TWENTY YEARS OF POST-FIRE PLANT SUCCESSION IN A "CERRADO", SÃO CARLOS, SP, BRAZIL

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ABSTRACT

Secondary succession in degraded areas is little studied, especially where long-term observation of evolutionary processes is concerned. The aim of this work was to follow the qualitative and quantitative changes in vegetation throughout the regeneration process after fire in a cerrado with forest physionomy. The area under study is a reserve on CPPSE-EMBRAPA's farm, São Carlos region of São Paulo State, Brazil. In 1981, an especially destructive fire eliminated the aerial part of the vegetation and litter. From that time, the vegetation in three permanent quadrats of 2 x 20 m was recorded for twenty years. The results demonstrated the rapid growth of herbs, shrubs, climbers and trees successively, with a great species richness and, after a certain time, a decline in density at a rate similar to the initial recovery. Both the soil seed bank and sprouting subterranean organs played important parts in the recovery of the vegetation. Three phases were observed in the plant succession: plant growth, followed by intraspecific competition with a reduction in the number of individuals and finally interspecific competition with the disappearance of some species from the quadrats. The different populations behaved similarly and the rise and fall in density of each species over time reflected their ecological role.

Keywords: post-fire succession, woody savanna, forest savanna, secondary succession.

RESUMO

Sucessão vegetal após fogo ao longo de trinta anos em um cerrado, São Carlos, SP, Brasil

A sucessão secundária em áreas degradadas é pouco estudada, principalmente em relação ao acompanhamento dos processos evolutivos por longo período. O objetivo deste trabalho foi de verificar as mudanças qualitativas e quantitativas da vegetação durante o processo de regeneração após fogo em um cerrado com fisionomia de cerradão. A área estudada pertence a uma reserva institucional da CPPSE-EMBRAPA, São Carlos, SP, Brasil. No ano de 1981 ocorreu um incêndio de proporções elevadas eliminando todo o folhedo e o dossel. O acompanhamento foi realizado em três parcelas fixas de 2 x 20 m ao longo de vinte anos. Os resultados demonstraram um rápido estabelecimento de indivíduos sucessivamente com plantas herbáceas, arbustivas, lianas e arbóreas, uma grande riqueza em espécies e, depois de determinado tempo, uma regressão em densidade na mesma ordem de estabelecimento. O banco de sementes do solo e o rebrotamento subterrâneo tiveram papel importante na recuperação da vegetação. No processo sucessional ocorreram três fases sucessivas: estabelecimento de plantas; competição intra-específica devido ao reajuste no número de indivíduos por espécies e competição interespecífica com a eliminação de algumas espécies das parcelas. As populações analisadas apresentaram padrões semelhantes de comportamento e a maior ou menor densidade ao longo do tempo refletiu o comportamento ecológico das espécies.

Palavras-chave: sucessão pós-fogo, cerradão, savana, sucessão secundária.

INTRODUCTION

It is common for humans to use fire to renovate the aerial biomass of vegetation, fertilize the soil and improve palatability of the plants for pasturing. Various authors such as Coutinho (1981) and Vicentini (in Dias *et al*., 1996) have mentioned fire occurrence, since prehistory, both of natural and anthropic origin. Frequent burning favors the maintenance and expansion of savanna formations in Brazil (Coutinho, 1982) and in others countries (Trollope, 1982; Sarmiento, 1983; Calvo *et al*., 2002).

Burning causes qualitative and quantitative modifications in plant community structure (Souza & Soares, 1983; Eiten & Sambuichi, 1996), in the timing and intensity of flowering (Coutinho, 1982), in population dynamics (Raw & Hay, 1985) and in the competitivity of species (Viro, 1974), making it possible to select plants with protective structures against fire (Rachid, 1956). As a consequence, it promotes open physiognomies with fewer woody elements, and abandoning burned areas permits the vegetation to return to a state equal or similar to pre-fire physionomy (Eiten & Sambuichi, 1996; Moreira, 2000). This constitutes a regeneration process of the vegetation, through successive phases, called secondary succession. The dynamics of populations and plant communities during the process of succession towards a state equal or similar to the original is poorly known, particularly in tropical regions, with little literature citation.

The aim of this work was to observe and record the post-fire regeneration process in a woody savanna to discover the patterns of community behavior and the dynamics of the species throughout this period.

METHODOLOGY

This study was conducted in a "cerrado" reserve with forest physiognomy (woody savanna) on the Canchim Farm, São Carlos (SP, Brazil) 22° 01' S and 47° 53' W, which belongs to CPPSE-EMBRAPA, and has been preserved for more than 60 years. Cool dry winters and hot rainy summers are typical of the region. There may also be frost once or twice a year. Embrapa-CPPSE (1999) described the local climate as tropical of altitude, Cwa in the Köppen system. The soil belongs to the dark-red Latosol group with areas of quartz sand.

This woody savanna constitutes an official reserve of 592 hectares divided into two parts by a main road. There was an accidental fire at the beginning of October, 1981 in one of these areas. Owing to a hard frost in that winter, followed by a dry season, there was a large quantity of dry biomass on the soil and in the canopies, providing fuel for a huge fire. In the affected area about 18.4% of the plants did not show signs of sprouting, 76.6% had basal shoots and 5% showed aerial shoots just six months after the fire (Souza & Soares, 1983).

For 20 years following the fire, the regeneration of vegetation in three permanent quadrats of 2 x 20 m was studied. They were separated by about 50 m from each other and subdivided into 2 x 2 m plots to facilitate the identification and counting of plants. To standardize the plant count, each sign of growth in the soil, or set of shoots emerging from a single burnt trunk was regarded as an individual. The plants that were difficult to identify in the seedling phase were marked for observation during development and, at the same time, other seedlings of the same species, located in adjacent areas of the quadrats, were collected for botanical study and integrated into a field catalogue. The unidentified seedlings were divided into morphospecies and counted as such. These procedures facilitated the identification and counting in subsequent surveys. Botanical material was collected only from plants that had grown sufficiently to allow part of the plant to be removed without altering the natural regeneration process. The plants were identified by comparing them with material in the HUFSCar herbarium. Some young plants disappeared during the observation period, without having been identified, and were included in the same category as unidentified seedlings. Classifications in trees, shrubs and climbers were based on Mendonça *et al*. (1998), and observation of the predominant habitat in the region.

Time intervals between surveys varied according to the stability of the vegetation during the regeneration process (Table 2). After the first year, the field surveys were conducted in the dry season to decrease the recording ephemeral seedlings.

The Shannon and Weaver Index - Log. N (Marrugan, 1988) was used to calculate the diversity

of species and the Jaccard Index to estimate floristic similarity between successive samples (before and after with the symbology of 1 year: 2 years, etc.) and floristic similarity between quadrats. The similarity was based on the presence/absence of species in the plots. Several authors have used these indices for similar purposes (Shafi & Yarranton, 1973; Torres *et al*., 1997).

