Chapter 6

ASSESSING THE ROLE OF THE CANOPY GAP CHARACTERISTICS IN THE REGENERATION OF SHRUB AND TREE SPECIES IN A SEMIDECIDUOS MESOPHYTIC FOREST IN SOUTH-EASTERN BRAZIL

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ABSTRACT

This study investigated the role of the canopy gap characteristics in the regeneration of shrub and tree species of differing successional category in a semideciduos mesophytic forest in the county of Campinas, São Paulo State, south-eastern Brazil. Ten gaps representing a size gradient were selected. All shrubs and trees in the gaps with height $\geq$ 0.5 m were sampled. The sampled species were classified in successional categories (pioneer, early secondary and late secondary species). The influence of the size and canopy openness of gaps on the regeneration of shrub and tree species was tested through regression analysis and canonical correspondence analysis (CCA). Except for a group of pioneer species and some late secondary species related to the larger and smaller gaps, respectively, several species did not show direct relationships with the size and canopy openness of the gaps. Therefore, it was not possible to generalize in terms of strict partitioning of species regeneration niches of different successional categories. The occurrence of large gaps in tropical forests is extremely important for the maintenance of pioneer species, while small gaps may stimulate the regeneration of late secondary species that compose the canopy and understorey. The comprehension of the factors that rule the gaps colonization is vital for the definition of strategies aiming at the maintenance of the last tropical forest fragments and the restoration of areas already degraded.

***Key words*: Canopy gaps, disturbance, forest succession, tropical forest, Brazil.**

INTRODUCTION

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Disturbances are a natural and integral part of forest ecosystems. The process of forest succession occurs only in the aftermath of disturbances and some forest species exist solely in disturbed sites (Dale et al., 2000). Natural disturbances in the forest canopy (gaps) are created by the fall of trees, either by snapping or uprooting. Also falling branches or the death of a tree may create gaps in the canopy (Van Der Meer and Bongers, 1996).

Canopy gaps in tropical forest facilitates a series of environmental changes in the forest understorey, such as an increase in light intensity (photosynthetically active radiation – PAR), alterations in the spectral quality of the light, increase in air and soil temperatures, temperature oscillations, reduction in relative air humidity and soil surface moisture. Gaps may also alter the spatial patterning of fine roots, soil nutrients and soil moisture (Brown, 1996)). These alterations tend to be more drastic as the level of the disturbance increases (Barton et al., 1989; Denslow et al., 1990; Ewel et al., 1998; Pascarella, 1998; Runkle, 1998). Through a series of ecophysiological responses to these environmental changes, the plants trigger a forest regeneration process which may be faster or slower depending on a series of factors related to the type of disturbance itself and to parameters of the surviving vegetation, whether represented by adult individuals around the disturbance area or by a seedling bank or even in the form of dormant seeds in the soil.

In an attempt to explain the high diversity of tree species in tropical forests, some hypotheses and theories start from the principle that a certain level of disturbance would be necessary to prevent competitive exclusion and enable the coexistence of different species in the same area (Connell, 1978; Vandermeer et al., 1996; Vetaas, 1997; Kneeshaw and Bergeron, 1998; Wiegand et al.,1998). Therefore, some theories put forward that tree species are specialized for regeneration niches, that is, there are specialist species for gaps of different sizes (Denslow, 1980) as well as specialist species in certain zones in the gaps (Orians, 1982). Results of recent studies corroborate this theory (Runkle et al., 1995; Sipe and Bazzaz,1995; Brown, 1996; Oliveira-Filho et al., 1998). However, several studies have questioned the differentiation of regeneration niches as the main mechanism of coexistence of tree species in tropical forests. They propose that there is a continuum of ecological conditions in the forest environment, mainly light, which ranges from the understorey to the big gaps. The species behave more as generalists, with superposition of distribution along the gradient formed by different sized gaps (Barton, 1984; Hubbel and Foster, 1986; Welden et al., 1991; Liberman et al., 1995; Tabarelli and Mantovani, 1997; Hubbel et al., 1999). Brokaw and Busing (2000) stand out that being common to all forest, and similar in process, gap dynamics cannot explain the latitudinal gradient in tree richness.

Gap size and canopy openness may not be enough to explain species selectivity. Seedling survival and growth are affected by the formation period of the gap and the position of the seedlings within it (Brown, 1993, 1996; Runkle, 1998).

Studies of tropical forests indicate that the effective dependence on a certain gap size may be valid only for a small group of pioneer species, which need alternating temperatures and/or a high ratio of red to far red of the light spectrum to germinate and a high light intensity for growth. These conditions are normally only available in large gaps (Barton, 1984; Brokaw, 1985; Van Der Meer et al., 1998). In these, the pioneer species are favored by the fact that a tree falls cause the soil to revolve in the root zone, creating a recruitment micro-site for these species (Putz, 1983). The heterogeneity tends to be greater in large gaps than in small gaps (Denslow, 1987) and some pioneer species may have different responses in terms of germination, survival and growth even within a single gap, which may mask the results of selectivity expected by the gap size gradient.

Shade tolerant species seem to be less affected by gap size than pioneer species. They are the main group involved in colonization of small gaps (Brokaw, 1985; Tabarelli and Mantovani, 1997; Runkle, 1998; Martins and Rodrigues, 2002; Martins et al., 2004). In medium sized and large gaps, factors such as surviving trees in their interior and canopy height of the surrounding forest may minimize the expected effects on understorey and late canopy species (Canham, 1988; Ulh et al., 1988; Webb, 1998). In these environments, where the light levels may be insufficient for pioneer species to grow, a gradual enrichment in soil fertility resulting from the decomposition of the fallen tree may be important for these shade tolerant species (Carlton and Bazzaz, 1998).

