

Point of View

“GAPS OF DECIDUOUSNESS”: CYCLICAL GAPS IN TROPICAL FORESTS

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ABSTRACT: A new concept named “gaps of deciduousness” is introduced for the momentary annual bright places that appear under tropical and subtropical deciduous canopy trees when they are leafless, a cyclical kind of gap totally different from treefall gaps, whose importance in the regeneration ecology of these forests until now had not been discussed or evaluated. The aim of this article is to highlight the most significant aspects related to the concept of “gaps of deciduousness” and suggest the importance of developing studies to evaluate its relevance in the discussion of plant species coexistence and biodiversity maintenance in some tropical forests.

Key words: gap dynamics, forest dynamics, light regimes, forest biodiversity

“CLAREIRAS DE DECIDUIDADE”: CLAREIRAS CÍCLICAS EM FLORESTAS TROPICAIS

RESUMO: Um novo conceito de “clareiras de deciduidade” é introduzido para os locais iluminados que surgem momentaneamente sob as copas de árvores decíduas do dossel de florestas tropicais e subtropicais, quando essas árvores estão sem folhas. Elas são um tipo de clareiras cíclicas totalmente diferente das clareiras formadas pela queda de árvores, cuja importância na ecologia da regeneração dessas florestas até agora não tinha sido avaliada ou discutida. O objetivo desse artigo é ressaltar os aspectos mais significantes relacionados com o conceito de “clareiras de deciduidade” e sugerir a importância de se desenvolverem estudos para avaliar sua relevância na discussão sobre a coexistência das espécies de plantas e a manutenção da biodiversidade em algumas florestas tropicais.

Palavras-chave: dinâmica de clareiras, dinâmica de florestas, regimes de luz, biodiversidade florestal

INTRODUCTION

The importance of treefall gaps in the ecology of tropical forests has been long recognized (*e.g.*, Whitmore, 1990). The presence of light regimes (gaps and understory) and different species tolerance or intolerance to shade has been considered the most important factor that explains the distribution of tree species in many tropical and subtropical forests (Whitmore, 1996).

Recently, Gandolfi et al. (2007) suggested a complementary model for forest gap dynamics, proposing that each tropical and subtropical forest canopy species may create specific microsite conditions beneath its crown, and discussed possible consequences of this pattern to the maintenance of forest biodiversity. While explaining this model, the authors briefly introduced the idea of “gaps of deciduousness”

(GD), for momentary increases of light irradiance in the forest understory beneath the crown of deciduous or semideciduous canopy trees when they are leafless. Many authors discussed the importance of these “gaps” in the ecology of temperate forests (*e.g.*, Kato & Komiyama, 2002), but no similar discussions have so far been presented for tropical and subtropical forests.

The aims of this point of view are to define and develop the GD concept and discuss its possible consequences and importance in regeneration ecology of tropical and subtropical forests. To introduce these ideas, some data about the light regimes are used, which were observed beneath different evergreen and deciduous canopy tree species in a Brazilian Moist Seasonal Semideciduous Forest, showing the heterogeneity of understory light conditions created by these different leaf phenology patterns. The Moist Seasonal

Semideciduous Forest formation, or Seasonal Tropical Forest (Whittaker, 1970), occurs in the South and Southeast of Brazil, presenting 30–50% of deciduous and/or semideciduous trees species, many of which attain the canopy.

From July 1994 to June 1995, a phytosociological and light regime study was carried in three plots of 3,500 m² (A, B and C) in the Santa Genebra Forest Reserve, a Moist Seasonal Semideciduous Forest fragment in Campinas, São Paulo state, Brazil (22°49' S; 47°06' W). More forest site information for this forest fragment can be found in Martins & Rodrigues (2002). This light regime study recorded light irradiance as photosynthetic photon flux density (PPFD = $\mu\text{mol m}^{-2} \text{s}^{-1}$) in 24 microsites spread over three sampling forest areas using eight quantum sensors (Li 190SA and Li190SZ, Li-COR, Inc. U.S.A.), connected to a data-logger (Li - 1000-35 Li-COR, Inc. U.S.A.), and taking measurements 1.5 m above forest floor. On each sampled day, eight microsites were simultaneously measured, but equipment availability restrictions only permitted to sample each microsite two days per month during 7.5 hours per day (09h30–7h00)

This study was designed to describe the light regimes existent in a semideciduous forest and not to present discussion about light regimes under canopy tree species, therefore not all recorded microsites are useful to us and data from only nine of the 24 recorded microsites are here presented. This represents a great restriction of data, but our aim is only to highlight one important fact that until now has been neglected in the ecology of tropical forests, so as to stimulate researches to design specific studies and to obtain larger samples to compare light intensities under evergreen, deciduous, semideciduous trees and gaps, permitting a more complete understanding of how “gaps of deciduousness” may affect plant species regeneration.