Concerning the population analyses, species from different synusia having different behavior and a large number of individuals were chosen.

RESULTS AND DISCUSSION

Studies on plant succession have indicated a number of difficulties: identification of species in the various development stages; the timescale required to detect patterns of a community's behavior and the fact that many species in the "cerrado" sprout from subterranean systems, making it hard to distinguish between plants deriving from germination or sprouting.

During the observation period of this study, 112 plant species were found (Table 1), of which 62 were shrubs, 37 trees and 13 climbers. The type of vegetation and the quadrat size can explain the dominance of shrub species. Larger quadrats would tend to sample more trees, while smaller species would be repeated. The analysis of herbaceous species has been published separately due to the shorter period of registering them (Soares & Lima, 2000).

Compared to the data from Silva (1996), who carried out a phytosociological survey using the point-centered quarter method of the species with PBH (perimeter at breast height) above 10 cm in a contiguous area among the 77 species found by this author, 39 were common to this work, being in general, those of higher Importance Value. This floristic similarity enables comparisons to be made between the two areas, taking into account methodological differences.

Tables 2, 3 and 4 show the number of plants per species, number of new species recorded, total numbers of plants and numbers of unidentified seedlings, with their respective morphospecies. The individual number rose geometrically between eight months and a year and half. After this, there was a decrease in plant density, which did not reach a stable value at the end of this study. Large numbers of individuals appeared in the first year. Quadrat 1 had a maximum of 972 individuals (24.2/m^2) and 69 species; quadrat 2, 1,057 individuals (26.4/m^2) and 81 species; and quadrat 3, 1,243 individuals (31.0/m^2) and 78 species. These values are much higher than those found by other authors in tropical forests. Uhl *et al*. (1982) found maximum values of 12.7 plants/1.5 m^2 in the forest of the upper Rio Negro (Amazon). Some species disappeared from our samples for a certain period perhaps due to death and were followed by the growth of new plants in the quadrat, or simply by death and regrowth of the aerial parts.

Regarding the species distribution, 45 species were common to all three quadrats; 26 occurred in two quadrats and 44 in only one. By the Jaccard Index, the floristic composition of the three quadrats was similar, with value of 51% between quadrats 1 and 2; 52% between quadrats 1 and 3 and 55% between quadrats 2 and 3. This similarity demonstrated that the quadrats of 2 m x 20 m were suitable to sample most species and were for the intended purpose as the majority of the plants were seedlings or very young plants having a high density per square meter.

The species with the largest numbers of individuals during the succession were: *Copaifera langsdorffii, Eugenia albotomentosa, Myrcia lingua, Ocotea pulchella, Roupala montana* and *Xylopia aromatica* among trees; *Memora peregrina, Campomanesia pubescens, Didymopanax vinosum, Gochnatia pulchra* and *Miconia albicans* among the shrubs and *Heteropteris byrsonimifolia* among the climbers.

Individuals and species grew rapidly, with peak values occurring between six months and one year in each quadrat. After this period, there was a rapid reduction in the number of plants and a slow and constant decrease of species, the latter becoming more evident after the tenth year.

After a fire there is a large supply of nutrients from the ashes and light, due to the canopy having been eliminated (Christensen, 1985), which helps a large number of seedlings to develop. Therefore, after the "installation" period, the competition process began for the growing plants, and this was brought on by the restriction of light, nutrients and available physical space. The number of individuals per species decreased more quickly than the number of species indicating that intra-specific competition

TABLE I
Plant species encountered over twenty years of post-fire regeneration in a woody savanna (cerrado) São Carlos, SP, Brazil and their life forms.

Families	Species	Life form
Anacardiaceae	*Anacardium humile* St. Hil.	Shrub
Annonaceae	*Xylopia aromatica* St. Hil.	Tree
Apocynaceae	*Aspidosperma tomentosum* Mart.	Tree
	Forsteronia velloziana (A. DC.) Woodson	Climber
	Temnadenia violacea (Vell.) Miers	Climber
Araliaceae	*Didymopanax vinosum* March.	Shrub
Arecaceae	*Attallea geraensis* Bar. Rodr.	Shrub
	Syagrus flexuosa (Mart.)Becc.	Shrub
Asteraceae	*Bacharis* sp.	Shrub
	Eupatorium maximilianum Schrad.	Shrub
	Eupatorium squalidum DC.	Shrub
	Gochnatia pulchra Cabrera	Shrub
	Hoenephyton trixoides (Garner) Cabrera	Shrub
	Piptocarpha rotundifolia (Less.) Baker	Tree
	Vernonia ruficoma Cham. & Schltdl.	Shrub
Bignoniaceae	*Distictella mansoana* (DC.) Bureau	Climber
	Jacaranda caroba DC.	Shrub
	Jacaranda decurrens Cham.	Shrub
	Memora peregrina (Miers.) Sandwich	Climber
	Pyrostegia venusta Miers	Climber
	Tabebuia ochracea (Cham.) Standl.	Tree
Bromeliaceae	*Ananas ananassoides* (Baker) L.B. Smith	Shrub
	Bromelia antiacantha Bertol.	Shrub
Burseraceae	*Protium heptaphyllum* (Aubl.) March	Shrub
Caryocaceae	*Caryocar brasiliense* Camb.	Tree
Connaraceae	*Connarus suberosus* Planch.	Shrub
Cucurbitaceae	*Cayaponia spelina* (Manso) Gogn.	Climber
Dilleniaceae	*Davilla rugosa* Poir.	Shrub
Erytroxylaceae	*Erytroxylum campestre* St. Hil.	Shrub
	Erytroxylum cuneifolium (Mart.) O.E.Schultz	Shrub
	Erytroxylum sp.	Shrub
	Erytroxylum suberosum St.Hil.	Shrub
Euphorbiaceae	*Croton* sp.	Shrub
	Ditassa mucronata Mart.	Climber
	Mabea fistulifera Mart.	Tree
	Pera obovata Baill	Tree
	Sapium glandulatum (Vell.)Pax	Shrub
Fabaceae – Caesalpinioidae	*Bauhinia holophylla* Steud.	Shrub
	Cassia langsdoffii Kunth	Shrub
	Copaifera langsdorffii Desf.	Tree
	Dimorphandra mollis Benth.	Tree
	Galactia sp.	Shrub
Fabaceae – Mimosoidae	*Anadenanthera falcata* (Benth.) Speg.	Tree
	Stryphnodendron adstringens (Mart.) Coville	Tree
	Stryphnodendron obovatum Benth.	Tree
	Stryphnodendron polyphyllum Mart.	Tree
Fabaceae – Papilionoidae	*Acosmium dasycarpum* (Vog.) Yakol.	Shrub
	Acosmium subelegans (Mohlembr.) Yacovlev	Shrub
	Andira humilis Mart.	Shrub
	Dalbergia miscolobium Benth.	Tree
	Machaerium acutifolium Vog.	Tree
	Pterodon emarginatus Vog.	Tree
Flacourtiaceae	*Casearia sylvestris* SW.	Shrub
Hypocrateaceae	*Peritassa campestris* (Camb.) A.C.Smith	Shrub
Lauraceae	*Ocotea pulchella* Mart.	Tree
Malphiguiaceae	*Heteropteris byrsonimifolia* L. Rich.	Climber
	Byrsonima coccolobifolia (Spr.) Kunth	Shrub

TABLE 1
Continued...

