Chapter 1

POST-FIRE REGENERATION IN A SEMIDECIDUOUS MESOPHYTIC FOREST, SOUTH-EASTERN BRAZIL

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ABSTRACT

Post-fire regeneration was analyzed in a semideciduous mesophytic forest fragment in the county of Campinas (22°49´45"S and 47° 06´33"W) São Paulo State, Brazil, in six surveys of the vegetation in natural regeneration, carried out at 20, 27, 35, 41, 48 and 66 months after a fire event. In each survey all the shrub and tree individuals with height > 1.0 m were sampled in permanent plots. Pioneer species dominated the initial regeneration, with predominating density of *Ricinus communis* L. and *Trema micrantha* (L.) Blume that were gradually substituted by shade tolerant species. In the last surveys the understorey and late secondary species substituted the pioneers, with predominating density for *Hybanthus atropurpureus* (A. St.-Hil.) Taub. and *Galipea jasminiflora* (A. St.-Hil.) Engl., that were probably favored by the shade produced by the species that started colonization in the area. The recovery of floristic richness in the forest fragment was relatively fast, since 27 months after the fire event 89 shrub and tree species were sampled and at 41 months this number had reached 116, that is close to the species richness values found in more preserved forest fragments in the region. Fire may be contributing to the great floristic heterogeneity in the semideciduous mesophytic forests, but in the long term the impact of this type of disturbance on the vegetation of fragments submitted to frequent fires is unknown.

Key words: Fire ecology; Forest regeneration; Succession; Tropical forest

INTRODUCTION

The occurrence of disturbances is responsible for the start of the secondary succession process in forest ecosystems and much has already been discussed on the ecological role of these disturbances in the structural organization and maintenance of high plant diversity in the forests (Denslow, 1987; Clark, 1990; Vandermeer et al., 1996; Charles-Dominique et al., 1998; Ferreira and Prance, 1999; Martins and Rodrigues, 2002). Fire, of the different types of natural or human origin to which tropical forests are subject, probably most infers in the functioning of these ecosystems because it alters the floristic composition and vegetation structure, the nutrient cycle and the different fauna components (Uhl et al., 1981; Kauffman et al., 1995; Martins et al., 1995; Cochrane and Schulze, 1999; Gerwing, 2002).

The evolution of the vegetation of certain ecosystems, such as the Brazilian savannah (Cerrado), is closely associated to the natural occurrence of fire, with clear adaptation in the plants to this type of disturbance (Coutinho, 1990; Andrade et al., 2002). However, forest formations in the tropics and sub-tropics submitted to fire can have their floristic composition and structure extremely descharacterized with local extinction of species, invasion of exotic pioneer species, uncontrolled growth of liana and grass populations and stagnation in the succession at a early stage (Corlett, 1987; Gerwing, 2002; Martins and Ribeiro, 2002). Obviously the negative effects of fire on these forests will be more severe the greater the intensity of the fire and the smaller the interval between occurrences (Gerwing, 2002).

The speed and sequence of the floristic and structural alterations in the post-fire succession are determined by factors such as: vegetation composition remaining from the disturbance, soil seed bank, plant tissues with resprouting capacity and proximity to seed sources (Uhl et al., 1981; Turner et al., 1997; Cochrane and Schulze, 1999; Pausas et al., 1999). Therefore, knowledge of the floristic composition and structure of the colonizing communities of forests degraded by fire and their alterations during succession are extremely important, not only for discussion of the predominant succession model, but also for understanding the factors involved in the colonization process of these degraded areas.

The regeneration potential of a forest fragment (resilience) is variable in space and time and can, if efficiently managed, promote total or partial restoration of the vegetation in the patterns of the colonization process of treefall gaps (Clark and Clark, 1987). The resilience of these forest fragments depends on the course taken during the degradation process (Aronson et al., 1995) that is, of the magnitude, time of occurrence, frequency and type of degradation. But this resilience is also dependent on vegetation and ecological characteristics of the phytogeographic unit of origin of the fragment (Rodrigues and Gandolfi, 2000).

In São Paulo State, south-eastern Brazil, the current remains of semideciduous mesophytic forest are fragments generally confined to areas of difficult access and considered unsuitable for agriculture, such as areas of steep slopes, valley floors, areas with marshy soil etc. The vegetation characteristics of these forest fragments depend on various factors, such as the fragment shape, size, degree of isolation, the types of neighbourhood (Viana and Tabanez, 1996) among which the type and history of human disturbance prevail as vegetation definers (Rodrigues and Gandolfi, 1996, 1998).

In addition to the fragmentation itself acting on the reduction of the biodiversity in these remnants of vegetation (Brown and Brown, 1992; Turner, 1996; Laurence, 2001) most of these semideciduous mesophytic forest fragments are still being submitted to constant disturbances. Fire originating from sugar cane cropping and extensive livestock raising are currently the most common degrading action of forest fragments (Rodrigues and Gandolfi, 1998). However, unlike the Amazon forest and the savannah (Cerrado), in which many studies have been carried out and resulted in important models for understanding of the succession and degradation of these ecosystems post-fire (Uhl et al., 1981; Coutinho, 1990; Ferreira and Prance, 1999; Williamson and Mesquita, 2001; Andrade et al., 2002; Gerwing, 2002), very little is known about the impact of fire and the regeneration capacity of the semideciduous mesophytic forest submitted to this type of disturbance.