This shows the polemic role of the environmental gradient represented by the understorey and different size gaps in species selectivity of distinct sucessecional categories in tropical forests. This gradient is influenced by several factors, many of which are not related to the gap size. In this context, this study investigated the role of the canopy gap characteristics in the regeneration of shrub and tree species of differing successional category in a semideciduos mesophytic forest in the county of Campinas, São Paulo State, south-eastern Brazil.

MATERIAL AND METHODS

Study area

This study was carried out in the Santa Genebra County Reserve (22°49’45”S and 47°06’33”W), located in the county of Campinas, São Paulo State, south-eastern Brazil. The total reserve area is 251.8 ha and altitudes vary from 580 to 610 meters. The climate is Cwa type by the Köeppen classification (Setzer, 1966) defined as warm and wet, with a dry winter and wet summer, 1381.2 mm mean annual rainfall and an average annual temperature of 21.6°C. The predominant soil type is Purple Latosol allic (Oliveira et al., 1979). The majority of the reserve area is covered by semideciduous mesophytic forest with some stretches of swamp forest, on permanently marshy soil (Leitão Filho, 1995).

The relationship between gap characteristics and regeneration of shrub and tree species was analyzed in 10 natural gaps localized in semideciduous mesophytic forest stretches. Were selected gaps with similar ages and sizes that represent a gradient of environmental disturbance caused by whole or partial tree fall.

Gap physical characteristics

Hemispherical photographs processed by the Winphot program (Ter Steege, 1993) were used to calculate the size of each gap (Brokaw, 1982a) and the corresponding canopy openness, following methodology used in studies of tropical forest canopy (Whitmore et al., 1993; Walter and Torquebiau, 1997; Trichon et al., 1998; Martins and Rodrigues, 2002). The canopy openness is a good indicador of the solar radiation penetration and microclimate in the gaps (Brown 1993; Rich et al., 1993; Whitmore et al., 1993; Martins and Rodrigues, 2002).

Floristic Data

All the shrubs and trees with height ≥ 0.5 m found in the gap were sampled. Only species with five or more individuals in the total of the gaps were used in the analysis. This procedure eliminated rare species from the analysis. Measurements of diameter at the soil level and of plant height were taken, and botanical material was collected for identification. The FITOPAC program (Shepherd, 1996) was used to calculate the density and dominance of the sampled species for each gap (Mueller-Dombois and Ellenberg, 1974).

Species Successional Classification

The species sampled in the gaps were classified in successional categories taking the studies of Gandolfi et al. (1995), Bernacci and Leitão Filho (1996), Santos et al. (1996) and Martins et al. (2002) as reference.

Four successional categories were adopted: pioneer, initial secondary, late secondary and unclassified, which correspond to the shade tolerance levels of the species. Thus the category of the late secondary species was considered the most tolerant and successionally advanced. Shade intolerant pioneer species were included at the other classification extreme. Based on their position in the forest vertical strata, the late secondary species were grouped as understorey, sub-canopy and canopy species. Understorey species were defined as reaching a maximum height of three meters, and the sub-canopy species were taller, but did not reach the forest canopy. The late secondary species which when adult occupy the forest canopy or emerge from it were classified as canopy species.

This successional classification was used to calculate the sum of the density values and dominance species by successional category. The percentage and dominance of species per successional category were then calculated for each gap.

Statistical Treatment

The correlation among percentage and dominance of pioneer and late secondary species with the gap sizes and with the canopy openness were analyzed by regression analysis. The analyses were carried out by the SYSTAT program (Wilkinson, 1991).

The hypothesis of whether there is a vegetation gradient correlated with gap characteristics was tested further using canonical correspondence analysis (CCA), a technique that enables a direct gradient analysis (Ter Braak, 1987). The “Monte Carlo” permutation test (Ter Braak, 1988) was used to test the matching probability of the relationship found between the gap characteristics and the species distribution in the gaps. The PC-ORD program (McCune and Mefford, 1997) was used to carry out the analyses.

The data processed by PC-ORD consisted of two matrices as a prerequisite for CCA. The main matrix was formed by density values of the shrub and tree species per gap. The second matrix was formed by the following variables (gap characteristics): a) gap size; b) canopy openness; c) canopy height; d) pioneer species dominance; e) late secondary species dominance; f) pioneer species density; g) late secondary species density; h) total basal area of individuals.

After a preliminary analysis, gap five, considered to unsuitable because of the extremely high density of a single species (*Actinostemon klotschii* (Muell. Arg.) Pax) was eliminated from the species matrix.

RESULTS

Floristic Data and Gap Physical Characteristics

Table 1 shows the 59 most abundant species (number of individuals ≥ 5) sampled in the gaps and their respective successional categories. The gap sizes and corresponding canopy openness, obtained by hemispherical photographs, are shown in Table 2. The larger gaps do not have percentages of canopy openness excessively higher from the others because of the presence of remaining individuals, that is, survivors of the tree fall which made the gap.

Regression Analysis

The results of the regression analysis, showing the correlation among gap physical characteristics and vegetation parameters are shown in Tables 3 and 4 and Figures 1 to 4.

The regression analysis showed that the dominance and percentage of pioneer species were significantly and positively correlated with the gap size (Table 3) and with the canopy openness (Table 4). On the other hand, the dominance and percentage of late secondary species correlated negatively with the gap size (Table 3) and with canopy openness (Table 4).

