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Gap Area and Tree Community Regeneration in a Tropical Semideciduous Forest

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1. Introduction

In tropical and temperate forests, the canopy gaps affect the architecture and the establishment of plants throughout their life-cycle. The gaps help to maintain the tree diversity by density effect and niche partitioning. The possibility of gap occurrence particularly interplays with recruitment limitation, allowing the coexistence of species that otherwise could not make it (Brokaw & Busing 2000; Lima, 2005; Gravel et al., 2010). A typical canopy gap goes through diverse stages, the initial one known as gap stage. In this stage, the invasion by lianas (Schnitzer & Carson, 2010) and bamboos (Larpkern et al., 2011) might occur. The next stage is the construction stage, in which the establishment of some species occurs, although they have not yet reached the canopy level. The last stage is the mature one, in which the canopy and the gap are virtually closed by true vegetation (Lima, 2005).

Natural gaps are caused by death (or injury) of one or more canopy trees (in some cases they are caused by the fall of large branches), and are defined as small openings on the canopy of forests, usually occupying a <0.1 ha (Yamamoto, 2000). This kind of transitory event is frequent in tropical forests (Brokaw, 1985), where plant species of early successional stages (pioneers and secondary ones) might take advantage of this kind of disturbance, since they can tolerate higher micro-climate and ecological variations (Mulkey et al., 1996).

The size distribution and frequency of gap occurrences in a forest is a function of local climate, topography, soil, bedrock and the composition and size distribution of trees (Deslow, 1980). All the trees, especially those in slopes, peaks, shallow or waterlogged soils, and the emerging ones, are subject to wind action, creating gaps proportional to their heights and crown sizes. Moreover, the gap-area is related to the number and orientation of falling trees. Each gap has specific geometry, climate and substratum (Lima, 2005; Deslow, 1980), which leads to important differences in spatial and temporal forest structure (Deslow 1980; Brokaw, 1982). The micro-climatic features of a canopy gap might change with its size from one season to another, and even with extreme climate events. These conditions may be

optimal for certain species at a certain point of time, though they can change in a mid/long term (Brown, 1993). Some plant species can only regenerate in a narrow range of light availability (Barton et al., 1989; Whitmore, 1990). In addition to the marked variation in the canopy opening, the reduction of basal area and the increase in gap-area found in canopy gaps, can also interfere in the process of regeneration and in the growth of tree seedlings (Sapkota & Odén, 2009).

The colonization of gaps by species of different categories or successional groups is influenced by ecophysiological responses of species in the area by the seed bank and by seedlings and/or remnant individuals, as well as by post-disturbance migrant species via dispersal processes (Martins et al., 2009). Moreover, it will also depend on the time the opening has occurred, the opening size, the substratum conditions, the relationship with herbivores as well as on density dependent factors (Hartshorn, 1980). Understanding the dynamics of gaps in tropical forests is paramount for forest restoration, sustainable management and conservation of forest remnants (Martins et al., 2009).

In this context, the present study aims to: 1. Identify ecological patterns related to richness and the potential of natural regeneration of tree species in natural gaps. 2. Investigate whether the tree community responds or not to different levels of canopy openings represented by gaps of different sizes found in tropical semideciduous forests (TSF).

2. Material and methods

2.1 Study area

We conducted this study in a 30 ha tropical semideciduous forest (TSF) remnant showing a good conservation status. The fragment is situated in the southern region of Uberlândia municipality located in Minas Gerais state, at a region known as "Triângulo Mineiro". The study site lies within a matrix of planted pasture for cattle mixed with cerrado *sensu stricto* fragments and secondary riparian forest areas.

The dystrophic red latosol ranging from slight to high acidity levels predominates in the region. There are soils with a base saturation of 50 to 65% - Marília Formation, Bauru Group - in some scarce areas (Embrapa, 1982). In tropical semideciduous forest conditions at "Fazenda do Glória (18° 57′ S to 48° 12′ W) the dystrophic red latosol has a base saturation varying from 7.4 to 29% and low availability of N, P and Ca (Haridasan & Araújo, 2005).

2.2 Location and size-class distribution of canopy gaps

We calculated the gap area percentage in the canopy using the intercept method (Floyd & Anderson, 1987; Bullock, 1996), according to Kneeshaw & Bergeron methodology (1998).The gap areas in the canopy were calculated as following:

$$E(X) = \frac{1}{L} \sum_{j=1}^{n} \frac{Xj}{dj} \tag{1}$$

Where: E (X) - estimation of canopy gaps proportion, L - transect length, X j - the gap area, dj - the gap diameter.

We marked each canopy gap center with a metal stake 90cm height.. Each stake was identified by a colorful tape bearing a numerical sequency. We recorded the geographic coordinates for each canopy gap using a Garmin GPS Etrex model. The geographic coordinates were obtained in the center of each canopy gap. For the purposes of analysis, each gap was regarded as a single sample. A total of 25 gaps were assessed and categorized into distinct size classes according to amplitude and size classes previously described by Brokaw (1985) for tropical rain forests. These classes were previously applied by Lima et al. (2008) who employed the same amplitude distribution in a tropical semideciduous forest at São Paulo state.

