



## Colonization of gaps produced by death of bamboo clumps in a semideciduous mesophytic forest in south-eastern Brazil

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### Abstract

The study was carried out in 16 gaps produced by bamboo clump death (*Merostachys riedeliana* Rupr. ex Doell) in a semideciduous mesophytic forest in the Santa Genebra County Reserve (22°49'45" S and 47°06'33" W), Campinas, SP, south-eastern Brazil. All shrub and tree individuals in the gap with height  $\geq 0.50$  m were sampled. The floristic similarity among the colonizing vegetation in these gaps and in gaps produced by treefall was assessed by the Jaccard similarity index and cluster analysis. The colonization process of these gaps was found to be similar to that in gaps formed by treefall, but this colonization only began after the bamboo clump death. The gap area varied from 35 m<sup>2</sup> to 454 m<sup>2</sup>, but small gaps predominated. In the set of gaps, 3677 individuals were sampled belonging to 40 families, 83 genera and 114 species. The families with the greatest species richness in the gaps were Myrtaceae (10), Euphorbiaceae (9) and Solanaceae and Rubiaceae (8 each). The species with the greatest number of individuals in the gaps were the pioneers *Celis tala* Gillies ex Planchon and *Croton priscus* Muell. Arg. and the shade-tolerant shrubs *Actinostemon klotzschii* (Muell. Arg.) Pax, *Polygala klotzschii* Chod., *Psychotria hastisepala* Muell. Arg. and *Galipea multiflora* Engl. Late secondary species predominated because of the greater number of small gaps. The gaps formed by bamboo clump death contributed to the successional and structural organization of the forest, creating suitable environments for colonization by shrub and tree species of the different successional groups.

### Introduction

Bamboos are widely distributed from 46° N to 47° S, but they prefer wet environments such as tropical and subtropical forests (Soderstrom and Calderón 1979; Londoño 1990), where they form the most important grass group (Soderstrom and Calderón 1971, 1979). However, the influence of bamboos in the structure and dynamics of Neotropical forest has only recently deserved attention (Oliveira-Filho et al. 1994).

Several bamboo species compensate long non-productive intervals that can last decades (Janzen 1976; Soderstrom 1981; Filgueiras 1988) with a complex system of rhizomes that occupy vast forest areas (Pohl 1991) and compete with tree and shrub species

for resources and space (Whitmore 1975; Oliveira-Filho et al. 1994; Guilherme 2000).

*Merostachys riedeliana* Rupr. ex Doell is found in forest fragments in São Paulo and Minas Gerais states, south-eastern Brazil (Gonçalves 2000; Guilherme and Ressel 2001), where the plants can reach the canopy. The plants have long culms, growing in dense clumps and reaching 10 m in height. The formation of dense clumps of this species can interfere negatively in the natural regeneration of shrub and tree species in these remains of semideciduous mesophytic forests, affecting forest physiognomy and structure (Oliveira-Filho et al. 1994; Guilherme 1999).

After synchronized flowering and fructification of this and other *Merostachys* species, at intervals of about three decades (Guilherme and Ressel 2001), death of the entire population (Filgueiras 1988) sets in and the quick rot of the bamboo clumps produces different gaps in the canopy (Oliveira-Filho et al. 1994).

The ecological role of disturbances in the maintenance of the high species diversity in tropical forests has been discussed by several authors (Connell 1989; Vandermeer et al. 1996; Vetaas 1997; Wiegand et al. 1998). In this regard, the ecological importance of canopy gaps in the successional and structural organization of the tropical forests, due to increased light levels favoring regeneration of various tree species groups, has been shown in a series of studies (Denslow 1980, 1987; Brown 1993; Brokaw 1985, 1987; Reader et al. 1995; Rebertus and Burns 1997; Carvalho et al. 2000).

Thus the objective of this study was to test the hypothesis that bamboo clump death produces openings in the forest canopy and promotes a colonization process similar to that which occurs in treefall gaps, and that the species is, therefore, an important disturbance factor in shrub and tree species regeneration.

## Study area

The study was carried out in the Santa Genebra County Reserve, located 22°49'45" S and 47°06'33" W in the county of Campinas, São Paulo state, in south-eastern Brazil. The total area of the reserve is 251.8 ha, with altitudes that vary from 580 to 610 m. The climate is Cwa type by the Köppen classification (Setzer 1966), defined as warm and wet, with a dry winter and wet summer, mean annual rainfall of 1381.2 mm and mean annual temperature of 21.6 °C. The predominant soil type is Purple Latosol allic (Oliveira et al. 1979).