For the sampled microsites under trees, leaf fall phenological behavior of each canopy tree was observed in the field during one whole year, but to simplify the discussion, semideciduous and deciduous trees were grouped and all taken as deciduous trees. Five microsites were beneath the crowns of deciduous canopy tree species, *Cabralea canjerana* (Vell.) Mart. (Meliaceae), *Esenbeckia leiocarpa* Engl. (Rutaceae), *Croton piptocalyx* Müll Arg. (Euphorbiaceae), *Piptadenia gonoacantha* (Mart.) J.F.Macbr. (Fabaceae) and *Jacaratia spinosa* (Aubl.) A.DC. (Cariaceae), two beneath evergreen canopy tree species, *Pachystroma longifolium* (Ness) I. M. Johnston (Euphorbiaceae) and *Metrodorea stipularis* Mart. (Rutaceae), and two placed in the center of two gaps (more details can be found in Gandolfi, 2000).

The light regimes beneath evergreen and deciduous canopy trees sampled during one year were very different, with low light levels below the evergreen all year long and with two different extreme light conditions beneath deciduous trees. When evergreen and deciduous canopy trees are leafy, the light regimes beneath them are similar; for example, on September 15, 1994, daily PPFDs were respectively, 0.62 mol m⁻² d⁻¹ and 0.97 mol m⁻² d⁻¹, beneath the crowns of one evergreen canopy tree (*Metrodorea stipulacea*) and a deciduous one (*Jacaratia spinosa*). On November 20, 1994, daily PPFDs reached, respectively, 0.85 mol m⁻² d⁻¹ and 10.82 mol m⁻² d⁻¹, when the perenifolius remained green and the deciduous tree was leafless, an almost 13 fold difference (Figure 1). Also on November 20, 1994, only 24 m away from that deciduous tree, daily PPFD reached only 8.84 mol m⁻² d⁻¹ in the center of a small gap (176 m²), showing that light levels below a deciduous tree can sometimes be higher than in a gap. Similar examples with other three canopy tree species were previously presented by Gandolfi et al. (2007).

Spatial light heterogeneity in the understory created by the simultaneous presence of evergreen and deciduous trees in the forest canopy has not been reported or discussed for tropical and subtropical moist or rain forests until now, even in long-term forest light studies. (Turnbull & Yates, 1993; Rich et al., 1993)

The displayed results for microsites 1, 4, 5, 6 and 7 (Table 1) are most commonly observed beneath evergreen and deciduous trees, but different patterns can also occur; for instance, the highest light irradiance beneath the evergreen canopy tree in microsite 2

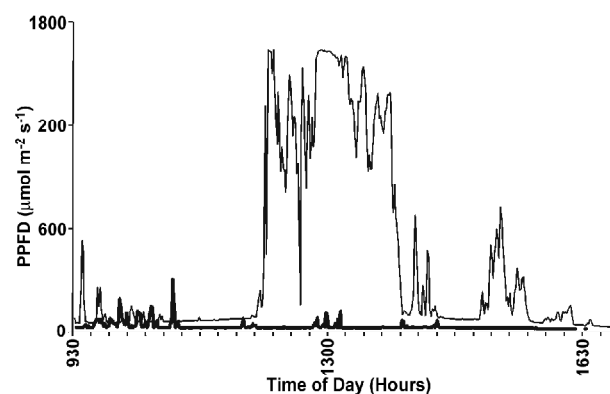


Figure 1 - Daily course of photosynthetic photon flux density (PPFD) for two microsites, beneath the crown of an evergreen canopy tree (*Metrodorea stipulacea*) (bold line) and beneath a deciduous one (*Jacaratia spinosa*) (normal line). Records were taken in the understory of a Moist Seasonal Semideciduous Forest fragment in the Southeast of Brazil, on November 20, 1994, when the perenifolius remained green and the deciduous tree was leafless.

