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Gap-phase regeneration in a semideciduous mesophytic forest, south–eastern Brazil

Sebastião Venâncio Martins[1,*] and Ricardo Ribeiro Rodrigues[2]
[1]*Departamento de Engenharia Florestal, Universidade Federal de Viçosa, 36571–000 Viçosa, MG, Brazil;* [2]*Departamento de Ciências Biológicas, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, SP, Brazil; *Author for correspondence*

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Abstract

The study was carried out in ten natural canopy gaps in the Santa Genebra County Reserve (22°49′45″S, 47°06′33″W) in the county of Campinas, São Paulo State, Brazil. The size and canopy openness of the gaps were studied using hemispherical photographs. The vegetation survey included all shrubs and trees with height $\geqslant$ 0.50 m in the gaps interiors and all the individuals with PBH (perimeter at breast height) $\geqslant$ 15 cm in a 3 m surrounding border of the gaps. The similarity among the gaps and among their surrounding areas was assessed by the Jaccard similarity index and by cluster analyzes. The gap size varied from 20.09 to 468 m^2, with a predominance of small gaps. The families with the greatest species richness in the gaps were Rutaceae, Rubiaceae and Euphorbiaceae. The species with the greatest number of individuals in the gaps were *Coffea arabica* L., *Hybanthus atropurpureus* (St. Hil.) Taub. and *Actinostemon klotschii* (Muell. Arg.) Pax, all widely distributed in the understorey. Shade-tolerant species (late secondary species) predominated in function of the predominance of small gaps. The high number of species found in the gaps reflects the importance of these disturbances in the maintenance of species diversity in the studied forest.

Introduction

Knowledge of the physical, floristic and structural characteristics of gaps is essential in gap dynamic studies, considering the interrelation existent among these characteristics and the natural regeneration process that occurs in these disturbance areas. Characteristics such as gap size, surrounding canopy height and the presence of remaining vegetation, that is, survivors of the disturbance, increase the heterogeneity of the forest and may provide specific environmental conditions for regeneration niches. These sites may meet the needs of different shrub and tree species groups (Denslow 1980, 1987; Orians 1982; Brown 1993).

The environmental alterations caused by the openness of gaps in the forest canopy such as increases in light levels and temperature and humidity reduction, may be minimized by the canopy height of the surrounding forest and by the remaining vegetation in the gaps (Brokaw 1982a; Uhl et al. 1988; Tabarelli 1997).

The floristic and structural study of gaps and their surrounding areas considering the classification of the species in successional groups is obviously important not only for the discussion of the predominant successional model, but also for the understanding of the factors involved in the occupation process of these areas. Data on the floristic composition and structure of a gap at a certain moment will reflect the responses of different species or groups of species to the environment of the disturbance. These will subsidize a better understanding of the ecology of such species and of the forest resilience. However, knowledge of the vegetation surrounding the gaps is also necessary, as colonization of these areas tends to be directly influenced by the closest vegetation by supplying or impeding seeds entry (Swaine and Hall 1983; Denslow and Gomez 1990; Martinez-Ramos and Soto-Castro 1993; Abe et al. 1995).

Gap size, which influences the main regeneration controlling factors such as light, air and soil temperature and relative air and soil humidity, is probably the most studied characteristic. The size of the gap defines its occupation by pioneer species or by shade-tolerant species (Hartshorn 1980; Pickett 1983). The greater the gap size the more different the microclimate in its interior tends to be compared to the conditions under the forest canopy. When there are small disturbances, such as the formation of a small gap, forest regeneration takes place mainly by the lateral growth of trees from the edges or of the remaining individuals of the late successional species already present in the area before the disturbance. In large gaps, occupation, at least at first, tends to be mainly by shade-intolerant species with rapid growth strategies and short life cycle, that is, pioneer species (Denslow 1980).

Recent studies have used hemispherical photographs to quantify the gap size and canopy openness, and the methodology has been considered very efficient (Brown 1993; Whitmore et al. 1993; Van der Meer and Bongers 1996; Valverde and Silvertown 1997; Walter and Torquebiau 1997; Trichon et al. 1998).

This study was carried out to test the hypothesis that natural gap colonization in the semideciduous mesophytic forest in the Santa Genebra County Reserve is defined by a great abundance of pioneer species, influenced by a set of physical and structural characteristics in the gaps and the surrounding vegetation.

The objectives were: 1) characterize gaps in the Santa Genebra County Reserve in terms of size, canopy openness and floristic composition; 2) apply the hemispherical photograph method to determine the gap size and canopy openness; 3) analyze the floristic relationships among the gaps and discuss their relationship with the surrounding vegetation; 4) identify the colonization pattern by species of different successional categories in the gaps.

Study area

The study was carried out in ten natural gaps in the Santa Genebra County Reserve (22°49′45″S and 47°04′33″W), in the county of Campinas, São Paulo State, south-eastern Brazil. The Reserve area is an isolated forest fragment of 251.8 ha, with altitudes varying from 580 to 610 m. The climate is Cwa type by the Köeppen 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 predominant soil type is Purple Latosol allic (Oliveira et al. 1979). The greatest part of the reserve area is covered by semideciduous mesophytic forest, with some stretches of swamp forest (Leitão Filho 1995).

