Point of View

PERMEABILITY - IMPERMEABILITY: CANOPY TREES AS BIODIVERSITY FILTERS

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ABSTRACT: Each tropical and subtropical forest canopy species may create specific microsite conditions below its crown, which works as a filter for those species that attempt to regenerate below it. In function of the permeability or impermeability level, each canopy species could partially determine a plant community structure and composition beneath its crown projection. Therefore, present and future forest plant community biodiversity could be partially determined by the present structure of the canopy tree species community (filter effect). Some theoretical and practical aftermaths are suggested.
Key words: tropical forest dynamics, tree regeneration, gap dynamics, ecological filters, forest biodiversity

PERMEABILIDADE - IMPERMEABILIDADE: ÁRVORES DO DOSSEL COMO FILTROS DA BIODIVERSIDADE

RESUMO: Cada espécie do dossel das florestas tropicais e subtropicais pode criar micrositios específicos sob sua copa, que funcionam como filtros para aquelas espécies que tentam regenerar sob elas. Em função da permeabilidade ou impermeabilidade, cada espécie do dossel poderia parcialmente determinar a composição e estrutura da comunidade de plantas sob a projeção da sua copa. Portanto a biodiversidade presente e futura da comunidade de plantas da floresta poderia ser parcialmente determinada pela estrutura atual da comunidade de árvores do dossel (efeito de filtro). Alguns desdobramentos teóricos e práticos deste novo enfoque são sugeridos.
Palavras-chave: dinâmica de florestas tropicais, regeneração de árvores, dinâmica de clareiras, filtros ecológicos, biodiversidade florestal.

Many authors have tried to explain the observed coexistence of a high number of tree species in some tropical and subtropical forests (Palmer, 1994; Chesson, 2000; Wright, 2002), but, unfortunately, until the present no single hypothesis or theory could elucidate the cause or causes of this pattern. This study introduces the idea that each canopy tree species may create specific microsites below its crown that will function as a biodiversity filter upon the plants that attempt to regenerate under it. This idea suggests that present and future biodiversity of forest plant communities could be partially determined by the different permeability levels created by present canopy tree species. This alternative model for forest dynamics helps to elucidate the regeneration and distribution of all types of forest tree species, and produces important theoretical and practical consequences for tropical and subtropical forest research and management.

Gap dynamics is a model used to explain tree regeneration, tropical forests auto-perpetuation and the coexistence of so many tree species (but see Hubbell et al., 1999, Lortie et al., 2004). In this model, forests are considered a mosaic of patches of different ages, with a continuous change in species composition, while gap phase patches convert themselves into building phase patches and then into mature phase patches (Cooper, 1913; Watt, 1947; Oldeman, 1983; Whitmore, 1990). During this regeneration cycle, shade-intolerant tree species (pioneers) growing in gaps (full sun microsites) are gradually replaced by more shade-tolerant species (secondary and climax species) that dominate building and mature patches (shaded microsites).

The adaptation of tree species to full sun or shaded microsites has been considered one of the most important traits to explain tree regeneration and distribution in tropical moist or rain forests. Therefore, gap studies and tree species distribution between gap/non-gap forest patches still constitute the paradigm in the discussion of tropical forest dynamics (Whitmore, 1996, Martins & Rodrigues, 2002). Gap dynamics may be a good model to explain pioneer, canopy and emergent tree regeneration. However, since the time necessary for a gap to develop into a mature patch and then to a gap again is very long, when compared with the short lives of understory tree species, this model does not explain how these species regenerate during the cycle of canopy trees.

A recent study in a tropical forest showed that shade-tolerant tree seedlings of different species are highly sensitive to the understory light heterogeneity (Montgomery & Chazdon, 2002). These authors found that differences in light regimes under distinct canopy microsites, with no canopy gaps, could significantly affect growth and recruitment of shade-tolerant species.

In a Moist Seasonal Semideciduous Forest, Gandolfi (2000) observed that along one year the light regimes beneath evergreen and deciduous canopy trees were different (Figure 1). When the crowns of all observed trees were covered by leaves (July 6, 1994 and June 8, 1995), light intensities in the understory underneath them were very low, remaining, in general, below 10 µmol m^{-2} s^{-1} of photosynthetic photon flux density (PPFD) (Figures 1a and 1d). In contrast, when deciduous trees are partially (*Piptadenia gonoacantha*, in October 5, 1994) or totally leafless (*Esenbeckia leiocarpa* in October 5, 1994 and *Piptadenia gonoacantha* in November 24, 1994), higher light levels were observed under their crowns. Underneath the evergreen tree *Pachystroma longifolium* light conditions remained very low, during all the measured period. (Figures 1a, 1b, 1c and 1d).

