

## **ABSTRACT**

LAU, ON LEE ANNIE. Evolution of Tree Architecture in the Brazilian Cerrado.  
(Under the direction of Dr. William Hoffmann).

The tropical savanna-forest boundary is commonly characterized by an abrupt transition in vegetation structure and in tree species composition. It has been hypothesized that differences in architecture between savanna and forest trees have an important role in determining the contrasting structural differences between savanna and forest ecosystems. Because of the importance the vegetation structure in determining the ecosystem properties of these systems, I performed a comparative study of tree architecture to examine differences in plant structure of savanna and forest species. To eliminate the potential bias from phylogenetic relatedness, I used congeneric species pairs containing trees of both habitat types that occur sympatrically in savannas of the Brazilian cerrado habitat at IBGE Ecological Reserve (RECOR). I found that relative to savanna species, forest species have larger crown volumes with more apical meristems and greater height for a given stem diameter. Other traits that influence patterns of light interception also differed, with savanna species exhibiting more convoluted leaf blades and shorter petioles. There was evidence that allometry and other traits are convergent in savanna and forest tree species across lineages, providing strong support for adaptive functions of these traits. Furthermore, the larger canopies of forest species imply that they play a role in reduced light in the understory and the exclusion of grasses, which potentially facilitates further expansion of forest tree species in the absence of fire.

Evolution of Tree Architecture in the Brazilian Cerrado.

by  
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## **DEDICATION**

For my family and friends.

## BIOGRAPHY

On Lee Lau was born in Hong Kong and immigrated to San Francisco with her family to spend her formative years learning what science was about as a volunteer and intern at the California Academy of Sciences, and gaining an appreciation for the outdoors on trail projects with the Student Conservation Association. She studied the ecophysiology of larkspur species (*Delphinium*) in an undergraduate Biology thesis at Reed College with Dr. Keith Karoly and measured three-spine sticklebacks (*Gasterosteus aculeatus*) as a lab manager and field technician at University of Texas at Austin with Dr. Dan Bolnick before pursuing a graduate degree. She has done various types of scientific and conservation work in Alaska, California, Costa Rica, Hawaii, Oregon, Texas, Trinidad and Tobago, Vancouver Island BC, and now North Carolina and Brazil. She hopes the future will bring fulfilling work and opportunities to explore more ecosystems.

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## CHAPTER I

### Introduction to the Brazilian Cerrado

The Cerrado region of Brazil is characterized by diverse xeromorphic vegetation that varies in structure from open grasslands (campo limpo) to dense woodlands (cerradao) and riparian gallery forests (Eiten 1972, Oliveira-Filho and Ratter 2002; Figure 1). The Cerrado occupies an area of approximately 2 million km<sup>2</sup> with a distinct seasonal climate in South America (Eiten 1972). However, much of the Cerrado habitat in the area has been lost due to human disturbance (de Siqueira and Peterson 2003, Silva et al 2006). Drier, savanna-like habitats in the Cerrado are characterized by high light levels penetrating to the ground level, low soil water and nutrients, and frequent fire (Hoffmann et al 2005). This is in stark contrast to adjacent habitats, such as riparian gallery forests that have low light levels at the forest floor due to a dense canopy. Forest habitat, even within 40 meters of the savanna boundary, is often associated with higher soil water, higher soil nutrients, and lower fire occurrence (Hoffmann et al 2009). The differences in these environments are likely mirrored by characteristic physiological traits and species composition in these habitats.

Two functional types of trees, associated with differences in forest and savanna habitats, contribute to the canopy cover and ecosystem structure in the Brazilian Cerrado (Silva and Santos 2005). And there are predictable differences between types in functional morphological traits, such as higher specific leaf area and bark thickness in savanna than forest types (Hoffmann et al 2005). Due to the strong contrasts between savanna and forests environments, it is expected that savanna species are adapted to seasonal drought and fire,

and forest species are adapted to strong competition for light. But under fire suppression, forest species can occur in both savanna and forest habitats, while savanna species tend only to occur in the savannas.