Families	Species	Life form
	Byrsonima intermedia A. Juss.	Shrub
	Byrsonima verbascifolia Juss.	Shrub
	Banisteriopsis stellaris (Griseb) B. Gates	Climber
Melastomaceae	*Leandra aurea* (Cham.) Cogn.	Shrub
	Miconia fallax DC.	Shrub
	Miconia albicans Triana	Shrub
	Miconia langsdorffii Cogn.	Tree
	Miconia ligustroides (DC.) Naud.	Shrub
	Miconia rubiginosa (Bonpl.)DC.	Tree
	Miconia stenostachia DC.	Shrub
	Tibouchina stenocarpa (DC.) Cogn.	Shrub
Monimiaceae	*Siparuna guianensis* Aubl.	Tree
Moraceae	*Brosimum gaudichaudii* Trécul	Shrub
Myristicaceae	*Virola sebifera* Aubl.	Tree
Myrsinaceae	*Rapanea guyanensis* Aubl./tree	Tree
	Rapanea umbellata (Mart.)Mez./tree	Tree
Myrtaceae	*Campomanesia pubescens* (DC.) O. Berg.	Shrub
	Eugenia albotomentosa Camb.	Tree
	Eugenia bimarginata DC.	Tree
	Eugenia obversa Berg.	Tree
	Eugenia pitanga (Berg.)Kiaersk	Shrub
	Eugenia polyphylla O. Berg.	Shrub
	Eugenia sp. 1	Shrub
	Eugenia sp. 2	Shrub
	Eugenia sp. 3	Shrub
	Eugenia spathophylla O. Berg.	Tree
	Myrcia lingua Berg.	Tree
	Myrcia sp.	Tree
	Psidium grandifolium Mart.	Shrub
Nyctaginaceae	*Guapira noxia* (Netto) Lund	Tree
	Neea theifera Oersted	Tree
Ochnaceae	*Ouratea spectabilis* (Mart.) Engl.	Shrub
Passifloraceae	*Passiflora villosa* Well.	Climber
Proteaceae	*Roupala montana* Aubl.	Tree
Rubiaceae	*Alibertia sessilis* (Vell.) K.Schum.	Shrub
	Alibertia sp.	Shrub
	Amaioua guianensis Aubl.	Tree
	Palicourea rigida H.B.K.	Shrub
	Psychotria barbifolia DC.	Shrub
	Psychotria capitata Ruiz & Pav.	Shrub
	Psychotria sessilis (Vell.) Muli. Arg.	Shrub
	Psychotria sp.	Shrub
	Rudgea viburnoides (Cham.) Benth.	Shrub
	Tocoyema formosa (C. & S.) K. Schum.	Shrub
Sapindaceae	*Serjania erecta Radlk.*	Shrub
	Serjania caracasana (Jacq.) Willd	Climber
	Serjania lethalis A.St. Hil.	Climber
Sapotaceae	*Pradosia brevipes* (Pierre) Penn.	Shrub
	Pouteria torta (Mart.) Radlk	Tree
Smilacaceae	*Smilax* sp.	Climber
Styracaceae	*Styrax camporum* Pohl	Tree
Verbenaceae	*Aegiphylla lhotzkiana Cham.*	Shrub
	Lippia lupulina Cham.	Shrub
Vochysiaceae	*Vochysia tucanorum* (Spr.) Mann.	Tree

TABLE 2
Plant species and number of individuals in post-fire regeneration in quadrat 1 (40 m²) in a Cerrado, São Carlos, SP, Brazil. Observation from 10/1981 to 06/2001.

	Time in days												
Species	**7**	**14**	**36**	**71**	**105**	**141**	**240**	**360**	**590**	**820**	**1517**	**3680**	**7300**
Didymopanax vinosum	-	13	40	33	34	37	33	30	27	24	25	17	2
Memora peregrina	-	19	39	56	51	50	50	54	48	44	50	25	15
Gochnatia pulchra	-	14	32	47	45	48	47	42	44	26	33	29	8
Bauhinia holophylla	-	3	9	11	14	16	15	12	11	10	11	11	3
Byrsonima intermedia	-	11	1	2	9	9	9	10	11	9	10	8	2
Distictella mansoana	-	10	12	11	16	15	12	11	10	8	12	30	4
Attallea geraensis	-	3	3	3	3	3	3	3	3	3	3	5	6
Cassia langsdorffii	-	3	3	3	3	3	3	3	2	1	1	1	0
Cayaponia spelina	-	1	5	8	12	14	12	11	8	8	2	3	0
Serjania lethalis	-	1	1	1	1	2	2	2	2	0	0	0	0
Ananas ananassoides	-	1	1	1	1	1	1	1	2	2	2	1	4
Syagrus flexuosa	-	1	1	1	1	1	1	1	1	1	1	0	0
Davilla rugosa	-	2	2	2	2	2	0	0	0	0	0	0	0
Banisteriopsis stellaris	-	2	2	4	4	3	3	3	3	1	1	2	2
Serjania caracasana	-	1	1	2	2	2	1	1	2	0	1	0	0
Myrcia lingua	-	-	15	21	27	31	33	40	43	32	28	19	16
Roupala montana	-	-	7	8	15	28	42	78	85	54	50	26	19
Ocotea pulchella	-	-	6	15	21	26	34	32	32	20	21	13	9
Miconia falax	-	-	3	19	43	78	82	65	70	47	54	39	20
Miconia albicans	-	-	3	17	40	75	81	64	70	46	53	40	21
Acosmium dasycarpum	-	-	5	9	11	15	15	16	16	11	13	11	8
Smilax sp.	-	-	3	9	13	16	18	16	19	11	12	13	0
Erytroxylum suberosum	-	-	3	6	5	5	5	8	9	10	9	11	4
Temnadenia violacea	-	-	1	2	2	2	3	2	3	3	3	3	2
Erytroxylum campestre	-	-	1	1	1	6	6	6	5	4	12	8	9
Ouratea spectabilis	-	-	1	2	4	5	5	5	7	6	4	6	2
Styrax camporum	-	-	2	2	2	4	4	4	5	3	3	3	2
Stryphnodendron adstringens	-	-	2	2	2	2	2	2	2	2	2	2	0
Anadenanthera falcata	-	-	1	1	1	1	1	1	3	1	3	1	1
Pouteria torta	-	-	1	1	1	1	1	1	1	1	1	0	0
Forsteronia velloziana	-	-	-	24	29	39	33	28	29	18	17	8	9
Eugenia albotomentosa	-	-	-	28	40	55	50	41	37	19	19	13	6
Xylopia aromatica	-	-	-	25	34	42	69	84	59	38	32	28	14
Casearia sylvestris	-	-	-	12	15	16	16	16	13	12	8	4	2
Miconia rubiginosa	-	-	-	7	8	12	12	12	9	6	9	8	6
Campomanesia pubescens	-	-	-	2	11	16	17	14	18	12	13	17	7
Eugenia sp. 2	-	-	-	4	2	6	10	12	18	7	10	10	0
Eugenia sp. 3	-	-	-	6	6	6	14	11	14	9	9	4	2
Miconia stenostachia	-	-	-	3	6	6	11	11	12	12	11	13	10
Peritassa campestris	-	-	-	6	6	6	6	4	3	2	2	1	1
Vochysia tucanorum	-	-	-	8	7	6	3	3	3	2	1	1	3
Protium heptaphyllum	-	-	-	2	2	2	2	2	2	2	1	2	0
Ditassa mucronata	-	-	-	2	1	3	4	4	10	7	9	3	0
Croton sp.	-	-	-	1	1	1	1	1	1	1	1	1	0
Pterodon emarginatus	-	-	-	1	1	1	2	2	1	1	1	1	0
Erytroxylum cuneifolium	-	-	-	3	7	4	4	4	2	2	0	0	0
Psidium grandifolium	-	-	-	2	2	2	2	2	3	0	0	0	0
Passiflora villosa	-	-	-	1	2	3	3	3	4	3	2	0	0

