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"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

PATTERNS, DRIVERS AND ECOLOGY OF TROPICAL LEAF PHENOLOGY

Mateus Geovane Lima da Silva

Rio Claro – SP
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Resumo

A fenologia foliar tropical é central para o funcionamento das florestas e para as interações ecológicas, embora o papel dos fatores abióticos e bióticos sobre o lançamento foliar ainda permanece sob investigação. Esta dissertação examina o lançamento foliar em florestas tropicais e sua relação com os fatores abióticos e bióticos, com atributos foliares relacionados à herbivoria e seu potencial papel mediando interação entre lianas e árvores em uma floresta na Amazônia Central. No primeiro capítulo, realizamos uma revisão sistemática sobre lançamento foliar e herbivoria, e uma meta-análise sobre a influência dos fatores abióticos no lançamento foliar nas florestas tropicais. A revisão revelou que poucos estudos abordam a pressão da herbivoria sobre o lançamento foliar, sendo o escape temporal e sincronia como as principais estratégias fenológicas de defesa. A meta-análise evidenciou um efeito positivo dos fatores abióticos sobre o lançamento foliar, mais forte para a luz, seguido da água e temperatura. Além disso, o efeito da disponibilidade de água e luz variou entre florestas com diferentes sazonalidade e entre os níveis de espécie e de comunidade, mas não entre formas de vida. No segundo capítulo, investigamos se o lançamento foliar está relacionado a atributos foliares associados à herbivoria em uma área da Amazônia Central. Usando imagens de uma câmera digital, identificamos o início e o pico do lançamento foliar em nível de comunidade e indivíduos, e testamos se árvores que lançavam folhas na estação seca e chuvosa diferiam em seus atributos foliares. O lançamento foliar foi sazonal no nível da comunidade, concentrado na estação seca, e a maioria das árvores lançaram folhas nesse período, enquanto uma menor proporção o fez na estação chuvosa. No entanto, o momento do lançamento foliar não apresentou relação com os atributos mensurados. Medições diretas das taxas de herbivoria são necessárias para avaliar se o lançamento foliar na estação seca atua como um escape temporal contra a herbivoria. No terceiro capítulo, descrevemos um desacoplamento temporal no lançamento foliar entre lianas e árvores em uma área da Amazônia Central. Através das imagens digitais da câmera, detectamos o início do lançamento foliar das lianas e das árvores. As lianas anteciparam o lançamento foliar comparado às árvores, que pode atuar como uma estratégia para maximizar a captura de luz e reduzir a competição. A antecipação do lançamento foliar pode representar uma estratégia fenológica potencialmente favorável às lianas, hipótese que deverá ser testada com maior amostragem. Em conjunto, esses resultados ampliam nossa compreensão dos fatores que influenciam o lançamento foliar e como a fenologia pode influenciar as interações ecológicas em florestas tropicais.

Palavras-chave: Florestas tropicais, fenologia foliar, floresta amazônica, fenocâmera.

Abstract

Tropical leaf phenology is central to forest functioning and species interactions, yet the relative influence of abiotic and biotic drives on leaf flushing remains unclear. This dissertation examines leaf flushing in tropical forests and its relation with abiotic and biotic factors, with herbivory-related leaf traits, and with liana-host tree interactions in a Central Amazonian forest. In the first chapter, we conducted a systematic review of leaf flushing and insect herbivory, and a meta-analysis of the effect of abiotic factors on leaf flushing in tropical forests. The review showed that few studies have addressed herbivory pressure on the timing of leaf flushing, with escape and synchronous leaf flushing most often proposed as phenological strategies against herbivores. The meta-analysis revealed a positive effect of abiotic factors on leaf flushing, strongest for light availability, followed by water and temperature. Furthermore, the effect of water and light availability varied among forests with different seasonality and between the species and community levels, but not among life forms. In the second chapter, we investigated whether leaf flushing timing is related to herbivory-associated leaf traits in a Central Amazonian forest. Using digital camera images, we identified the onset and peak of leaf flushing at the community and individual-tree levels, and tested whether trees flushing in the dry and wet season differed in leaf traits. Flushing was seasonal at the community level, concentrated in the dry season, and most individual trees flushed leaves during this period, while a smaller proportion did so during the wet season. However, leaf flushing timing was not associated with any of the measured herbivory-related leaf traits. Direct measuring of herbivory rates and leaf damage are needed to evaluate whether dry-season leaf flushing provides temporal escape from herbivory. In the third chapter, we described a temporal displacement in leaf flushing between lianas and their host trees in a Central Amazonian forest during 2016. Based on the digital camera images, we identified the onset of leaf production corresponding to liana and tree. Lianas and trees started to flush leaves during the dry season, but lianas flushed earlier than their host trees, a behavior that may maximize light capture and reduce competition. This suggests that leaf phenological may be a potential mechanism contributing to liana success in tropical forest. Together, these findings can advance our comprehension of the drivers of leaf flushing and its influence on ecological interactions in tropical forests.