2.3 Canopy opening and gap-areas

We estimated the canopy opening and gap area for each canopy gap (N=25) using hemispherical photographs.

The hemispherical photographs were taken using a Sigma 8 mm fish-eye lens attached to a Nikon D80 camera (Figure 1). The camera was mounted on a leveled tripod 1.3 m above ground (Nascimento et al., 2007), with the fish eye focus setting into infinity, as previously described by Mitchell & Whitmore (1993).
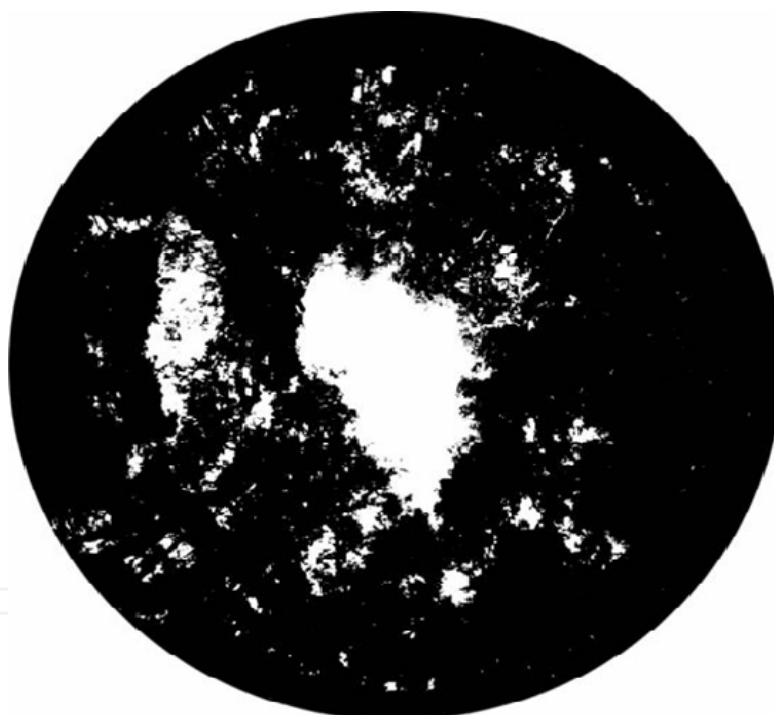

Fig. 1. Hemispherical photograph taken 1.3 m above ground in a canopy gap – open area in the center of the image – formed by the fall of one large sized tree.

The photographs were taken in full-color tones, always between 8-10 a.m., and 2-6 p.m., as recommended by Whitmore et al., (1993). Afterwards, we turned all the pictures taken into images in grey tones (8 bits) and reduced the resolution to 968 x 648 pixels. This is a necessary transformation in order to run the software Winphot 5.0 (Steege 1997), which we applied to analyze the set of hemispherical photographs and the area of each canopy gap. The function "gap area" is available as a tool of this software (Steege 1997). This kind of canopy gap area estimation had already been disseminated by other authors (Whitmore,

1990; Whitmore et al., 1993; van der Meer & Bongers, 1996; Eysenrode et al., 1998; Martins et al., 2002) and provides an accurate estimation of canopy opening as well as the occupied area by gaps in different vegetation types.

2.4 Natural regeneration in canopy gaps

We measured in each canopy gap the number of individuals (seedlings, saplings and some adults), height and number of all tree species higher than 10 cm and bearing a minimum 5 cm DBH (Diameter at Breast Height taken 1.3 cm above ground). The DBH is an inclusion criterion for tree species in forest formations at Cerrado biome (Felfili et al. 2005). When it was not possible to identify the species in the field, we collected botanical material (flowering or vegetative parts) of each plant and compared to specimens at reference herbariums (HUB, CENARGEN) both situated in Brazil. When the identification by comparison was not possible, we sent the material to specialists. All the species and families were identified and classified according to APG III (Chase & Reveal, 2009).

We studied the correlation between species richness, number of individuals and canopy–gap size using a linear correlation (Zar, 1999), investigating whether or not species show a response to size variation in canopy openings caused by gaps of different sizes. According to literature, larger gaps tend to hold a higher density of ruderals or invasive species (Whitmore, 1990). The presence of ruderal or invasive species within vegetation fragments is regarded as an important aspect of integrity of tropical plant communities (Tabarelli et al., 1999; Tabarelli et al., 2000; Tabanez & Viana, 2000).

