analyses of the physical-edaphic hydric characteristics (Grego and Vieira 2005).

This study aimed at assessing the differences in distribution between two savanna physiognomies, *cerrado sensu stricto* (*s.s.*) and *cerradão*, in a savanna fragment over 43 years of fire absence. Therefore, the distribution patterns of these physiognomies were correlated with edaphic texture using ordinary kriging. The analyses

and considerations presented herein were supported by information on the composition and structure of important populations found in both physiognomies.

MATERIALS AND METHODS

THE STUDY AREA AND ITS PLANT COVER

The 38.8 ha study area is located in the municipal district of Corumbataí, São Paulo State (22°15′S e 47°00′W), Brazil (Fig. 1). The climate in this region is characterized as moist tropical, with a dry period between April and September, and a wet season from October through March, *i.e.*, the climate is of the Cwa type in the Köppen classification (Pagano et al. 1989). The soil, defined as red-yellow latosol sandy phase or medium texture, is the predominant type in the Corumbataí river basin (Tauk-Tornisielo and Esquierro 2008).

The terrain has a declivity of approximately 70 m, and lies on a plateau in *Serra dos Padres* (or *Serra de Santana*), in the transition area between the topographical regions North Peripheral Depression and Cuestas (Troppmair 2000). It has remained isolated since 1981, surrounded by sugarcane and grazing fields. The closest plant remainings, which consist of fragments of semidecidual seasonal forest, are found at least one kilometer away on the sides and at the top of the surrounding hills. There are no records of fire since its acquisition over 40 years ago (Camargo and Arens 1967, Piccolo et al. 1971). The water table is very deep – after digging 30 m without finding water, the attempt of building a well was discarded (Camargo and Arens 1967).

Corumbataí *Cerrado* currently features two physiognomies, *cerradão* and *cerrado s.s.* According to the description of *cerrado sensu lato* physiognomies by Eiten (1983), *cerradão* shows forest characteristics, with trees forming a closed canopy of 7 m or more in height, besides an understory forest of scattered shrubs. *Cerrado* comprises trees usually shorter than those found in *cerradão* in addition to herbaceous-subshrub species, though trees taller than 7 m were also found, which is infrequent in similar physiognomies (Eiten 1983).

Few are the savanna fragments located in the State of São Paulo, or even in other regions of the country, with a history of fire suppression such as that of the Corumbataí *cerrado* that has been fire-protected since

its acquisition in 1962. Fire absence was confirmed by the observation of no charred tree trunks.

In a phytosociological study in Corumbataí, sampling only plants of height ≥ 1.5 m in both physiognomies, Marcelo H.O. Pinheiro (unpublished data) found a total basal area of 20.1 m² in *cerradão* and 16.0 m² in *cerrado s.s.*, while total volume was 148,48 m³ and 102,8 m³, for *cerradão* and *cerrado s.s.*, respectively. The included plants had the measured perimeter at 30 cm above the soil. In this study, of the 43 (10 m \times 20 m) plots, 26 (5,200 m²) were installed in the *cerradão* and 17 plots (3,400 m²) in the *cerrado s.s.*

Although the presence of *campo limpo* in the Corumbataí *cerrado* has been previously reported (Camargo and Arens 1967, Piccolo et al. 1971), this study considered the presence of *cerradão* and *cerrado s.s.* alone, based on the analysis of aerial photographs and satellite images.

STUDY OF SAVANNA SPECIES

Both physiognomies were divided into sampling parcels of 200 m² each, 26 of the parcels were located in *cerradão* and 17 in *cerrado s.s.* The parcels were established in a transect that ran along the terrain declivity. The total sample area was 8,600 m². All the tree and shrub plant at least 1.5 m in height were included in the phytosociological survey. The software FITOPAC 1 (Shepherd 1995) was used to calculate the phytosociological descriptors density, relative dominance and frequency, and importance value index (IVI), that it results of the sum of the relative density, relative frequency and relative dominance of each analyzed species. The phytosociological descriptors above were calculated by FITOPAC 1, from the input data of the individuals' heights and diameters belonging to the analyzed species in the study.

Abiotic factors that might have influenced *cerradão* expansion in the absence of fire were discussed based on floristic and phytosociological information about the six most important species sampled in *cerradão*, as determined by IVI. A similar phytosociological study performed in the same region by Cesar et al. (1988) in the 80's was also utilized, so that the past and present structural features of the study savanna area could be compared.

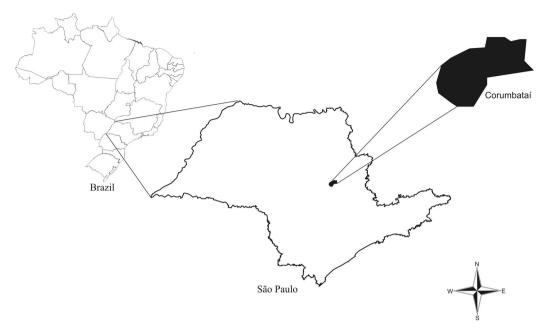


Fig. 1 – Localization of the municipal district of Corumbataí in the State of São Paulo, Brazil.