The colonization process in ten gaps located in the semideciduous mesophytic forest was analyzed. Natural gaps were selected, separated from each other by at least 100 m, located in areas where the forest is in a better state of conservation and with sizes that represent an environmental disturbance gradient.

Methods

Gap physical characterization

Hemispherical photographs were used to determine the size of each gap (sensu Brokaw (1982b)) and the corresponding canopy openness. The main advantages of this method are the speed with which the photographs are obtained and processed and the increased accuracy because it is possible to consider the gap perimeter irregularities. The canopy openness, which is a good indicator of the solar radiation penetration potential, can also be calculated. This physical characteristic is highly correlated with the microclimate of the gaps (Whitmore et al. 1993; Green 1996; Walter and Torquebiau 1997).

The photographs were taken with an 8mm 180° angle lens ("fish eye") fixed on a photographic camera pointed to the sky. After developing, the images were read with a scanner and classified by the IDRISI program (Eastman 1995), defining the sky areas, that is, the open and the closed canopy areas (Chazdon and Field 1987; Whitmore et al. 1993).

The size and canopy openness of gaps were calculated using the WINPHOT program (Steege 1993) using the relationship between the sum of the pixels classified by the INDRISI as sky and the total hemisphere of the photograph.

Correlations between the canopy openness and the gap size and between the gap size and canopy height were tested by regression analysis using the program SYSTAT (Wilkinson 1991).

Vegetation characterization in the gaps

All the shrubs and trees with height ⩾ 0.50 m were sampled in the gaps and botanical material was collected for identification.

In a 3 m wide band around the gap areas, called the gap surrounding areas, all shrubs and trees with perimeter at breast height (PBH = 1.30 m) ⩾ 15 cm were sampled and identified.

The taxonomic identification was made by consulting the herbariums of the State University of Campinas and Escola Superior de Agricultura "Luiz de Queiroz" of the São Paulo State University. Specialist help was obtained whenever necessary. The plants classification system of Cronquist (1988) was adopted.

Successional species categories

The species sampled in the gaps were classified in successional categories using studies of Gandolfi et al. (1995); Bernacci and Leitão Filho (1996); Santos et al. (1996), the work of specialist advisors and field observations as references.

Four successional categories that correspond to the species shade tolerance were adopted: pioneer, early secondary, late secondary and unclassified. The late secondary species was considered the most shade-tolerant and advanced successional category. The shade-intolerant species were included at the other classification extreme (pioneers). Depending on the position of occurrence in the vertical forest strata, the late secondary species were grouped in understorey or sub-canopy and canopy species. Understorey species were defined as those that reached a maximum height of 3m, and the sub-canopy species as those taller, but not reaching the forest canopy. Species occupying the forest canopy or emerging from it when adult were considered late canopy species.

Floristic similarity

The FITOPAC program (Shepherd 1996) was used to analyze the floristic similarity between the gaps and between their surrounding areas. A Jaccard similarity matrix (Mueller-Dombois and Ellenberg 1974) was elaborated from the species present in the gaps and the gap surrounding areas. Cluster Analysis by average linkage method (UPGMA) was used to interpret the floristic similarity. Principal Coordinates Analysis (PCO) was also used to confirm the results of the classification analysis (Gauch 1982).

The Mantel test was used to evaluate the relationship between the similarity matrices based on floristic composition in the gaps and in the gap surrounding areas (McCune and Mefford 1997).

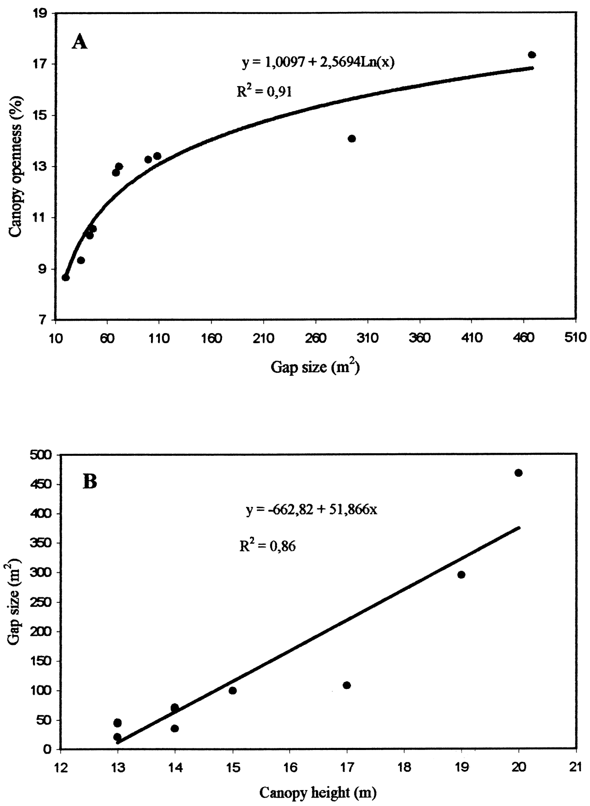

Figure 1. Relationship between: (A) canopy openness and gap size, (B) gap size and canopy height, in a semideciduous mesophytic forest, south-eastern Brazil.