Table 1 - High and low observed daily photosynthetic photon flux density (PPFD) from July 1994 to June 1995, in the center of two gaps, beneath the crown of two evergreen and five deciduous canopy tree species of a Moist Seasonal Semideciduous Forest in Campinas (SP, Brazil). (M = microsite number - the values presented were not the highest and lowest ones in the year, since each microsite was only recorded two days per month).

Sensor placed ^a	M	Daily PPFD ^b	
		Low	High
		----- mol m ⁻² d ⁻¹ -----	
Beneath evergreen canopy tree belonging to species			
<i>Pachystroma longifolium</i>	1	0.07	1.00
<i>Metrodorea stipularis</i>	2	0.27	2.71
Beneath deciduous canopy tree belonging to species			
<i>Cabrlea canjerana</i>	3	0.14	1.43
<i>Esenbeckia leiocarpa</i>	4	0.07	2.90
<i>Croton piptocalyx</i>	5	0.09	5.04
<i>Piptadenia gonoacantha</i>	6	0.09	7.39
<i>Jacaratia spinosa</i>	7	0.41	10.90
In the center of			
Small new gap (176 m ²) ^c	8	0.51	13.47
Large old gap (688 m ²)	9	0.61	16.80

^aMore details in Gandolfi (2000). ^bDaily PPFD = 0930h–1700 h. ^cGap area according to Gandolfi (2000) and similar to Runkle (1981).

was caused by the presence of two canopy deciduous trees around it, which when leafless produced a great bright area under them and increased the background diffuse radiation in the surrounding understory. Differently, the relatively low levels of light observed beneath a deciduous tree in microsite 3 were caused by evergreen vines that covered it, maintaining the understory shaded even when it was leafless.

Differences in high light irradiances among leafless trees (e.g., in microsites 4, 5 and 6) are commonly observed in the field and may be related to crown shapes and sizes, patterns of leaflessness (deciduous or semideciduous), differences in season and duration of leaflessness, relation between leaflessness duration and solar elevation, etc., but the highest irradiance observed in microsite 7 was probably related to the fact that this tree occurred on the edge of a treefall gap.

Some factors can explain why the highest irradiances recorded in gaps shown in Table 1 were higher than those below deciduous trees; for instance, in each displayed microsite, the highest values occur at different times - in gaps, the highest levels occurred in the summer, when solar elevation was highest, but when the considered deciduous trees were again leafy. Beneath some deciduous trees (microsites 3 and 4), light irradiances were not so different from under evergreen trees (microsites 1 e 2), but under some other deciduous trees (microsites 5, 6 and 7) high light irradiances were, shade tolerance-wise, more similar to

gaps (microsites 8 and 9) than beneath the evergreens. We suggest naming these bright places beneath the crowns of deciduous canopy trees as “gaps of deciduousness”(GD), once these microsites are more similar in light irradiance to the conditions observed on the edge or in the center of some treefall gaps than to those beneath evergreen canopy crowns.

The number of deciduous and semideciduous trees in forest canopies can vary according to the considered tropical forest (Morellato et al., 2000; Condit et al., 2000); these numbers in each of our three sampled forest areas (3,500 m² each) were respectively 25 (41.7%) in area A, 51 (82%) in area B and 42 (56.8%) in area C, showing the importance of considering this light regime in the study of semideciduous forests.

The spatial distribution of these deciduous trees in forest canopies can also vary, a deciduous tree may appear surrounded by evergreen trees (single GD) or forming patches produced by two, three or more deciduous trees (complex GD). In our study, we observed 13 single and 4 complex GDs in area A, and, respectively, 11 and 13 in area B and 10 and 10 in area C. When many of the deciduous trees simultaneously lose their leaves, in these complex GDs, great bright areas can appear in the understory. In 11 of 27 complex GDs the cluster of deciduous tree crowns produced areas ranging from 50 to 150 m².

Many deciduous and semideciduous canopy trees can occur on the edge of treefall gaps and, when

leafless, they can increase bright areas of gaps. In area A, 15 deciduous trees occurred on the edge of present gaps, or 34% of the total of trees on these edges, in area B, 22 trees or 50%, and in area C, 22 trees as well, or 65%. Similar GDs are expected to occur in other tropical forest formations, since many species of deciduous and semideciduous trees also occur in the canopies of these forests (Condit et al., 2000; Willians-Linera & Meave, 2002).