Thus the objective of this study was to test the hypothesis that the regenerative capacity (resilience) of a semideciduous mesophytic forest fragment degraded by fire is expressed in time, with a large increase in plant density and diversity.

MATERIAL AND METHODS

Study Area

The study was carried out in a semideciduous mesophytic forest fragment with an area of 15.87 ha at a mean altitude of 694 m, located in the Campinas Experimental Center (CEC) of the Agronomic Institute (IAC), Campinas (22°49′45”S and 47°06′33”W), São Paulo State, Brazil. The climate is the Cwa type by the Köppen classification (Setzer, 1966), defined as warm and wet, with a dry winter and wet summer. The average annual rainfall is 1381.2 mm and the mean annual temperature is 21.6 °C. The soil type of the area studied in the forest fragment was classified as Dark Red Latosol, clay texture.

The forest fragment presents an extremely irregular canopy, 15-20 m high when it exists, with some emergent trees of up to 30 m in height (*Cariniana estrellensis* (Raddi) Kunt, *C. legalis* (Mart.) Kunt, *Aspidosperma polyneuron* M. Arg and others).

A fire reached the fragment in September 1988 and resulted in different levels of vegetation destruction. The area chosen for the study was the most external of the fragment, where the vegetation was severely degraded by the fire.

VEGETATION ANALYSIS

The vegetation in regeneration in the forest fragment affected by fire was sampled using four blocks divided into twelve 6 x 6 m plots, totaling 1728 m^2 of total sample area.

Six surveys were carried out in each plot on the natural regeneration, at 20, 27, 35, 41, 48 and 66 months after the September 1988 fire. In each survey all the shrubs and trees > 1.0m were sampled from which botanical material was collected for identification.

The taxonomic identification of the botanical material was made by consulting the herbarium (ESA) at the Escola Superior de Agricultura “Luis de Queiroz”/University of São Paulo (USP) and with the help of specialists whenever necessary. The scientific names were updated and standardized according to the Missouri Botanical Garden (http:mobot.mobot.org/W3T/Search/vast.html).

For each survey the diversity was determined by the Shannon (H') diversity index (Magurran, 1987; Zar, 1984):

$$H' = -\sum p_i \ln p_i,$$

where p_i is the proportion of the individuals in the ith species.

The diversity values (H') among surveys were compared by the t-test, according to Magurran (1987), used in similar studies (Vidal et al., 1998; Rodrigues et al., 2004).

Regression analysis was used to test the correlation among the vegetation parameters such as number of individuals and number of species, with the post-fire time.

SPECIES SUCCESSIONAL CLASSIFICATION

The species sampled were classified in successional categories, using reference studies by Gandolfi et al. (1995), Santos et al. (1996), Gandolfi (2000) and Martins and Rodrigues (2002), consultations with specialists and field observations.

Four successional categories were adopted: pioneers, early secondary, late secondary and unclassified, that corresponded to the species level of tolerance to shade. The late secondary species category was considered the most shade-tolerant and advanced successional category. The shade-intolerant species were included at the other classification extreme (pioneers).

The unclassified category included the species that have not yet been classified successionally because of lack of data on their ecological characteristics and the exotic species sampled.

In addition to these successional categories, a group of species was included in the understorey category because they completed their life cycles in this shaded forest strata. They were shrub species or small trees that tolerate the shade produced by the canopy.

RESULTS

Floristic Changes Over Time

As expected, there were floristic alterations during the study period. Thus the regression analysis showed tendencies to increase in the number of individuals and the number of species up to the fifth survey (48 months after the fire) and reduction of both in the last survey (66 months) (individuals/time: $r^2 = 0.85$, $P < 0.01$; species/time: $r^2 = 0.97$, $P < 0.01$). The number of families was positively related with post-fire time ($r^2 = 0.77$, $P < 0.05$) (Table 1, Figure 1).

Table 1 Floristic characteristics of vegetation in post-fire regeneration in a semideciduous mesophytic forest fragment, Campinas, SP, Brazil

Time after fire (months)	Number of species	Number of families	Number of individuals	Shannon diversity (H')
20	60	28	488	3.18
27	89	36	1001	3.58
35	99	40	936	3.74
41	116	42	1363	3.72
48	117	43	1787	3.26
66	112	45	1493	3.17

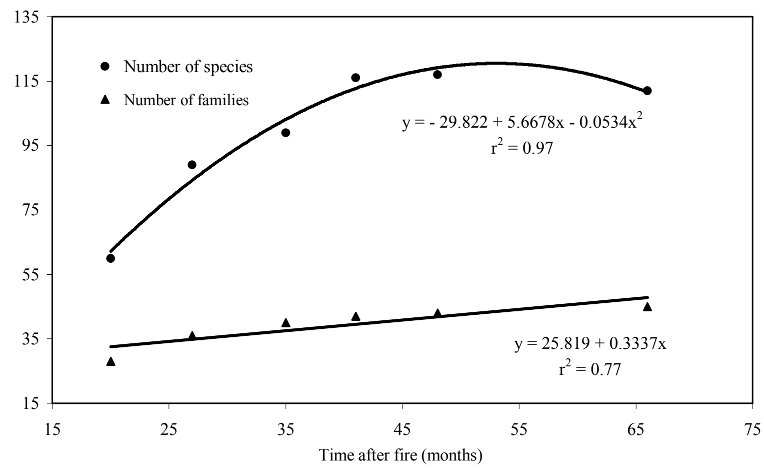

Figure 1. Relationship between the number of species and families and the time after the fire event, in a semideciduous mesophytic forest in south-eastern Brazil.