Results

Gap size and canopy openness

The canopy openness varied from 8.7% to 17.3% and the gap size from 20.09 m^2 to 468 m^2 (Table 1). The largest gaps did not have canopy openness values very different from the others because of the presence of colonizing or remaining individuals at the time of their formation. (Figure 1A) shows that the canopy openness was positively and significantly correlated with the gap size ($P < 0.0001$, $r^2 = 0.91$).

The gap size was significantly and positively correlated with the height of the surrounding forest can-

Table 1. Physical and floristic characteristics of ten gaps in the Santa Genebra County Reserve, Campinas, SP, Brazil.

Number of the gap	Size (m^2)	Canopy openness (%)	Number of species	Number of individuals	Density (ind. m^{-2})
1	108,35	13,39	39	147	1,36
2	20,09	8,65	22	64	3,19
3	68,48	12,75	35	146	2,13
4	99,40	13,25	41	215	2,16
5	46,13	10,55	20	96	2,08
6	34,95	9,33	24	111	3,17
7	71,57	12,98	35	170	2,37
8	43,47	10,29	27	70	1,61
9	295,00	14,06	57	373	1,26
10	468,00	17,32	60	630	1,35

opy ($P < 0.001$, $r^2 = 0.86$) (Fig. 1B). A positive relationship was also found between the gap canopy openness and the canopy height ($P = 0.003$, $r^2 = 0.73$). Larger gaps were formed where the canopy is composed of larger trees capable of causing large openness when they fall.

Floristic composition

The gaps and gap surrounding areas sampled species, their families, successional characterization and number of individuals are listed in (Table 2).

In the set of ten gaps, 2.022 individuals belonging to 41 families, 70 genera and 105 species were sampled.

The families with the greatest species richness were: Rutaceae, with ten species (9.5% of the total); Rubiaceae, with nine (8.6%); Euphorbiaceae, with seven (6.7%); Fabaceae, Meliaceae and Myrtaceae, with five each (4.8%); and Piperaceae and Mimosaceae, with four each (3.8%). The Cecropiaceae, Flacourtiaceae, Myrsinaceae, Sapindaceae and Ulmaceae families were sampled with three species each (2.9%).

The families with greatest number of individuals were: Rubiaceae, with 385 individuals; Euphorbiaceae with 359; Violaceae with 260 and Rutaceae with 167. They corresponded to 57.9% of the total of plants sampled.

The prominence of the Rubiaceae family is due to the high number of *Coffea arabica* L. (coffee) individuals. The Violaceae family stood out by the high density of *Hybanthus atropurpureus* (St. Hil.) Taub. in most of the gaps. *Actinostemon klotschii* (Muell. Arg.) Pax was mainly responsible for the high number of individuals in the Euphorbiaceae family.

The species with greatest number of individuals were *C. arabica* with 271 individuals, *H. atropurpureus* with 260, *A. klotzschii* with 236, *Polygala klotzschii* Chod. with 92, *Psychotria hastisepala* Muell. Arg. with 92 and *Galipea multiflora* Engl. with 88, totaling 51.4%.

Only three (2.9%) of the 105 species sampled were found in all the gaps *C. arabica, P. klotzckii* and *Aspidosperma polyneuron* Muell. Arg. Two species (1.9%) occurred in nine gaps, *H. atropurpureus* and *P. hastisepala*, while five species (4.8%) were found in eight gaps: *A. klotschii*, *Urera baccifera* (L.) Gaud., *Esenbeckia febrifuga* (St. Hil.) A. Juss., *Seguieria floribunda* Benth. and *Myrciaria floribunda* (Wild.) Berg. A large number of species (33) was observed in only one gap.

Among the gaps the number of individuals varied from 64 to 630 and the number of species from 20 to 60 (Table 1). This variation was related with the increase of their size. The number of individuals was positively and significantly correlated with the gap size ($P < 0.0001$, $r^2 = 0.97$). A positive relationship was also found between the number of species and the gap size ($P < 0.0001$, $r^2 = 0.93$), however this relationship was non-linear (Figure 2).

The gaps had on average 2.07 individuals/m^2. The gap average density of pioneer and late secondary species was 0.25 individuals/m^2, and 1.33 individuals/m^2, respectively.

Taking the gap surrounding areas as a whole, 189 individuals were sampled distributed in 20 families, 37 genera and 46 species (Table 2).

The families with the greatest number of species in the gap surrounding areas were: Rutaceae with eight species (17.4% of the total); Euphorbiaceae, with seven (15.2%); Myrtaceae, with five (10.9%);

Table 2. Species sampled in ten gaps and surroundings areas, in the Santa Genebra County Reserve, Campinas, SP, Brazil. Successional category: P, pioneer species; ES, early secondary species; LS, late secondary species; UC, unclassified. Classification by vertical strata: U, understorey; SC, sub-canopy; C, canopy. N, number of individuals. Sampling locations: gp, gap; sa, surrounding area.