The greatest part of the reserve is covered by semideciduous mesophytic forest (Leitão Filho 1995).

The bamboo clumps (*M. riedeliana*) in the reserve flowered, fructified and then died in 1994, producing gaps in the forest canopy. The colonization process in these 16 gaps was analyzed two years after this event.

## Methods

### *Physical and floristic characterization of the gaps*

The gap size produced by bamboo clump death was measured by the method proposed by Brokaw (1982a) where eight coordinates of direction and distance to gap edge were marked from a central point within the gap.

All the shrub and tree individuals with height  $\geq$  0.50 m in the gaps were sampled for the floristic survey of the colonizing vegetation and the botanical material was collected for identification. Taxonomic identification was carried out by consulting the herbariums UEC at Campinas State University and ESA at the Escola Superior de Agricultura "Luiz de Queiroz" at the University of São Paulo and, when necessary, with specialist help. The plant classification system of Cronquist (1988) was adopted.

Regression analysis was used to determine the influence of the gap size on the floristic composition of the colonizing vegetation.

### *Successional species categories*

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

Four successional categories were adopted: pioneers, early secondary, late secondary and unclassified, which 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).

Regression analysis was used to analyze the influence of gap size on the selectivity of the colonizing vegetation in the different successional categories.

### *Floristic similarity*

Floristic comparisons were made to assess the floristic similarity among the gaps in this study and typical gaps produced by treefall in the same forest.

A matrix of binary data was constructed from this analysis, containing 139 shrub and tree species and 26 gaps, 16 produced by bamboo clump death (this study) and 10 gaps produced by treefall (Table 1),

Table 1. Sizes of ten treefall gaps in a semideciduous mesophytic forest, south-eastern Brazil.

Number of the gap	18 (2)*	22 (6)	24 (8)	21 (5)	19 (3)	23 (7)	20 (4)	17 (1)	25 (9)	26 (10)
Size (m <sup>2</sup> )	20.09	34.95	43.47	46.13	68.48	71.57	99.4	108.35	295.00	468.00

\*Original numbers of the gaps (Martins and Rodrigues 2002).

Table 2. Physical and floristic characteristics of 16 gaps produced by bamboo clump death in a semideciduous mesophytic forest, south-eastern Brazil.

Number of the gap	Size (m <sup>2</sup> )	Number of species	Number of individuals	Density (ind. m <sup>-2</sup> )
1	34.8	23	73	2.10
4	40	22	45	1.13
8	50.5	27	97	1.92
2	51.8	34	182	3.51
15	60.4	27	121	2.00
7	65.6	32	191	2.83
3	71.5	33	119	1.66
6	72.7	38	219	3.01
5	87.4	45	265	3.03
13	89.2	31	82	0.92
9	93.9	30	251	2.67
16	118.9	39	204	1.72
12	185.9	30	100	0.54
11	254.3	55	414	1.63
14	293.2	60	508	1.73
10	453.8	55	805	1.77

which were studied by Martins and Rodrigues (2002). The floristic similarity was calculated from this matrix by the Jaccard index (Mueller-Dombois and Ellenberg 1974):

$$IS_J = \left( \frac{c}{a + b + c} \right) \times 100,$$

where  $a$  = number of exclusive species of the plot 1,  $b$  = number of exclusive species of the plot 2 and  $c$  = number of species common to the two plots.

Cluster analysis was used to interpret the floristic similarity among gaps by average linkage method (UPGMA). These analyses were performed by the FITOPAC 1 computer program (Shepherd 1996).

This floristic comparison was possible because the same criteria of individual inclusion had been used in both studies, and because the field surveys were carried out in the same period.

## Results

### *Physical and floristic characterization of the gaps*

The gap size varied from 35 m<sup>2</sup> to 454 m<sup>2</sup>, but the majority of the gaps was considered small, with a size of less than 100 m<sup>2</sup> (Table 2).

In the set of 16 gaps, 3677 individuals belonging to 40 families, 83 genera and 114 species were sampled (Table 3).

The families with the greatest species richness were: Myrtaceae, with ten species (8.77% of the total), Euphorbiaceae, with nine species (7.89%), Rubiaceae and Solanaceae with eight species each (7.02%), Meliaceae and Rutaceae with six species each (5.26%), Fabaceae and Mimosaceae with five species each (4.39%).