Table 1
The 59 most abundant species (number of individuals ≥ 5) sampled in 10 gaps in the Santa Genebra County Reserve, Campinas, SP, Brazil. (Successional classification: P = pioneer species, IS= initial secondary species, LS = late secondary species, UC = unclassified; classification by vertical strata: U = understorey, SC = sub-canopy, C = canopy).

Abbreviations	Species	CLASSIFICATION
Aca pan	*Acacia paniculata* Willd.	P
Aca pol	*Acacia polyphylla* DC.	P
Act klo	*Actinostemon klotschii* (Muell. Arg.) Pax	LS, U
Alc gla	*Alchornea glandulosa* Poep. and Endl.	P
Asp pol	*Aspidosperma polyneuron* Muell.Arg.	LS, C
Asp ram	*Aspidosperma ramiflorum* Muell.Arg.	LS, C
Ast gra	*Astronium graveolens* Jacq.	IS
Bal rie	*Balfourodendron riedelianum* (Engl.) Engl.	IS
Cas gos	*Casearia gossypiospermum* Briquet.	IS
Cec hol	*Cecropia hololeuca* Miq.	P
Cel igu	*Celtis iguanaea* (Jacq.) Sargent	P
Cel tal	*Celtis tala* Gillies ex Planchon.	P
Cen tom	*Centrolobium tomentosum* Guill.	IS
Chr gon	*Chrysophyllum gonocarpum* (Mart. and Eichl.) Engl.	IS
Cof ara	*Coffea arabica* L.	UC
Cor eca	*Cordia ecalyculata* Vell.	IS
Cou com	*Coussarea contracta* Benth and Hook.	LS, U
Cro flo	*Croton floribundus* Spreng.	P
Cro pri	*Croton priscus* Muell.Arg.	P
Cyb cun	*Cybianthus cuneifolius* Mart.	UC
Ese feb	*Esenbeckia febrifuga* (St.Hil.) A. Juss.	LS, U
Ese lei	*Esenbeckia leiocarpa* Engl.	LS, SC

Cont.

Table 1 (continued.)

Abbreviations	Species	Classification
Eug lig	*Eugenia ligustrina* Willd.	LS, SC
Eug ver	*Eugenia verrucosa* D. Legrand	LS, U
Gal mul	*Galipea multiflora* Engl.	LS, U
Hol bal	*Holocalyx balansae* Mich.	LS, C
Hyb atr	*Hybanthus atropurpureus* (St.Hil.) Taub.	LS, U
Ing lus	*Inga luschnatiana* Benth.	IS
Jac spi	*Jacaratia spinosa* (Aubl.) A.DC.	P
Lon gui	*Lonchocarpus guilleminianus* (Tul.) Malme	IS
May ili	*Maytenus ilicifolia* Reiss.	LS, U
Met sti	*Metrodorea stipularis* Mart.	LS, SC
Myr ros	*Myrcia rostrata* DC.	P
Myr cau	*Myrciaria culiflora* (DC) Berg.	LS, SC
Myr flo	*Myrciaria floribunda* (Wild.) Berg.	LS, U
Oco bea	*Ocotea beaulahiae* Baitello	UC
Ott pro	*Ottonia propinqua* Kunth.	P
Pac lon	*Pachystroma longifolium* (Ness) I. M. Johnston	LS, C
Pal mar	*Palicourea marcgravii* St.Hil.	LS, U
Pav sep	*Pavonia sepium* St.Hil.	P
Pic war	*Picramnia warmingiana* Engl.	LS, SC
Pip ama	*Piper amalago* (Jacq.) Yunker	P
Pip amp	*Piper amplum* Kunth.	UC
Pip gon	*Piptadenia gonoacantha* (Mart.) Macbr.	IS
Pol klo	*Polygala klotzschii* Chod.	LS, U
Pro cru	*Prockia crucis* L.	IS
Psy has	*Psychotria hastisepala* Muell. Arg.	LS, U
Rud jas	*Rudgea jasminoides* Muell. Arg.	LS, SC

Sav dic	*Savia dictiocarpa* Kuhlm	LS
Seb klo	*Sebastiania klotschiana* Pax and Hoffman	LS, U
Seg flo	*Seguieria floribunda* Benth.	IS
Sol arg	*Solanum argenteum* Roem. and Schultz.	P
Tre mic	*Trema micrantha* (L.) Blume.	P
Tri cat	*Trichilia catigua* Adr. Juss.	LS, U
Tri cla	*Trichilia claussenii* C. DC.	LS, SC
Tri ele	*Trichilia elegans* A. Juss.	LS, U
Tri pal	*Trichilia pallida* Sw.	LS, SC
Ure bac	*Urera baccifera* (L.) Gaud.	P
Ver dif	*Vernonia diffusa* Less.	P

Table 2
Gap size and canopy openness measurements obtained from hemispherical photographs in 10 gaps in the Santa Genebra County Reserve, Campinas, SP, Brazil.