On October 5, 1994 (Figure 1b), when *Esenbeckia leiocarpa* was leafless and *Piptadenia gonoacantha* was only partially leafless, daily PPFD intensities were respectively 6.6 and 5.8 times higher than those registered under the evergreen *Pachystroma longifolium*. But on November 24, 1994, daily PPFD under *Piptadenia gonoacantha* (Figure 1c), totally

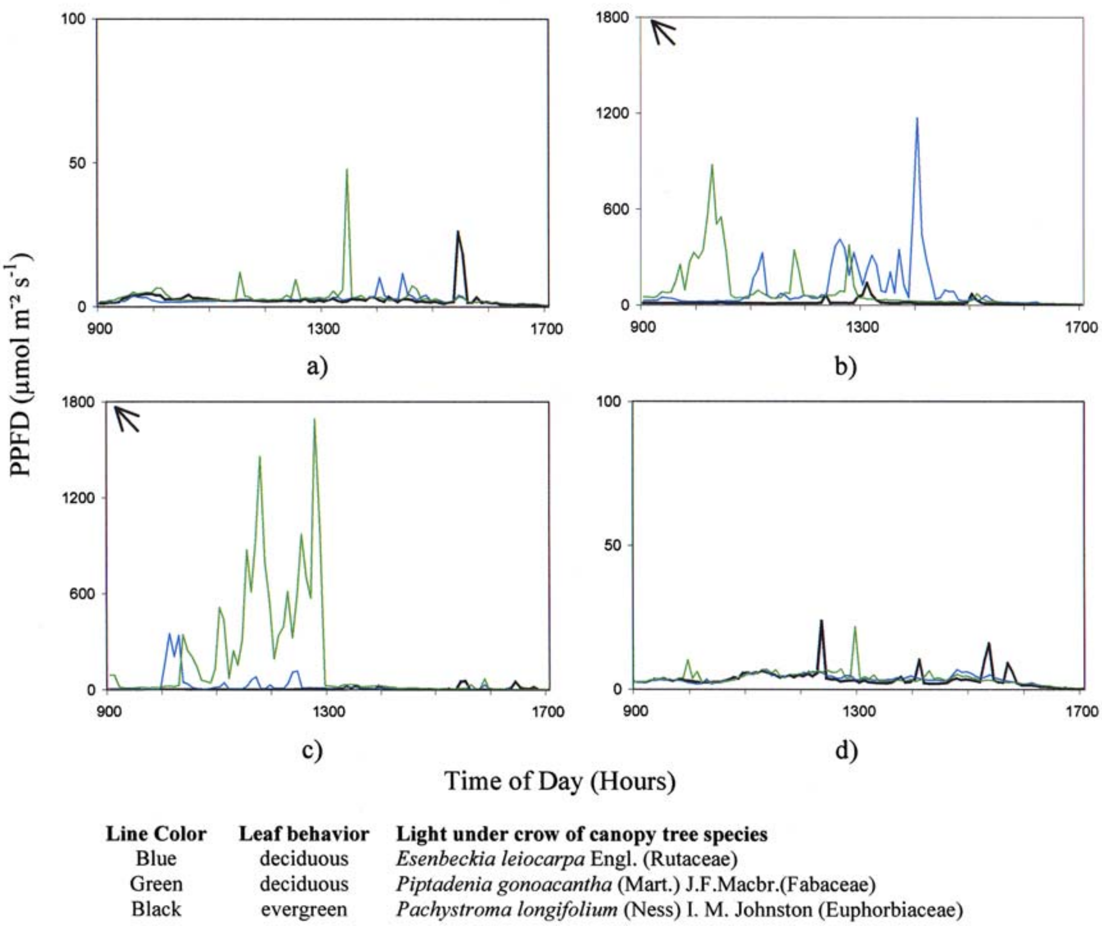

Figure 1 - Time–course variation of light intensities in photosynthetic photon flux density (PPFD) under the crowns of two deciduous canopy tree species, *Esenbeckia leiocarpa* and *Piptadenia gonoacantha*, and one evergreen canopy tree species, *Pachystroma longifolium*, in four days (a: July 6, 1994, b: October 5, 1994, c: November 24, 1994 and d: June 8, 1995) in a Moist Seasonal Semideciduous Forest (Santa Genebra Reserve, Campinas/SP, Brazil).

leafless, was 23.6 times higher than under the evergreen tree, and 6.6 times higher than under the other deciduous trees, which were then partially covered by new leaves.