The species with greatest number of individuals were *Celtis tala* Gillies ex Planchon. with 365 individuals, *Croton priscus* Muell. Arg. with 321, *Actinostemon klotzschii* (Muell. Arg.) Pax with 304, *Polygala klotzschii* Chod. with 285, *Coffea arabica* L. with 250 and *Galipea multiflora* Engl. with 202, totalling 46.9%.

Table 3. Species sampled in 16 gaps produced by *M. riedeliana* clump death in a semideciduous mesophytic forest, south-eastern Brazil. Successional category: ST, late secondary; ES, early secondary; P, pioneer; UC, unclassified. N, number of individuals.

Species	Families	Succes. category	N
<i>Justicia</i> sp1	Acanthaceae	UC	10
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	ES	157
<i>Aspidosperma polyneuron</i> Muell.Arg.	Apocynaceae	LS	92
<i>Aspidosperma ramiflorum</i> Muell. Arg.	Apocynaceae	LS	101
Asteraceae 1	Asteraceae	UC	1
Asteraceae 2	Asteraceae	UC	1
<i>Vernonia diffusa</i> Less.	Asteraceae	P	42
<i>Pseudobombax grandiflorum</i> (Cav.) A. Rob.	Bombacaceae	P	1
<i>Cordia ecalyculata</i> Vell.	Boraginaceae	ES	6
<i>Copaifera langsdorffii</i> Desf.	Caesalpiniaceae	LS	1
<i>Senna macranthera</i> (Collad.) Irwin et Barn.	Caesalpiniaceae	P	2
<i>Holocalyx balansae</i> Mich.	Caesalpiniaceae	LS	36
<i>Carica quercifolia</i> (St. Hil.) Hieron.	Caricaceae	P	2
<i>Jacaratia spinosa</i> (Aubl.) A.D.C.	Caricaceae	P	11
<i>Cecropia pachystachya</i> Trec.	Cecropiaceae	P	1
<i>Maytenus ilicifolia</i> Reiss.	Celastraceae	LS	15
<i>Maytenus robusta</i> Reiss.	Celastraceae	LS	1
<i>Diospyros inconstans</i> Jacq.	Ebenaceae	LS	2
<i>Sloanea monosperma</i> Vell.	Elaeocarpaceae	LS	2
<i>Actinostemon klotzschii</i> (Muell. Arg.) Pax	Euphorbiaceae	LS	304
<i>Actinostemon concolor</i> (Spreng.) Muell.Arg.	Euphorbiaceae	LS	5
<i>Alchornea glandulosa</i> Poep. & Endl.	Euphorbiaceae	P	3
<i>Croton floribundus</i> Spreng.	Euphorbiaceae	P	17
<i>Croton priscus</i> Muell.Arg.	Euphorbiaceae	P	321
<i>Margaritaria nobilis</i> L.	Euphorbiaceae	LS	1
<i>Pachystroma longifolium</i> (Ness) I.M. Johnston	Euphorbiaceae	LS	29
<i>Savia dictyocarpa</i> Kuhlman	Euphorbiaceae	LS	20
<i>Sebastiania klotzchiana</i> Pax & Hoffman	Euphorbiaceae	LS	32
<i>Centrolobium tomentosum</i> Guill.	Fabaceae	ES	5
<i>Lonchocarpus guilleminianus</i> (Tul.) Malme	Fabaceae	ES	24
<i>Machaerium brasiliensis</i> Vog.	Fabaceae	ES	1
<i>Machaerium stipitatum</i> Vog.	Fabaceae	ES	4
<i>Myroxylon peruiferum</i> L.	Fabaceae	UC	4
<i>Casearia gossypiosperma</i> Briq.	Flacourtiaceae	ES	8
<i>Casearia sylvestris</i> Sw.	Flacourtiaceae	P	1
<i>Prockia crucis</i> L.	Flacourtiaceae	ES	7
<i>Nectandra megapotamica</i> (Spreng.) Mez	Lauraceae	ES	3
<i>Ocotea beaulahiae</i> Baitello	Lauraceae	UC	23
<i>Ocotea minarum</i> Mart. ex Ness	Lauraceae	UC	1
<i>Cariniana estrellensis</i> (Raddi) O. Kuntze	Lecythidaceae	LS	55
<i>Strychnos brasiliensis</i> (Spreng.) Mart.	Loganiaceae	LS	2
<i>Abutilon bedfordianum</i> St.Hil. & Naud.	Malvaceae	P	3
<i>Pavonia sepium</i> St.Hil.	Malvaceae	P	1
<i>Cedrela fissilis</i> Vell.	Meliaceae	ES	1
<i>Guarea macrophylla</i> Vell.	Meliaceae	LS	1
<i>Trichilia catigua</i> Adr. Juss.	Meliaceae	LS	19
<i>Trichilia claussoni</i> C. DC.	Meliaceae	LS	17
<i>Trichilia elegans</i> A. Juss.	Meliaceae	LS	39
<i>Trichilia pallida</i> Sw.	Meliaceae	LS	22

Table 3. Continued.