MAPPING OF THE PHYSIOGNOMIES AND SOIL ANALYSIS

Cartography was performed by compiling the 1:10000 topographic charts, Corumbataí I (SF-23-Y-A-I-2-SO-E) (São Paulo 1979a) and Fazenda da Toca (SF-23-Y-A-I-2-SO-F) (São Paulo 1979b) sheets, from which the study area was drawn. The distribution of the Corumbataí cerrado physiognomies into cerradão and cerrado s.s. was determined by building maps of savanna physiognomy distribution based on the interpretation of aerial photographs produced by a mirror stereoscope. Photographs dated from 1962 (1:25000), 1988 (1:40000), 1995 (1:25000) and 2000 (1:30000) were produced by the company BASE Aerofotogrametria e Projetos SA, and those taken in 1972 (1:25000) and 1978 (1:35000) were produced by IBC/GERCA. The map showing the distribution of the physiognomies in the year 2005 was built with MOLDIS satellite images provided by Digital Globe.

The sequence of aerial photographs showing the distribution of the two savanna physiognomies was used to assess the variation of the area occupied by the two physiognomies over the 43 years considered in this study. Topographic values including declivity and altimetry in the study area were defined with the software SIG IDRISI for Windows (Eastman 1997) using the terrain isolines presented in the 1:10000 topographic charts.

Soil sample collection for physical and chemical analysis was restricted to a regular 100 m² grid defined by 17 randomly chosen georeferenced points (Fig. 2). Steel probes were used to collect soil material at up to 40 cm. The results were interpreted according to the guidelines of Raij et al. (1996) and POTAFOS (1998). Since, according to Landim (2003), who said that randomly collected samples usually provide useful information, we used this method to select samples in a regular grade (Newton 2007).

Soil texture was classified by grain size as follows: 2.0 to 0.2 mm grains – coarse sand; 0.2 to 0.05 mm grains – fine sand; 0.05 to 0.002 mm grains – silt; and grains smaller than 0.002 mm – clay. This classification system, presented by Lemos and Santos (1996), is similar to that proposed by the International Society of Soil Sciences (Klar 1988).

GEOSTATISTICAL ANALYSIS

Geostatistical analysis was performed by the interpolation of soil texture data, *i.e.*, percentage of clay, fine sand, coarse sand and silt, through the ordinary kriging method. This technique was used to build isopletic maps, from which it was possible to infer the distribution of textural components in the study area (Sturaro et al. 2000, Landim 2003).

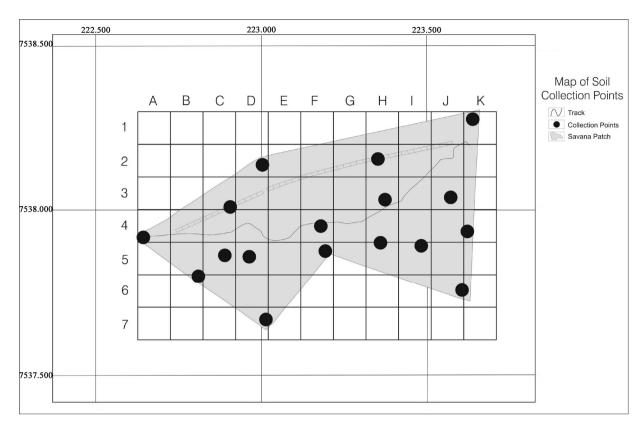


Fig. 2 – Localization of soil collection sites in the Corumbataí fragment in $200 \, \text{m}^2$ regular grids. The smaller numbers are Universal Transverse Mercator (UTM) coordinates.

Kriging allows the estimation of the value of variables distributed over space and/or time from surrounding measured values. It is an exact procedure that takes into consideration all the observed values, and might serve as the basis for automatic computer-assisted cartography, based on values of a regionalized variable distributed over an area (Landim 2003).

The values resultant from chemical soil analysis were not considered for ordinary kriging, but only the percentages of silt, clay, fine sand and coarse sand. Chemical analysis results were not utilized because they reflect the current chemical properties of the savanna soil under study, which have resulted from the influence exerted by the vegetation on the soil chemical status, especially by litter fall decomposition (Daubenmire 1974, Barnes et al. 1997). The edaphic surface horizon tends to quickly respond to the incorporation of the plant biomass generated by its plant cover (Furley 1992). Soil texture, in turn, requires a longer period than that covered by this study, to undergo significant changes

caused by the action of biotic and climatic weathering in conjunction with the type of the rock of origin (Furley and Newey 1983).

The following equation was used to calculate the mean variation of *cerradão* expansion at time intervals defined by different years:

$$\Delta A = \frac{a_2 - a_1}{t_2 - t_1}$$

where ΔA is the mean variation of expansion of the *cerradão* area during the studied time period; a_1 is the initial *cerradão* area during the studied period; a_2 is the final *cerradão* area during the same time; t_1 is the initial year of the studied period and t_2 is the final year of study.