TABLE 2
Continued...

	Time in days												
Species	**7**	**14**	**36**	**71**	**105**	**141**	**240**	**360**	**590**	**820**	**1517**	**3680**	**7300**
Rapanea guianensis	-	-	-	-	19	29	26	33	25	17	15	14	8
Eugenia pitanga	-	-	-	-	7	14	23	23	16	15	11	6	4
Leandra aurea	-	-	-	-	5	9	9	5	6	5	7	5	5
Miconia ligustroides	-	-	-	-	4	4	4	3	8	5	5	6	2
Tibouchina stenocarpa	-	-	-	-	4	6	6	5	7	8	3	1	3
Neea theifera	-	-	-	-	1	1	1	1	1	1	1	0	0
Rapanea umbellata	-	-	-	-	5	3	1	2	0	0	0	0	1
Virola sebifera	-	-	-	-	-	2	13	11	21	22	23	18	7
Copaifera langsdorffii	-	-	-	-	-	3	3	4	21	14	9	6	0
Siparuna guianensis	-	-	-	-	-	8	8	8	7	4	4	2	10
Piptocarpha rotundifolia	-	-	-	-	-	1	1	1	1	1	2	1	0
Eugenia polyphylla	-	-	-	-	-	6	8	4	3	0	1	1	0
Eugenia sp. 1	-	-	-	-	-	-	1	2	3	4	4	2	2
Jacaranda caroba	-	-	-	-	-	-	2	0	6	3	0	2	0
Jacaranda decurrens	-	-	-	-	-	-	1	0	0	0	0	0	0
Vernonia ruficoma	-	-	-	-	-	-	-	-	-	1	1	0	0
Distictella mansoana	-	-	-	-	-	-	-	-	-	-	-	1	3
Mabea fistulifera	-	-	-	-	-	-	-	-	-	-	-	-	9
Number of identified plants	0	85	206	437	611	813	890	880	907	641	651	506	273
Non identified seedlings	6	22	38	57	65	69	69	64	65	64	64	9	-
Non identified species	4	6	8	4	4	5	3	4	2	2	8	-	-
Total number of plants	6	107	244	494	676	882	959	944	**972**	705	715	515	273
Total number of species	6	19	35	56	59	66	**69**	65	66	61	61	63	42
New species	6	19	21	24	11	9	8	3	4	3	2	9	1

occurs prior to inter-specific competition. This fact may be expected as individuals of the same species compete for the same resources.

Since the heat from the fire only penetrates the first few centimeters of the soil´s surface, the seed bank and subterranean structures which remain are protected against scorching (Coutinho, 1982), although heat can be a stimulus for germination of some seeds (Willians, 2000; Hanley *et al.,* 2003). In addition, fire induces a high incidence of light, elimination of pests and competitors (Castro Neves & Miranda, 1996) and degradation of allelopathic substances (Christensen, 1985).

During the observation period, a large number of seedlings appeared, which were confirmed by the presence of cotyledons and marked heterophylly in some species. Likewise, many shoots emerged from subterranean parts, however the counting method did not enable us to distinguish them from those arising from the seed bank. Any digging in search of subterranean organs could affect the natural development of vegetation. While it cannot be proved, it is probable that individuals which arose in the first 15 days after the fire, originated as vegetative shoots, given the low precipitation during this period, less than 50 mm (Souza & Soares, 1983). The fire can stimulate sprouting form subterranean organs in the cerrado and in other vegetation types of the word (Calvo *et al.,* 2002; Hoffmann *et al.,* 2003; Rodrigo *et al.,* 2004, Vesk & Westoby, 2004) and in some species it was observed that sprouting was the first sign of plants living on after a fire. The re-sprouting capacity of subterranean organs is due to the presence of active buds and allocation of biomass to these organs (Hoffmann, 1999). The re-sprouting from aerial organs is possible due to bark protection and modified leaves (cataphylls) that protect aerial buds (Souza & Soares, 1983; Guedes, 1993 in Silva, *et al*., 1996).

The importance of the seed bank in secondary succession in tropical rainforests is very well studied (Whitmore, 1983). However, in the “cerrado” and

TABLE 3
Plant species and number of individuals in post-fire regeneration in quadrat 2 (40 m²) in a Cerrado, São Carlos, SP, Brazil. Observation from 10/1981 to 06/2001.