The similarity of species present in canopy gaps was investigated using the Cluster Analysis (Hair et al. 2005) and applying the Jaccard similarity index. We used the medium distance from the group as the linkage method (UPGMA) (Kent & Coker, 1992). We ordinate the plots and the species within them, using a correspondence analysis by segments applying DECORANA (Detrended Correspondence *Analysis*) method (Hill, 1979). We created a matrix, species x plot, using the number of individuals in each sample (plot) as variable, following recommendations of Kent & Coker (1992). This type of multivariate analysis positions the species and plots along two ordination axis, permitting the investigation of ecological patterns in vegetational studies (ter Braack, 1995; Felfili et al., 2004). Both the multivariate techniques employed in this study (ordination and cluster analysis) were performed using the PC-ORD software version 5.10 (McCune & Mefford, 2006).

3. Results and discussion

The tree community species richness is represented by 80 species distributed among 65 genera and 37 families (Table 1). The families with the highest species richness were Fabaceae (13 species), Myrtaceae (8 species), Rubiaceae (8 species) and Annonaceae (4 species), totalling 40% of the total amount of species surveyed in this study. The genera with the highest species richness were *Myrcia* (4 species), *Myrsine* (3 species), *Trichilia* (3 species) and *Aspidosperma* (2 species). Most of the species found belong to initial colonization stages (successional and initial secondary), contributing 62.2% of the total amount surveyed. Most of the timber trees were late secondary species, and sometimes early secondary ones, which produce high or medium value timber.

Tree species	Family	Number of individuals	Number of gaps
Alibertia sessilis (Vell.) K. Schum.	Rubiaceae	11	7
Amaioua intermedia Mart.	Rubiaceae	2	2
Annona cacans Warm.	Annonaceae	2	1
Apuleia leiocarpa (Vogel) J.F. Macbr.	Fabaceae	4	1
Aspidosperma cylindrocarpon Müll. Arg.	Apocynaceae	10	7
Aspidosperma discolor A. DC.	Apocynaceae	7	6
Astronium nelson-rosae D. A. Santin	Anacardiaceae	25	17
Bauhinia rufa (Bong.) Steud.	Fabaceae	11	7
Bauhinia ungulata L.	Fabaceae	2	2
Campomanesia velutina (Cambess.) O. Berg	Myrtaceae	2	2
Cardiopetalum calophyllum Schltdl.	Annonaceae	21	15
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	3	3
Casearia grandiflora Cambess.	Salicaceae	27	14
Casearia sylvestris Sw.	Salicaceae	2	2
Cedrella fissilis Vell.	Meliaceae	1	1
Celtis iguanaea (Jacq.) Sarg.	Cannabaceae	1	1
Cestrum sp.	Solanaceae	1	1
Cheiloclinium cognatum (Miers) A.C. Sm.	Celastraceae	9	4
Coccoloba mollis Casar.	Polygonaceae	2	2
Copaifera langsdorffii Desf.	Fabaceae	10	8
Cordia sellowiana Cham.	Boraginaceae	3	2
Cupania vernalis Cambess.	Sapindaceae	35	19
Dasyphyllum sp.	Asteraceae	2	1
Duguetia lanceolata A. St.-Hil.	Annonaceae	7	5
Dyospirus hispida A. DC.	Ebenaceae	2	2
Eriotheca candolleana (K. Schum.) A. Robyns	Malvaceae	1	1
Erythroxylum daphnites Mart.	Erythroxylaceae	3	3
Eugenia florida DC.	Myrtaceae	3	3
Faramea cyanea Müll. Arg.	Rubiaceae	2	1
Garcinia gardneriana (Planch. & Triana) Zappi	Clusiaceae	1	1
Genipa americana L.	Rubiaceae	4	3
Guapira areolata (Heimerl) Lundell	Nyctaginaceae	2	2
Handroanthus serratifolius (Vahl) S. O. Grose	Bignoniaceae	3	3
Hirtella gracilipes (Hook. f.) Prance	Chrysobalanaceae	10	4
Heisteria ovata Benth.	Olacaceae	9	7
Hymenaea courbaril L.	Fabaceae	1	1
Inga laurina (Sw.) Willd.	Fabaceae	13	5
Inga sessilis (Vell.) Mart.	Fabaceae	54	16
Ixora sp.	Rubiaceae	1	1
Ixora warmingii Müll. Arg.	Rubiaceae	3	2