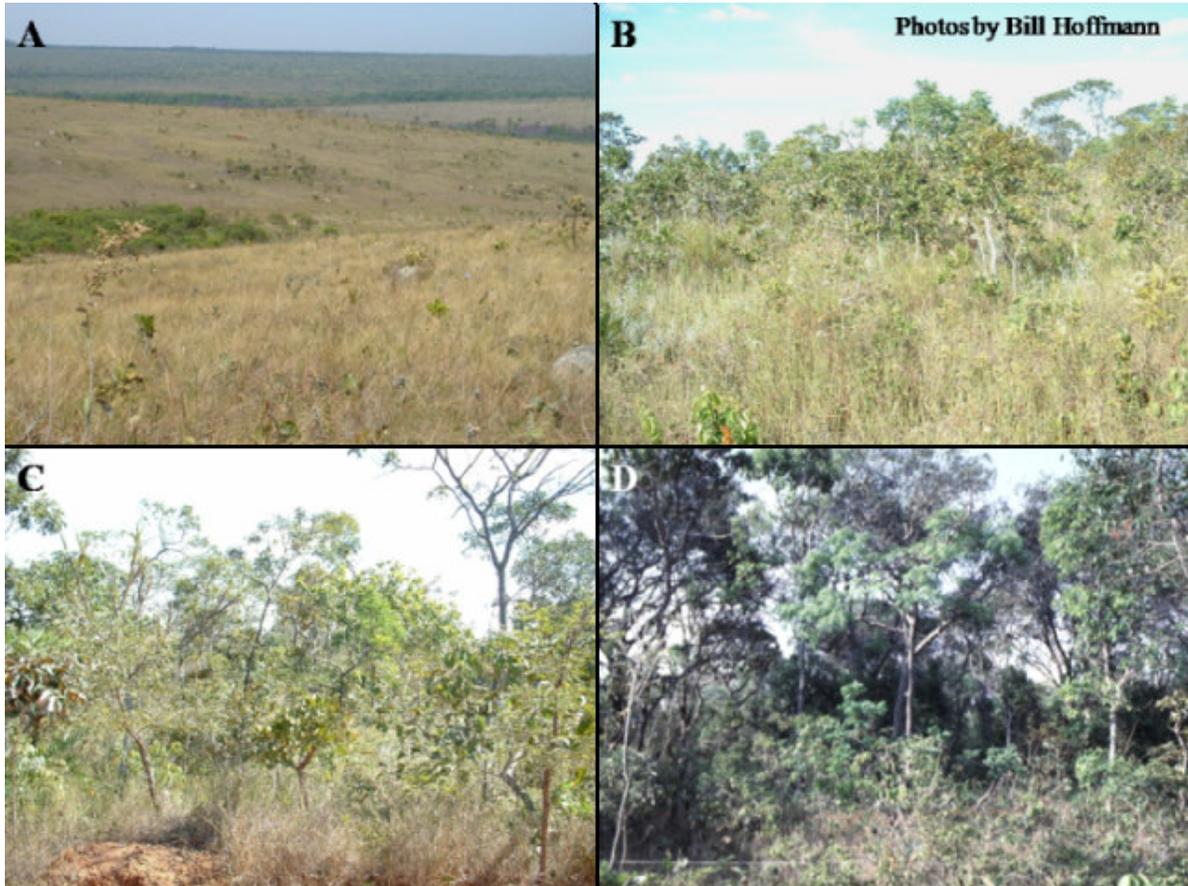


Figure 1. Representative habitats of the Cerrado biome at or near IBGE Ecological Reserve in Brasilia, DF, Brazil: (A) Campo limpo – open grassland with few trees and shrubs, (B) Campo sujo – low tree woodland, (C) Cerrado *sensu stricto*, (D) Cerradao – dense woodland

Both fire activity and low soil resources may limit the establishment of forest trees in the savanna (Eiten 1972). However, forest trees able to colonize the savanna may be competitively superior and displace savanna trees. A number of factors may favor the expansion of gallery forests into the savanna, including: increased growth of woody

vegetation near savanna-forest boundaries, decreased prevalence of grasses and reduced frequency of fires (King et al 1997, Silva et al 2008). Species traits (i.e., morphology and physiology) associated with adaptation to habitat are likely to affect many of those factors that govern the expansion of gallery forests (Wright et al 2007) and generally determine the distribution of species in the Cerrado.

The Cerrado is an excellent system for the study of convergent evolution of tree architectural traits. The diverse flora is characterized by particular functional groups that appear to have evolved repeatedly (Bucci et al 2004, Hoffmann et al 2005a, Silva and Batalha 2008). The forest-to-savanna transition has occurred many times with over 30 genera containing both forest- and savanna-type tree species which are morphologically distinct and many often co-occur sympatrically (Hoffmann et al 2003, Silva and Santos 2005).

Convergence is an evolutionary force that produces similar phenotypes under similar conditions across multiple lineages and provides strong evidence that selection has acted to shape those phenotypes or traits through adaptation (Ackerly 2004). Of particular interest in this study is convergent evolution toward a savanna-type strategy which decreases light interception and as a consequence, does not exclude growth of (pyrogenic) grasses. The biogeographic history of many savanna species is poorly understood but savanna species appear to be derived from earlier colonizations by forest species (Hoffmann et al 2003). As in other cases of convergent evolution, multiple traits may converge in a correlated fashion in response to a single selective pressure, or may converge independently to different aspects of the selective environment (Harmon et al 2005). This complexity makes predicting and testing for patterns both more difficult and more interesting.