Keywords: Tropical forests, leaf phenology, Amazon forest, phenocam.

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General introduction

Leaf phenology e.i. the timing of leaf production, leaf longevity, and senescence connect multiple ecological processes that drive tropical forest dynamics. In particular, the timing of leaf flushing influences not only plant photosynthesis but also forest productivity seasonality, biogeochemical cycles, water and carbon fluxes, and plant-plant competition, while also mediating herbivory interactions (Van Schaik, Terborgh, Wright, 1993; Reich, 1995; Myneni et al., 2007). Given its influence across a broad range of ecological processes, leaf phenology is a structuring process in ecology (Ratche, Lacey, 1985; Forrest, Abraham, Miller-Russing, 2010). Understanding leaf flushing seasonality, its drivers and how it affects ecological interactions is therefore fundamental to understanding forest dynamics and ecological interactions.

The time of leaf flushing is shaped by both abiotic and biotic factors (Wright 1996; Fenner, 1998). In tropical forests, abiotic factors such as precipitation, moisture availability, photoperiod, and temperature have been suggested as proximate cues that directly determine leaf flushing patterns (Wright, Van Schaik, 1994; Sakai, Kitajima 2019) or act as signals that trigger the plant's endogenous process (Borchert, 1994; Reich et al., 2004). The effect of these abiotic factors on leaf flushing, however, remains ambiguous in tropical forests (Morellato et al., 2000), likely because abiotic factors tend to be correlated with one another, making it difficult to isolate their relative contribution and infer causal relationship. In addition to these proximate abiotic cues, herbivory pressure has also been proposed as an ultimate, evolutionary driver of leaf flushing timing (Aide, 1992; Murali, Sukumar, 1993), although this hypothesis remains less investigated. In this sense, the onset of leaf production reflects a trade-off between resource acquisition and minimizing herbivory damage (Aide 1992; Kikuzawa, 1994; Aide, Angulo, 2000; Lamarre et al 2014),

Plants experience a high herbivory pressure in tropical forests, which can reduce plant fitness (Straus, Agrawal, 1999; Coley, Barone, 1996). This pressure is particularly high on immature and expanding leaves, where most damage tends to occur due to their high nutritional quality and lower physical defenses (Coley, Barone, 1996; Dubey et al., 2011), suggesting that leaf flushing seasonality may be under selective pressure for defense against herbivory (Aide, 1992; Coley, Barone, 1996; Fenner, 1998). To withstand insect herbivores, plants can rely on phenological strategies such as adjusting the timing of leaf production to period of low activity of herbivores (i.e. dry season) or synchronizing leaf production with co-occurring species to overwhelming herbivores (Fenner, 1998; Lamarre et al., 2014). In

addition to phenological strategies, plants rely on morphological leaf traits, such as trichome density, leaf toughness, thickness, leaf mass per area (LMA), and chemical to deter insect herbivores (Agrawal, Fishbein, 2006), traits that affect leaf quality and herbivory feeding preference (Straus, Agrawal, 1999; Hanley et al., 2007; Pearse, Karban, 2013). Because defense investment is costly, diverting resources from growth (Hermes, Mattson, 1992), defensive traits may be allocated according to the herbivory risk a leaf experiences. Since leaf flushing behavior and leaf lifespan influence this exposure, leaf defensive traits may therefore vary among species and functional groups with contrasting phenological strategies (Dirzo, Boege, 2008; Marquis, Morais, 2021).