Data of Figure 1 only confirm a common visual observation made in South and South-Eastern Brazilian Moist Seasonal Semideciduous Forests, that is, during the leaf fall of canopy deciduous trees, light levels in their understories were more similar to those previously observed in some gaps than to those beneath evergreen canopy trees. Thus, this leaf fall creates "gaps of deciduousness" in the understory below deciduous trees and results in a light regime totally different from those observed in tropical and subtropical rain forests (Rich et al., 1993; Turnbull & Yates, 1993). These observations are of great importance because in fragments of Brazilian Moist Seasonal Semideciduous Forests, deciduous trees represent 30 to 50% of the canopy trees (Morellato, 1991). Great part of the deciduous tree species loses their leaves during the winter and part of the spring, usually periods of low water availability. In general, these trees will remain leafless for two months, but individually this period may vary from one to twenty weeks (Morellato, 1991).

In some days, during the winter, the increase of light and the low water availability under the "gaps of deciduousness" might create more stressful conditions for seedlings that live beneath deciduous canopy trees than for those beneath evergreen canopy trees. In contrast, when the first spring rains return, more light and water availability under the "gaps of deciduousness" might favor seedlings and saplings under deciduous trees rather than those under evergreen canopy trees. For instance, after two months without rain, the monthly rainfall totals in October and November, 1994 were respectively 55 and 169 mm, and light availability under leafless *Piptadenia gonoacantha* in November 24, 1994, was almost 24 times higher than beneath evergreen *Pachystroma longifolium*, 14 m away (Gandolfi, 2000).

Considering that in South-Eastern Brazilian Moist Seasonal Semideciduous Forests the length of time a tree is leafless varies among deciduous species and even between individuals of the same species (Morellato, 1991), the positive or negative effects of deciduous or evergreen canopy trees upon seedlings vary in time and space.

Many studies about tree species of these forests have shown that they respond differently to distinct light intensities (Souza & Válio, 2001; 2003; Válio, 2001; 2003). Hence, as our data for Moist Seasonal Semideciduous Forests show, seeds, seedlings or saplings living beneath different canopy tree species are, in reality, submitted to different light regimes that may eventually generate distinct biological responses, such as germination, stress, growth, photoinhibition or death, in individuals situated at short distances from each other.

The description of a new type of light regime in tropical and subtropical semideciduous forests represents an important advancement with possible consequences in different aspects of the dynamics of these forests. However, differences in light regimes created by distinct canopy trees are only a small part of the heterogeneity created by canopy trees.

Jones et al. (1997) highlighted that each canopy tree species is a physical ecosystem engineer that creates many specific abiotic conditions beneath its crown, like specific litter accumulation, soil composition, allelochemical compounds composition, among others (for details see Zinke, 1962; Lodhi, 1977; Binkley, 1995; Denslow, 1996; Carnevale & Montagnini, 2002). Many authors have shown that such different conditions can affect germination, seed predation, pathogens attacks, tolerance, and herbivory in a species-specific way (Chou & Yang, 1982; Denslow, 1996; Cintra, 1997; Wardle & Lavelle, 1997; Metcalfe & Turner, 1998; Nicotra et al., 1999; Van Oijen et al., 2005). These species-specific biological responses can result in the selection of specific communities of seedlings, soil fauna, bacteria, micorrhiza, and pathogens composition (e.g., see Boettcher & Kalisz, 1990, Dobson & Crawley, 1994; Denslow, 1996; Cintra, 1997; Ettema & Wardle, 2002).

George & Bazzaz (1999a; 1999b) observing the effect of ferns, and Peters et al. (2004), observing the effect of a palm-tree on tree regeneration, showed that different forest species of plants can act as ecological filters affecting the composition, structure and distribution of seedlings or saplings of understory and canopy species. The occurrence of different light regimes under deciduous and evergreen canopy trees here presented also suggests that canopy species could potentially act in a similar way. Several other results (e.g., Augspurger, 1984) suggest that explanations are need for forest tree species regeneration and distribution using more factors than only light regimes.

Observing the spatial distribution pattern of five canopy tree species, in the understory of Hemlock-Northern Hardwood Forests, Woods & Whittaker (1981) showed that those canopy species could affect saplings in different ways. Due to a filter effect, the probability of the sapling of a given species to remain or be replaced under the crown of each one of the canopy trees varied among species. Based on these results, Woods & Whittaker (1981) suggested that these interactions could explain the coexistence of those species in a stable community.