Gap number	Gap size (m^2)	Canopy openness (%)
2	20.09	8.65
6	34.95	9.33
8	43.47	10.29
5	46.13	10.55
3	68.48	12.75
7	71.57	12.98
4	99.40	13.25
1	108.35	13.39
9	295.00	14.06
10	468.00	17.32

Table 3
Results of regression analysis between vegetation parameters and gap sizes (x)

Vegetation parameters	r^2	**Equation**	P
Pioneer species dominance (y)	0.77	y = -48.659 + 15.78 Ln(x)	< 0.01
Pioneers species percentage (y)	0.67	y = -11.635 +6.959 Ln(x)	< 0.01
Late species dominance (y)	0.58	y = 136.53 –19.007 Ln(x)	< 0.05
Late species percentage (y)	0.65	y = 83.998 – 7.524 Ln(x)	< 0.01

Table 4
Results of regression analysis between vegetation parameters and canopy openness (x)

Vegetation parameters	r^2	**Equation**	P
Pioneer species dominance (y)	0.76	y = -50.766 + 5.808x	< 0.01
Pioneers species percentage (y)	0.67	y = -12.741 + 2.576x	< 0.01
Late species dominance (y)	0.60	y = 142.453 – 7.271x	< 0.01
Late species percentage (y)	0.60	y = 83.563 – 2.652x	< 0.05

Table 5
Correlation coefficients among the gap physical variables and the first ordination axes of the canonical correspondence analysis

Variables	Axis 1	Axis 2	Axis 3
Gap size	0.822	-0.230	0.131
Canopy openness	0.672	0.053	0.364
Pioneer species dominance	0.654	0.159	0.329
Late secondary species dominance	-0.791	-0.239	0.116
Pioneer species density	0.152	0.787	0.215
Late secondary species density	-0.766	-0.467	-0.342
Canopy height	0.779	-0.332	0.147
Total basal area	0.769	-0.172	0.033

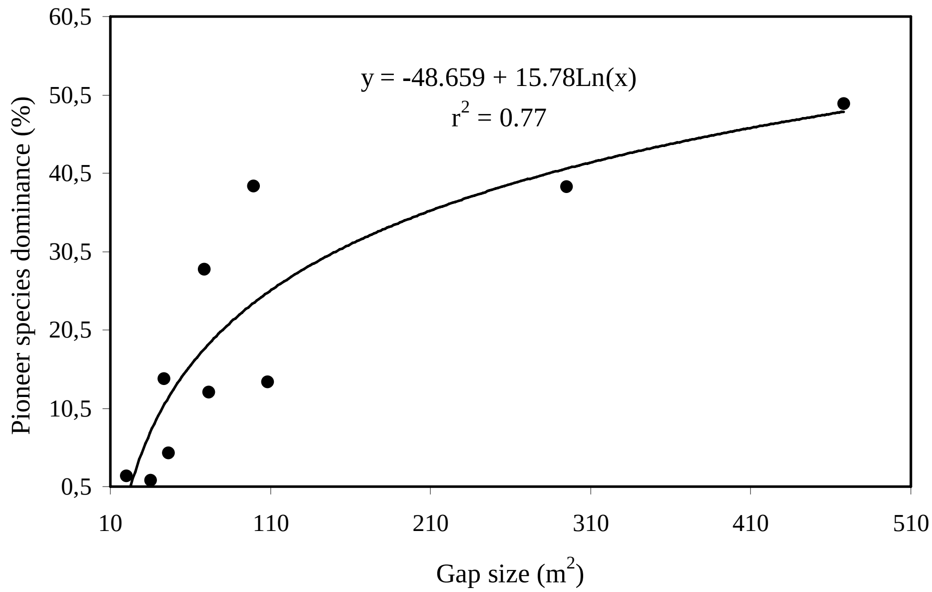

Figure 1. Relationship between pioneer species dominance and gap size in a semideciduos mesophytic forest, south-eastern, Brazil.

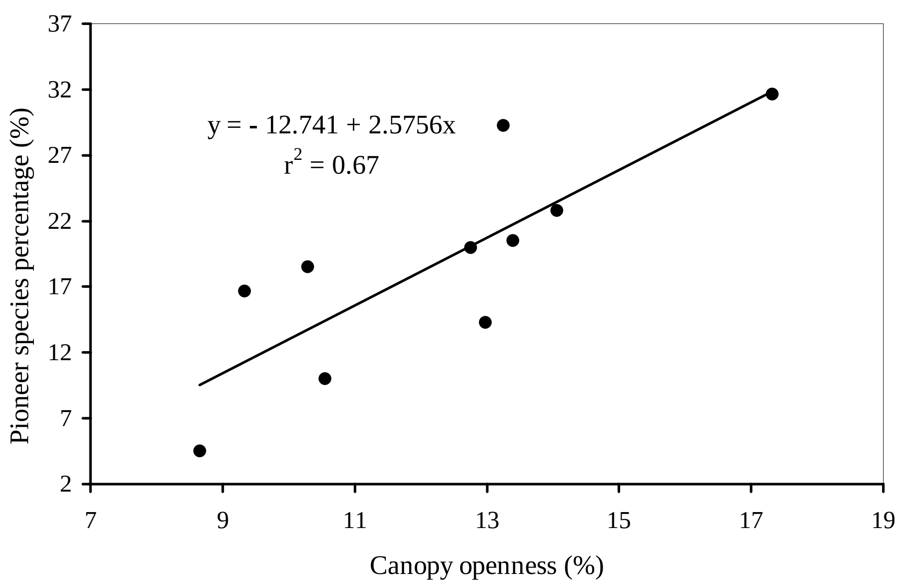

Figure 2. Relationship between pioneer species percentage and canopy openness in a semideciduos mesophytic forest, south-eastern, Brazil.