Beyond herbivory interaction, leaf flushing phenology may be an important trait mediating tree-liana competitions for resources. Lianas are climbing plants that rely on trees for structural support to reach the canopy and display their leaves above the host tree's crown, thus competing intensively for light (Putz, 1984; Schnittzer, Bongers, 2002; Media-Vega et al., 2020). Because liana remains rooted in the soil, they also compete belowground for water and nutrients (Schnitzer, 2005). Their efficient colonization of disturbance-created niches make lianas particularly abundant in tropical forests favoured by large-scale disturbances, such as fragmentation, and by localized disturbances, such as tree-falls gaps (Schnitzer, Bongers, 2011). Rapid growth and stem elongation, for instance, favors liana success in disturbed conditions (Schnitizer, 2005). Once lianas reach the canopy, however, leaf phenology may become an equally important trait favoring successful colonization, since the timing of leaf flushing determines a plant's ability to capture resources (Kikuzawa, 1995). In tropical forests, light is thought to drive leaf flushing patterns, with plants flushing leaves in response to increased light availability (Wright, 1996; Wu et al., 2016). The timing of leaf flushing between liana and trees may represent a key trait mediating their competition for light, and potentially, an underlying aspect of liana success in tropical forests that remains poorly understood.

Climatic conditions influence vegetation distribution, as a result leaf flushing patterns can differ across tropical forests (Osada, 2002; Reich, et al., 2004; Elliot, Baker, Borchert, 2006). The main climatic difference between more seasonal and less seasonal tropical forest lies in the length and intensity of dry season (Reich, Borchert, 1982). In more seasonal tropical forests (e.g. tropical dry forests) characterized by a pronounced dry period, rainfall seasonality may be a determining determinant of leaf phenology activity, with the onset of leaf flushing responding to water availability (Borchert, 1998). On the other hand, in less seasonal tropical forests such as rainforest, where water availability is less limiting, solar

radiation and photoperiod may instead be more relevant in driving leaf production, since light availability represents a more invariant cue (Wright, 1991), even within this forests types, leaf flushing response to the cue can vary among species.

The high diversity of plant species found in tropical forests is followed by an equally diverse leaf phenology pattern (Wright 1996; Morellato et al., 2000). Variation in leaf flushing is commonly observed at multiple, such as among individuals within the same species, among species, communities, and among different life forms, resulting in a mosaic of phenological strategies (Reich, 1995; Singh, Kushwa, 2005). Phenology response to multiple external abiotic and biotic factors, therefore whether this variation reflects heterogeneous abiotic drivers, plasticity or genetically mediated differences in sensitivity to external cues remains an open question (Forrest et al., 2010). To track this variability requires different approaches to accurately monitor leaf phenology dynamics in tropical forests (Song et al., 2024). Monitoring approaches include ground-based observation, digital cameras, which provide a high frequency observation (Alberton et al., 2014; 2017), and satellite that adds a new scale of observations (Piao et al., 2019). These methods are not mutually exclusive, combined, they provide integrated information on leaf phenology pattern, variation across sites, and phenological behavior trends (Song et al., 2024).

Although the Amazon forests maintains an evergreen canopy, it display seasonality in leaf phenology, with a short period of aggregated leaf flushing (green-up) concentrated during the driest months (Huete et al., 2006; Myneni et al., 2007; Wu et al., 2016). Leaf exchange during the dry season has been reported to alter leaf demography (i.e. the proportion of young, mature, and old leaves) and, consequently, canopy photosynthetic capacity (Albert et al 2018), highlighting the role of leaf phenology and leaf age driving seasonal forest productivity (Rastrepo-Coupe et al., 2013; Wu et al 2017; Chen et al 2019). This phenomenon, however, fueled an intense debate regarding seasonality in the Amazon forest, with studies claiming that the apparent green-up could be explained by changes in sun-sensor geometry rather than by an actual increase in canopy leaf area (Galvão; Morton et al., 2014), since shifts in the angle among sun, sensor, and canopy affect the near-infrared (NIR) reflectance detected by the sensor. Other studies, however, have confirmed that the dry-season green-up reflects a real increase in canopy leaf area (Bi et al., 2015).

This dry-season leaf flushing has been attributed to increased light availability, associated with lower cloud cover during this period (Xiao et al., 2006; Green et al., 2020), indicating that trees are not water-limited during the dry season, probably due to deep root systems that access deep water tables or hydraulic lift (Nepstad, 1994; Oliveira, 2005).

Aggregating leaf flushing during the period of peak solar radiation may represent an opportunistic strategy to maximize photosynthesis (Kitajima, Mulkey, Wright, 1997; Rivera et al 2002, Myneni et al., 2007). In this sense, leaf renewal could be interpreted through the lens of the Leaf Demography-Ontogeny Hypothesis, whereby trees replace old leaves with a low photosynthetic capacity for leaves with a more photosynthetic capacity (Doughty, Goulden, 2008; Wu et al., 2017). In addition, high solar radiation during the dry season has also been shown to co-vary with lower insect herbivores abundance (Van Schaik, Terborgh, Wright, 1993), leading to the hypothesis that dry-season leaf production may represent a phenological escape strategy from herbivores (Aide, Coley, Lopes et al., 2016), yet this question remains under investigation.