Species	Families	Succes. category	N
<i>Acacia paniculata</i> Willd.	Mimosaceae	P	3
<i>Acacia polyphylla</i> DC.	Mimosaceae	P	9
<i>Inga luschnathiana</i> Benth.	Mimosaceae	ES	9
<i>Inga marginata</i> Willd.	Mimosaceae	ES	3
<i>Piptadenia gonoacantha</i> (Mart.) Macbr.	Mimosaceae	ES	68
<i>Mollinedia widgrenii</i> A.DC.	Monimiaceae	LS	2
<i>Ardisia latipes</i> Mart.	Myrsinaceae	LS	16
<i>Ardisia semicrenata</i> Mart.	Myrsinaceae	UC	19
<i>Rapanea guianensis</i> Aubl.	Myrsinaceae	ES	1
<i>Rapanea umbellata</i> (Mart.) Mez.	Myrsinaceae	ES	9
<i>Calycorectes acutatus</i> (Toledo) Miq.	Myrtaceae	LS	3
<i>Campomanesia guazumaefolia</i> Berg.	Myrtaceae	LS	1
<i>Eugenia excelsa</i> O. Berg.	Myrtaceae	LS	3
<i>Eugenia florida</i> DC.	Myrtaceae	LS	3
<i>Eugenia hiemalis</i> Camb.	Myrtaceae	LS	1
<i>Eugenia ligustrina</i> Willd.	Myrtaceae	LS	1
<i>Eugenia verrucosa</i> D. Legrand	Myrtaceae	LS	2
<i>Myrciaria cauliflora</i> (DC) Berg.	Myrtaceae	LS	5
<i>Myrciaria floribunda</i> (Wild.) Berg.	Myrtaceae	LS	50
<i>Psidium sartorianum</i> Niedenzu	Myrtaceae	UC	1
<i>Bougainvillea arborea</i> Glaziou	Nyctaginaceae	ES	1
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	ES	5
<i>Pisonia ambigua</i> L.	Nyctaginaceae	ES	5
<i>Agonandra englerii</i> Hoehne.	Opiliaceae	ES	2
<i>Gallesia integrifolia</i> (Spreng.) Harms	Phytolaccaceae	ES	5
<i>Seguiera floribunda</i> Benth.	Phytolaccaceae	ES	41
<i>Ottonia propinqua</i> Kunth.	Piperaceae	P	15
<i>Piper amalago</i> (Jacq.) Yunker	Piperaceae	P	77
<i>Piper gaudichaudianum</i> Kunth.	Piperaceae	P	43
<i>Polygala klotzschii</i> Chod.	Polygalaceae	LS	285
<i>Colubrina glandulosa</i> Perk.	Rhamnaceae	ES	1
<i>Rhamnidium elaeocarpum</i> Reiss.	Rhamnaceae	ES	1
<i>Coffea arabica</i> L.	Rubiaceae	UC	250
<i>Coussarea contracta</i> Benth. & Hook.	Rubiaceae	LS	12
<i>Coutarea hexandra</i> Schamann	Rubiaceae	LS	1
<i>Ixora venulosa</i> Benth.	Rubiaceae	LS	2
<i>Palicourea marcgravii</i> St.Hil.	Rubiaceae	LS	8
<i>Psychotria hastisepala</i> Muell. Arg.	Rubiaceae	LS	33
<i>Psychotria sessilis</i> (Vell.) Muell. Arg.	Rubiaceae	LS	1
<i>Rudgea jasminoides</i> Muell. Arg.	Rubiaceae	LS	10
<i>Balfourodendron riedelianum</i> (Engl.) Engl.	Rutaceae	ES	7
<i>Esenbeckia febrifuga</i> (St.Hil.) A.Juss.	Rutaceae	LS	4
<i>Esenbeckia leiocarpa</i> Engl.	Rutaceae	LS	55
<i>Galipea multiflora</i> Engl.	Rutaceae	LS	202
<i>Metrodorea nigra</i> St.Hil.	Rutaceae	LS	1
<i>Metrodorea stipularis</i> Mart.	Rutaceae	LS	60
<i>Zanthoxylum juniperinum</i> Poepp.	Rutaceae	ES	2
<i>Chrysophyllum gonocarpum</i> (Mart. & Eichl.) Engl.	Sapotaceae	ES	7
<i>Picramnia warmingiana</i> Engl.	Simaroubaceae	LS	59

Table 3. Continued.