Brazilian tree species of Moist Seasonal Semideciduous Forests respond differently to distinct levels of light (Souza & Válio, 2001, 2003), and since evergreen and deciduous canopy trees cast different shade intensities, they may eventually produce divergent biological responses in terms of germination, growth, stress, death, etc. on the species attempting to regenerate under each one of them.

As already discussed in Gandolfi et al. (2007), leaf fall span varies widely in deciduous trees species in the Santa Genebra Forest Reserve (from one week to four months) and thus in some GDs high light levels occurring simultaneously with low soil water availability during the winter might create more stressful conditions for seedlings that live beneath these deciduous canopy trees than for those beneath the evergreen. But other GDs occur during or after the early rains in spring, allowing for high light levels and soil water availability to occur at the same time, possibly favoring more the seedlings and saplings under deciduous trees than those under evergreen canopy trees.

In a more general sense, we expect that positive or negative biological responses of plants growing below GDs probably will vary according to forest formation, characteristics of the canopy trees and the considered season of deciduousness (summer, winter, etc., which affects the levels of light that attains the forest floor), the correspondence or non-correspondence of this leaflessness with the dry season, (which in turn affects soil water availability), the characteristics of the regenerating plants, as the considered tree species and their ecological group (tolerant or intolerant to shade), the development stage of individuals (seedlings, saplings, poles, etc.), and so on.

Over the last decades, many authors showed that different light regimes affect the survival and development of seeds, seedlings, saplings and poles of tropical moist and rain forests (Whitmore, 1996), as in Moist Seasonal Semideciduous Forests the presence of GDs in these other formations needs to be described and discussed, given its possible great importance for the ecology of these formations. However, many other plant life forms, like herbs, vines, epiphytes, etc. could also respond to these different light regimes with consequences in forest biodiversity

patterns. Nonetheless, we believe the most important feature to highlight about these GDs is that according to the phenological leaf fall behavior of the considered deciduous canopy species, GDs can exist for some days, weeks or months, but like they open and close every year GDs can exist during years or decades, while the considered deciduous and semideciduous canopy trees remain alive in the forest canopy. So they are cyclical, being therefore totally different from treefall gaps that open canopy and then slowly close over the years.

The gap dynamics model proposes that moist and rain tropical forests are dynamic patchworks, where one patch converts into another in a predetermined cycle of three stages maintaining forest composition and biodiversity (Whitmore, 1990). This model assumes that higher shade conditions will appear in the understory of one patch, according to this cycle evolution, suggesting that all replacements of canopy trees will always be between evergreen species. However, in tropical forests many important genera have deciduous or semideciduous canopy species, as *Aspidosperma*, *Cariniana*, *Cedrella*, *Ceiba*, *Copaifera*, *Ficus*, *Ochroma*, *Pseudobombax*, *Tabebuia*, *Tecoma*, etc., and thus in these forests pioneer, early secondary and climax species can be evergreen or deciduous. Therefore, in gap dynamics the expected three stages of transition in each formed patch could have eight possible sequences involving evergreen or deciduous canopy species, with a single replacement sequence involving only evergreen species. These consequences of GD occurrences suggest that the inferred progressive more shaded conditions during this dynamics could not even occur or be much more complex than expected.

Many other important considerations could be proposed, but one, specifically, must be stressed. Light conditions do not affect only plant species regeneration, but also many plant-animal interactions, e.g. pollination or dispersion, and many animal-animal interactions, e.g. predation, camouflage, reproduction, etc., which depend on animal visual orientation and are thus affected by light conditions present in each forest understory spot (Endler, 1993). Finally, even if we are proposing here that GDs are a significant subject to tropical and subtropical forest ecology, it is important to underline that, as observed by Gandolfi et al. (2007), the possible different impacts of these “cyclical gaps” in forest regeneration could be only a special case of a more general process, the ecological filter effect created by abiotic and biotic conditions produced by each different canopy tree species on plant species regeneration, not necessarily involving light changes in the understory.

ACKNOWLEDGEMENTS

The authors thank Francisco Carlos Antonioli for assistance in the field and permanent friendship. This study was funded by FAPESP (Project n° 93/1026-8). Carlos A. Joly was supported by a CNPq Productivity Fellowship (Grant 520334/99-0).

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Received July 22, 2008

Accepted August 29, 2008