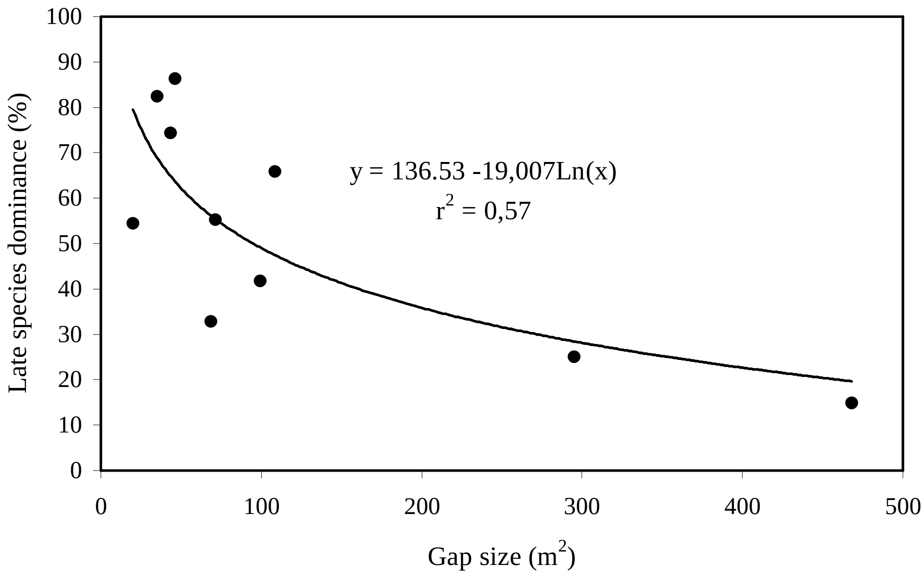

Figure 3. Relationship between late secondary species dominance and gap size in a semideciduos mesophytic forest, south-eastern, Brazil.

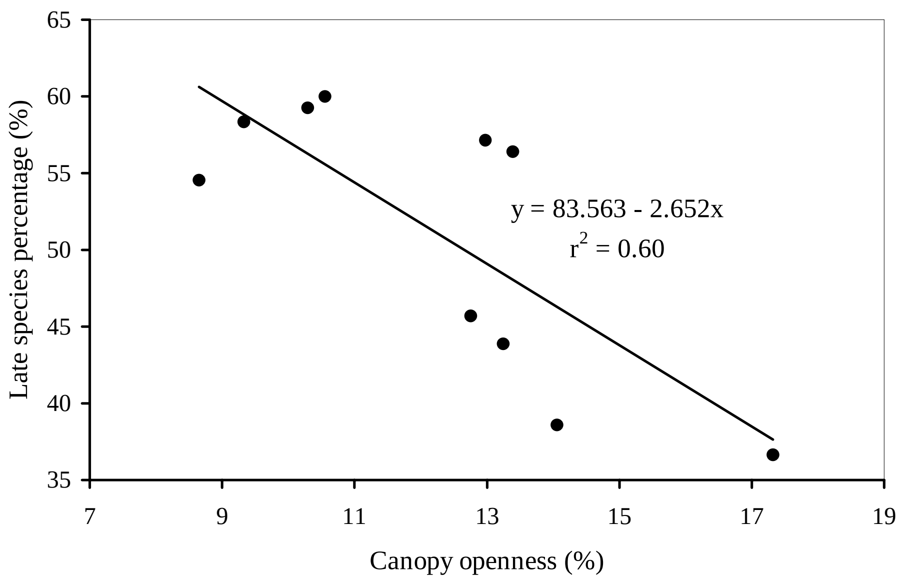

Figure 4. Relationship between late secondary species percentage and canopy openness in a semideciduos mesophytic forest, south-eastern, Brazil.

Canonical Correspondence Analysis

The results of the CCA with the relationship between gap characteristics and shrub and tree species distribution are shown in the ordination diagrams in Figures 5 and 6 and in Table 5.

The eigenvalues for the first three canonical axes were 0.311, 0.220 and 0.167. The first canonical axis accounted for 25.4% of the total variance in the analysis, while the other two axes accounted for 43.4% and 57.9%, respectively. Low percentages variances are expected in vegetation data and do not impair the significance of species-environment relations (Ter Braak, 1988). The Monte Carlo permutation test for the three axes, showed that the species abundances and gap physical variables were significantly correlated (P<0.05). These results indicate that the most species occurred throughout the gap size gradient, varying principally in their abundances (Ter Braak, 1987, 1995).

Table 5 shows the correlation coefficients among the gap physical variables and the three main canonical axes.

The first canonical axis discriminated with positive scores the gaps considered of medium or large size and with negative scores the small gaps (Figure 5).

The first canonical axis in Figure 6 shows that the species which had the greatest positive scores were, in decreasing order or importance: *Piper amplum* (Jacq.) Yunker, *Centrolobium tomentosum* Guill., *Aspidosperma ramiflorum* Muell. Arg., *Alchornea glandulosa* Poep. and Endl., *Cecropia hololeuca* Miq., *Trema micrantha* (L.) Blume. and *Vernonia diffusa* Less. The greatest negative scores were for *Acacia polyphylla* DC., *Savia dictiocarpa* Kuhlm, *Trichilia catigua* Adr. Juss., *Palicourea marcgravii* St. Hill., *Lonchocarpus guilleminianus* (Tull.) Malme, *Myrciaria cauliflora* (DC.) Berg. e *Chrysophyllum gonocarpum* (Mart. and Eichl.) Engl.

The second axis assigned the greatest positive scores in decreasing order of importance to *Croton floribundus* Spreng., *Croton priscus* Muell. Arg., *Cordia ecalyculata* Vell., *Ottonia propinqua* Kunth. and *Urera baccifera* (L.) Gaud. and the greatest negative scores to *P. amplum, C. tomentosum, A. ramiflorum, Metrodorea stipularis* Mart. and *Galipea multiflora* Engl. Two small gaps and the species *C. floribundus* and *C. priscus* were polarized on this axis with positive scores.