Species	Families	Succes. category	N
<i>Cestrum laevigatum</i> Schlecht.	Solanaceae	P	2
<i>Solanum</i> sp1	Solanaceae	UC	1
<i>Solanum</i> sp2	Solanaceae	UC	1
<i>Solanum acerifolium</i> Mil.	Solanaceae	P	9
<i>Solanum argenteum</i> Roem. & Schultz.	Solanaceae	P	2
<i>Solanum concinnum</i> Schott ex Sendtn.	Solanaceae	ES	11
<i>Solanum erianthum</i> D. Don	Solanaceae	ES	4
<i>Solanum gemellum</i> Mart. ex Sendt.	Solanaceae	ES	1
<i>Luehea divaricata</i> Willd.	Tiliaceae	ES	4
<i>Triumfetta semitriloba</i> Jacq.	Tiliaceae	P	3
<i>Celtis iguanae</i> (Jacq.) Sargent	Ulmaceae	P	36
<i>Celtis tala</i> Gillies ex Planchon	Ulmaceae	P	365
<i>Trema micrantha</i> (L.) Blume.	Ulmaceae	P	58
<i>Ureca baccifera</i> (L.) Gaud.	Urticaceae	P	173
<i>Aegiphila sellowiana</i> Cham.	Verbenaceae	P	3
<i>Hybanthus artropurpureus</i> (St.Hil.) Taub.	Violaceae	LS	143

The most frequent species in the set of gaps were *C. arabica*, sampled in all the gaps, and *Aspidosperma polyneuron* Muell. Arg., sampled in 15 gaps. A large number of species (37) was observed in only one gap.

Among the gaps the number of individuals varied from 45 to 805 and the number of species from 22 to 60 (Table 2). This variation was related to the increase in gap size. The gaps had on average of 2.01 individuals/m<sup>2</sup>. The number of individuals was positively and significantly correlated with the gap size ( $P < 0.0001$ ,  $r^2 = 0.84$ ). A positive and significant relationship ( $P < 0.0001$ ,  $r^2 = 0.72$ ) was also found between the number of species and the gap size (Figure 1).

#### Floristic similarity

The Jaccard index obtained in the floristic comparison among the colonizing vegetation in the set of gaps in this study and the set of treefall gaps (Martins and Rodrigues 2002) was 56.67%, indicating floristic similarity (Mueller-Dombois and Ellenberg 1974).

Cluster analysis showed that there was no individualization of gap groups by their cause of origin, that is, groups did not form from gaps produced by bamboo clump death or by treefall (Figure 2). On the contrary, there was linking between the two types of gaps, which was expected as the two sets of gaps are similar floristically.

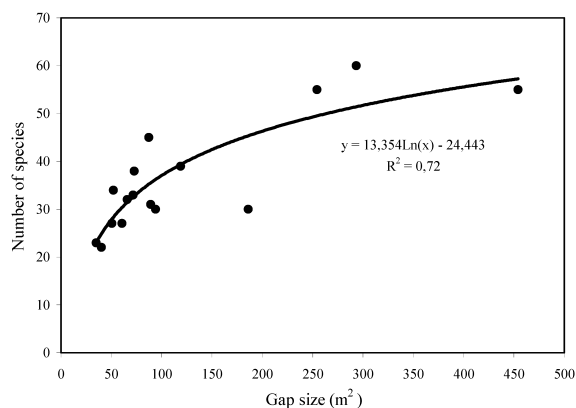


Figure 1. Relationship between number of species and gap size produced by bamboo clump death in a semideciduous mesophytic forest, south-eastern Brazil.

However, the influence of the gap size could be detected in the definition of floristic groups. Gaps 10, 11, 14, 25 and 26, that formed a single group, were the only ones that could be considered big, with areas greater than 250 m<sup>2</sup>. In this group, gaps 10, 11 and 14 were the largest in this study (Table 2), and 25 and 26 were the largest gaps produced by treefall (Table 1), with 295 m<sup>2</sup> and 468 m<sup>2</sup>, respectively (Martins and Rodrigues 2002).