RESULTS

MAPPING OF THE PHYSIOGNOMIES AND EDAPHIC ANALYSES

The distribution of the two physiognomies over the years, represented in the maps indicated a pattern of

continuous *cerradão* expansion with the concurrent retraction of *cerrado s.s.* The analysis of the aerial photographs shows this expansion since 1962, the first year of study (Fig. 3).

By comparing the sequence of distribution maps with the areas occupied by the physiognomies, it was possible to observe the time intervals of more or less intense *cerradão* expansion.

The comparison between two intervals of equal duration, *e.g.*, ten years (1962-1972 and 1978-1988), allows the identification of differences in the intensity of *cerradão* expansion into areas formerly occupied by *cerradão* in 1962-1972 (4.5 ha) was smaller than in 1978-1988 (11.9 ha). Moreover, the areas occupied by *cerradão* in 1995-2000 (2.53 ha) and 2000-2005 (5.62 ha), two five-year periods, were also slightly distinct.

The values obtained in the chemical analyses performed on the 17 collected samples are showed in Table I. The majority of soil samples, P Resin (<2 mg/ dm³, Raij et al. 1996), K (< 0,7 mmol_c/dm³, Raij et al. 1996), Ca (< 3 mmol_c/dm³, Raij et al. 1996) and Mg (<4 mmol_c/dm³, Raij et al. 1996) were low. Sum of bases values (SB) for both physiognomies were considered average values (average values between 2.1-5 mmol_c/dm³, POTAFOS 1998), except in point A4 where it was 17.5, considered as high. Base saturation values (BS) were very low (< 2.5%, POTAFOS 1998) in all points, except for point A4. Organic matter values (OM) in the samples showed slight differences (low values $\leq 15 \text{ g/dm}^3$, POTAFOS 1998). Values of pH were very low (< 4.3, Raij et al. 1996) in almost all edaphic samples collected, which were all defined as dystrophic. Once more, the sample collected at point A4 was an exception, showing base saturation higher than 50%.

The percent variation in texture components, *i.e.* clay, silt, fine sand and coarse sand is observable through the isopletic maps (Fig. 4). The highest rates of clay and fine sand were found in the West of the fragment, whereas the highest rates of coarse sand were seen in the East portion.

GEOSTATISTIC ANALYSIS

The isopletic maps generated by ordinary kriging on the basis of the results obtained in the analyses of the edaphic material collected at the random points (Fig. 2) allowed the establishment of a possible relationship between edaphic texture variation and the expansion of the forest savanna physiognomy (Fig. 4). Cerradão expansion coincided with the occurrence of edaphic texture components defined as having greater hydric retention capacity, e.g., clay and fine sand. However, cerradão occupation started in an area where coarse sand prevails, as shown in the 1972 map in the southeast boundary of the study fragment (Fig. 3). Expansion, however, was not as intense on the west side where, according to kriging, finer textures, i.e., clay and fine sand predominated. In the center of the fragment, high percentages of silt were found. Coincidentally, this fragment area was intensely occupied by cerradão from 1972 to 1988 (Fig. 3).

The rates of variation of occupied area are presented in Table II. It is noteworthy how the rate of variation in areas occupied by $cerrad\tilde{a}o$ (ΔA) over the 1978-1988 10-year period (1.2) is close to that over the 2000-2005 5-year period (1.1).

STRUCTURE OF SAVANNA POPULATIONS

As determined by IVI, the six most important species found in *cerradão* were *Daphnopsis fasciculate* (Meisn.) Nevling (Thymeliaceae), *Amaioua guianensis* Aubl. (Rubiaceae), *Pera glabrata* (Schott) Poepp. ex Baill. (Euphorbiaceae), *Miconia chartacea* Triana (Melastomataceae), *Ocotea pulchella* (Nees) Mez (Lauraceae) and *Copaifera langsdorffii* Desf. (Caesalpiniaceae). These species are listed in Table III, in a decreasing order, according to their IVI in the *cerradão* sampling parcels. Interestingly, in *cerrado s.s.*, the IVI sequence was different.

Total IVI for the *cerradão* species was 41%. The same species sampled in *cerrado s.s.*, contributed to 32.3% of total IVI. In the study performed by Cesar et al. (1988), these species, with the exception of *M. chartacea*, which was not sampled, contributed with 24.6% of total IVI (Table III).

The *D. fasciculate* population showed the highest density (R.De.), dominance (R.Do.) and relative frequency (R.Fr.) in both physiognomies, in agreement with the values reported by Cesar et al. (1988). Therefore, *D. fasciculate* showed the highest IVI values.