The Shannon diversity variation (H´) did not present a pattern over the study period (Table 1), increasing significantly only at the interval of 20 to 27 months post-fire (t-test, t = 6.04, $P < 0.001$) and from 27 to 35 months (t-test, t = 3.20, $P < 0.001$) and reducing from 41 to 48 months (t-test, t = 8.27, $P < 0.001$). There were no significant differences in the diversity values obtained between 35 and 41 months post- fire (t-test, t = 0.66, $P > 0.05$) and between 48 and 66 months (t-test, t = 1.48, $P > 0.05$).

Considering all the surveys of natural regeneration carried out after the fire event in the forest fragment, 163 shrub and tree species were sampled, distributed in 45 families (Table 2).

Table 2 Species sampled in a semideciduous mesophytic forest fragment degraded by fire in Campinas, SP, Brazil. Successional category (SC): P, pioneer species; ES, early secondary species; LS, late secondary species; U, understorey species; UC, unclassified. N, number of individuals. Time after fire: S1, 20 months; S2, 27 months; S3, 35 months; S4, 41 months; S5, 48 months; S6, 66 months

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Ricinus communis *L.*	Euphorbiaceae	P	78	80	46	8		
Trema micrantha (L.) Blume	Ulmaceae	P	78	107	89	77	61	31
Solanum erianthum D. Don	Solanaceae	P	37	57	42	41	32	5
Schizolobium parahyba (Vell.) S.F. Blake	Caesalpiniaceae	P	28	43	48	42	47	34
Guazuma ulmifolia Lam.	Sterculiaceae	P	22	47	59	74	96	61
Solanum robustum H.L. Wendl.	Solanaceae	P	22	1	1			
Croton floribundus Spreng.	Euphorbiaceae	P	22	29	24	28	27	20
Centrolobium tomentosum Guill. ex Benth.	Fabaceae	ES	18	40	35	45	42	41
Galipea jasminiflora (A. St.-Hil.) Engl.	Rutaceae	U	16	55	70	91	204	165
Machaerium stipitatum (DC.) Vogel	Fabaceae	ES	14	21	25	24	37	27
Bauhinia forficata Link	Caesalpiniaceae	P	18	11	12	18	14	9
Cupania vernalis Cambess.	Sapindaceae	ES	10	29	24	38	48	47
Casearia gossypiosperma Briq.	Flacourtiaceae	ES	10	32	28	40	55	37
Colubrina glandulosa Perkins	Rhamnaceae	ES	10	25	22	30	18	20
Peltophorum dubium (Spreng.) Taub.	Caesalpiniaceae	ES	9	16	11	23	14	12
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	LS	7	11	25	21	12	27
Esenbeckia febrifuga (A. St. Hil.) A. Juss. ex Mart.	Rutaceae	U	7	36	37	52	62	45
Aegiphila sellowiana Cham.	Verbenaceae	P	6	9	7	12	10	9

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Zanthoxylum rhoifolium Lam.	Rutaceae	P	5	5	4	1	2	4
Zeyheria tuberculosa (Vell.) Bureau	Bignoniaceae	LS	4	4	1	3	1	2
Trichilia pallida Sw.	Meliaceae	U	4	3		1	12	6
Helicteres ovata Lam.	Sterculiaceae	P	4	12	11	17	17	9
Croton piptocalyx Müll. Arg.	Euphorbiaceae	P	4	13	17	21	20	12
Cryptocaria moschata Nees	Lauraceae	LS	3	3	4	4	8	4
Eriotheca candolleana (K. Schum.) A. Robyns	Bombacaceae	LS	3	6	5	7	6	5
Cecropia pachystachya Trécul	Cecropiaceae	P	3	5	5	6	5	7
Lonchocarpus muehlbergianus Hassl.	Fabaceae	ES	3	4	2	1	4	2
Vernonia diffusa Less.	Asteraceae	P	3				6	
Guettarda viburnoides Cham. and Schltdl.	Rubiaceae	U	3	6	6	7	12	6
Casearia sylvestris Sw.	Flacourtiaceae	P	2	2	10	7	12	17
Melia azedarach L.	Meliaceae	UC	2		3	3	4	1
Metrodorea stipularis Mart.	Rutaceae	LS	2	7	9	9	10	13
Pothomorphe umbellata (L.) Miq.	Piperaceae	U	2					
Phyllanthus acuminatus Vahl	Euphorbiaceae	LS	2	5	2	2	2	4
Aloysia virgata (Ruiz and Pav.) Juss.	Verbenaceae	P	2	7	9	13	8	6
Solanum bullatum Vell.	Solanaceae	P	2	5	3	5		
Carica papaya L.	Caricaceae	UC	2	2	5	2		
Cedrela fissilis Vell.	Meliaceae	LS	2	3		5	2	4
Vernonia polyanthes Less.	Asteraceae	P	2	73	19	29	19	4
Myrtaceae 1	Myrtaceae	UC	2				5	