#### Successional species categories

The shrub and tree species sampled in the gaps were distributed in 48 (42.11% of the total) late secondary

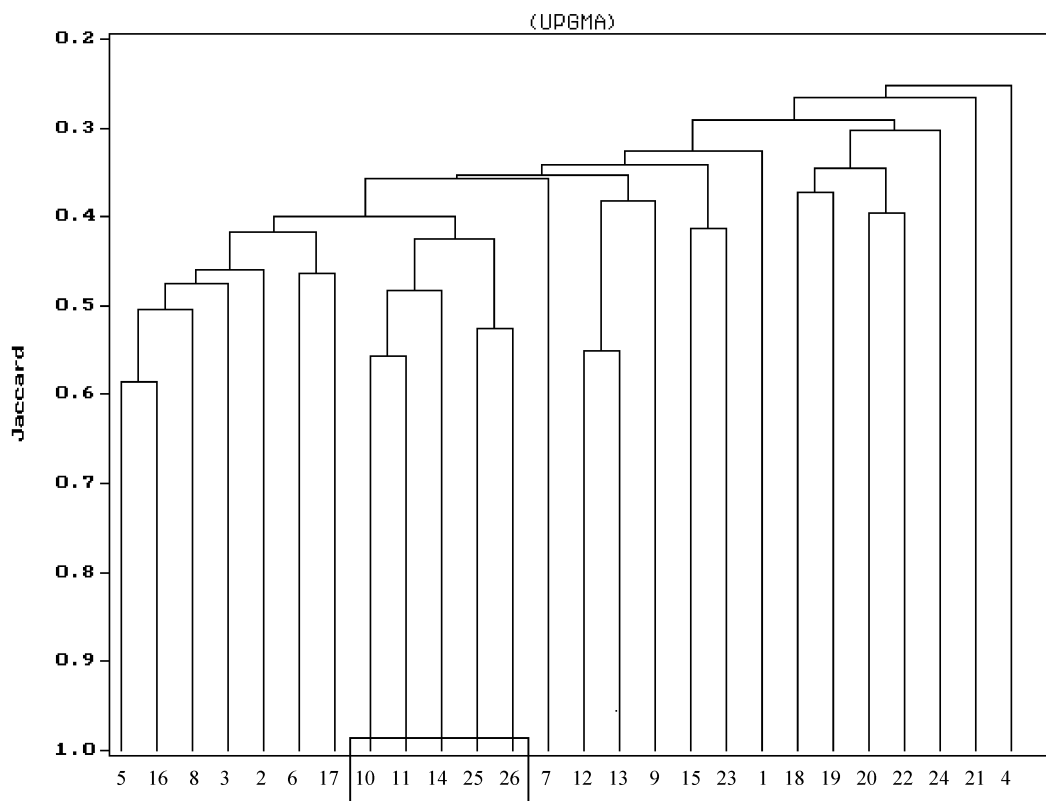


Figure 2. Dendrogram obtained using the Jaccard similarity index and average linkage method (UPGMA), for gaps produced by bamboo clump death: observations 1 to 16; and by treefall (Martins and Rodrigues 2002): observations 17 to 26, in a semideciduous mesophytic forest, south-eastern Brazil. The observations 10, 11, 14, 25 and 26 (marked group) represent the largest gaps.

species, 29 (25.44%) early secondary species and 26 (22.81%) pioneer species. Only 11 species (9.65%) could not be characterized successional (Figure 3A). The number of pioneer species increased significantly ( $P = 0.003$ ,  $r^2 = 0.70$ ) with the increase in gap size (Figure 4).

Of the total of individuals sampled in the gaps, 1759 (47.84%) were late secondary species, 1203 (32.72%) pioneer, 407 (11.07%) early secondary species and 300 (8.38%) individuals were species not characterized (Figure 3B). The high number of individuals of not characterized species was due to the high *C. arabica* density, an exotic species that has invaded the forest fragment.

Considering only the two extreme successional categories, the mean density of pioneer species and late secondary species among gaps was 0.60 individuals/m<sup>2</sup> and 1.01 individuals/m<sup>2</sup>, respectively.

## Discussion

The predominance of small gaps produced by bamboo clump death reproduced a pattern reported in most studies on canopy treefall gaps in tropical forests, where small gaps are more frequent than large ones (Brokaw 1985; Costa and Mantovani 1992; Whitmore et al. 1993; Tabarelli and Mantovani 1997a, 1997b; Martins and Rodrigues 2002).

The canopy height determines treefall gap size (Brokaw 1985; Tabarelli 1994; Martins and Rodrigues 2002). However, the size of the gaps in this study was determined by the space occupied by the bamboo clump in the forest canopy. The predominance of small gaps is related to the small space occupied by the isolated *M. riedeliana* bamboo clumps in the forest. Only three large bamboo clumps occupied large spaces in the forest and when they died they produced the largest gaps in this study.