Jacaranda cuspidifolia Mart. ex A. DC	Bignoniaceae	2	2
Lacistema aggregatum (P.J. Bergius) Rusby	Lacistemataceae	7	6
Maprounea guianensis Aubl.	Euphorbiaceae	2	2
Margaritaria nobilis L. f.	Euphorbiaceae	2	2
Matayba guianensis Aubl.	Sapindaceae	7	7
Miconia albicans (Sw.) Steud.	Melastomataceae	15	7
Miconia sellowiana Naudin	Melastomataceae	18	8
Myrcia splendens (Sw.) DC.	Myrtaceae	3	3
Myrcia sp.	Myrtaceae	4	4
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	2	2
Myrcia variabilis DC.	Myrtaceae	1	1
Myrsine densiflora Scheff.	Primulaceae	1	1
Myrsine umbellata Mart.	Primulaceae	1	1
Myrsine sp.	Primulaceae	4	4
Nectandra megapotamica (Spreng.) Mez	Lauraceae	29	9
Ocotea corymbosa (Meisn.) Mez	Lauraceae	35	16
Ocotea spixiiana (Nees) Mez	Lauraceae	19	8
Ormosia arborea (Vell.) Harms	Fabaceae	1	1
Ormosia fastigiata Tul.	Fabaceae	1	1
Ouratea castaneifolia (DC.) Engl.	Ochnaceae	5	4
Platycyamus regnellii Benth.	Fabaceae	1	1
Pouteria torta (Mart.) Radlk.	Sapotaceae	2	2
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	5	3
Pseudolmedia laevigata Trécul	Moraceae	2	2
Pterodon pubescens (Benth.) Benth.	Fabaceae	1	1
Rudgea viburnoides (Cham.) Benth.	Rubiaceae	1	1
Sclerolobium paniculatum Vogel	Fabaceae	2	2
Simira viridiflora (Allemao & Saldanha) Steyerm.	Rubiaceae	15	5
Siparuna guianensis Aubl.	Siparunaceae	106	20
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Wess. Bôer	Moraceae	1	1
Sweetia fruticosa Spreng.	Fabaceae	13	9
Siphoneugena densiflora O. Berg	Myrtaceae	6	6
Tapirira obtusa (Benth.) J.D. Mitch.	Anacardiaceae	20	8
Terminalia glabrescens Mart.	Combretaceae	12	6
Trichilia catigua A. Juss.	Meliaceae	2	2
Trichilia pallida Sw.	Meliaceae	40	14
Trichilia elegans A. Juss.	Meliaceae	2	1
Virola sebifera Aubl.	Myristicaceae	3	2
Vitex polygama Cham.	Lamiaceae	1	1
Xylopia aromatica (Lam.) Mart.	Annonaceae	2	2

Table 1. Regenerating species of tree community sampled in 25 canopy gaps in tropical semideciduous forest (TSF), Uberlândia, Minas Gerais.

The species with highest number of individual values within the 25 surveyed gaps were *Siparuna guianensis* Aubl. (106 individuals), *Inga sessilis* (Vell.) Mart. (54 ind.), *Trichilia pallida* Sw. (40 ind.), *Ocotea corymbosa* (Meisn.) Mez (35 ind.), *Trichilia pallida* Sw. (40 ind.) and *Cupania vernalis* Cambess. (35 ind.). This cluster of species was found regenerating in gaps of different sizes, and they are probably favored by occurrence of canopy gaps in TSF conditions.

The cluster analysis identified 4 different canopy gap groups based on tree species composition (Figure 2), with a cut-off level of 0.5 or 50% of floristic similarity. The analysis categorized most part of the gaps into a huge group (C1, C11 up to C17). The other groups formed had shown a lower species similarity. These results underscore the heterogeneity in the species composition within gaps, separating the huge gaps (C4, C10 and C24) from the other, based on the occurrence of tree species that compound the regeneration in this environment. These three gaps are of large size (≥ 1000.0 m²) and contribute to a greater number of individuals sampled over the small gaps.
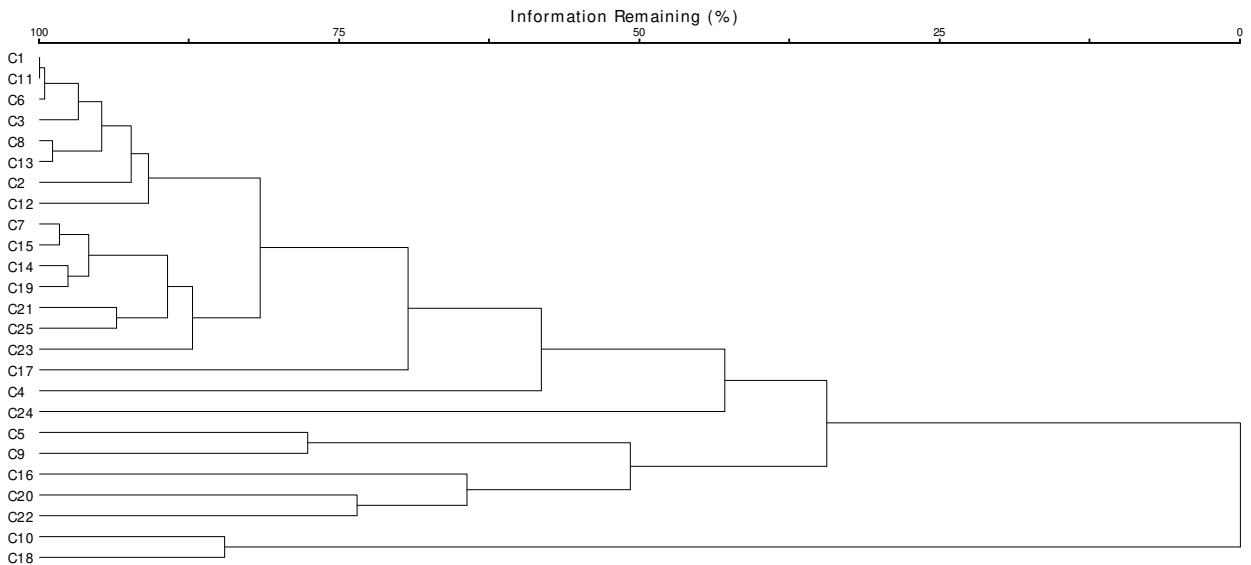