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Mollinedia widgrenii A. DC.	Monimiaceae	U	1	1	5	3	10	1
Holocalyx balansae Mich.	Fabaceae	LS	1	4	5	5	5	6
Senna macranthera (DC. ex Collad.) H.S. Irwin and Barneby	Caesalpiniaceae	P	1	1		1	1	1
Piptadenia gonoacantha (Mart.) J.F. Macbr.	Mimosaceae	ES	1	6	8	11	13	8
Jacaranda macrantha Cham.	Bignoniaceae	ES	1			1	1	
Lonchocarpus cultratus (Vell.) H.C. Lima	Fabaceae	ES	1	6	6	10	8	10
Acacia polyphylla DC.	Mimosaceae	P	1	1	3	4	6	6
Lonchocarpus pentandrus (A.St.-Hil.) Kallunki and Pirani	Rutaceae	UC	1					
Annona cacans Warm.	Annonaceae	UC	1	2	2	2		
Siparuna guianensis Aubl.	Monimiaceae	U	1	1	1	1	2	1
Machaerium hirtum (Vell.) Stellfeld	Fabaceae	ES	1	2	3	4	4	2
Diospyros inconstans Jacq.	Ebenaceae	LS	1	6	10	7	6	12
Asteraceae 1	Asteraceae	UC	1					
Cariniana legalis (Mart.) Kuntze	Lecythidaceae	LS	1	1	4	4	4	4
Trichilia hirta L.	Meliaceae	U	1	2	2	1		4
Cordia trichotoma (Vell.) Arráb. ex Steud.	Boraginaceae	ES	1	2	2	7	3	2
Cecropia glaziovi Snethl.	Cecropiaceae	P	1	6	7	12	12	3
Merostachys riedeliana Rupr. ex Döll	Poaceae	UC	1	2	1	14	1	5
Chorisia speciosa A.St.-Hil.	Bombacaceae	ES	1	1	2	1	2	3
Rollinia sylvatica (A. St.-Hil.) Martius	Annonaceae	ES	1	1	1	2	9	2
Solanum pycnanthemum Mart.	Solanaceae	P		44	40	51	39	11
Wulffia baccata (L.) Kuntze	Asteraceae	UC		12		8	3	2

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Solanum paniculatum L.	Solanaceae	P		7	8	9	15	7
Ottonia propinqua Miq.	Piperaceae	U		7	9	8	1	
Picramnia sp. 1	Simaroubaceae	UC		7	14	10	9	7
Celtis iguanaea (Jacq.) Sarg.	Ulmaceae	P		8	7	7	12	11
Hybanthus atropurpureus (A. St.-Hil.) Taub.	Violaceae	U		5	12	229	521	502
Piper aduncum L.	Piperaceae	U		4	2	7	1	
Spathodea nilotica Seem.	Bignoniaceae	UC		6	1	1		1
Calycorectes sp. 1	Myrtaceae	UC		3	3	2	8	
Acacia paniculata Willd.	Mimosaceae	P		3	8	6	9	2
Eugenia pyriformis Cambess.	Myrtaceae	U		2	1	2	3	2
Maytenus aquifolium Mart.	Celastraceae	U		2	1	4	3	7
Cecropia hololeuca Miq.	Cecropiaceae	P		2	1	1	1	5
Platypodium elegans Vogel	Fabaceae	ES		2	2	2	1	1
Lantana camara L.	Verbenaceae	UC		2	3	11	7	7
Zanthoxylum hiemale A.St.-Hil.	Rutaceae	ES		2	1	6	5	
Dalbergia frutescens (Vell.) Britton	Fabaceae	ES		2		1		
Solanum sp. 1	Solanum	UC		2			1	
Eugenia florida DC.	Myrtaceae	U		2	2	8	2	13
Coffea arabica L.	Rubiaceae	UC		1		1	1	1
Guapira opposita (Vell.) Reitz	Nyctaginaceae	ES		1	1	1	2	7
Matayba elaeagnoides Radlk.	Sapindaceae	ES		1	2	3	1	
Hymenaea courbaril L.	Caesalpiniaceae	LS		1			1	1