Except for the pioneer species density variable, which correlated strongly with axis 2, the other variables correlated strongly with axis 1. The variables gap size, canopy openness, canopy height, total basal area of individuals and pioneer species dominance had the greatest correlation coefficient for axis 1 (Table 5). Thus, the largest gaps were polarized on the first canonical axis in the sense of increase of those variables. On the opposite side, the gaps with smaller sizes and canopy openness were placed in this axis in the sense of increase of the late secondary species dominance and density variables.

The species considered pioneers *C. hololeuca, T. micrantha, V. diffusa, A. glandulosa, Jacaratia spinosa* (Aubl.) DC. and *Piper amalago* (Jacq.) Yunker are strongly correlated with the larger gaps where the canopy openness is larger (Figure 5 and 6), but the typical understorey species *G. multiflora* and *A. klotsckii* were also present. Other understorey late secondary species such as *Hybanthus atropurpureus* (St. Hil.) Taub., *Polygala klotzsckii* Chod., *Psychotria hastisepala* Muell. Arg. and *Trichilia elegans* A. Juss. and late secondary canopy species such as *S. dictiocarpa* preferred small gaps with a fairly close canopy.

However, several species did not show any definite preference for gap size and canopy openness.

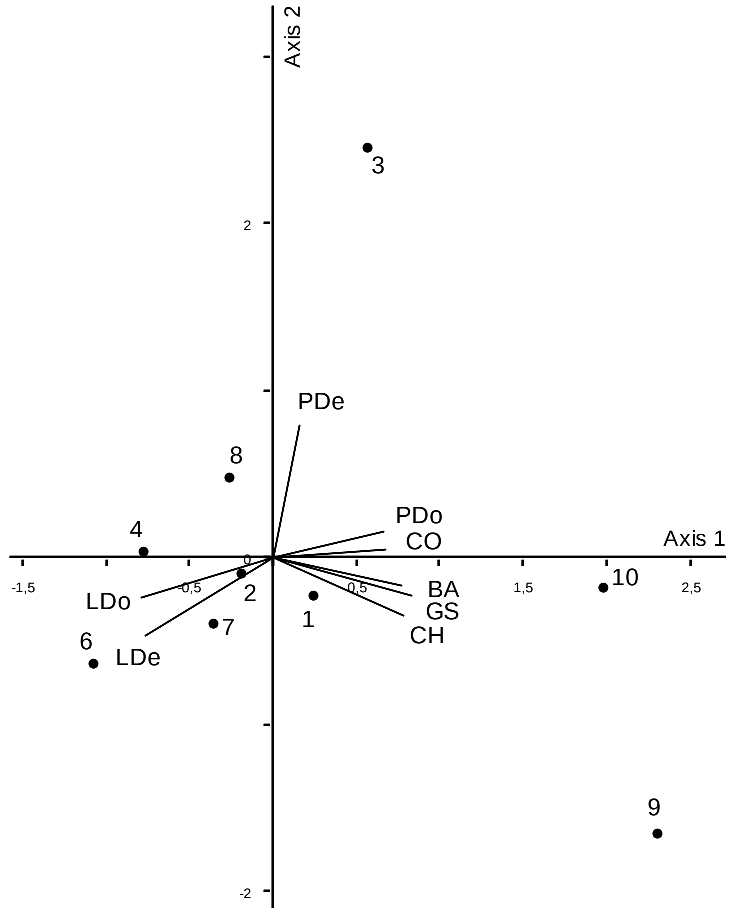

Figure 5. Canonical correspondence analysis: ordination biplot showing the distribution of the gaps in the first two axes. The gaps (●) are represented by numbers and the gap physical variables by vectors. The gap physical variables are: BA = total basal area, CH = canopy height, CO = canopy openness, GS = gap size, LDe = late secondary species density, LDo = late secondary species dominance, PDe = pioneer species density, PDo = pioneer species dominance.