Fig. 2. Cluster analysis of 25 canopy gaps in TSF conditions, using UPGMA and the Jaccard index, Uberlândia, MG. The cut level for small groups was 0.5 or 50% of floristic similarity. The abbreviations C1-C25 reefer to the sequential number of each canopy gap sampled in this study.

On the other hand, the ordination by DECORANA (Figures 3 a and b) showed a density gradient, in which the species bearing the highest number of individuals, such as *Siparuna guianensis*, *Trichilia pallida* and *Ocotea corymbosa* formed a huge group, standing in the central portion of the ordination space (Figure 3b). The eigenvalue for the first value was significant (>0,3), denoting strong relationships from an ecological point of view (Kent & Coker, 1992).

The species *Virola sebifera* Aubl. and *Handroanthus serratifolius* (Vahl) S. O. Grose had the lowest number of individuals, separating from the main group formed by the most part of the species and occurring only in few gaps. The ordination also separated the largest gaps with different values for the two ordination axis (C4, C10 and C24), from the smaller ones based on density values, which in turn, had agreed with the cluster analysis.

Fig. 3. Ordination of the 25 natural canopy gaps (a) and tree species (b) by DECORANA method in TSF forest, Uberlândia, MG. The first letters refer to the number of each gap.

More than half of the canopy gaps in the study area were formed by the fall of whole canopy trees (52% of the gaps) followed by break of branches and crowns (Table 2). The fall of more than one tree also played some role in the formation of large sized "linked gaps".

We could also observe, only one time, a whole collapsed tree, which probably was caused by strong winds. In this context, Nelson (2005) mentions that pioneer species which form the canopy are susceptible to wind damages, which can cause the fall of individuals in open areas and edges of tropical forest fragments.

The majority of the canopy gaps documented in the study area are small to medium sized ones (up to 500 m² area) (Figure 4). The average area of the surveyed gaps are 573.0 m² ranging from 52.6 m² for small gaps formed by the fall of a single tree to 3468.0 m² for the larger ones. We found a significant correlation (Figure 5) between the gap area and the number of tree species (r=0.68; p<0.001). When the number of sampled individuals were taken into account we found a less significant relationship (r=0.45; p<0.05). This parameter shows a higher variation rate (10-82 ind. per gap) when compared to the number of species (7-24 species per gap) therefore, the relationship found becomes weaker as the gap areas increase.
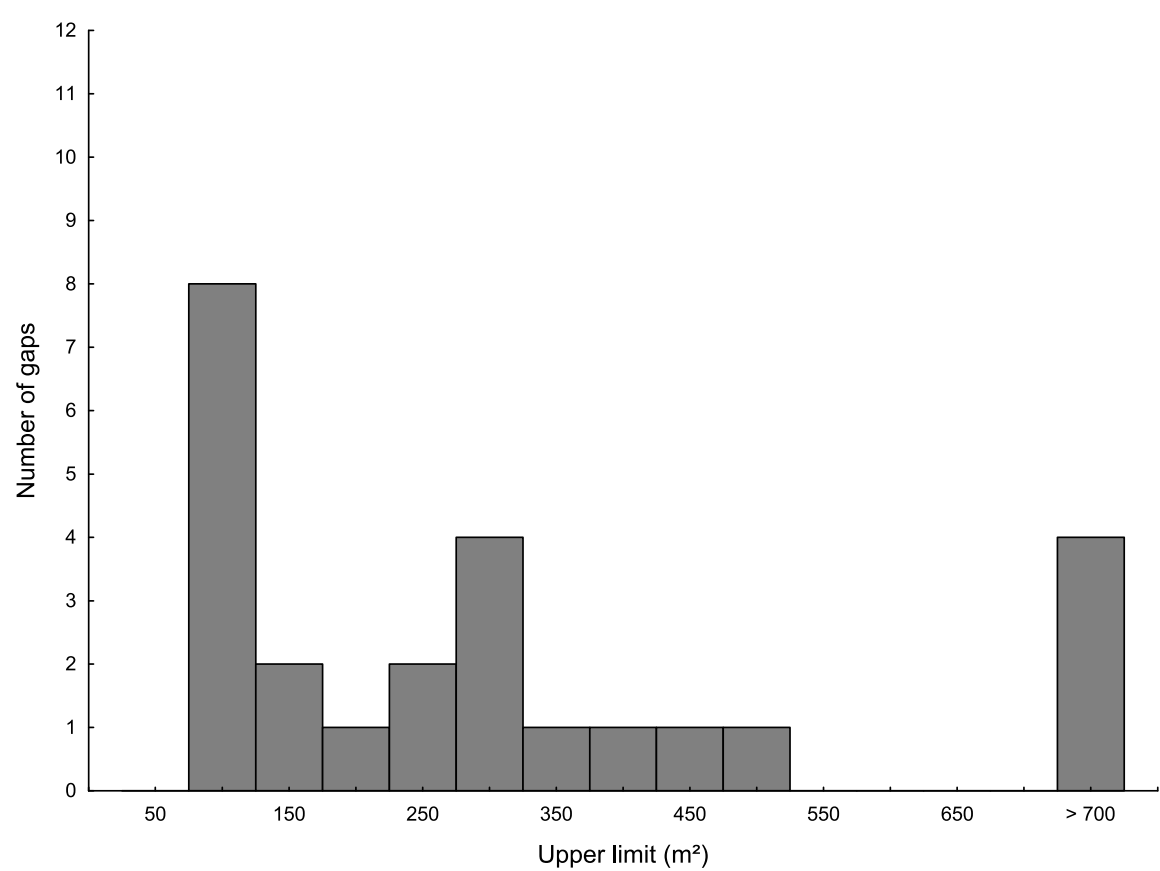