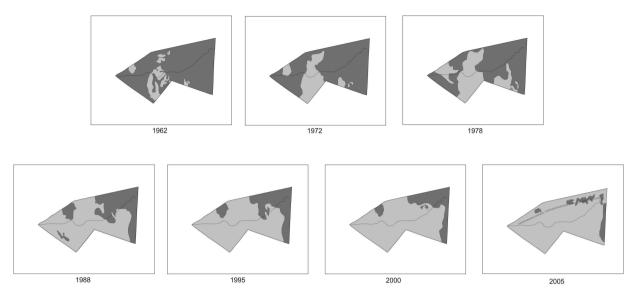


Fig. 3 – Space-temporal variations in both $cerrad\tilde{a}o$ and cerrado s.s. physiognomies over 43 years. Light gray = $cerrad\tilde{a}o$; dark gray = cerrado s.s.

TABLE I

Variations in the chemical analysis of soil samples collected (0-40 cm) from the 17 collection points located in both physiognomies (Fig. 2). K, Ca, Mg, H+Al, SB and CEC values are expressed as mmol_c/dm³. Organic matter (OM); sum of bases (SB); cation exchange capacity (CEC); base saturation (BS).

Collect	resin-P	OM	pН	K	Ca	Mg	H+A1	SB	CEC	BS
points	mg/dm ³	g/dm ³	CaCl ₂	mmol _e /dm ³						%
A4	1	11	5.2	0.5	9	8	14	17.5	31.5	56
B6	1	14	4.2	0.6	3	2	31	5.6	36.6	15
C3	1	25	3.9	0.5	1	1	42	2.5	44.5	6
C5	1	18	4.0	0.6	1	1	47	2.6	49.6	5
D2	1	14	4.0	0.4	1	1	42	2.4	44.4	5
D5	1	20	3.9	0.4	1	1	47	2.4	49.4	5
D7	1	20	4.0	0.9	1	1	50	2.9	52.9	5
F4	1	18	3.9	0.4	1	1	40	2.4	42.4	6
F5	1	14	3.9	0.5	1	1	38	2.5	40.5	6
H2	1	16	3.9	0.4	1	1	45	2.4	47.4	5
Н3	1	20	3.9	0.4	1	1	40	2.4	42.4	6
H4	2	14	4.0	0.4	1	1	31	2.4	33.4	7
I4	1	14	3.9	0.5	1	1	36	2.5	38.5	6
Ј3	1	14	4.0	0.4	1	1	28	2.4	30.4	8
K1	1	11	4.1	0.7	1	1	25	2.7	27.7	10
K4	1	11	4.1	0.2	1	1	20	2.2	22.2	10
K6	1	14	4.1	0.9	1	1	21	2.9	23.9	12

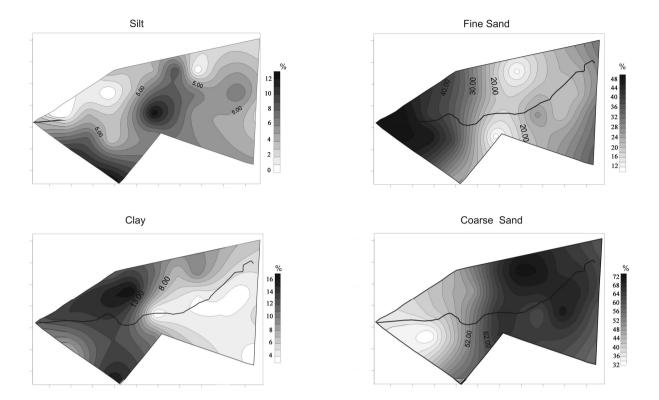


Fig. 4 – Isopletic maps showing variations in the distribution (%) of the four edaphic textures studied (clay, silt, fine sand and coarse sand) as determined by ordinary kriging.

TABLE II

Mean rates of the areas occupied by $cerrad\tilde{a}o$ expansion in the Corumbataí reservation over the different periods (ΔA) ; hectares occupied by $cerrad\tilde{a}o$ expansion over the different periods (EC).

	1962-1972	1972-1978	1978-1988	1988-1995	1995-2000	2000-2005
ΔA	0.45	0.74	1.2	0.34	0.5	1.1
EC	4.5	4.4	12	2.4	2.5	5.6

TABLE III

Phytosociological descriptors of the most important species (as determined by IVI) in cerradão and cerrado s.s., by M. H. O. Pinheiro (unpublished data) and Cesar et al. (1988). Relative density (R.De.); relative dominance (R.Do.); relative frequency (R.Fr.); importance value index (IVI). M. chartacea was not found by Cesar et al. (1988).