	Time in days												
Species	**7**	**14**	**36**	**71**	**105**	**141**	**240**	**360**	**590**	**820**	**1517**	**3680**	**7300**
Heteropteris byrsonimaefolia	-	87	175	166	141	152	141	124	26	61	23	73	29
Banisteriopsis stellaris	-	18	21	26	26	33	34	41	16	21	23	14	1
Memora peregrina	-	11	16	28	23	27	28	29	20	22	13	11	11
Gochnatia pulchra	-	18	29	35	33	32	28	34	14	21	18	12	3
Distictella mansoana	-	6	20	10	6	6	6	5	7	4	3	2	3
Aspidosperma tomentosum	-	2	2	3	4	4	7	1	1	1	2	1	1
Syagrus flexuosa	-	1	2	2	2	2	2	2	2	2	2	2	3
Serjania lethalis	-	8	26	25	19	23	24	17	7	10	17	4	3
Serjania caracasana	-	5	6	9	14	18	18	18	8	12	11	3	3
Bromelia antiacantha	-	1	2	2	1	1	1	1	1	1	1	2	1
Didymopanax vinosum	-	-	10	14	21	19	16	16	11	14	11	4	5
Ocotea pulchella	-	-	8	12	12	16	28	31	32	25	23	18	15
Neea theifera	-	-	3	7	23	28	29	23	4	4	4	2	1
Caryocar brasiliense	-	-	1	16	20	10	21	19	11	8	6	5	1
Davilla rugosa	-	-	2	10	10	10	9	10	7	4	2	3	0
Dalbergia miscolobium	-	-	9	11	12	12	10	7	9	2	4	1	1
Eugenia albotomentosa	-	-	3	3	3	8	15	13	16	13	17	13	10
Pouteria torta	-	-	6	7	10	8	11	6	7	6	4	4	4
Styrax camporum	-	-	1	4	4	6	15	17	13	12	7	3	1
Andira humilis	-	-	4	5	5	7	4	1	1	1	2	4	0
Stryphnodendron obovatum	-	-	4	5	5	5	4	4	3	2	1	7	0
Eugenia bimarginata	-	-	1	1	1	1	3	3	3	3	3	2	2
Palicourea rigida	-	-	1	1	2	2	2	2	2	2	2	2	2
Serjania erecta	-	-	1	1	1	1	1	1	1	2	1	1	0
Tabebuia ochracea	-	-	1	1	1	1	1	1	0	0	0	2	0
Forsteronia velloziana	-	-	-	93	132	175	201	150	156	92	76	39	37
Copaifera langsdorffii	-	-	-	27	25	29	24	24	23	24	22	9	12
Xylopia aromatica	-	-	-	2	36	34	30	36	26	26	19	17	13
Casearia sylvestris	-	-	-	2	11	19	24	22	22	11	6	6	0
Myrcia lingua	-	-	-	4	4	20	21	40	24	17	16	15	8
Miconia stenostachia	-	-	-	8	7	22	36	37	43	29	40	30	23
Miconia albicans	-	-	-	7	5	19	30	32	37	27	33	27	23
Miconia fallax	-	-	-	2	2	7	10	11	13	10	12	10	1
Aegiphylla lhotzkiana	-	-	-	4	4	10	6	6	2	3	4	3	0
Pterodon emarginatus	-	-	-	4	4	4	4	5	3	2	1	3	1
Ouratea spectabilis	-	-	-	3	3	3	3	3	3	3	3	1	1
Smilax sp.	-	-	-	2	3	3	6	7	3	3	4	3	0
Ditassa mucronata	-	-	-	1	1	3	2	7	0	0	0	0	0
Erytroxylum campestre	-	-	-	1	1	3	3	3	3	3	2	2	1
Tocoyema formosa	-	-	-	1	1	1	2	2	2	3	3	2	0
Stryphnodendron adstringens	-	-	-	1	1	1	1	1	1	1	1	1	0
Protium heptaphyllum	-	-	-	2	2	2	1	1	1	1	1	2	0
Peritassa campestris	-	-	-	1	1	1	1	1	1	0	0	0	0
Dimorphandra mollis	-	-	-	1	1	2	1	0	0	0	0	0	0

TABLE 3
Continued...

	Time in days												
Species	**7**	**14**	**36**	**71**	**105**	**141**	**240**	**360**	**590**	**820**	**1517**	**3680**	**7300**
Roupala montana	-	-	-	-	2	17	35	47	51	40	42	24	11
Rudgea viburnoides	-	-	-	-	12	28	26	17	14	7	3	1	1
Anadenanthera falcata	-	-	-	-	11	4	5	3	3	3	4	2	2
Bauhinia holophylla	-	-	-	-	2	2	1	1	1	1	2	3	0
Rapanea umbellata	-	-	-	-	-	8	32	26	40	33	24	12	10
Eugenia sp. 1	-	-	-	-	-	4	13	13	13	17	11	4	2
Psidium grandifolium	-	-	-	-	-	1	27	20	20	16	9	3	0
Miconia rubiginosa	-	-	-	-	-	5	9	7	7	5	3	8	7
Alibertia sp.	-	-	-	-	-	1	1	9	7	8	1	0	0
Eugenia pitanga	-	-	-	-	-	10	10	9	5	3	0	0	0
Erytroxylum suberosum	-	-	-	-	-	2	2	1	1	0	0	0	0
Byrsonima verbascifolia	-	-	-	-	-	5	5	2	1	0	0	0	0
Virola sebifera	-	-	-	-	-	-	6	8	11	17	13	10	9
Guapira noxia	-	-	-	-	-	-	1	1	10	2	2	1	1
Campomanesia pubescens	-	-	-	-	-	-	3	0	2	3	2	3	1
Eugenia obversa	-	-	-	-	-	-	3	3	10	6	11	4	1
Brosimum gaudichaudi	-	-	-	-	-	-	3	1	2	3	3	1	1
Erytroxylum cuneifolium	-	-	-	-	-	-	1	1	1	1	1	2	1
Machaerium acutifolium	-	-	-	-	-	-	1	2	1	2	1	1	0
Byrsonima coccolobifolia	-	-	-	-	-	-	1	1	2	1	1	1	0
Eugenia spathophylla	-	-	-	-	-	-	2	2	1	1	1	0	0
Byrsonima intermedia	-	-	-	-	-	-	-	1	3	2	5	2	0
Siparuna guianensis	-	-	-	-	-	-	-	3	3	4	3	9	29
Psychotria barbiflora	-	-	-	-	-	-	-	3	4	2	5	4	2
Vochysia tucanorum	-	-	-	-	-	-	-	1	1	1	1	0	0
Vernonia ruficoma	-	-	-	-	-	-	-	-	2	0	6	9	0
Amaioua guianensis	-	-	-	-	-	-	-	-	-	1	1	1	1
Stryphnodendron polyphyllum	-	-	-	-	-	-	-	-	-	-	2	2	1
Miconia ligustroides	-	-	-	-	-	-	-	-	-	-	1	1	1
Acosmium subelegans	-	-	-	-	-	-	-	-	-	-	1	0	0
Leandra aurea	-	-	-	-	-	-	-	-	-	-	3	0	0
Eugenia sp. 2	-	-	-	-	-	-	-	-	-	-	1	0	0
Psychotria capitata	-	-	-	-	-	-	-	-	-	-	1	0	1
Pradosia brevipes	-	-	-	-	-	-	-	-	-	-	1	0	0
Pyrostegia venusta	-	-	-	-	-	-	-	-	-	-	-	1	0
Pera obovata	-	-	-	-	-	-	-	-	-	-	-	1	1
Rapanea guianensis	-	-	-	-	-	-	-	-	-	-	-	-	3
Miconia langsdorffii	-	-	-	-	-	-	-	-	-	-	-	-	2
Number of identified plants	0	157	354	570	670	877	1051	996	801	687	608	475	308
Non identified seedlings	6	7	6	14	3	14	6	2	112	3	13	36	-
Non identified species	-	6	6	11	3	10	5	1	11	2	10	10	0
Total number of plants	6	164	360	584	673	891	**1057**	998	913	690	621	511	308
Total number of species	5	16	31	53	51	66	70	68	80	65	**81**	76	53
New species	5	17	21	30	7	18	14	5	12	3	17	12	4

TABLE 4
Plant species and number of individuals in post-fire regeneration in quadrat 3 (40 m²) in a Cerrado, São Carlos, SP, Brazil. Observation from 10/1981 to 06/2001.