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Roupala brasiliensis Klotzsch	Proteaceae	U		1	1	2	2	3
Aspidosperma polyneuron Müll. Arg.	Apocynaceae	LS		1	1	1	1	
Senecio brasiliensis (Spreng.) Less.	Asteraceae	UC		1				
Inga marginata Willd.	Mimosaceae	ES		1	2	1	1	2
Jacaratia spinosa (Aubl.) A. DC.	Caricaceae	P		1	1	1	2	2
Brunfelsia uniflora (Pohl) D. Don	Solanaceae	UC		1	1	1	1	
Maytenus robusta Reiss.	Celastraceae	U		1	4	4	6	7
Guatteria nigrescens Mart.	Annonaceae	LS		1				2
Abutilon peltatum K. Schum.	Malvaceae	P		1	1	1	1	1
Metrodorea nigra A. St.-Hil.	Rutaceae	U		1	1	3	4	4
Maclura tinctoria (L.) D. Don ex Steud.	Moraceae	ES		1	1	1	1	1
Machaerium nyctitans (Vell.) Benth.	Fabaceae	ES		1	1	1	1	
Eugenia sp. 1	Myrtaceae	UC			3	7	1	1
Cestrum laevigatum Schltdl.	Solanaceae	P			2	6	3	2
Eugenia sp. 2	Myrtaceae	UC			2			
Copaifera langsdorffii Desf.	Caesalpiniaceae	LS			2	2	1	2
Connarus regnellii G. Schellenb.	Connaraceae	LS			2	2	1	3
Zanthoxylum caribaeum Lam.	Rutaceae	ES			2	1	3	1
Pilocarpus pauciflorus A. St.-Hil.	Rutaceae	LS			2	1	1	2
Campomanesia guaviroba (DC.) Kiaersk.	Myrtaceae	LS			1			
Luehea divaricata Mart.	Tiliaceae	ES			1	2	1	1
Rhamnidium elaeocarpum Reiss.	Rhamnaceae	ES			1			
Schinus terebinthifolius Raddi	Anacardiaceae	P			1			
Sebastiania serrata (Baill. ex Müll. Arg.) Müll. Arg.	Euphorbiaceae	U			1		8	5

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Actinostemon communis (Müll. Arg.) Pax	Euphorbiaceae	U			1			
Solanum swartzianum Roem. and Schult.	Solanaceae	P			1	2	2	1
Solanaceae 1	Solanaceae	UC			1			
Trichilia elegans A. Juss.	Meliaceae	U			1	2	4	3
Trichilia pallens C. DC.	Meliaceae	U			1	1		
Eupatorium laevigatum Lam.	Asteraceae	P			1	3		
Uncertain 1	Uncertain	UC			1	1	1	
Piper amalago L.	Piperaceae	U				9	17	16
Coutarea hexandra (Jacq.) K. Schum.	Rubiaceae	U				4	1	
Chomelia obtusa Cham. and Schltdl.	Rubiaceae	U				4		
Rapanea umbellata (Mart.) Mez	Myrsinaceae	ES				3	1	3
Olyra sp. 1	Poaceae	UC				3	1	
Inga fagifolia G. Don	Mimosaceae	ES				3	4	3
Poaceae 2	Poaceae	UC				2		
Lonchocarpus subglaucescens Mart. ex Benth.	Fabaceae	UC				2		
Chomelia ribesioides Benth. ex A. Gray.	Rubiaceae	U				2	12	2
Pisonia ambigua Heimerl	Nyctaginaceae	ES				1		
Cordia sellowiana Cham.	Boraginaceae	ES				1	1	
Baccharis dracunculifolia DC.	Asteraceae	UC				1		
Polygala klotzschii Chodat	Polygalaceae	U				1	5	5
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae	UC				1		1
Ficus guaranitica Chodat	Moraceae	ES				1	3	1
Rubiaceae 1	Rubiaceae	UC				1	2	

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Luetzelburgia guaissara Toledo	Fabaceae	LS				1		1
Campomanesia guazumifolia (Cambess.) O.Berg	Myrtaceae	LS				1		2
Enterolobium contortisiliquum (Vell.) Morong	Mimosaceae	ES				1		
Piper gaudichaudianum Kunth	Piperaceae	U					7	15
Solanum concinnum Sendtn.	Solanaceae	P					4	
Matayba juglandifolia (Camb.) Radlk.	Sapindaceae	UC					3	
Esenbeckia leiocarpa Engl.	Rutaceae	LS					2	16
Myrcia rostrata DC.	Myrtaceae	P					1	3
Oxalis latifolia Kunth	Oxalidaceae	UC					1	1
Cordia sp. 1	Boraginaceae	UC					1	
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. and Wess. Boer	Moraceae	U					1	
Ocotea corymbosa (Meisn.) Mez	Lauraceae	ES					1	
Ocotea sp. 1	Lauraceae	UC					1	
Allophylus edulis (A. St.-Hil., Cambess. and A. Juss.) Radlk.	Sapindaceae	P					1	
Astronium graveolens Jacq.	Anacardiaceae	ES					1	
Alchornea glandulosa Poepp. and Endl.	Euphorbiaceae	ES					1	
Solanum megalochiton Sendtn.	Solanaceae	P					1	
Canna indica L.	Cannaceae	UC						7
Psychotria sp. 1	Rubiaceae	UC						5
Trichilia catigua A. Juss.	Meliaceae	U						3
Prunus myrtifolia (L.) Urb.	Rosaceae	ES						1
Salvia splendens Ker Gawl.	Lamiaceae	UC						1
Nectandra megapotamica (Spreng.) Mez	Lauraceae	ES						1