importance three index (1+2), 12, comment that not round by Coont or an (2,000).												
	Cerradão					cerraa	lo s.s.		Cesar et al. (1988)			
	R.De.	R.Do.	R.Fr.	IVI	R.De.	R.Do.	R.Fr.	IVI	R.De.	R.Do.	R.Fr.	IVI
Daphnopsis fasciculata	19.66	8.5	3.22	31.38	20.29	7.47	2.74	30.51	10.76	7.66	6.53	24.96
Amaioua guianensis	13.31	7.29	3.22	23.82	8.96	5.37	2.74	17.08	2.53	1.47	2.37	6.37
Pera glabrata	3.08	13.84	3.22	20.14	2.5	5.08	2.74	10.32	1.44	2.59	1,90	5.93
Miconia chartacea	8.89	4.17	3.1	16.16	2.16	1.21	2.26	5.62	_	_	_	_
Ocotea pulchella	5.65	6.84	3.22	15.72	4.33	4.21	2.58	11.12	8.76	6.69	6.02	21.47
Copaifera langsdorffii	6.18	6.17	3.22	15.58	7.15	12.28	2.74	22.18	1.97	10.48	2.57	15.02

DISCUSSION

BRIEF HISTORICAL ANALYSIS

Comparing descriptions of the physiognomies present in the Corumbataí cerrado decades ago (Camargo and Arens 1967, Piccolo et al. 1971) with their current status corroborate that, in the absence of fire, cerradão has undergone an expansion process combined with structural and floristic changes. Both Camargo and Arens (1967) and Piccolo et al. (1971) reported the existence of a savanna physiognomy defined as campo limpo in the Corumbataí cerrado fragment. In this study, especially when aerial photos taken in 1962 and 1972 were considered, no campo limpo physiognomy was found. Only cerradão and cerrado s.s. physiognomies were identified. Although the campo limpo reported by Camargo and Arens (1967) and Piccolo et al. (1971) may make some of the maps showed herein seem contradictory, particularly those of 1962 and 1972, it is possible that these authors misdefined the *campo limpo* physiognomy. In their description of the Corumbataí campo limpo, Camargo and Arens (1967) mentioned Dimorphandra mollis Benth. (Fabaceae) and Ouratea spectabilis (Mart. ex Engl.) Engl. (Ochnaceae), besides species of the genera Bauhinia L., Campomanesia Ruiz and Pav., Kielmeyera Mart. and Zucc. (Clusiaceae), and Stryphnodendron Mart. (Mimosaceae), in which tree and shrub species predominate. Such a physiognomy cannot be considered as a campo limpo according to the classification systems proposed by Eiten (1977) and Oliveira-Filho and Ratter (2002), unless tree and shrub individuals were small and covered by herbaceous plants across the entire area, a fact not confirmed by the aerial photographs taken at that time. Moreover, Camargo and Arens (1967) reported a less dense cerrado s.s. in an area subjacent to the supposed campo limpo. So, perhaps variation was, then, subtle between cerrado s.s. and a probable campo cerrado that comprises shrubs besides herbaceous plants.

Also important is the information provided by Camargo and Arens (1967) and Piccolo et al. (1971) regarding the occurrence of the physiognomy *cerradão* in the Corumbataí fragment in the late 60's. Camargo and Arens (1967) reported the occurrence of taller trees, with up to 12 m, in the southeast of the fragment

where a larger amount of organic matter has now been found, and also the presence of equally dense vegetation at the northwestern most border of the fragment (Camargo and Arens 1967), coinciding with the arrangement shown in Figure 4. Nonetheless, Piccolo et al. (1971) reported a higher tree density close to the center of the fragment where, according to these authors, higher rates of organic matter were found in the soil.

FLORISTIC AND PHYTOSOCIOLOGIC CONSIDERATIONS

The sequence of images showing the distribution of both physiognomies over 43 years of fire suppression evidenced *cerradão* expansion into the areas formerly covered by *cerrado s.s.* Such expansion is consistent with the information provided in several works reporting increased vegetation density in the absence of fires following the occupation of savanna physiognomies by formations of forest characteristics (Coutinho 1990, Hopkins 1992, Ratter 1992, Hoffmann 2000, Moreira 2000, Henriques and Hay 2002, Durigan and Ratter 2006).

Some tree species, e.g., D. fasciculate and Pera glabrata, cited as examples of taxa that can be found in ciliary forests, even in the cerrado biome (Mendonça et al. 1998, Rodrigues and Nave 2000), have played an important role in *cerradão* expansion. These plants currently found in practically the entire Corumbataí, are characteristic of wetter areas and cannot be defined as pyrophitic (Mistry 1998). This information corroborates the absence of fire in the study area, a condition necessary for the progressive expansion of cerradão. Notwithstanding, the greater hydric retention capacity of finer edaphic textures, i.e., fine sand, silt and clay, would be another factor to contribute to the success of the colonization of these species. Haridasan (1992) also considered hydric retention capacity an important feature for the establishment and expansion of cerradão in the absence of fire.