This greater number of small gaps explained the predominance of late secondary species, corroborat-

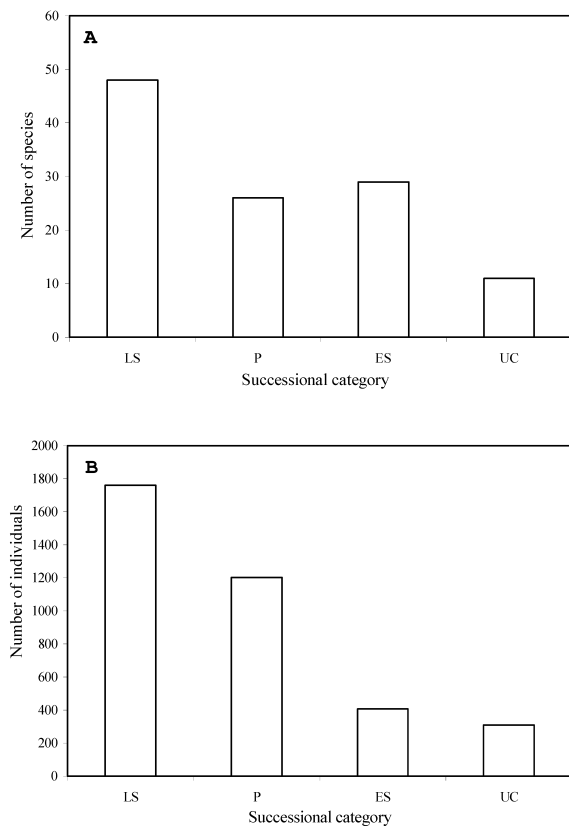


Figure 3. Number of species (A) and number of individuals (B) for successional category (LS, late secondary; P, pioneer; ES, early secondary; UC, unclassified) samples in gaps produced by *M. riedeliana* death in a semideciduous mesophytic forest, south-eastern Brazil.

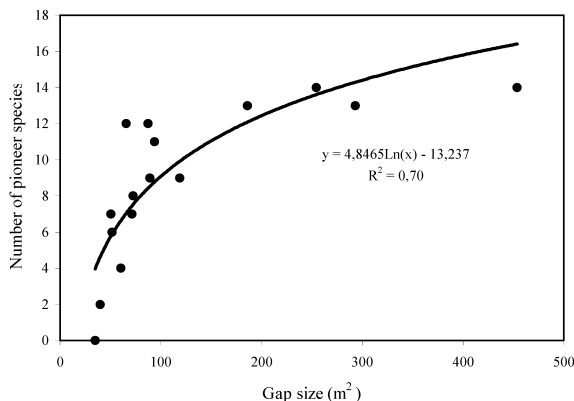


Figure 4. Relationship between number of pioneer species and gap size produced by bamboo clump death in a semideciduous mesophytic forest, south-eastern Brazil.

ing studies carried out on treefall gaps in the same forest (Martins and Rodrigues 2002) and in other Brazilian forests (Rollet 1983; Negrelle 1995; Tabarelli

and Mantovani 1997a, 1997b). In these small gaps, the regeneration of late secondary species begins only after bamboo death. It should be pointed out, however, that the three large gaps, with areas greater than 250 m<sup>2</sup>, totaled 50% of the total gap size, 47% of the total number of individuals and 43.6% of the total number of individuals from pioneer species, and therefore are important in terms of species representatives of this successional group. These results corroborate studies on gap dynamics in tropical forests, where large gaps are less numerous than smaller ones but account for the greater proportion of the total area of disturbance and play an important role in the maintenance and diversity of the pioneer species group in these forests (Hartshorn 1980; Brokaw 1982b, 1985; Martins and Rodrigues 2002).

The mean density value found for the set of 16 gaps was superior to the values obtained in gaps in other Brazilian forests, which varied from 0.13 (Tabarelli and Mantovani 1997a) to 0.99 individuals/m<sup>2</sup> in Atlantic forest (Tabarelli and Mantovani 1997b) and close to 2.07 individuals/m<sup>2</sup> reported in treefall gaps produced in the Santa Genebra forest (Martins and Rodrigues 2002).