Table 2

Species	Family	SC	N					
			S1	S2	S3	S4	S5	S6
Ruellia tetragona Link	Acanthaceae	UC						1
Diatenopteryx sorbifolia Radlk.	Sapindaceae	ES						1
Eugenia obovata O. Berg.	Myrtaceae	U						1
Myrcia formosiana DC.	Myrtaceae	P						1
Sweetia fruticosa Spreng.	Fabaceae	LS						1
Randia armata (Sw.) DC.	Rubiaceae	U						1
Myrtaceae 2	Myrtaceae	UC						1
Himatanthus obovatus (Müll. Arg.) Woodson	Apocynaceae	UC						1
Eugenia oblongata Mattos and D. Legrand	Myrtaceae	U						1

The most abundant species during the surveys were *Ricinus communis* L., *Trema micrantha* (L.) Blume, *Solanum erianthum* D. Don, *Guazuma ulmifolia* Lam., *Schizolobium parahyba* (Vell.) S.F. Blake, *Galipea jasminiflora* (A. St.-Hil.) Engl. and *Hybanthus atropurpureus* (A. St.-Hil.) Taub.. The densities of these species altered during the study period, with a significant reduction in the number of *R. communis* individuals ($r^2 = 0.77$, $P < 0.05$), that wasn't sampled 48 months post-fire, *T. micrantha* ($r^2 = 0.73$, $P < 0.05$) (Figure 2) and *S. erianthum* ($r^2 = 0.68$, $P < 0.05$) and increase in the number of *H. atropurpureus* ($r^2 = 0.78$, $P < 0.01$) and *G. jasminiflora* individuals ($r^2 = 0.73$, $P < 0.05$). *G. ulmifolia* and *S. paraiba* did not present a significant relationship between the number of individuals and the post-fire time ($P > 0.05$).

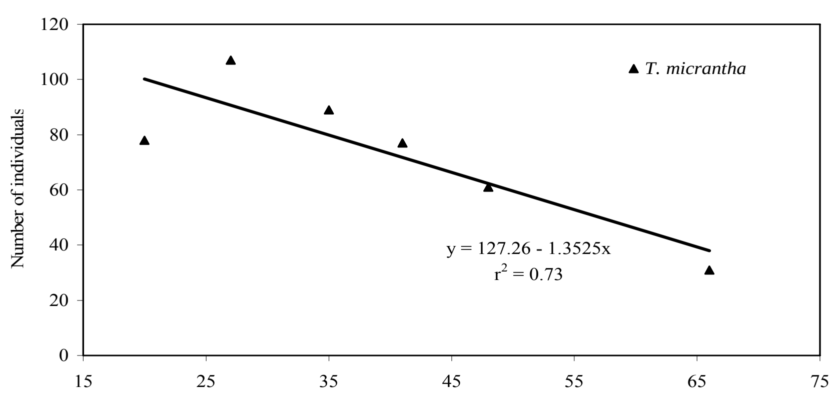

Figure 2. Relationship between the number of individuals of the pioneer species *Trema micrantha* and the time after the fire event, in a semideciduous mesophytic forest in south-eastern Brazil.

Species Successional Classification

The number of pioneer species wasn't significantly correlated with the post-fire time ($P > 0.05$) and a significant and positive relationship was detected between the number of understorey species and time ($r^2 = 0.72$, $P < 0.05$) and late secondary species and time ($r^2 = 0.93$, $P < 0.01$).

The number of understorey species individuals increased with the post-fire time ($r^2 = 0.79$, $P < 0.05$) (Figure 3) that was also detected for late secondary species individuals ($r^2 = 0.83$, $P < 0.05$) (Figure 4), but no significant relationship was found between number of pioneer species individuals and time ($P > 0.05$).

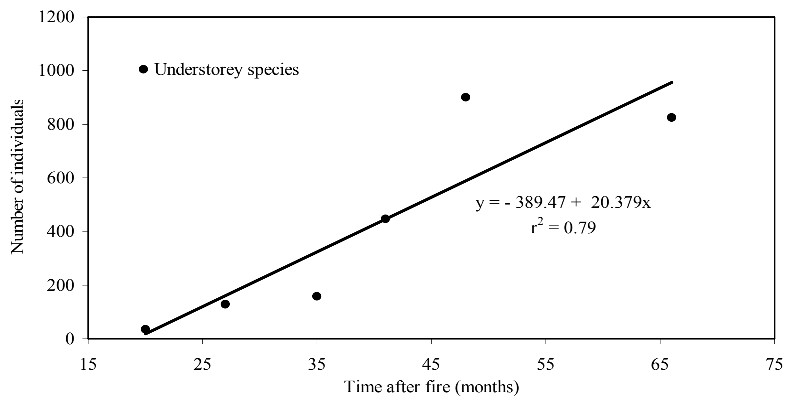

Figure 3. Relationship between the number of individuals of understorey species and the time after the fire event, in a semideciduous mesophytic forest in south-eastern Brazil.