The increased IVI for both species cited above demonstrates the continuous increase in *cerrado s.s.* occupation by *cerradão*. The values for *D. fasciculate* in both *cerradão* and *cerrado s.s.* (31.38 and 30.51, respectively) were higher than the 24.96 found by Cesar et al. (1988). *P. glabrata* IVI was 20.14 in *cerradão*, 10.32 in *cerrado s.s.*, and 5.93 in the survey by Cesar et al. (1988). On the other hand, an important consequence

of fire absence in the study area relates to the decrease in savanna trees and shrubs, such as *Ouratea spectabilis*, *Qualea multiflora* Mart. (Vochysiaceae), *Tocoyena Formosa* (Cham. and Schltdl.) K. Schum. (Rubiaceae) and *Vochysia tucanorum* Mart. (Vochysiaceae) (Durigan et al. 2004, Pinheiro and Monteiro 2006) according to our observations. This phenomenon can be noticed by comparing the IVIs of these species over the two distinct periods described by Cesar et al. (1988) and M.H.O. Pinheiro (unpublished data).

Thus, the occurrence of fire-sensitive forest species, e.g. Calyptranthes clusiaefolia (Miq.) O. Berg (Myrtaceae), Nectandra megapotamica (Spreng.) Mez (Lauraceae) and Palicourea macgravii St. Hil. (Rubiaceae) in the Corumbataí cerrado is concurrent with the results obtained by Moreira (2000), Henriques and Hay (2002) and Hoffmann and Moreira (2002), who observed the same phenomenon in cerrado areas after fire suppression. One of the species mentioned by those authors was Miconia albicans (Sw.) Triana, also present in both physiognomies studied. These results seem to also corroborate the successional model proposed by Pivello and Coutinho (1996), who considered cerradão as a transition stage to the occupation of forest formations.

Other species were defined as forest taxa or components of ciliary woods found in the cerrado biome, e.g., Amaioua guianensis Aubl. (Rubiaceae), Croton floribundus Spreng. (Euphorbiaceae), Miconia chartacea Triana (Melastomataceae) and Trichilia hirta L. (Meliaceae). The occupation of the studied fragment by fire-sensitive species was probably intensified by the increase in generalist tree species, e.g., Copaifera langsdorffii Desf. (Caesalpiniaceae), that contributed to change microenvironmental conditions, e.g. greater shading, lower soil temperatures and higher edaphic moisture, favoring the recruitment of the small plants that started to become part of the savanna forest physiognomy (Setterfield 2002, Banfai and Bowman 2007). M. chartacea, found by us, but not by Cesar et al. (1988), is a good example of this facilitating phenomenon. However, if the study area had tended towards an opposite condition, i.e., occasional fires still occurred, the floristic composition and the density of cerrado s.s. species would probably be favored (Felfili et al. 2000).

The facilitating mechanism proposed above proba-

bly played an important role in the expansion observed in the Corumbataí cerradão fragment over the study period. In addition, the possible influence of the reduced occurrence of savanna bird species and the increase in the number of forest birds in the study fragment (Willis 2006) should also be considered. This would have been influenced by the absence of fire that would have caused the vegetation to become denser, changing the structure of phytocenoses (Macedo 2002). Similarly, Skowno and Bond (2003) observed that the increase in vegetation density in South-African grassy savannas following fire exclusion resulted in the loss of avifauna species dependent on these phytocenoses. It is probable that the growing colonization of the Corumbataí savanna fragment by forest woody plants occurred via propagules, found in the forest remaining areas located nearby, brought by forest avifauna. The importance of the floristic influence exerted by the nearness of remainings was pointed out by Bowman et al. (2001), Ribeiro and Tabarelli (2002) and Pinheiro and Monteiro (2006).

GEOSTATISTIC ANALYSIS AND EDAPHIC CHARACTERISTICS

The results of ordinary kriging combined with the analysis of the images of the spatial variation of occupation in both physiognomies corroborated the information reported by Hopkins (1992), who correlated the occupation of savanna forest formations with clay and sand edaphic textures, respectively, in regions of contact between both formations. The same results also corroborated Moreno and Schiavini (2001), Ruggiero et al. (2002) and Marimon Júnior and Haridasan (2005). These studies indicated the importance of fine edaphic textures for greater soil water retention as they increased edaphic hydric availability to the plants (Ruggiero et al. 2002, Marimon Júnior and Haridasan 2005), hence the regulation of nutrients in the soil (Marimon Júnior and Haridasan 2005). Nevertheless, the present work resorted to chemical soil analyses to show that the study area presents no significant edaphic fertility differences. Furthermore, the occurrence, in the whole studied area, of a soil defined as dystrophic, would be a considerable indicator of the importance of the edaphic structure on the increase in vegetation density, in the absence of fires, and in areas that used to be occupied by open

savanna physiognomies, as *cerrado senso stricto* and *campo cerrado*.

Based on the distribution of edaphic textures predicted by kriging, it was possible to infer how such distribution might have influenced the increase in the area occupied by *cerradão* over the study period. As suggested by Sollins (1998) and Hibbard et al. (2001), the greater capacity to retain water in the soil shown by finer textures, such as clay, might have facilitated *cerradão* expansion in the absence of fire. However, it was possible to notice *cerradão* occupation in an area located in the southeast of the fragment where there was a greater predominance of coarse sand (Fig. 4). This can be observed in the 1962 image of the fragment (Fig. 3). In images taken over the subsequent years, however, expansion in this area was visibly less intense and comparable to that where finer textures predominated.