## **Evolution of Tree Architecture in High vs. Low Light Environments**

Plant form has an important role for light interception in contrasting ecosystems (Pearcy et al 2005). Plant morphological traits likely reflect a balance between effective light interception, transport of water, and structural integrity (Westoby et al 2002, Falster and Westoby 2005a, Westoby and Wright 2006, Wright et al 2007). Architectural traits are particularly important for light interception because tree height and crown size determine the amount and intensity of light exposure on leaves. High and low light environments may impose different selective pressures on these functionally important traits. At a global scale, plants are differentiated by size and a suite of correlated traits that function in resource capture, usage, and release (Diaz et al 2004). This suggests that allometric relationships between size and architectural traits may reflect growth strategies in contrasting environments.

The size of a tree is determined by its success in acquiring light, water, and nutrients. In turn, the shape of a tree is likely determined by the allocation of those resources (Makela and Valentine 2006). When light is limiting, growth is slow and many individuals do not have adequate carbon storage to survive (Baltzer and Thomas 2007). Species adapted to low light environments like the understory of tropical forests often display specialized tree architecture to display leaves that maximize light interception (Valladares et al 2000, Falster and Westoby 2005b). In high light environments, other factors such as water and nutrients are likely limiting to growth. High rates of water loss through transpiration likely drive plants in high light environments to adopt a conservative growth strategy (Grime 1977, Bucci et al

2004). For example, high leaf angles and self shading can be used for structural photoprotection in high light environments at the cost of a reduction in light interception (Pearcy et al 2005).

Farnsworth and Niklas (1995) theorized that there are multiple strategies to optimizing tree architecture and allometry. For example, wide tree crowns are likely to optimize light interception in low competition environments with high light, while taller tree height will intercept more light in high competition environments. However, both traits are constrained by the limits of mechanical stability (Osunkoya et al 2007). There are multiple trade-offs in crown design such that there are multiple viable phenotypes (Halle 1999, Sterck et al 2006) that may be adaptive in different light environments.

### **Effects of Tree Architecture on Ecosystem Properties in the Cerrado**

The fundamental difference between savanna and forest habitats in the Cerrado is decreased light levels and the exclusion of grasses in the forest. Transitions between habitats can be abrupt, with dramatically different light environments within 20 meters on either side of the savanna-forest boundary in the Brazilian Cerrado. For example, forest understory environments often have less than 5% of the ambient light levels of 'open' savanna areas nearby (Hoffmann et al 2009). Tree productivity affects grass productivity, which is critical to maintaining a frequent fire regime (Belsky 1994, Hoffmann et al 2003). Canopy structure determines light transmission through the canopy, which influences grass productivity and

understory microclimate, and ultimately the fire regime (Higgins et al 2000, Hoffmann et al 2002, Gardner 2006).

Tree architecture may both affect fire intensity (Schwilk 2003) and be affected by fire (Eiten 1972, Kennedy and Potgieter 2003). Therefore, because architectural patterns that favor allocation towards greater or less light interception may change the properties of that environment (Westoby and Wright 2006), the determinants of architecture and allometry at the sapling stage is particularly important (Kohyama 1987, Kohyama and Hotta 1990). In tropical environments, architectural differences between savanna and forest species may be analogous to differences between pioneer and understory species. Pioneer trees exploit available light as they are adapted to high competition environments (Osada 2006, Poorter et al 2006), much like forest species that establish in savannas. In the savanna, these trees are not likely to be overtopped and may become the dominant vegetation if the ecosystem is not disturbed or nutrient limited (Eiten 1972, King et al 1997, Jeltsch 2000). The structure of woody vegetation determines ecosystem properties in the Cerrado partly by regulating the amount of light that reaches the understory. So, quantifying the architectural traits of different species in the Cerrado will likely increase our understanding of processes that govern ecosystem properties.

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## CHAPTER II

### Evolution of Tree Architecture and Allometric Relationships in the Brazilian Cerrado

#### INTRODUCTION

The ability of a tree to intercept light once it reaches the canopy depends largely on the size and shape of its crown (Valladares and Niinemets 2007). Trees with wide crowns and minimal self-shading can increase light interception by exposing more leaf area to direct light, but these trees tend to have restricted height due to structural constraints (Farnsworth and Niklas 1995, Pearcy et al 2005). However tree height is important for light competition, as trees may overtop others for primary access to direct light (Moles et al 2009). Herein lies a critical tradeoff between traits that allow rapid acquisition of resources and traits that conserve limiting resources within well protected tissues (Diaz et al 2004). Trees that adopt different strategies have contrasting impacts on light penetration. Allometric relationships describe how these shape characteristics change with size. Therefore, the adaptive evolution of architectural traits and allometry has significant consequences for ecosystems (Westoby and Wright 2006).