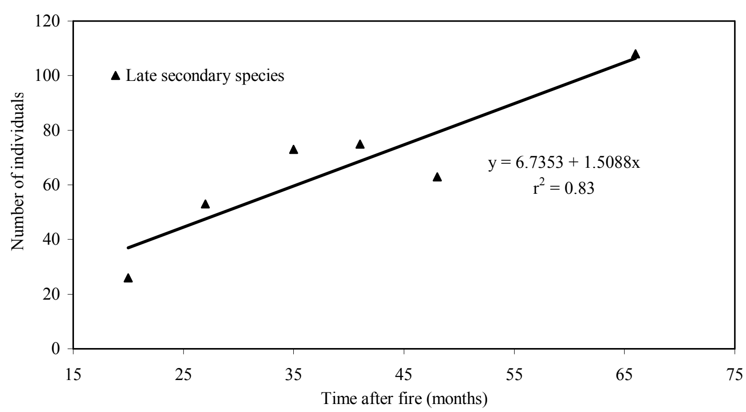

Figure 4. Relationship between the number of individuals of late secondary species and the time after the fire event, in a semideciduous mesophytic forest in south-eastern Brazil

DISCUSSION

The recovery of floristic richness in the forest fragment was relatively fast, since 27 months after the fire event 89 shrub and tree species were sampled and at 41 months this number had reached 116, that is close to the species richness values found in more preserved forest fragments in the region (Gandolfi et al., 1995; Salis et al., 1995; Bernacci and Leitão Filho, 1996). An increase in the number of families was detected over the surveys and the families sampled with great species richness are those normally reported as typical of this formation (Gandolfi et al., 1995; Salis et al., 1995; Bernacci and Leitão Filho, 1996).

The high number of species already in the first post-fire surveys and the high diversity values indicate a great floristic heterogeneity in the vegetation, that is explained by the very irregular action of fire in space, generating different regeneration niches (Uhl et al., 1981, 1988; Mellick and Ahton, 1991; Castellani and Stubblebine, 1993; Cochrane and Schulze, 1999; Martins and Ribeiro, 2002). These results corroborate studies in tropical forests, where disturbances play an important role in the maintenance of the richness and diversity (Denslow, 1987; Clark, 1990; Vandermeer et al., 1996; Charles-Dominique et al., 1998; Ferreira and Prance, 1999; Martins and Rodrigues, 2002).

The increase in the number of individuals and species from the first survey (20 months after the fire) to the fifth survey (48 months) confirmed the great post-fire resilience of the fragment analyzed, as suggested for semideciduous mesophytic forests (Rodrigues and Gandolfi, 1998). In the last survey (66 months) there was a reduction in the number of individuals and species because support capacity of the area was reduced with the growth of the regenerate individuals that eliminated the regeneration niches of some pioneer species because of shading of the area, that has been widely demonstrated in gap dynamic studies (Brokaw, 1985; Abe et al., 1995; Charles-Dominique et al., 1998; Martins and Rodrigues, 2002).

Among the pioneer species that effectively began the colonization process of the area, *R. communis* and *T. micrantha* were outstanding for the number of individuals in the first surveys. The high density of these species in the colonization of degraded areas (fragment edges and burnt areas) has already been reported in other studies in semideciduous mesophytic forests of the region (Viana and Tabanez, 1996; Amador, 1999; Rozza and Rodrigues, 1999).

A particularity of the studies on forest fragments degraded by fire in this region has been the regenerative capacity of *R. communis* in the initial stages of the secondary succession (Castellani and Stubblebine, 1993; Tabanez et al., 1997; Rozza and Rodrigues, 1999; Santin, 1999) with very rapid and intense population reduction, practically disappearing from the sampling 24-30 months after the fire. The regenerative performance of *R. communis*, an exotic species very common in natural regeneration of areas with human occupation, indicated that there is no need for initial control of its population for forest restoration post-fire (Rodrigues and Gandolfi, 1996) because it exercises the function of a short life cycle pioneer, disappearing from the area quickly in addition to inhibiting the invasion of aggressive herbaceous species such as *Panicum maximum* Jacq., due to the shading that it causes (Rozza and Rodrigues, 1999). In another forest fragment degraded by fire in the south-eastern of Brazil, where *R. communis* did not occur in the regeneration, colonization by aggressive grasses, mainly *Melinis minutiflora* P. Beauv., inhibited post-fire forest regeneration (Martins and Ribeiro, 2002).

T. micrantha has been found quickly colonizing large open areas such as forest edges and large treefall gaps or those produced by fire (Brokaw, 1985; Castellani and Stubblebine, 1993; Martins and Rodrigues, 2002; Rodrigues et al., 2004). In these areas, the species presented greater growth in height and dry matter accumulation and leaf area, indicating good capacity for exploiting the high irradiation levels (Souza, 1996).

Other pioneer species besides *R. communis* and *T. micrantha* that also colonized the area quickly, such as *S. parahyba, Solanum robustum* H.L. Wendl., *Croton piptocalyx* Müll. Arg., *Vernonia polyanthes* Less. and *Solanum pycnanthemum* Mart., did not present regeneration by resprouting after the fire. This indicates that these species used as regeneration strategy the germination of seeds that were already in the soil and resisted the fire action or that arrived in the area after the fire event, from other areas of the fragment less affected by the fire, or nearby fragments.