The high number of species and individuals sampled indicates that the colonization process in these gaps produced by bamboo clump death is similar to that in treefall gaps in the same forest (Martins and Rodrigues 2002). This reflects the resilience of the Santa Genebra forest to natural disturbances, characterized by the abundant regeneration of shrub and tree species in canopy gaps and the ecological role of these disturbance areas in maintaining the forest structure and species richness, as suggested by several authors (Denslow 1987; Ashton 1989; Vandermeer et al. 1996; Vetaas 1997; Okuda et al. 1997; Tabarelli and Mantovani 1997b).

The families with the greatest species richness in this study were also important in the gaps produced by treefall (Martins and Rodrigues 2002) and in a stretch of one hectare of this same fragment (Santos et al. 1996). Euphorbiaceae, Meliaceae, Myrtaceae and Rutaceae stand out in species richness in most of the phytosociology surveys carried out in semideciduous mesophytic forests in São Paulo state (Toniato et al. 1998; Gandolfi 2000). The Rubiaceae family were second in species richness in treefall gaps in the Cantareira Mountain forest (Tabarelli 1994).

Only *C. tala* and *C. priscus* of the most abundant species group are colonizing pioneers of disturbed areas, such as large gaps and forest edges, while the



other species are typical of the understorey. In this group *A. klotschii*, *P. klotzchii*, *Psychotria hastisepala* Muell. Arg. e *G. multiflora* are shrubs tolerant to the shade of the understorey and are also among the most abundant species in small treefall gaps (Martins and Rodrigues 2002), which certainly reflects their plasticity to variable environmental conditions. *A. klotschii* is of high density in the majority of phytosociology surveys in semideciduous forests in the Paulista Peripheral Depression (Rodrigues 1992; Santos et al. 1996).

The emphasis on richness and abundance of species typical of the understorey in gap environments has already been reported in studies in tropical forests and has been attributed to the predominance of small gaps and seasonal leaf fall of the trees that form the canopy, resulting in variation in light levels during the year (Tabarelli and Mantovani 1997a, 1997b; Svenning 2000). Understorey shrubs are exposed to a wide range of light variation throughout their lives in these forests, and show strong plasticity in growth response (Canham 1988; Pascarella 1998) and even reproduction (Amézquita 1998) for canopy openness.

The two most frequent species in the gap set, *C. arabica* and *A. polyneuron*, are abundant in different environments in the forest. *C. arabica* is distributed in the understorey and treefall gaps (Martins and Rodrigues 2002), possibly competing with the regeneration of autochthon species. *A. polyneuron*, a late secondary emergent species in the forest canopy, has been sampled with high density values both in treefall gaps (Martins and Rodrigues 2002) and in a well-preserved stretch of forest with a little-disturbed forest canopy (Santos et al. 1996).

The floristic similarity among the gaps in this study and those produced by treefall (Martins and Rodrigues 2002) confirm the ecological role of the *M. riedeliana* bamboo clumps after their death, creating regeneration niches similar to those produced by treefalls. This importance is even more evident when the formation of a group consisting of large gaps is found regardless of their cause of origin. The biggest gaps in the two studies, which are similar in floristic composition, have several pioneer species in common. In these large gaps, pioneer species seed germination and seedling growth may be stimulated by the high ratio red/red extreme of spectral light and high light intensity, respectively (Válio and Joly 1979; Vázquez-Yanes and Orozco-Segovia 1987; Van Der Meer et al. 1998).

Several studies in forests of the São Paulo state indicate a great floristic heterogeneity of the arboreal component in the space (Salis et al. 1995; Pagano et al. 1995; Metzger et al. 1998; Gandolfi 2000; Scudeller et al. 2001) and this is attributed to the low constancy (patchy distribution) of most tree species (Scudeller et al. 2001). In this context, the colonization of group gaps produced by bamboo clump death by different sets of species may result in patches with different floristic compositions and contribute to the generation and maintenance of floristic heretogeneity of these forests.

Although *M. riedeliana* forms dense clumps that can prevent the regeneration of shrub and tree species by interfering with seed germination and seedling growth (Whitmore 1975; Oliveira-Filho et al. 1994; Guilherme 1999, 2000), they produce open spaces in the forest after death that are colonized in a process similar to that which occurs in treefall gaps (Denslow 1980, 1987; Chandrashekara and Ramakrishnan 1993; Vandermeer et al. 1996; Tabarelli and Mantovani 1997a, 1997b; Martins and Rodrigues 2002). As the intervals between reproductive events in the species are from 30 to 32 years (Guilherme and Ressel 2001) and these events precede clump death, we suggest that canopy gaps produced by *M. riedeliana* are important regeneration sites of the shrubs and trees in Santa Genebra forest and other semideciduous mesophytic forests, at three decade intervals.

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