Species	Families	Succes. category	N	
			gp	sa
Astronium graveolens Jacq.	Anacardiaceae	ES	27	14
Duguetia lanceolata St. Hil.	Annonaceae	LS, C	2	
Rollinia sylvatica Mart.	Annonaceae	ES	4	
Aspidosperma polyneuron Muell.Arg.	Apocynaceae	LS, C	73	34
Aspidosperma ramiflorum Muell.Arg.	Apocynaceae	LS, C	23	2
Syagrus romanzoffiana (Cham.) Glass.	Arecaceae	ES	1	1
Vernonia diffusa Less.	Asteraceae	P	5	
Jacaranda micranttha Cham.	Bignoniaceae	ES	1	
Zeyheria tuberculosa (Vell.) Bur.	Bignoniaceae	ES	1	
Chorisia speciosa St.Hill.	Bombacaceae	ES	1	
Pseudobombax grandiflorum (Cav.) A. Rob.	Bombacaceae	P	1	
Cordia ecalyculata Vell.	Boraginaceae	ES	7	1
Patagonula americana L.	Boraginaceae	ES	2	
Copaifera langsdorffii Desf.	Caesalpiniaceae	LS, C	3	1
Holocalyx balansae Mich.	Caesalpiniaceae	LS, C	22	4
Senna macranthera (Collad.) Irwin et Barn.	Caesalpiniaceae	P		1
Jacaratia spinosa (Aubl.) A.DC.	Caricaceae	P	9	
Cecropia glazioui Sneth.	Cecropiaceae	P	2	
Cecropia hololeuca Miq.	Cecropiaceae	P	5	
Cecropia pachystachya Trec.	Cecropiaceae	P	2	
Maytenus ilicifolia Reiss.	Celastraceae	LS, U	14	
Maytenus robusta Reiss.	Celastraceae	LS, U	1	
Diospyrus inconstans Jacq.	Ebenaceae	LS, C	2	
Actinostemon klotschii (Muell. Arg.) Pax	Euphorbiaceae	LS, U	236	5
Alchornea glandulosa Poep. & Endl.	Euphorbiaceae	P	7	2
Croton floribundus Spreng.	Euphorbiaceae	P	9	7
Croton priscus Muell.Arg.	Euphorbiaceae	P	36	8
Pachystroma longifolium (Ness) I. M. Johnston	Euphorbiaceae	LS, C	37	33
Savia dictiocarpa Kuhlm	Euphorbiaceae	LS, C	16	3
Sebastiania klotschiana Pax & Hoffman	Euphorbiaceae	LS, U	18	
Phyllanthus acuminatus Vahl.	Euphorbiaceae	UC		1
Centrolobium tomentosum Guill.	Fabaceae	ES	5	1
Lonchocarpus guilleminianus (Tul.) Malme	Fabaceae	ES	6	
Machaerium stipitatum Vog.	Fabaceae	ES	1	
Machaerium villosum Vog.	Fabaceae	LS, C	1	
Sweetia fruticosa Spreng.	Fabaceae	LS, C	2	
Casearia gossypiospermum Briquet.	Flacourtiaceae	ES	9	
Casearia sylvestris Sw.	Flacourtiaceae	P	3	1
Prockia crucis L.	Flacourtiaceae	ES	8	1
Ocotea beaulahiae Baitello	Lauraceae	UC	11	2
Ocotea odorifera (Vell.) Rohwer	Lauraceae	LS, C		1
Nectandra megapotamica (Spreng.) Mez	Lauraceae	ES	2	
Cariniana estrellensis (Raddi) O. Kuntze	Lecythidaceae	LS, C	2	
Cariniana legalis (Mart.) O. Kuntze	Lecythidaceae	LS, C	3	
Abutilon bedfordianum St.Hil. & Naud.	Malvaceae	P	3	
Pavonia sepium St.Hil.	Malvaceae	P	5	

Table 2. continued.