We propose that another level of heterogeneity exists inside the patches of the forest mosaic, because each canopy tree species would be an ecological filter to the species that try to develop below it. Thus, different canopy tree species would be equally permeable for one "focal" species while presenting different levels of permeability (or impermeability) for another "focal" species. Therefore, the filter effect would depend on the relation between each "focal species" and each "filter canopy tree species" affecting the structure and composition of populations and communities.

The present differences observed in plant species composition beneath different canopy species would partially depend on this differential permeability of each canopy species to those species that arrived under it. Today's forest canopy structure is partially determining present plant diversity below it, and will also partially determine the future forest canopy diversity, because part of the current regeneration will grow, reach and remain in the future canopy.

It is also suggested that the selective action of specific conditions created and maintained during decades beneath the crown of each canopy tree would be, hierarchically, much more important to define the fate of seedlings and saplings living in the understory than sporadic stochastic disturbance events. Consequently, they are a key factor to determine forest biodiversity.

This filter model is not new. Weaver & Clements (1938), Tansley (1946), Lodhi (1977), Woods & Whittaker (1981) and many other have also described or suggested something similar. However, it is desired to suggest here that this filter effect would be a more general process that complements the Gap Dynamics Model in many tropical and subtropical forests. Moreover, a specific mechanism (permeability-impermeability levels) is proposed linking canopy trees to forest regeneration, tree distribution and biodiversity maintenance. This view reinforces the importance already explored by Watt (1964) of dominant species in determining the patterns in communities.

Light regimes are only one of the important components of the effect produced by canopy trees that can select species underneath them, but it is not necessarily the most important. Obviously soil fauna and microorganisms will also be affected. So, observing and testing other abiotic and biotic factors related to canopy trees may open the possibility of looking at forests with new eyes. Detailed studies of forests communities probably will demonstrate that canopy trees may show high, low and very low permeability to epiphytes, to vines, to herbs, to understory treelets and/or to canopy trees. The use of each canopy species as a parameter that integrates many abiotic and biotic factors related with tree species regeneration allows us to surpass the gap/non-gap dichotomy, changing the focus of forest dynamics studies.

This new proposition explains better the regeneration of all types of tree species that live under a canopy, making it possible to relate the maintenance of tree biodiversity with canopy composition and structure of tropical and subtropical forests.

There are other theoretical consequences, for instance, according to Janzen-Connell's hypothesis, seedlings survival chances increase with the increase of the distance between seedlings and their mother or conspecific trees. With the model here suggested, no previous pattern of seedling survival and distribution would be expected, because they depend not only on their mother or conspecific trees but also on the effects of permeability levels of each canopy tree that is covering them.

Practical implications can also be raised. The use of few canopy species in restoration projects and the intense selective timber log of few tropical forest species reduce the availability of species-specific microsites for regeneration and would possibly affect the future biodiversity in these forests. The use of high diversity of canopy species in projects of tropical and subtropical forest restoration and an adequate combination of these species can improve the restoration process and favor biodiversity restoration (Rodrigues et al., 2007).

Recent papers suggest that canopy filter effect can be a possible explanation for some observed patterns of tree regeneration (Vieira & Gandolfi, 2006; Souza, 2007). Vieira & Gandolfi (2006) show that density and species richness of seed rain and species diversity and sapling height in natural regeneration vary under the three studied canopy tree species in a restored Moist Semideciduous Forest with 15 years old and suggest that these observed patterns could be explained by neighborhood or by filter effects. After analyzing the canopy trees species sampled in a 10 ha permanent plot of a Moist Semideciduous Forest, Souza (2007) selected nine species that have more than five individuals in the canopy, the necessary condition to be statistically tested. Analysis revealed that three species had presented species-specific responses in the associations between overstory and understory trees, species that might have been acting as "ecological filters".

Finally, it is important to stress that results like those observed by George & Bazzaz (1999a; 1999b) and field observations suggest that inside the forest other plant life forms may act too as ecological filters. Therefore, in spite of canopy tree due to their size, biomass, resources invested and life span, these being hierarchically the most important filters, the superimposition with other filters needs to be considered to understand the regeneration, distribution and coexistence of tree species. We believe too that aspects like the effects of superimposed filters, the modulation of the filter effects of one tree by surrounding canopy trees and some other aspects related to tropical and subtropical forests are difficult to simulate, so that, in spite of the evolution of Forest Gap Models (Bugmann, 2001; Busing & Mailly, 2004), probably the use of individual-based simulation models to discuss the ideas here presented may not be a good strategy.

It is believed that the model here presented, named "canopy trees as filters of biodiversity", is a step forward to understand many cases of observed plant species coexistence and the natural forest dynamics. However, it does not explain all the complexity of tropical and subtropical forest dynamics.

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