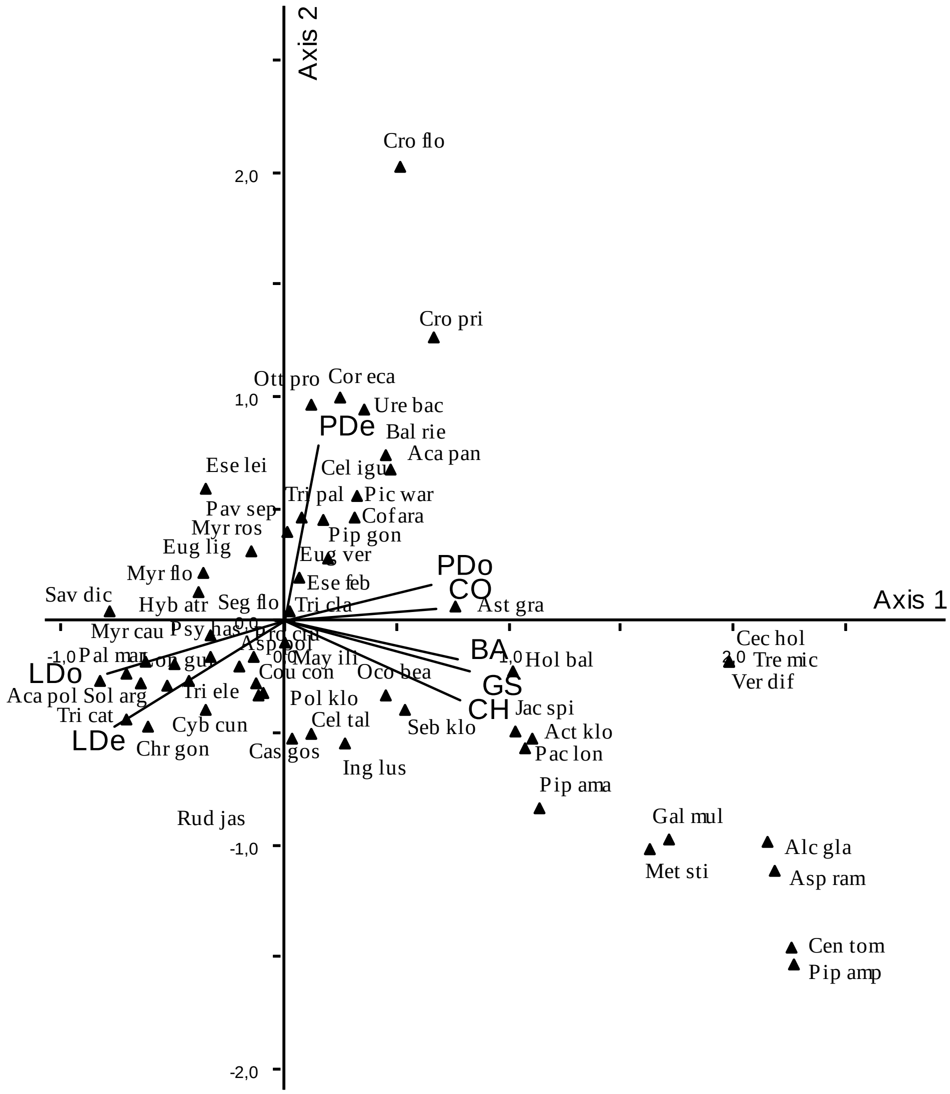

Figure 6.Canonical correspondence analysis: ordination biplot showing the distribution of the most abundant 59 species in the first two axes. The species are represented by abbreviations of their scientific names (Table 1) and the gap physical variables by vectors.

DISCUSSION

Regression Analysis

In spite of the heterogeneity of the responses, some patterns of behavior could be identified in the vegetation in response to the gap physical characteristics that result from the specific disturbances in the opening of these gaps.

The positive correlation between gap size and canopy openness with the percentage and dominance of pioneer species, and the negative correlation with the percentage and dominance of late secondary species, suggests that in more open canopy environments there may have been a greater selectivity on the late secondary species. On the other hand, the formation characteristics and the milder ecological restriction in the small gaps enabled a greater number of understorey and late canopy/sub-canopy species to share space and resources, to the detriment of the pioneers, as has been suggested in various studies (Canham, 1989; Abe et al., 1995; Runkle, 1998).

Tabarelli (1997) obtained similar results in the Atlantic Forest, suggesting that the gap size seems to have great influence on the late secondary species group but limited influence on the pioneer species. Increase in gap size can result in late secondary species plant death because of: a) the physical damage caused by tree fall; b) physiological stress caused by light and air temperature increase and reduced relative humidity in the air and soil; c) damage by herbivorous agents and d) competition with pioneer species (Barton, 1984; Brandani et al., 1988). The combination of these factors may have resulted in more deaths of individuals from this successional group in the larger gaps compared to the small gaps, where the environmental alterations were less drastic.

Canonical Correspondence Analysis

The pioneer species occurred with greater density values and/or dominance in the three large gaps and two small gaps. This polarization was expected for the three larger gaps, because of the higher canopy openness values. However, for the smaller gaps this polarization can be attributed to the conservation state of vegetation stretches where the gap was formed.

The largest gaps were formed in more preserved stretches of the forest fragment where the forest is at a more advanced successional stage (Martins, 1999). Thus in the CCA diagram, canopy height and total basal area are polarized together with the largest gaps. This positive relationship between gap size and forest development stage indicated that with the forest maturity, the canopy becomes higher causing the opening of larger gaps (Brokaw, 1982b; Martins and Rodrigues, 2002).

The greatest dominance values of pioneer species and the greatest percentages of species of this successional group were found in the largest Santa Genebra gaps. The typical pioneers, *Cecropia* spp. and *T. micrantha*, were sampled only in the gap with area greater than 400 m^2. The selectivity of these species for large gaps has already been shown in several studies (Brokaw, 1985; Myster and Walker, 1997; Van Der Meer et al., 1998; Guariguata and Ostertag, 2001).

To germinate, *Cecropia* species seeds need a high ratio of red to far red light, which typically occurs in large gaps (Valio and Joly, 1979; Vázquez-Yanes and Orozco-Segovia, 1987; Scarpa and Valio, 2001). High levels of light availability (Souza, 1996) and temperature alterations are important for *T. micrantha* seed germination (Castellani, 1996), which may also be related to selectivity of this specie for large gaps where alteration in the light availability and great diurnal temperature oscillations happens (Vázquez-Yanez and Orozco-Segovia, 1982, 1994).

The photosynthesizing photon flux density (PPFD) in gaps larger than 400m^2 is significantly greater than that reaching the soil in smaller gaps (Chazdon and Fetcher, 1984;

Barton et al., 1989). Within the gaps studied at Santa Genebra forest, those larger than 400 m^2 may have been the only ones where PPFD levels were sufficiently high for germination and growth of those pioneer species thus supporting the results of this study.