Species	Families	Succes. category	N	
			gp	sa
Miconia inaequidens Naud.	Melastomataceae	P	1	
Cedrela fissilis Vell.	Meliaceae	ES	1	
Trichilia catigua Adr. Juss.	Meliaceae	LS, U	13	2
Trichilia claussenii C. DC.	Meliaceae	LS, SC	20	8
Trichilia elegans A. Juss.	Meliaceae	LS, U	55	
Trichilia pallida Sw.	Meliaceae	LS, SC	8	1
Acacia paniculata Willd.	Mimosaceae	P	15	
Acacia polyphylla DC.	Mimosaceae	P	19	4
Inga luschnatiana Benth.	Mimosaceae	ES	8	1
Piptadenia gonoacantha (Mart.) Macbr.	Mimosaceae	ES	37	7
Ficus glabra Vell.	Moraceae	ES	1	
Ardisia latipes Mart.	Myrsinaceae	LS, U	1	
Cybianthus cuneifolius Mart.	Myrsinaceae	UC	5	
Rapanea umbellata (Mart.) Mez	Myrsinaceae	ES	1	
Eugenia ligustrina Willd.	Myrtaceae	LS, SC	11	3
Eugenia verrucosa D. Legrand	Myrtaceae	LS, U	11	1
Myrciaria culiflora (DC) Berg.	Myrtaceae	LS, SC	5	
Myrciaria floribunda (Wild.) Berg.	Myrtaceae	LS, U	15	1
Myrcia rostrata DC.	Myrtaceae	P	7	2
Gomidesia affinis (Chamb.) Legr.	Myrtaceae	LS, SC		1
Pisonia ambigua L.	Nyctaginaceae	ES	2	
Oxalis rhombeo-ovata St.Hil.	Oxalidaceae	UC	4	
Seguieria floribunda Benth.	Phytolacaceae	ES	29	
Ottonia propinqua Kunth.	Piperaceae	P	17	
Piper amalago (Jacq.) Yunker	Piperaceae	P	41	
Piper amplum Kunth.	Piperaceae	UC	8	
Piper gaudichaudianum Kunth.	Piperaceae	P	3	
Polygala klotzschii Chod.	Polygalaceae	LS, U	92	
Colubrina glandulosa Perk.	Rhamnaceae	ES	1	
Rhamnidium elaeocarpum Reiss.	Rhamnaceae	ES	3	1
Chomelia obtusa Cham. & Schllecht.	Rubiaceae	LS, U	1	1
Coffea arabica L.	Rubiaceae	UC	271	
Coussarea contracta Benth & Hook.	Rubiaceae	LS, U	6	
Guettarda viburnioides Cham. et Schllecht	Rubiaceae	LS, SC	1	
Palicourea marcgravii St.Hil.	Rubiaceae	LS, U	9	
Psychotria carthagenensis Jacq. sensu L.B.Sm.	Rubiaceae	LS, U	3	
Psychotria hastisepala Muell. Arg.	Rubiaceae	LS, U	81	
Psychotria leiocarpa Cham et Schl.	Rubiaceae	LS, U	2	
Rudgea jasminoides Muell. Arg.	Rubiaceae	LS, SC	11	4
Balfourodendron riedelianum (Engl.) Engl.	Rutaceae	ES	29	
Esenbeckia febrifuga (St.Hil.) A. Juss.	Rutaceae	LS, U	26	
Esenbeckia leiocarpa Engl.	Rutaceae	LS, SC	7	8
Galipea multiflora Engl.	Rutaceae	LS, U	88	6
Metrodorea nigra St. Hil.	Rutaceae	LS, U	2	
Metrodorea stipularis Mart.	Rutaceae	LS, SC	8	1
Pilocarpus pauciflorus St. Hil.	Rutaceae	UC	1	1
Zanthoxylum hiemale St.Hil.	Rutaceae	ES	1	2
Zanthoxylum juniperinum Poepp.	Rutaceae	ES	3	1

Table 2. continued.

Species	Families	Succes. category	N	
			gp	sa
Zanthoxylum monogynum A.St.Hill.	Rutaceae	ES	2	3
Allophylus edulis (St.Hil.) Radlk.	Sapindaceae	P	1	
Cupania vernalis Camb.	Sapindaceae	ES	2	
Diatenopteryx sorbifolia Radlk.	Sapindaceae	ES	2	1
Chrysophyllum gonocarpum (Mart. & Eichl.) Engl.	Sapotaceae	ES	10	
Picramnia warmingiana Engl.	Simaroubaceae	LS, SC	13	1
Solanum acerifolium Mil.	Solanaceae	P	2	
Solanum argenteum Roem. & Schultz.	Solanaceae	P	7	
Solanum concium Schott ex Sendtn.	Solanaceae	ES	3	
Luehea divaricata Wild.	Tiliaceae	ES	2	1
Celtis iguanaea (Jacq.) Sargent	Ulmaceae	P	14	
Celtis tala Gillies ex Planchon.	Ulmaceae	P	15	
Trema micrantha (L.) Blume.	Ulmaceae	P	5	1
Urera baccifera (L.) Gaud.	Urticaceae	P	72	3
Hybanthus atropurpureus (St.Hil.) Taub.	Violaceae	LS, U	260	

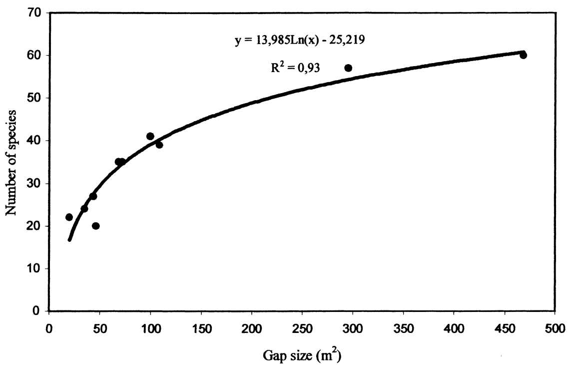

Figure 2. Relationship between number of species and gap size, in a semideciduous mesophytic forest, south-eastern Brazil.

Meliaceae, Mimosaceae and Caesalpiniaceae with three each (6.5%).

The families with greatest number of individuals in the gap surrounding areas were: Euphorbiaceae, with 60 individuals, Apocynaceae, with 36; Rutaceae, with 22 and Anacardiaceae, with 14. These families formed 69.8% of the total number of sampled plants.

The three species with greatest number of individuals in the gap surrounding areas were: *A. polyneuron*, with 34 individuals (18.0% of the total); *Pachystroma longifolium* (Ness.) I.M. Johnston, with 33 (17.5%) and *Astronium graveolens* Jacq., with 14 (7.4%). These species formed 42.9% of the total number of individuals.