Fig. 4. Distribution by size-classes of natural canopy gaps (using hemispherical photographs) in a tropical semideciduous forest remnant (TSF), Uberlândia, MG.

Lima et al., (2008) found a high variation rate in the canopy gap sizes, ranging from 507.0 to 1109.0 m², in a tropical semideciduous forest, using the Runkle method for area estimation. The huge canopy gaps documented by the authors were, in many occasions, larger than the plots they had set. In our study area, the large sized gaps occupy areas over 1000 m², tending to hold a marked environmental variation (center, edges and limits with closed canopy) with higher light radiation rates reaching the soil surface (Figure 6).
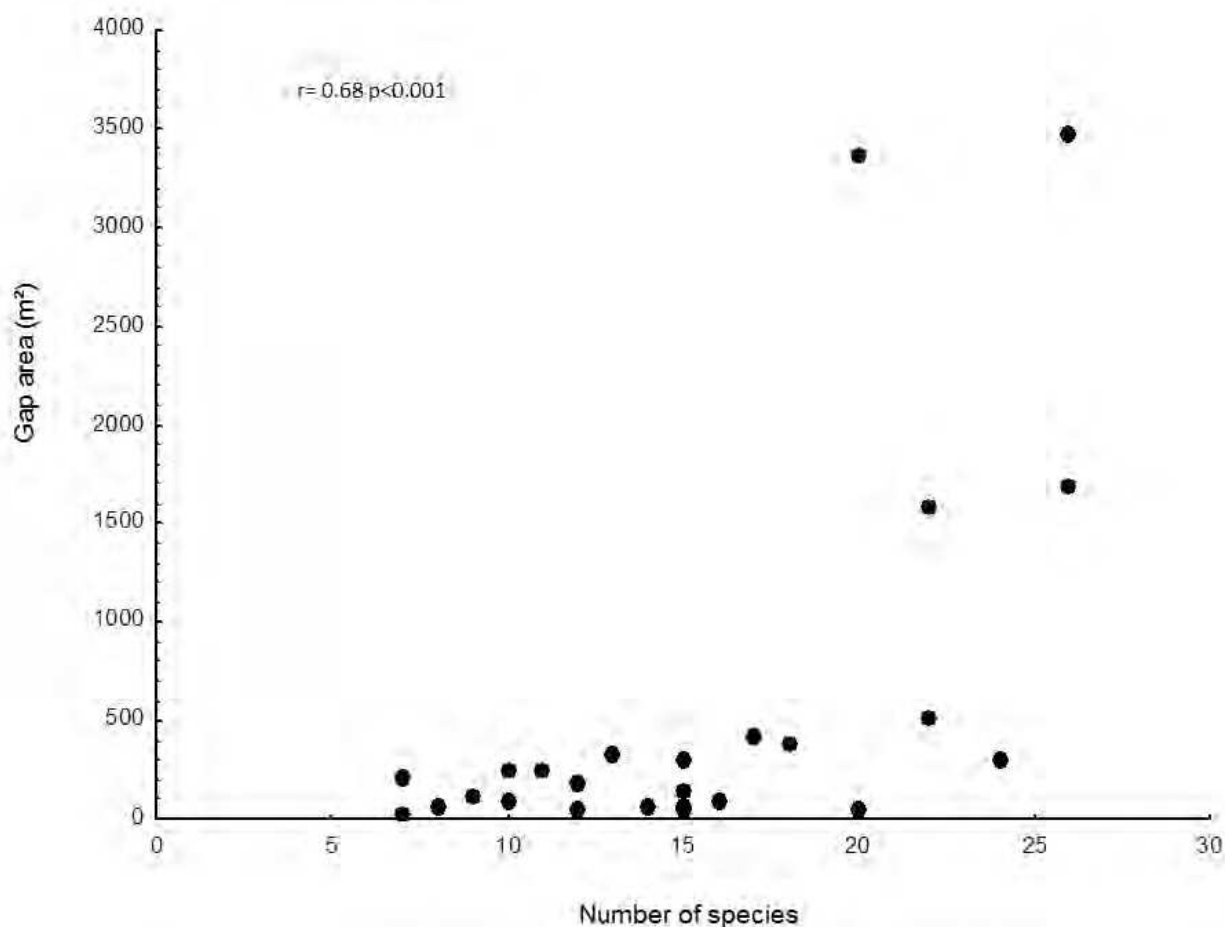
Fig. 5. Relationships between gap area and number of species, in a tropical semideciduous forest remnant (TSF), Uberlândia, MG.