The CCA polarization of the typical understorey species *G. multiflora* and *A. klotschii* and the late secondary canopy species *Holocalix balansae* Mich. and *Pachystroma longifolium* (Ness) I. M. Johnston with the largest gaps indicates two aspects of these gap dynamics: first, the confirmation of the advanced development stage of the forest stretches where the gaps were located, characterized by a well structured understorey and late secondary canopy species with abundant regeneration (Martins and Rodrigues, 2002); second, the survival of individuals of these species after gap formation, which must be related with shading conditions at the edges of these gaps provided by a higher surrounding canopy and by the remaining shrubs and trees and with your positions inside the gaps (Brown, 1996).

The light period and intensity received by a gap is related not only to its size, but also to other characteristics, such as shape, exposition, terrain inclination, surrounding vegetation height and surviving vegetation after tree fall (Brokaw, 1985; Denslow and Hartshorn, 1994). Thus, the increase in gap size also increased environmental heterogeneity in the interior of these gaps (Denslow, 1987) because of remaining trees, understorey patches and fallen tree trunks (Carlton and Bazzaz, 1998). This was observed in the field in the large gaps, where large tree falls with uprooting clearly produced the three zones (roots, trunk and crown) proposed by Orians (1982), which did not occur in the small gaps. Futhermore, remaining shrubs and trees were more abundant in the large gaps, which is reflected in the basal area of individuals values positively correlated with the gap area. This certainly increased the heterogeneity in theses areas. The spatial variation in the litter (seeds, leaves, branches, etc) deposition in the gaps (Martins and Rodrigues, 1999) must also have contributed to the environmental heterogeneity, especially in the large gaps.

Therefore, the heterogeneity of light and microclimate conditions in large gaps may favor the development of certain understorey or late canopy species, as observed in this study.

The two small gaps polarized on axis two together with the pioneer density are located in more degraded forest stretches compared to the stretches where the large gaps are located. This was confirmed by high density values of some pioneer species, such as *C. priscus* and *C. floribundus*, in the surroundings of these gaps (Martins, 1999). The individuals of these species are at reproductive age, and by autochory, allow local seed rain (Martins and Rodrigues, 1999), which certainly contributes to the high density of saplings of these species in the gaps. This is in accordance with the studies on the relationship between the distance of the seeds source and the regeneration of pioneer species in canopy gaps and degraded areas (Swaine and Hall, 1983; Denslow and Gomez, 1990; Abet et al., 1995; Rodrigues et al., 2004).

The greatest concentration of late secondary species in the smaller size gaps and, therefore with smaller canopy openness, reflects the forest resilience and the plasticity of this successional group in using different forest environments. Typical understorey shrubs and trees species, such as *H. atropurpureus*, *P. klotzsckii*, *P. hastisepala*, *P. marcgravii*, *Myrciaria floribunda* (Wild.) Berg. e *T. elegans* achieved to survive and/or reproduce in the smaller gaps, while others typical of sub-canopy condition such as *T. catigua*, *M. cauliflora*, *Rudgea jasminoides* Muell. Arg. and some late secondary canopy species such as *Aspidosperma polyneuron* Muell. Arg. e *S. dictiocarpa* achieved to regenerate in environments where the canopy openness must have provided less drastic microclimatic alterations than the large gaps (Brown ,1993).

This late secondary species behavior was found in the majority of studies where small gaps predominate (Tabarelli and Mantovani, 1997; Canham, 1988; Svenning, 2000). For these species, an event, such as a tree fall, may increased light avaibility to the seedeling bank, speeding the growth of its individuals and favouring the regeneration (Duarte et al., 2002). Already understorey species may have plasticity to forest light conditions and be benefited mainly with the opening of small gaps, with recruitment, growth and reproduction responses (Canham, 1989; Amézquita, 1998; Pascarella, 1998).

In spite of the selectivity tendencies of some species from certain successional categories in relation to the gap size and canopy openness – pioneer species in the largest gaps or in small gaps but located in more degraded forest stretches and influenced by the surrounding pioneers; and late secondary species in the small gaps – it must be pointed out that several species do not give clear responses for gap physical characteristics and therefore, to their environmental conditions. Therefore, this study corroborates the theory that many tropical tree species do not have strict regeneration niches partitions represented by different sized gaps, but compose guilds of generalists (Barton, 1984; Hubbel and Foster, 1986; Welden et al., 1991; Lieberman et al., 1995; Tabarelli and Mantovani, 1997).

These statements have been reinforced by eco-physiological studies of germination, survival and growth, which also indicate that several tropical shrubs and trees species are generalists for forest light conditions (Augspurger, 1984; Denslow et al., 1990; Popma and Bongers, 1991; Souza, 1996).

Besides the physical and structural gap characteristics analyzed, others such as gap opening time, geographic orientation, micro-sites formed by litterfall, degradation of the surrounding vegetation and the presence of remaining shrubs and trees, must also influence the colonizing vegetation parameters.

CONCLUSIONS

The results of this study indicates that the relationship between the canopy gap characteristics and the regeneration of shrub and tree species is very complex. Except for a group of pioneer species and some late secondary species related to the larger and smaller gaps, respectively, several species did not show direct relationships with the size and canopy openness of the gaps.

Once some pioneer species (e.g., *Trema micrantha* and *Cecropia*) exits solely in very disturbed forest sites, the occurrence of large gaps in tropical forests is extremely important for the maintenance of pioneer species, while small gaps may stimulate the regeneration of late secondary species that compose the canopy and understorey.

The comprehension of the factors that rule the gaps colonization is vital for the definition of strategies aiming at the maintenance of the last tropical forest fragments and the restoration of areas already degraded.

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