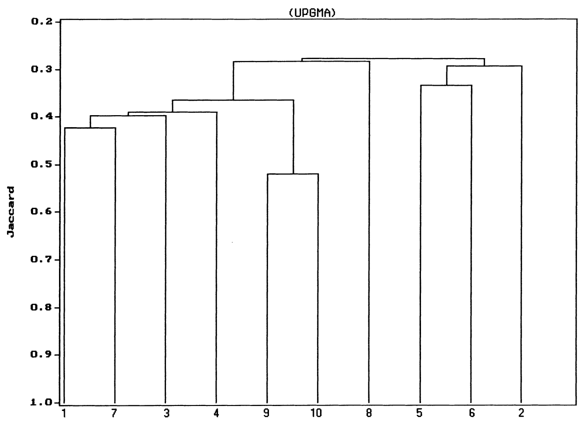

Figure 3. Dendrogram obtained using Jaccard similarity index and average linkage method (UPGMA), for canopy gaps in a semideciduous mesophytic forest, south-eastern Brazil.

Floristic similarity

The greatest floristic similarity (51.9%) was found between gaps 9 and 10 (Figure 3), which had the largest sizes, followed by that found between the medial size gaps (gaps 1, 3, 4 and 7) and between the small gaps (gaps 2, 5 and 6). The least similarity (18.8%) was between gaps 2 and 10, the smallest and largest gaps studied, respectively. Therefore, the floristic similarity between gaps is associated with gap sizes.

The ranking of the gaps by the Principal Coordinates Analysis (PCO) confirmed the results of the

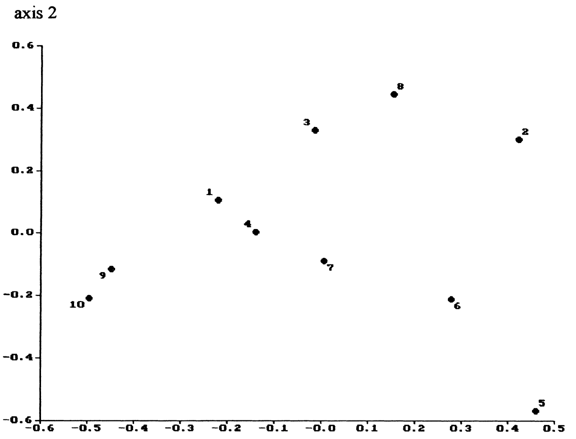

Figure 4. Scatter diagram showing the positions of the gaps on the first two axes of PCO (Principal Coordinates Analysis), using presence and absence data of the species sampled in ten gaps in a semideciduous mesophytic forest, south-eastern Brazil.

cluster analysis, that is, the occurrence of a group formed by gaps 9 and 10 (Figure 4) and the others forming a gradient both on axis 1 and on axis 2.

The floristic similarity pattern between gap surrounding areas was similar to that found for the gaps. The greatest value of the Jaccard similarity index (41.2%) was also found between the surrounding areas of gaps 9 and 10. Positive association between similarity matrices based on floristic composition in the gaps and in the gap surrounding areas was indicated by the Mantel test (Standardized Mantel Statistic: $r = 0.86$, $t = 6.84$, $P = 0.001$).

Successional species categories

The shrub and tree species sampled in the gaps are distributed in 26 (24.8% of the total) pioneer species, 32 (30.5%) early secondary species and 41 (39.0%) late secondary species. Only six species (5.7%) could not be classified (into a successional category) (Figure 5A).

Of the total of individuals sampled in the gaps, 306 (15.1%) were pioneer, 212 (10.5%) early secondary species, 1204 (59.6%) late secondary species, while 300 (14.5%) individuals were species not classified (Figure 5B). The high number of individuals in the not characterized group was mainly due to the high *C. arabica* density, an exotic species which has invaded the fragment as a result of the agricultural use of the neighboring areas.

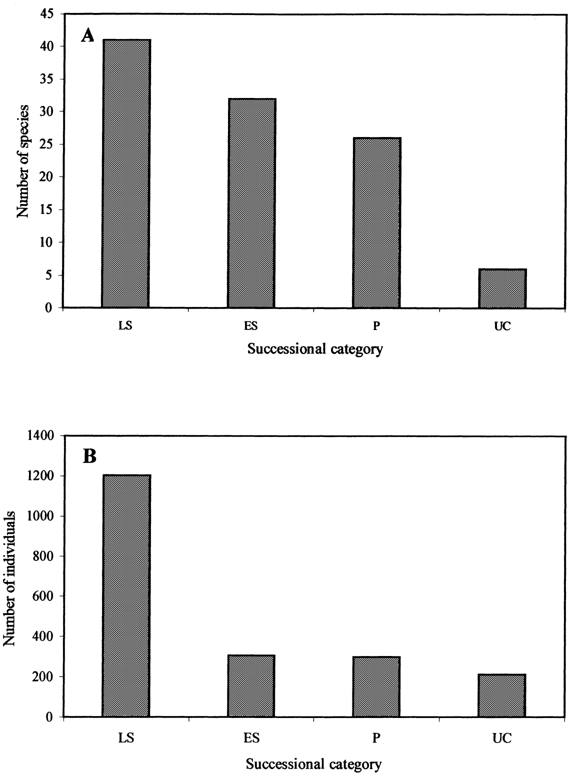

Figure 5. Successional species categories (P, pioneer; ES, early secondary; LS, late secondary; UC, unclassified) in ten canopy gaps in a semideciduous mesophytic forest, south-eastern Brazil: (A) number of species, (B) number of individuals for successional category.