The tropical plant species usually have their growth genetically determined by low or high light intensity rates (Lüttge, 1997). Therefore, some species are able to survive in the overstory or under the canopy in shaded environments. We can find in the same individual adapted leaves for sunny and shaded environments and these two distinct features related to different rates of light/radiation exposure are vital to understanding the ecophysiological variations of plants associated to their environments (Lüttge, 1997).

The estimation of gap areas in the canopy varied from 6.03 to 7.81% alongside the lines we had set for this purpose (Table 3). These are higher values than those mentioned by Van der Meer & Bongers (1996) for a tropical rain forest at Guiana and similar to the values of 7.1% found by Kneeshaw & Bergeron (1998) in a temperate boreal forest at secondary successional stage, in this case using the same methodology applied in this work.

Martins et al., (2004) described canopy gap size classes ranging from 35 to 454 m² in a tropical semideciduous forest (TSF) in Southeast Brazil. The canopy gaps formed by death of Bamboo groupings (*Merostachis riedeliana* Rupr.), had played some role in the structural and successional forest organization, creating successional environments for gaps colonization by tree and shrub species belonging to different ecological groups. In a TSF fragment situated at São Paulo state, Oliveira (1997), mentions that the majority of natural gaps were

created by the fall of branches and dead trees, providing small sized gaps ($\cong 46{,}9$ m²). This event, on a small scale, maintains a diversity of patches in the forest, forming renovation and degradation of eco-units surrounded by patches at later successional stages (Oldeman, 1990).
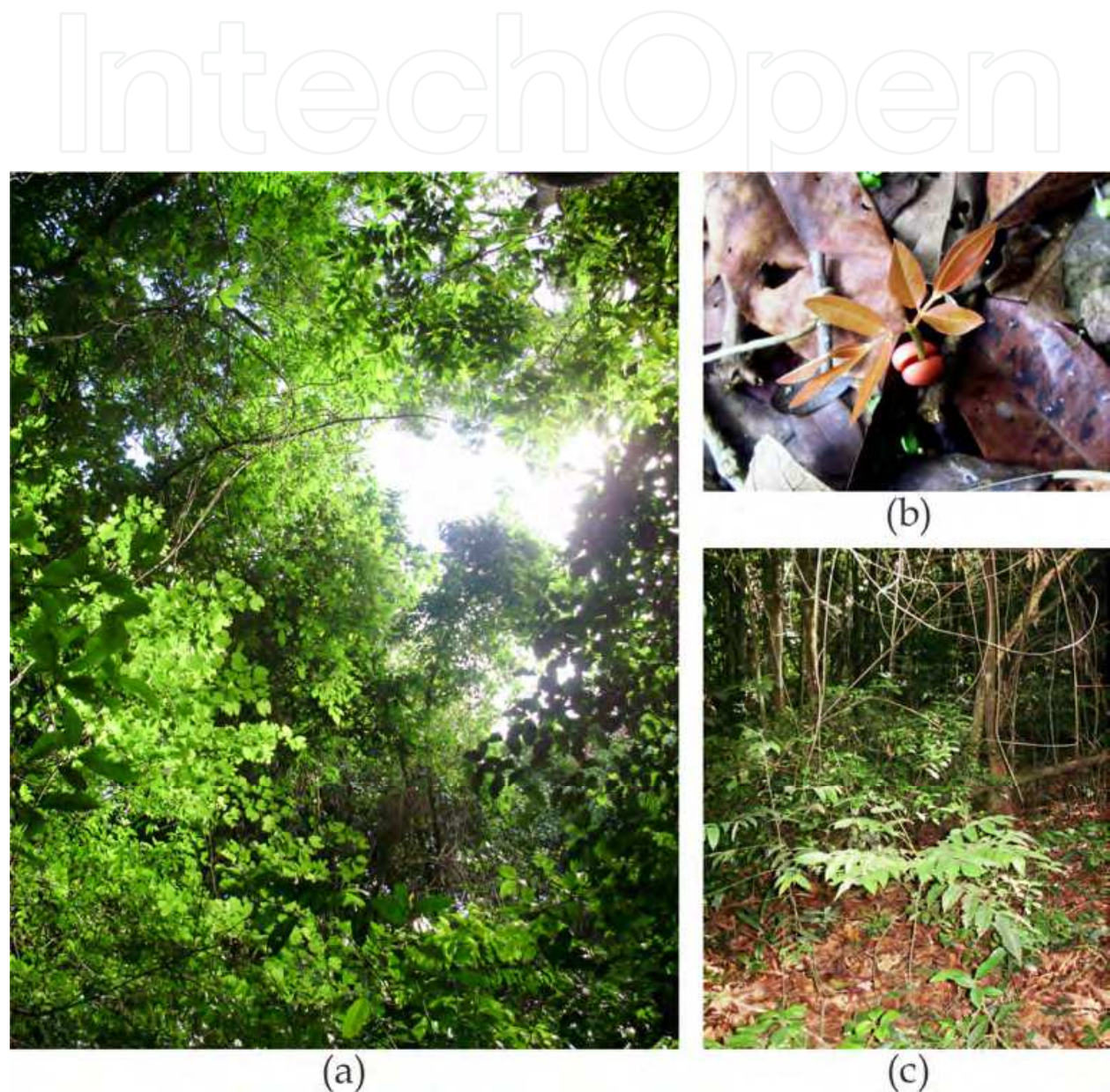