The proximity of seed sources has been considered as one of the main factors in defining the secondary succession in forest areas that suffer natural or human disturbances, and a negative relationship is expected between distance from the source and quantity of seeds that reach the degraded area (Guevara et al., 1986; McClanahan, 1986; Gorchov et al., 1993; Barik et al., 1996; Silva et al., 1996; Holl, 1999).

The fire action reduces the soil seed bank in the most superficial layers by causing loss of seed viability because of exposure to very high temperatures, as has been demonstrated for several forests (Miller, 1999; Andrade et al., 2002). However, in the studied fragment the seeds of some species must have resisted the fire action because they were buried in deeper layers of the soil or even because of their morphological characteristics, that protect them from heating, as is the case of *S. parahyba* seeds which have a very hard seed coat.

Seed germination in some pioneer species may have been triggered by the fire itself, as reported in some studies. High percentages of *T. micrantha* seed germination have been obtained in alternated temperatures (Matthes, 1992; Castellani, 1996) that can also be related to the adaptation of the species to large open areas and forest fragments submitted to fire, in which, in addition to the alteration in the light spectral quality, there are also great temperature oscillations (Vázquez-Yanez and Orozco Segovia, 1982, 1994) favoring the germination of seeds that were stored in the soil.

The pioneer species were gradually substituted by late secondary species and by a group of species typical of more shady environments in the forest, that although they had occurred in the initial colonization stages, began to standing out in density in the community after 27 months after the fire event, reaching high densities 48 months post-fire. These species are defined as typical of the understorey in semideciduous mesophytic forest fragments (Bernacci and Leitão Filho, 1996; Santos et al., 1996; Gandolfi, 2000). The characteristic species of this group were: *G. jasminiflora, H. atropurpureus* and *Esenbeckia febrifuga* (A. St. Hil.) A. Juss. ex Mart.

Another group of typical understorey species and therefore, shade tolerant, was only sampled in the last survey and included: *Eugenia oblongata* Mattos and D. Legrand, *Eugenia obovata* O. Berg., *Randia armata* (Sw.) DC. and *Trichilia catigua* A. Juss.

H. atropurpureus, the most abundant species 66 months after the fire, is very common in the understorey (Rodrigues, 1992; Bernacci and Leitão Filho, 1996) and in small gaps (Martins and Rodrigues, 2002; Martins et al., 2004) in forest fragments in this region.

Individuals of this species regenerated by resprouting at the stem base and reached the reproductive stage two years after the fire event in a forest fragment close to the area of this study (Castellani and Stubblebine, 1993).

The high plasticity of these typical species of the understorey has already been reported in gaps in semideciduous mesophytic forest where many were able to survive and even reproduce (Martins and Rodrigues, 2002; Martins et al., 2004). The occurrence of small gaps and the seasonal leaf fall in these semideciduous mesophytic forests expose understorey species to a wide variation in light during their lives, that may favor the plasticity of response in growth and reproduction after the occurrence of a disturbance (Canham, 1989; Amézquita, 1998; Gandolfi, 2000; Svenning, 2000; Martins and Rodrigues, 2002).

Besides this adaptive capacity to variable light level conditions, the predominating density of these understorey and late secondary species only in the last surveys indicated that the shade produced mainly by the pioneer species must have favored the recruitment of individuals from these final species of the succession. Thus the most abundant pioneer species were very important in the generation of ecological conditions, especially shade, favorable to the establishment of shade tolerant species, suggesting a facilitation model (Connel and Slayter, 1977).

Similar studies carried out on semideciduous mesophytic forest fragments affected by fire revealed a complexity of responses by the vegetation to this type of disturbance. Similar results in terms of successional dynamic have been obtained among these studies, but with variation in the composition of the most abundant species and in the speed of the succession process (Matthes, 1992; Castellani and Stubblebine, 1993; Martins and Ribeiro, 2002). Comparison of these studies confirmed the complexity of the successional process in forest fragments (Whitmore, 1991, 1997) with the spatial and temporal heterogeneity of the environmental characteristics and of disturbance defining the particularities of the forest dynamic (Abe et al., 1995).

Sporadic fire events may be contributing to the large spatial floristic heterogeneity in the forests in São Paulo state, Brazil, shown in several studies (Salis et al., 1995; Torres et al., 1997; Schudeller et al., 2001). However, a question needs to be clarified: what is the time interval without a fire event needed by the semideciduous mesophytic forest fragments to recover their floristic composition and structure. In the eastern Amazon Forest this interval without fire must be long, for example 10 to 20 years, because at smaller intervals, after each fire there is complete reposition of individuals in the regeneration that do not reach reproductive age, resulting in the disappearance of seed sources and local extinction of tree species from the mature forest (Cochrane and Schulze, 1999).

CONCLUSIONS

The increase in the number of individuals and species from the first survey (20 months after the fire) to the fifth survey (48 months) confirmed the great post-fire resilience of the fragment analyzed, as suggested for semideciduous mesophytic forests of the São Paulo State, Brazil.

The high number of species already in the first post-fire surveys and the high diversity values indicate a great floristic heterogeneity in the vegetation, that is explained by the very irregular action of fire in space, generating different regeneration niches.

The most abundant pioneer species were very important in the generation of ecological conditions, especially shade, favorable to the establishment of shade tolerant species, suggesting a facilitation successional model.

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