Discussion

Gap size and canopy openness

The majority of the analyzed gaps was considered small, with a size of less than 100 m^2. Only the two bigger than 200 m^2 can be considered large, which is in accordance with the pattern found for the majority of tropical forests: small gaps being more frequent than large ones (Brokaw 1985; Costa and Mantovani 1992; Whitmore et al. 1993; Yavitt et al. 1995; Tabarelli and Mantovani 1997a, 1997b).

The larger gaps were formed where the canopy reaches a mean height of 20 m, and are the results of fell with the uprooting of one or more *P. longifolium* or *A. polyneuron* individuals. The small gaps were opened where the canopy is low, with height varying from 13 to 15 m, and resulted from the fell of small individual trees or from breakage of part of the crown.

The predominance of small gaps in the county of São Paulo and boundary region is the consequence of the successional stage of the forests, which are secondary and, consequently, have a low canopy. Therefore, small individuals do not open big gaps when they fall (Tabarelli 1994).

The positive correlations between gap size and canopy openness found in this study is in accordance with studies based on hemispherical photographs in other tropical forests in Asia, Central and South America (Brown 1993; Whitmore et al. 1993; Van der Meer and Bongers 1996; Trichon et al. 1998).

The use of hemispherical photographs has the advantages of greater speed and accuracy compared to the traditional methods of determining gap size, as the eight (Brokaw 1982a) or the 16 (Green 1996) sided polygon methods, the elipse (Barton et al. 1989; Tabarelli and Mantovani 1997a, 1997b) or Runkle (1981) methods, that have already been emphasized in other studies of canopy gaps (Whitmore et al. 1993; Van der Meer and Bongers 1996; Trichon et al. 1998). It was possible during the image processing to delimit the gap perimeter considering its irregularities. Besides the gap size, the hemispherical photographs allowed the quantification of the canopy openness, which is considered a good indicator of light and microclimate conditions in the gaps (Brown 1993; Rich et al. 1993; Whitmore et al. 1993).

Floristic composition

The mean density value found for the set often gaps was superior to the values obtained in natural gaps of other tropical forests, which varied from 0.13 (Tabarelli and Mantovani 1997a) to 0.99 individuals/m^2 (Tabarelli and Mantovani 1997b). This reflects the resilience of the Santa Genebra forest to natural disturbances.

The mean density of pioneers found in this study was superior to the value found (0.14 pioneer species/m^2) in gaps in the Atlantic Forest (Tabarelli 1997). The greatest density of pioneers in the Santa Genebra gaps may be a consequence of the great degree of disturbance in this forest and its seasonal characteristics, defining a pronounced deciduousness in the canopy, with consequent seasonal increase of light levels.

The high number of sampled species indicates that the gaps in the Reserve are rich in species and are not being colonized only by pioneer species, as suggested in the initial hypothesis. Therefore, the role of these disturbance areas in maintaining the forest structure, richness and diversity becomes clear, as suggested by several authors for other tropical forests (Denslow 1987; Ashton 1989; Vandermeer et al. 1996; Okuda et al. 1997; Tabarelli and Mantovani 1997b).

Among the most numerous families sampled in the gaps, the Violaceae and Polygalaceae were represented exclusively by understore species. The most numerous family, Rubiaceae, also stood out for density in surveys of other stretch of this forest (Santos et al. 1996) and in gaps in the Cantareira Mountain, São Paulo (Tabarelli 1994). The families Euphorbiaceae and Rutaceae also appear among the most numerous in the gap surrounding areas.

The families with greatest species richness in the gaps were the same as in the gap surrounding areas and in the stretch of one hectare of this same fragment (Santos et al. 1996). Therefore, it may be suggested that natural gaps are important regeneration sites of the shrubs and trees in Santa Genebra. Among the families with greatest species richness, Euphorbiaceae, Meliaceae, Myrtaceae and Rutaceae are outstanding for richness in the majority of phytosociology surveys made in semideciduous mesophytic forests in São Paulo state (Toniato et al. 1998). The Rubiaceae family occupied the second position for species richness also in gaps in the Cantareira Mountain forest (Tabarelli 1994).

The typical understorey shrub species, *H. atropurpureus, A. klotschii, P. klotzchii, P. hastisepala* and *G. multiflora* showed high plasticity, remaining abundant and also reproducing in the gap environments. Of these species, *A. klotschii* stood out for density in the majority of phytosociological survey in the semideciduous mesophytic forest of the São Paulo State Peripheral Depression (Rodrigues 1992; Santos et al. 1996).

The richness of typical species of the understorey in tropical forests is especially important for the diversity of these ecosystems (Gentry & Emmos 1987). Understorey species decisively contribute to diversity in small gaps, because they remain in these environments during the regenerative process, as observed in this and other studies in São Paulo State forests (Knobel 1995; Tabarelli and Mantovani 1997a, 1997b).