Understanding leaf flushing and its drivers across tropical forests, how trees with contrasting leaf flushing differ in leaf defensive traits, and the role of leaf flushing in mediating plant competition is therefore essential to comprehend tropical forests functioning, ecological interaction, and forest structure. Thus, this dissertation aims to investigate the influence of abiotic and biotic factors on leaf flushing in tropical forests, its association with herbivory-related leaf traits, and its role in mediating liana-tree interaction. Hence, based on the information mentioned above, this dissertation is organized into three chapters. The chapter one comprises a systematic review of leaf flushing and herbivory and a meta-analysis of the relationship between leaf flushing and abiotic aspect across tropical forests, evaluating how this relationships can vary across tropical forests with different climatic seasonality, between species and community levels, and among life forms. The second chapter investigates the relationship between the timing of leaf flushing and herbivory-related leaf traits, asking whether trees flushing during the dry and wet season differ in leaf traits associated with herbivory. The third chapter reports a contrasting leaf flushing phenology behavior, in which lianas exhibit an earlier leaf flushing than their host trees.

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General conclusion

This dissertation investigated tropical leaf flush phenology by assessing the effect of biotic and abiotic drivers on leaf flush across tropical forests through systematic review and a meta-analysis, the interplay between leaf flushing and leaf ant-herbivory traits in a Central Amazonian forest, and the potential role of leaf phenology underlying liana success in high canopy. Together, the outcomes reveal a complex leaf flush phenology in tropical forests and its relation with abiotic and biotic factors, and leaf flush behavior as a potential underlying liana strategy to thrive in tropical forests.

Chapter 1, provided a systematic review of the role of herbivory in leaf flushing and a global meta-analysis of the role of water availability, light availability, and air temperature on leaf flushing across tropical forests, and how these effects vary across biological scale and forests differing in climatic seasonality. The systematic review identified a very few studies addressing herbivory, limiting the possibility of a quantitative synthesis. Even so, the available evidences suggest that leaf flushing tends to occur during period of lower herbivory activity (dry season), with escape and synchronous leaf flushing as two phenological defense strategies, although herbivores can sometimes circumvent these strategies, highlighting the complex ecological interaction and the need for further studies on how herbivory shapes leaf flushing time in tropical forests. Regarding the meta-analysis of abiotic factors, results indicate a positive effect of abiotic factors on leaf flushing, with light availability showing the higher effect, followed by water availability and air temperature. The effect of light and water availability on leaf flushing tended to differ between species and community levels and across tropical forests with distinct climatic seasonality, while no significant effects were observed across life forms.

The chapter 2 described leaf flush behavior at the community and individual tree levels, and investigated the relationship between leaf flushing and herbivory-related leaf traits. At the community level, leaf flushing was aggregated during the driest months. At the tree level, most trees flushed leaves during the driest months, while fewer trees flushed during the wettest months. Moreover, leaf flushing intensity did not differ between trees flushing leaves in the dry and vs wet season, but did differ between phenological groups, with deciduous trees showing a faster increase in leaf flushing than evergreen trees. Trees that flushed leaves during the dry and wet season did not differ in measure of herbivory-related leaf traits (LMA, leaf toughness, thickness, and Carbon:Nitrogen). Further studies measuring herbivory damage and integrating additional chemical and morphological leaf traits are need

to better understand the role of herbivory in modulating leaf flushing and defense investment.

The chapter 3 examined a temporal displacement in leaf flushing between two liana and their host trees. Both lianas and host trees produced leaves during the dry season. However, liana flushed leaves earlier than trees. This earlier liana flushing may reflect a strategy to enhance light uptake and minimize direct competition with host trees. This temporal niche adjustment in leaf flush might be a possible mechanism favoring liana success because they benefit from increased light availability and reduced competition favoring, potentially supporting explain high abundance of liana in tropical forests.

Together, these findings demonstrate that abiotic drivers, particularly light availability, are an important control on leaf flushing in tropical forests, with their relative influence varying across forest types and biological scales. Although assessing herbivory remains challenging in highly diverse tropical forests, this dissertation underscores the need for further studies evaluating how biotic pressure shapes not only when plants flush leaves, but also how they invest in defenses against herbivory. Ultimately, leaf flushing may also mediate tree-liana competition interaction and represent an underlying mechanism contribution to liana success in tropical forests, a question we encourage future studies to investigate.