Fig. 6. Light input in a medium sized (a) canopy gap (500 m²), seedling establishment in a recently formed canopy gap (b) and natural regeneration in advanced stage at an old gap (c) in TSF, Uberlândia-MG.

Formation cause	N	% of total	Type of event (*)
Tree Fall	13	52,0	Falling of a whole tree, creating small sized gaps (< 100 m²)
Fall of more than one tree	4	16,0	Falling of more than one tree creating large sized gaps and linked gaps (> 1000 m²)
Crown break	6	24,0	Breaking of branches, and usually, the whole crown of a tree
Collapsed tree	1	4,0	Collapsing of large sized tree caused by tension or weight
Unidentified	1	4,0	Old canopy gap where we could not identify its formation cause

Table 2. Identified causes of canopy gaps in a tropical semideciduous forest remnant (TSF), Uberlândia, Minas Gerais.

Lines (*)	Covered distance (m)	Occupied area (%)
Line 1	320	7,81
Line 2	320	6,03
Line 3	320	7,68
Line 4	320	6,45

(*) According to Kneeshaw & Bergeron methodology (1998).

Table 3. Estimations of occupied area by natural canopy gaps in a tropical semideciduous forest remnant (TSF), Uberlândia, MG.

In many canopy gaps at natural forests there is a strong regeneration of fast growing pioneer species, , as well as the regrowth of previously stablished species by vegetative growth of roots and stumps (Harstshorn, 1989; Putz & Brokaw, 1989; Whitmore, 1990; Riéra, 1995, Vieira & Scariot, 2006), improving the natural regeneration of tropical vegetation. We observed this fact in our study area, mainly at large sized gaps, where the overstory is subject to higher light radiation rates, showing a higher development of early secondary and pioneer species, besides ruderal and lianes. These species, even though were not accounted in our sample design, can surely interfere in the regeneration of tree species through either competition at ground level or reproducing vegetative in a pretty much shorter time scale than do the tree species.

4. Conclusions

The class-size distribution of canopy-gaps showed a trending towards a bimodal distribution, being the most part of gaps represented by short to medium sized classes (≤ 500 m²). The distribution of tree species is influenced by gap size, community composition

and by the number of individuals of species present in this transitory event in STF conditions.

The environmental heterogeneity represented by canopy gaps of different sizes provides an important regeneration niche for pioneer and early secondary species, which we observed in colonizing gaps of different sizes and distinct micro-environments present in these locations. The variations in canopy openings within gaps of different sizes tend to increase the environmental variability in STF conditions improving thus, the natural regeneration in this type of vegetation.

5. Acknowledgments

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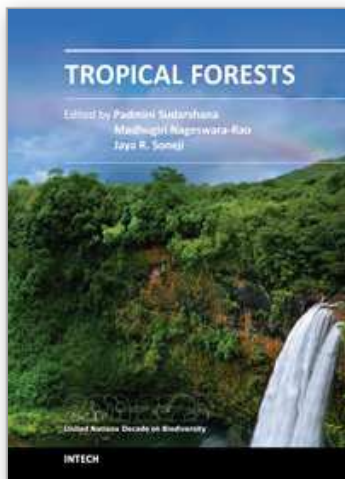
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Tropical Forests

Edited by Dr. Padmini Sudarshana

The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

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