The understorey shrubs in the tropical forests have a wide range of light environments during their lifetime showing strong plasticity in growth response for the canopy openness (Gandolfi 1991; Pascarella 1998). Thus, canopy gaps may favour understorey species in several ways, e.g. enhancing seedling establishment, growth and reproduction (Amézquita 1998).

The occurrence of young individuals of the late secondary canopy species *A. polyneuron* in all the gaps resulted from the high abundance of the species in the gap surrounding areas and in other stretch of this forest (Santos et al. 1996) and from the presence of remaining vegetation, which provided some level of shading for the regenerating individuals.

The pioneer *U. baccifera* was sampled in the majority of the gaps. This was expected because it is a typically pioneer species, colonizer of open environments. Other pioneer species commonly cited as gap colonizers (Gandolfi et al. 1995; Bernacci and Leitão Filho 1996; Santos et al. 1996) such as *Cecropia glazioui* Sneth., *Cecropia holoeuca* Miq., *Cecropia pachystachya* Tree., *Trema micrantha* (L.) Blume, *Celtis tala* Gillies ex Planchon., *Celtis iguanaea* (Jacq.) Sargent and *Vernonia diffusa* Less, were sampled in the gap set but at low densities, probably because of the predominance of small gaps.

Floristic similarity

The floristic similarity between gaps was associated with gap sizes and floristic composition in the immediately surrounding forest. It has been demonstrated for several species of trees with different tolerances to the shade that gap size influences seed germination, survival and growth of the seedlings (Denslow 1980; Brokaw 1987; Chandrashekara and Ramakrishnan 1993; Abe et al. 1995; Cintra and Horna 1997; Kneeshaw and Bergeron 1998). Thus, gaps with similar sizes had similar floristic compositions since they also offer seeds and seedlings more homogeneous environmental conditions, mainly light, as it became evident in the positive relationship between canopy openness and gap size.

The two biggest gaps, similar in floristic composition, are the only ones which may be considered large and have several pioneer species in common. The larger canopy openness and increase in light must have favored the establishment of these pioneer species which are common to both areas. On the other hand, the high floristic similarity between the stretches of the forest where these two largest gaps are located must also have contributed to the floristic similarity between them. The least similarity found between the smallest and largest gaps confirms the pattern of environmental characteristics defining the heterogeneity among gaps with different sizes.

For the small gaps, regeneration was mainly of the understorey and sub-canopy species also present in their surrounding areas. Therefore, the floristic similarity among these small gaps was influenced by the vegetation present before the disturbance. A similar colonization pattern was found by Tabarelli (1994) in small gaps in the Cantareira Mountain forest, São Paulo, emphasizing that the recruitment of understorey species may be maintained after opening the small gaps.

One of the factors which must have influenced the colonization of the gaps and the floristic differences among them is the proximity of the seeds sources as suggested by several authors (Abe et al. 1995; Masaki and Nakashizuka 1995; Reader et al. 1995; Webb 1998). This assumption is based on the fact that the comparison between the gaps showed a similarity pattern associated with what was found in the gap surrounding areas. Shrub and tree individuals remaining in the gaps or present in their surrounding areas would be dispersing seeds to the gap interiors, as verified by Martins and Rodrigues (1999), and increasing their diversity.

The floristic heterogeneity among the continuous stretches of the respective forest fragment should have originated from the heterogeneity of the colonization of the gaps with different sizes. This is confirmed by the floristic differences among them. The colonization of the group gaps by different sets of species may result in patches with different floristic compositions within the forest. Therefore, there is a probable cause/effect relationship where the gaps have their floristic diversity and heterogeneity influenced by the surrounding forest, but also play an important role in the generation and maintenance of spatial diversity and floristic heterogeneity in the forest as a whole.

Successional species categories

The percentage of species and individuals by successional category in the ten gaps shows that the late secondary species were more abundant than the initial species. Therefore, the initial hypothesis is rejected, and studies in natural gaps of other Brazilian forests are confirmed (Rollet 1983; Negrelle 1995; Tabarelli and Mantovani 1997a).

The classic studies consider that pioneer species are more abundant in big gaps, with sizes over 150 m^2 (Brokaw 1982b) or greater than 400 m^2 (Hartshorn 1980) or even 1000 m^2 (Whitmore 1982). Considering that only 20% of the gaps in the present study had a size over 150 m^2, the observed data may have resulted from the importance that species of the end of the forest succession have in comparison to pioneers species in smaller gaps. It should be pointed out, however, that only the two large gaps totaling 60.8% of the total gap size, 49.6% of the total number of individuals and 55.8% of the total number of individuals from pioneer species. They are, therefore, important in terms of species representatives in this successional group and of the forest dynamic as a whole. Furthermore, the pioneer species *C. glazioui, C. hololeuca, C. pachystachya* and *T. micrantha* occurred exclusively in the large gap. These results confirm studies which indicated the existence of a model for tropical forests where large gaps, although less numerous than the small, account for the greater proportion of the total area of disturbance. Consequently, they play an important role in the maintenance and in the diversity of the pioneer species group in tropical forests (Hartshorn 1980; Brokaw 1982b, 1985).

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