	Time in days												
Species	**7**	**14**	**36**	**71**	**105**	**141**	**240**	**360**	**590**	**820**	**1517**	**3680**	**7300**
Syagrus flexuosa	1	10	14	12	13	13	12	12	12	12	13	14	14
Bauhinia holophylla	1	3	7	8	8	9	9	8	5	6	5	5	1
Memora peregrina	-	7	17	28	34	37	37	37	33	32	30	20	9
Vochysia tucanorum	-	15	15	14	13	18	20	13	10	5	2	1	0
Heteropteris byrsonimaefolia	-	9	60	56	54	57	52	57	44	63	50	43	8
Guapira noxia	-	1	9	20	23	30	31	22	15	12	4	4	0
Miconia albicans	-	3	26	21	48	60	68	60	60	46	41	40	17
Miconia stenostachia	-	3	20	20	48	60	64	56	55	44	40	40	16
Miconia fallax	-	1	5	10	12	15	16	14	14	11	9	10	2
Distictella mansoana	-	4	7	9	9	9	8	7	6	5	4	11	4
Ananas ananassoides	-	4	5	5	7	9	9	8	7	8	9	7	3
Erytroxylum cuneifolium	-	1	2	3	8	11	10	8	10	6	7	7	5
Jacaranda caroba	-	1	4	6	5	5	5	6	4	4	3	1	1
Serjania lethalis	-	1	2	3	3	6	6	6	5	5	7	3	3
Eupatorium sp.	-	1	1	1	1	1	1	2	2	1	1	0	0
Tabebuia ochracea	-	3	3	3	4	6	2	0	1	0	0	1	0
Didymopanax vinosum	-	-	10	16	12	10	11	10	10	9	6	5	3
Gochnatia pulchra	-	-	10	12	12	12	16	17	9	6	7	4	1
Forsteronia velloziana	-	-	4	26	41	54	58	63	34	37	23	24	14
Aspidosperma tomentosum	-	-	2	6	6	8	8	7	6	6	5	4	0
Erytroxylum campestre	-	-	6	8	8	8	8	11	11	8	5	4	1
Davilla rugosa	-	-	3	5	5	5	6	6	5	4	2	3	0
Vernonia ruficoma	-	-	7	7	4	4	3	8	2	0	1	0	0
Compositae unidentified	-	-	3	3	3	3	4	10	7	1	3	0	1
Smilax sp.	-	-	2	4	6	7	5	6	4	4	5	5	0
Connarus suberosus	-	-	1	1	1	1	1	1	1	1	0	1	0
Virola sebifera	-	-	12	12	16	51	80	84	94	90	50	33	21
Roupala montana	-	-	2	6	30	53	71	71	75	69	48	28	10
Ocotea pulchella	-	-	11	25	17	19	31	37	36	30	23	25	14
Andira humilis	-	-	13	13	13	8	7	9	8	10	12	1	5
Stryphnodendron obovatum	-	-	3	8	8	10	12	11	5	8	6	2	2
Byrsonima intermedia	-	-	1	1	5	6	13	15	10	11	7	6	4
Casearia sylvestris	-	-	2	5	7	7	7	5	3	2	1	2	0
Ouratea spectabilis	-	-	2	2	3	5	5	5	2	6	7	5	4
Pouteria torta	-	-	6	6	5	7	6	6	6	5	4	5	3
Aegiphylla lhotzkiana	-	-	5	6	7	6	4	3	4	0	0	1	0
Erytroxylum sp.	-	-	6	0	0	10	7	6	7	5	3	3	0
Temnadenia violacea	-	-	3	12	12	12	11	11	6	5	4	4	3
Serjania caracasana	-	-	2	5	6	6	4	2	2	2	2	4	0
Xylopia aromatica	-	-	-	31	25	46	59	64	67	54	38	41	15
Eugenia bimarginata	-	-	-	33	62	76	74	66	49	56	49	11	7
Copaifera langsdorffii	-	-	-	14	21	28	34	34	27	25	15	12	6
Campomanesia pubescens	-	-	-	6	15	18	22	25	25	31	20	15	6
Eugenia albotomentosa	-	-	-	8	12	20	31	28	36	27	11	32	13

TABLE 4
Continued...

	Time in days												
Species	**7**	**14**	**36**	**71**	**105**	**141**	**240**	**360**	**590**	**820**	**1517**	**3680**	**7300**
Miconia ligustroides	-	-	-	3	11	17	18	14	8	6	8	9	1
Myrcia lingua	-	-	-	2	4	16	40	37	25	25	12	5	4
Peritassa campestris	-	-	-	4	4	4	4	3	2	2	3	6	1
Tibouchina stenocarpa	-	-	-	5	5	6	5	5	4	2	3	3	1
Siparuna guianensis	-	-	-	1	1	1	1	1	6	5	2	6	11
Dalbergia miscolobium	-	-	-	1	1	1	1	1	1	1	1	1	0
Hoenephyton trixoides	-	-	-	1	1	1	1	1	1	2	1	1	0
Psychotria sp.	-	-	-	2	2	2	3	4	5	6	6	0	0
Styrax camporum	-	-	-	1	1	1	2	1	1	0	0	0	0
Lippia lupulina	-	-	-	1	1	1	1	1	1	1	1	0	0
Rapanea umbellata	-	-	-	-	18	53	83	62	47	45	30	22	13
Rapanea guianensis	-	-	-	-	5	28	37	43	25	40	27	28	17
Eugenia pitanga	-	-	-	-	4	7	17	18	24	21	36	16	1
Psychotria sessilis	-	-	-	-	9	9	9	8	7	7	7	5	1
Unidentified	-	-	-	-	5	8	12	11	11	9	5	5	2
Leandra aurea	-	-	-	-	3	4	3	2	2	2	4	14	8
Neea theifera	-	-	-	-	2	2	5	3	2	1	1	5	2
Eugenia obversa	-	-	-	-	4	4	7	7	10	7	1	0	1
Sapium glandulatum	-	-	-	-	1	1	1	3	2	2	0	0	0
Galactia sp.	-	-	-	-	1	2	2	2	1	0	0	0	0
Myrcia sp.	-	-	-	-	2	2	1	1	1	0	0	0	0
Eugenia sp. 2	-	-	-	-	-	9	8	7	3	2	2	2	2
Stryphnodendron adstringens	-	-	-	-	-	1	2	2	1	3	2	5	2
Acosmium dasycarpum	-	-	-	-	-	7	5	0	0	0	2	1	0
Piptocarpha rotundifolia	-	-	-	-	-	1	3	4	4	6	1	0	0
Psychotria barbifolia	-	-	-	-	-	-	10	9	8	9	8	30	8
Pera obovata	-	-	-	-	-	-	5	6	3	2	5	2	0
Erytroxylum suberosum	-	-	-	-	-	-	1	1	1	1	1	2	0
Eugenia sp. 3	-	-	-	-	-	-	4	3	2	1	1	0	0
Anadenanthera falcata	-	-	-	-	-	-	-	1	1	1	3	2	2
Eugenia polyphylla	-	-	-	-	-	-	-	2	3	1	3	0	1
Alibertia sessilis	-	-	-	-	-	-	-	-	5	2	5	5	1
Amaioua guianensis	-	-	-	-	-	-	-	-	-	5	5	3	1
Bacharis sp.	-	-	-	-	-	-	-	-	-	1	1	0	1
Eupatorium squalidum	-	-	-	-	-	-	-	-	-	1	1	0	1
Stryphnodendron polyphyllum	-	-	-	-	-	-	-	-	-	-	1	1	3
Miconia rubiginosa	-	-	-	-	-	-	-	-	-	-	12	12	9
Anacardium humile	-	-	-	-	-	-	-	-	-	-	-	2	0
Number of identified plants	2	67	313	521	737	1034	1239	1200	1051	991	783	680	310
Non identified seedlings	0	11	11	13	2	3	4	3	9	10	12	7	-
Non identified species	-	9	7	8	2	3	4	2	7	8	6	7	-
Total number of plants	2	78	324	534	739	1037	**1243**	1203	1060	1001	795	687	310
Total number of species	2	23	40	56	61	66	73	71	**78**	75	74	68	56
New species	2	21	26	23	13	7	10	4	8	10	8	9	0