Cerradão expansion, apparently more intense over some of the study time periods of equal duration, e.g. 10-year periods, i.e., 1962-1972 and 1978-1988 (expansion rates of 0.45 and 1.2, respectively), may as well have resulted from climatic influences, specifically differences in rainfall over both 10-year periods. In this case, the higher cerradão expansion rates observed during periods of higher precipitation show similarities with the results reported by Jeltsch et al. (1997), Bowman et al. (2001), Fensham et al. (2003) and Tews et al. (2005), and some proposed models such as that developed by Jeltsch et al. (1998) to explain competition for hydric resources between woody and herbaceous components of African semi-arid savannas.

Future studies of climatic influence including correlation analyses of the variations between the areas occupied by both physiognomies along the years, and precipitation values over this period, can determine the importance of the climate, particularly pluviometric variation in the absence of fire, for the expansion of forest formations and denser savanna physiognomies in Brazilian *cerrados*. These data would help achieving a better understanding of the dynamics of forest-savanna tension areas under similar conditions.

High annual precipitation rates and soils of higher hydric retention capacity would not particularly favor savanna plant species, but would be greatly beneficial to forest tree and shrub species that require a greater hydric availability and can bear greater edaphic moisture (Medina and Silva 1990). Thus, the combination of high-rates of fine edaphic textures, *e.g.* clay, to maintain moisture (Ruggiero et al. 2002), organic matter and soil microorganisms (van Keulen 2001) with fire suppression for decades would provide the ideal environmental conditions for the establishment of many forest tree and shrub species in the *cerrado* of Corumbataí.

Although Bowman et al. (2001) pointed out the importance of the water table for the increase of woody species biomass, this factor should be ruled out in the case of the Corumbataí area. The fact that the depth of the local water table exceeds 30 m prevents woody plants to reach it. This information also points to the importance of fine soil textures for hydric retention as they meet plant water demand in the Corumbataí savanna fragment before percolation accentuates hydric restriction, especially over periods of drought.

The results of kriging combined with the information found by Camargo and Arens (1967) and Piccolo et al. (1971) allowed interesting inferences. In the sites mentioned by Camargo and Arens (1967) as of occurrence of denser vegetation, the soil, according to the results provided by the kriging, would present higher percentages of silte. Kriging also showed the distribution tendency of fine edaphic textures, such as clay and silt, in the fragment area previously described as a site where denser vegetation occurred (Fig. 4) by Piccolo et al. (1971).

In this study, the analysis of edaphic texture characteristics could not support Haridasan (1992) and Marimon Júnior and Haridasan (2005), who suggested that, in the absence of fire, savanna soils require enough nutrients to start secondary succession when local plant biomass increase occurs. However, information provided by Cesar et al. (1988) in the Corumbataí fragment revealed that, although values were very high on the surface layer, deeper horizons (circa 100 cm) could be defined as dystrophic. Thus, as this study was based on the collection of edaphic samples at a maximum depth of 40 cm, the chances that the results obtained masked more elevated values for base addition, for example, should be taken into account. If the soil samplings were restricted to the surface horizon, i.e., above 20.0 cm, fertility results would be more elevated, then supporting the hypothesis of Haridasan (1992) and Marimon Júnior and Haridasan (2005).

Nonetheless, an increasing number of studies, such as those conducted by Moreira (2000), Henriques and Hay (2002) and Marimon Júnior and Haridasan (2005), even cannot be ignored as they indicate that, in the absence of fire, savanna dystrophic soils are likely to bear succession mechanisms towards a climax where forest physiognomies dominate. According to Marimon Júnior and Haridasan (2005), clay soils under *cerradão* can hold a larger amount of water, playing a role in processes of active edaphic fertility. The greater hydric availability in these soils regulates the dynamics of nutrients and plant absorption.

Within this framework, Haridasan (1992) suggested that greater edaphic hydric availability may favor savanna-forest transition and play an important role in the establishment of forest formations (Furley 1992). However, for the same author, in soils currently exhibiting this texture, which maintains *cerradão* formations, and may be defined as dystrophic, nutrient availability was probably greater in the past (Haridasan 1992). This mechanism, which would also include an efficient cycling of nutrients, allowed the increase in plant biomass over secondary succession, and maintained plant biomass even when the concentrations of edaphic nutrients declined (Haridasan 1992).

INFORMATION ABOUT SIMILAR SAVANNA AREAS

The historical analysis of two savanna remainings described by Coutinho (1990) and Rizzini (1997) at Emas Experimental Station in Pirassununga, São Paulo State, and Paraopeba Horto Florestal in Paraopeba, Minas Gerais State, respectively, leads to an impasse regarding the effect of the absence of fires on savanna formations.

