FUNCTIONAL LEAF TRAITS OF TREE SPECIES SAPLINGS IN THE ATLANTIC LOWLAND TROPICAL FOREST OF SOUTHEASTERN BRAZIL: RELATIONSHIPS BETWEEN TRAITS AND DIFFERENCES BETWEEN FAMILIES

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INTRODUCTION

Tropical forests typically have a great richness of trees and shrub species, with up to 250 species per hectare. Species composition and community structure is partly determined by functional traits, which mediate the relationship between individuals and its environment. The regeneration niche is considered to be of great importance to survival and growth of tree species in tropical forests, and is fundamentally linked to the light requirements of species. In a heavily shaded understory, light is available mostly in the form of brief and unpredictable sunflecks, hence traits that grant an efficient radiation capture and use should enhance growth rates. Moreover, traits that confer resistance to mechanical damage and herbivory increase survival rates under the deprived conditions met at the forest floor.

Shade plants often have a high investment in total leaf area. This may occur either through large leaves, or through leaves with a high specific leaf area (SLA). Additionally, shade plants may display a large leaf area ratio, defined as total leaf area per unit dry mass of the whole branch. A drawback of possessing large leaves is a requirement of heavier support structures, decreasing the potential carbon gain per unit leaf area under poor irradiance. On the other hand, leaves with high SLA are often thin and soft, possessing high nitrogen content per unit dry mass. High SLA is also negatively correlated with leaf longevity, increasing the turnover of photosynthetic tissue and hence nutrients requirements. Soft leaves are also prone to suffer damage from herbivory, or from vertebrate trampling or falling debris. Thus, there is a potential trade - off between light capture efficiency and resistance to damage. Overcoming this trade - off is paramount for a given species to regenerate successfully in the forest understory.

Functional traits affecting light requirements and resistance to damage of juveniles are thought to be under heavy selective pressure in tropical tree saplings. Nevertheless, functional traits are also subject to phylogenetic constraints. Phylogenetic constraints and past selective pressure may thus have shaped leaf morphology in divergent directions in several lineages. Different methods were proposed to detect the effect of phylogeny on the evolution of functional traits. Although more sofisticated methods are available, a simple and straightforward approach is to study closely related species, such as species in the same genus or family. The diverse flora of the Atlantic Rain Forest presents an opportunity to study the relationships between leaf traits from several species of species - rich families sharing the same habitat.

OBJECTIVES

The aims of this work are to characterize functional leaf traits of saplings of tree species at the Lowland Atlantic Tropical Rain Forest, and to search for bivariate relationships between leaf traits, focusing especially on the most important families found at the Atlantic Rain Forest.

MATERIAL AND METHODS

Sampling was conducted during random walks, spanning *ca.* 2 ha, at Picinguaba, Serra do Mar State Park, São Paulo state, Brazil. A total of 104 woody saplings with 1 - 2 m high were sampled. Large canopy gaps were avoided. We cut one terminal branch from each sapling. Each branch was cut at the base of the node supporting the oldest leaves, and divided in photosynthetic (leaf blades) and support structures (stem and petioles). Leaves were digitized in a bed scanner, and leaf area measured with ImageJ software (http://rsb.info.nih.gov/ij/). Leaf blade thickness (T) was measured at the median portion of each leaf with a digital caliper, avoiding thick veins. Leaves and support structures were oven dried for 3 days then weighted. Specific leaf area (SLA) was calculated as leaf area per unit leaf dry mass, and leaf area ratio (LAR) as leaf area per unit branch dry mass (including leaves, petioles and stems, up to the fifth oldest metamer). Leaf dry matter density (DD) was estimated as thickness divided by SLA (Witkowski & Lamont 1991).

Individuals were identified, whenever possible, to species level, by comparison with herbaria material. Species were then grouped according to taxonomic criteria: Myrtaceae (9 species), Rubiaceae (8 species), and Fabaceae (4 species), and a pool of species belonging to other families (17 species from 11 families).

Species mean values were used as sampling units. Leaf area was log - transformed to meet the assumption of normal distribution. Functional traits were compared between groups by a one - way Analysis of Variance followed by Tukey post - hoc test. Regression analyses were performed between pairs of traits, separately for each group, and with all species pooled.

RESULTS AND DISCUSSION

We identified 38 species: 9 Myrtaceae, 8 Rubiaceae, 4 Fabaceae, 17 species from several other families, and 3 non - identified species. SLA, LAR, T and DD were significantly different between groups ($F_{3,37} > 6.3$; $p < 0.05$). On the other hand, leaf area was similar between groups ($F_{3,37} = 0.7$; $p > 0.05$). Myrtaceae species displayed significantly lower SLA and LAR than Rubiaceae species. Myrtaceae also presented significantly higher T than the group of several families. Rubiaceae presented lower DD than Myrtaceae. SLA presented a tight positive relationship with LAR, either within each group separately ($R^2 = 0.42$ - 0.99; $p < 0.05$) or when all species were pooled ($R^2 = 0.82$; $p < 0.05$). Species of Fabaceae presented a significantly steeper relationship between SLA and LAR, when compared to the other groups. SLA and T were negatively correlated in Myrtaceae species only ($R^2 = 0.57$, $p < 0.05$), and SLA and DD were negatively correlated in Rubiaceae species only ($R^2 = 0.56$, $p < 0.05$). Leaf area showed no significant relationship with any other trait.

LAR, as a stem trait, is in principle a more integrative trait than SLA, a leaf trait, and more time - consuming to measure. The good relationship between both indicates that SLA may be used as a proxy for LAR, on tree saplings at the lowland Atlantic rain forest. Moreover, SLA is related to leaf longevity, leaf physiology, and light capture (Reich *et al.,* 2003), all important factors for the maintenance of a positive carbon balance under dense canopy shade. Variation of SLA between species was related to T in Myrtaceae, and to DD in Rubiaceae. These two components of SLA have distinct implications for photosynthetic capacity: leaf C assimilation per unit area increase with T, but have no relation with leaf DD (Niinemets 1999). Thus, the relationship between SLA and T found in Myrtaceae may be related to a greater variation in photosynthesis than in Rubiaceae, reflecting a greater variation in maximum height, as Rubiaceae is comprised of understory treelets and shrubs only. Moreover, T and DD are important components of physical protection against herbivory and mechanical damage, an important cause of mortality in shaded seedlings. Thus, the differences in SLA found among the compared groups of species would suggest that Myrtaceae species, with tougher and thicker leaves, have a greater probability of survival under shaded conditions. But Rubiaceae species are at least as abundant as Myrtaceae species in the understory, and have a grater proportion of understory shrubs to canopy trees. Leaf chemical defenses may play a role in enhancing understory survival. Rubiaceae is a family characterized by widespread occurrence of alkaloids (Soto - Sobensis *et al.,* 2001), a qualitative N - based defense, while many species of Myrtaceae have terpenes, a C - based defense. Thus, these families may be associated to the 'defense' and 'escape' strategies against herbivory (Kursar & Coley 2003), with Rubiaceae defending young leaves with extremely toxic compounds, and Myrtaceae escaping herbivory by relying on tough leaves.

CONCLUSION

SLA may be used as a proxy for LAR in tree saplings of the Atlantic Rain Forest. Two of the richest and more abundant families from the Atlantic rain forest, Myrtaceae and Rubiaceae, markedly differ in leaf morphology, indicating contrasting strategies for survival under the shaded understory. Further research should address leaf expansion rates, herbivory rates, leaf longevity, and synchrony of leaf production in shaded saplings, focusing especially on families Rubiaceae, Myrtaceae and Fabaceae.

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