more specifically in woody savannas, this matter remains little explored. In the first piece of ecological work on the "cerrado", Lund (in Warming & Ferri, 1973) considered plant multiplication by seeds to be a "pure exception". Ferri (1960) suggested that this form of reproduction was restricted to new or developing "cerrados", but absent in the old "cerrados". Labouriau *et al*. (1963) reported the renewal of species by sexual reproduction in various areas of the natural "cerrado".

Santos Jr. (1992) observed seedling dynamics in various conditions, such as an intact canopy, natural and artificial gaps in the same area of this study. He reported the growth of new individuals in various seasons of the year and also found a larger number of seedlings in artificial gaps after burning. The presence of many seedlings after burning means some inferences can be drawn regarding their importance during post-fire regeneration in woody savanna, although the survival rate of seedlings has not been studied. Thus, as new studies are carried out, the importance of seeds for the "cerrado" regeneration process, in large areas and in gap healing, tends to gain value.

The soil seed bank appears to be of fundamental importance in the recovery of the "cerrado" as many tree seedlings in the sample belong to species with large seeds, not transported by wind, and are present in numbers that rule out the hypothesis of allochthonous sources. Santos Jr. (1992) observed a large number of seeds in the soil of this "cerrado" - above 200,000/m^2 - which could account for the large number of individuals found in the first stages of succession in this work.

Deiller *et al.* (2003) observed that germination after disturbance occurs rather from seeds in the litter than in the soil itself. The litter was completely burnt in the area we studied having a high temperature in the surface layer of the soil. This led us to believe that most of the seedlings derived from seeds of the subsurface layer of the soil, probably below one-centimeter in depth.

Plant density in synusia revealed a behavior similar to that of the community in each quadrat. There are successive population decreases in herbaceous synusias after four months (Soares & Lima, 2000), for climbers after eight months, shrubs after one year and trees after a year and half (Fig. 1). At the end of the sampling period, the plant survival rate per synusia, regarding the maximum values, were 20% for climbers, 30% for shrubs and 32% for trees. Although not sampled, rare herbs were seen in the plots at 10 and 20 years.

Differences in the synusias, throughout the community regeneration (Fig. 2), were tested with the Shannon-Weaver diversity index. For the first 6 months, increasing values were seen in all three synusias. After this period, which coincided with the plant and species establishment phase, they behaved differently. After a maximum of about two years, the diversity of shrubs decreased gradually and that of climbers declined after five years, whereas the rate for trees remained constant up to twenty years after the fire.

Natural or accidental fires in protected areas such as the case studied occur at intervals long enough to allow species to reproduce and replenish the seed bank. Thus, the community composition

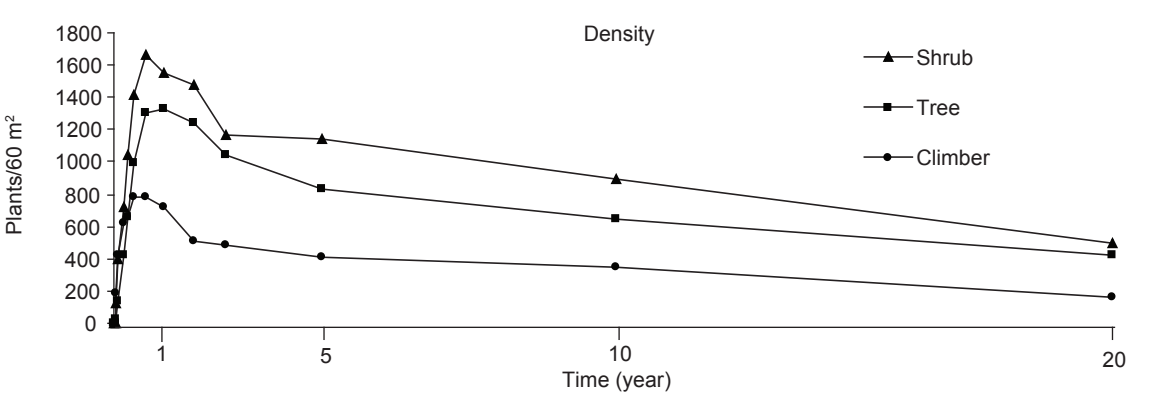

Fig. 1 — Plant density in different synusias in 60 m^2 over twenty years of post-fire secondary succession of a woody savanna in São Carlos, SP, Brazil.

and structure, after regeneration, are not affected much by burning, as can be observed in the data obtained here. However, successive burning can exhaust the seed bank stock, causing certain species to be excluded, mainly those which are not able to resprout or produce phelloderm sufficiently thick to protect the living tissues (Souza & Soares, 1983). By eliminating more susceptible species, spaces are cleared for herbs and shrubs to occupy, as observed in the first year of regeneration. Thus, successive hard burning led to the vegetation being lower and having a more open physiognomy by suppressing arboreal species without fire resistance (Moreira, 2000).