These savanna remainings, cited by Rizzini (1997) as examples of *cerrado* areas that would not undergo further changes in the absence of fire, were the same that Coutinho (1990) mentioned as examples of less dense savanna remainings, which in opposition to the description of Rizzini, suffered floristic and structural changes after long periods of fire suppression. According to Coutinho, these changes culminated with the occupation of these areas by *cerradão*. This information was confirmed by Delitti et al. (2001), in a study of the *Emas cerrado* as

well as by other works developed in other savanna areas in different parts of Brazil (Toledo-Filho et al. 1989, Ratter 1992, Moreira 2000, Henriques and Hay 2002, Durigan and Ratter 2006).

The information above raises questions about the length of observations. Rizzini (1997) reported a period of 35 years in his study of the Emas cerrado, whereas Coutinho (1990) stated that, after 43 years of fire protection in Emas, campo sujo was replaced by cerradão. Would eight years, which is the difference among the observation periods used by these authors, be enough to change the savanna physiognomy of Emas as described by Coutinho (1990)? As previously said, periods of higher precipitation combined with fire absence could have caused Emas and even Paraopeba to be occupied by cerradão species, leading to later marked expansion (Durigan and Ratter 2006), as observed in different savanna formations (Bowman et al. 2001, Sankaran et al. 2005, Banfai and Bowman 2007), and even in a forest formation in North America (Harcombe et al. 2004). The absence of pronounced dry periods as reported by Fensham et al. (2003), about the occupation of an Australian savanna by wet forest, as well as by the model developed by Tews et al. (2005), combined with fire suppression (Durigan and Ratter 2006), might have represented a positive conjunction of factors for the thickening of the woody vegetation in these savanna reserves.

Another aspect of no less importance for the composition and structural changes of the areas occupied by savanna physiognomies in Corumbataí, and also discussed by Jeltsch et al. (2000) and Setterfield (2002), is the potential influence of microsites originated from the accumulation of organic matter, as in the case of Corumbataí, and also by finer edaphic textures, as described by Moreno and Schiavini (2001) in a study developed in Minas Gerais. As suggested by us, microsites might have arisen as a consequence of the very establishment and expansion of cerradão. If the accumulation of edaphic organic matter can affect, over a long time, the increase in soil water retention efficiency (Daubenmire 1974, Barnes et al. 1997) and edaphic fertility (Durigan and Ratter 2006), and, in consequence, in the establishment and development of small plants of different species (Richards 1983, Svenning 2001, Santos and Válio 2002), the increment in the production and decomposition of litter fall in areas occupied by *cerradão* may have synergistically worked for the success of the occupation of the Corumbataí savanna by *cerradão* over the decades of fire absence.

CONCLUSIONS

In the Corumbataí *cerrado*, higher edaphic hydric retention capacity might have minimized, in the absence of fire, the competitive advantage of savanna species as the fragment was increasingly occupied by forest species. The developed root system characteristic of the tree and shrub savanna species, which is capable to ensure vegetative reproduction even after burns, as well as water obtention deep in the soil, no longer represents a potential advantage for these species. This might have occurred when fire started to be suppressed. Furthermore, the retention of water in the soil for a longer time provided by finer edaphic textures before percolation to deeper horizons would have also favored forest species.

In the absence of fire, savanna fragments similar to that in Corumbataí are likely to be increasingly occupied by forest species and, thus, affect the permanence of *cerrado sensu lato*. Adequate management techniques including controlled fires applied at appropriate times should be developed and employed by conservation organizations to the benefit of savanna plant and animal species.

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RESUMO

A influência de texturas edáficas finas, como fator de facilitação para a expansão de formações florestais sobre áreas savânicas, através da maior retenção hídrica edáfica, na ausência de incêndios, foi possível ser estudada graças às características encontradas em um fragmento savânico com 38,8 ha, situado em Corumbataí (SP). A supressão total do fogo por quatro décadas, e a ocorrência de duas fisionomias, cerrado sensu stricto e cerradão, permitiram a condução deste estudo. Amostras de solo foram coletadas em uma grade regular de 200 m², abrangendo toda a área do fragmento. Foram produzidos mapas isopléticos, com a distribuição das porcentagens de argila, areia fina, areia grossa e silte, utilizando-se o método geoestatístico krigagem ordinária. As mudanças nas áreas ocupadas por ambas as fisionomias foram definidas a partir de fotografias aéreas abrangendo um período de 43 anos. Essas imagens também permitiram o cálculo das taxas médias de ocupação das fisionomias nas quatro décadas. Além de corroborar a hipótese de retenção edáfica hídrica, como um fator de facilitação para a expansão de fisionomias florestais, sobre áreas savânicas, foi possível também inferir sobre a influência positiva de períodos de maior pluviosidade, para a expansão mais acentuada do cerradão.

Palavras-chave: cerrado, supressão do fogo, geoestatística, dinâmica de savanas.

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