The similarity rate in the successive stages (Fig. 3) demonstrates that the same species occurred throughout the study period. The small variation that occurred after the maximum similarity around 90% (between the first and second year) is primarily due to suppressing species rather than to replacement. This is supported by the low incidence of new species being recruited over time. It may be concluded that during the twenty years after the fire, the succession process occurred mainly by adjusting the plant density and species frequency in the quadrats.

Although the species appeared at different times, it was not possible to confirm the presence of pioneers or secondary species, except for *Siparuna guianensis*, which appeared somewhat later than others. It is well known that this species develops as undergrowth in the woody savanna (Silva, 1996).

In approximately the first year and a half, there was a fast population increase for the various species in the quadrats. After this period, species behaved in different ways.

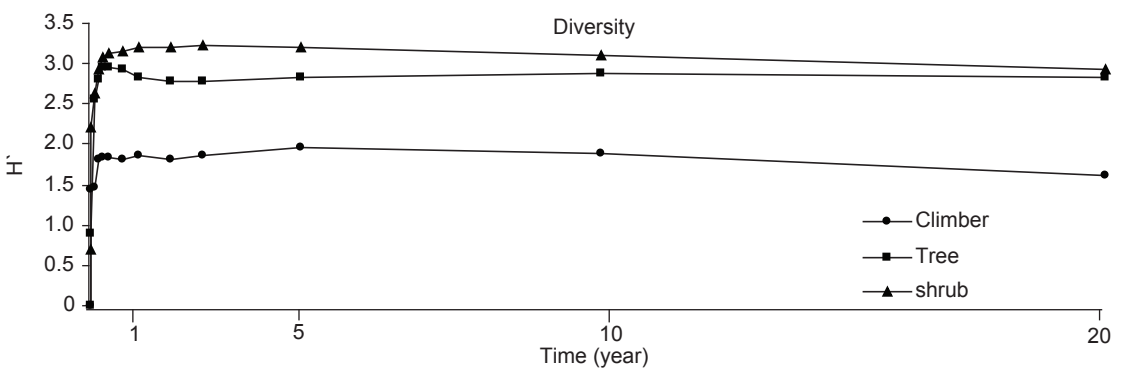

Fig. 2 — Species diversity by Shannon Index (H') in nats/individual during post-fire secondary succession of a woody savanna in São Carlos, SP, Brazil.

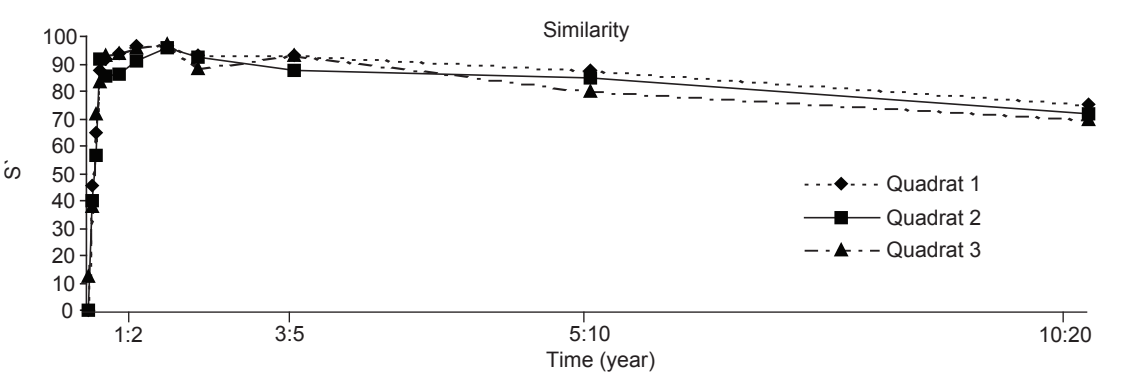

Fig. 3 — Sorensen Similarity Index (S') of successive samples, during post-fire secondary succession of a woody savanna in São Carlos, SP, Brazil. (1:2 is the similarity between first and second year and 3:5 similarity between third and fifth year etc.).

Vochysia tucanorum is a tree whose population both increased and decreased rapidly over the years, resulting in few remaining individuals at the end of the work. The early increase in population was due to resprouting (Souza & Soares, 1983). This is likely to be the standard behavior of species that sprout from subterranean parts.

Miconia rubiginosa is a tree that showed two growth population peaks. The decrease after the first year coincided with a denser community of herbs and shrubs.

Rapanea umbellata is a tree and seems to represent species that reproduce essentially by seeds with a slow growing population peak that decreases later by competition.

Andira humilis is a very low shrub common in open physiognomy, with a well-developed subterranean structure (xylopodium) having significant vegetative reproduction. This was reflected in its rapid appearance after burning and was followed by a population decrease due to the increase in the density of plant cover and consequent shading.

Miconia albicans is a shrub with predominantly sexual reproduction, very common in areas with medium-open canopy. This characteristic is reflected in its behavior during the succession, with slow population decrease over time, demonstrating good tolerance to shading and vegetation densification.

Campomanesia pubescens showed successive behavior which was very similar to the previous species, differing only in its preference for scrub, even in vegetation of high density. Hence, the population decreases when the vegetation becomes taller.

Casearia silvestris, a shrub common in open areas behaved in a common way found among species with fast population growth followed by a decrease due to intra- and inter-specific competition.

Memora peregrina is a climber that readily sprouts from subterranean organs with slow growth, which can live in open areas as a shrub. Due to these characteristics, it multiplied quickly, after which the population decreased slowly, mainly after the fifth year after the fire.

Distictella mansoana is a climber with tendrils and heterophylly when young. It rapidly established after the fire, then suffered a population decrease, coinciding with the rising density of vegetation. A second period of multiplication occured as the herb and shrub populations decreased. Climbers perform an important function in forest dynamics, mostly in areas disturbed by man (Putz, 1984), however their ecological function is little known (Hora & Soares, 2002). In this study, this species seems to be dependent on vegetation density for its development. The behavior of other climbers during the succession was apparently similar to this species.

Syagrus flexuosa is a very short palm-tree with a persistent leaf sheath, which protects the apical bud against fire. Its seeds are protected by a lignified endocarp, less susceptible to burning and, probably, fire acts as a stimulus for germination. This and other palm trees are commonly dominant in fields submitted to periodic burning (Sambuichi & Eiten, 1996).

The behavior and the successional dynamics of communities do not always reflect the dynamics of the populations. The latter behave differently during the regeneration process, depending on their reproductive characteristics, biology, ecological preference and temporal variation in the community structure.

CONCLUSIONS

A great number of seedlings with cotyledons or heterophylly were observed, which emphasize the importance of soil seed bank to replace "cerrado" vegetation at the first stage of sucession, after a severe fire.

The absence of replacing shrubs and arboreal species during the period and the marked variation in the numbers of plants per area demonstrate that the woody savanna regeneration after fire involves, from the start, the definitive species (installation phase). Over time it only has one adjustment, first in density of individual per species (competition intra-specific) and then in the number of species (competition inter-specific).

The populations had different patterns of development during the succession after the fire.

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