Allometric relationships between stem size and crown size are fundamental aspects of tree architecture that govern light interception (Falster and Westoby 2003). There is strong evidence for a number of tradeoffs between mechanical stability in architectural traits and optimal light interception (Farnsworth and Niklas 1995, Sterck et al 2006, Westoby and Wright 2006), such as small stems that cannot supply the water flow needed to support many large leaves. Recognition of such constraints has led to the formulation of Corner's rules,

which characterize many of the allometric relationships between stem traits (number and thickness) and leaf size (Ackerly and Donoghue 1998, King 1998, Olson et al 2009).

Farnsworth and Niklas (1995) theorized that that different environmental challenges lead to multiple viable architectural strategies, such as light-demanding dominant plants that tend to increase size and subordinate plants that conserve available resources. Each strategy may require certain combinations of architectural traits, leading to the large diversity of architectural forms observed (e.g. Halle 1999). While a given habitat will favor particular architectural traits, species traits may also be influenced by their phylogenetic history. Convergence – the repeated evolution of the same trait combinations in distinct lineages in the same environment – would provide evidence for the role of natural selection (Ackerly, 2004). On the other hand architectural similarity among related species would indicate trait conservatism and a lack of adaptive evolution in response to the environment.

Trees adapted to open environments tend to display very different architectural and life-history characteristics than those in forest environments (Archibald and Bond 2003). In low light environments, trees are expected to exhibit allometric relationships between architectural traits that favor light interception, such as greater tree height and crown diameter relative to overall size (King 1999, Archibald and Bond 2003). There is also little evidence that efficiency in height gain, calculated as plant height per stem diameter, is attributed to shade tolerance as there was no difference between canopy species and understory species across multiple rainforest species tested (Poorter and Werger 1999, Sterck et al 2001). The benefit of growing to a greater height is likely greater in low light environments such as forests where a high density of individuals causes competition for light.

In environments where light is not a limiting resource, trees are not likely to be selected for traits associated with light competition.

The variability in architecture among tree species can be described by a few basic traits, the relationships between them, and with overall size. Stem diameter is a common metric of overall plant size that allows standardization of size-dependent traits, such as tree height describes allocation to vertical growth and crown diameter describes allocation to lateral growth. Crown shape can also be described by crown area (the two-dimensional projected area of all leaves on a tree) and crown volume (the three-dimensional polygon that encloses all leaves on a tree). The number of branch tips has important consequences for growth and crown development; branch tips refer to the same structures in active growing tips/apical meristems (Ackerly and Donoghue 1998) and shoot number (Archibald and Bond 2003). Trees with large numbers of branch tips also have large amounts of stem tissue, which may regulate the number and size of leaves (Farnsworth and Niklas 1995). Different environments would likely favor different allocations to these structures during plant growth, and thus differences in allometry across independent lineages in the same environment would provide strong evidence of selection on architectural traits.

The savanna biome in central Brazil known as the Cerrado is an ideal system in which to study functional differences in diverse tree families under the framework of phylogenetically independent contrasts. Two functional types of trees dominate the landscape: species that are usually only found in high light savanna habitats (savanna type) and species that are found predominantly in low light forest habitats, but are also found in savanna under fire suppression (forest type). Although, the biogeographic history of many

savanna species is poorly understood, savanna species appear to be derived from earlier colonizations by forest species (Hoffmann et al 2003). The forest-to-savanna transition has occurred many times with over 30 genera containing both forest and savanna tree species, many of which co-occur sympatrically (Hoffmann et al 2003, Silva and Santos 2005).

There is evidence of convergence in plant traits among savanna species. Savanna trees tend to have higher specific leaf area (SLA) (Hoffmann et al 2005) and higher stem growth rates than forest trees, while there is no difference in rate of leaf production per branch between types (Rossatto et al 2009). One possible explanation for this observation is that while the number of leaves per branch remains similar, the number of active branches increases in forest trees. Forest trees may have more leaves that fill the crown area to capture more light energy, which makes them strong competitors for light in the cerrado.

Architectural differences between savanna and forest species not only influence plant success in their respective light environments, but also have consequences for ecosystem structure (Westoby and Wright 2006). Canopy structure determines light transmission through the canopy, which influences grass productivity and understory microclimate, and consequently the success of different species in the environment (Hoffmann 2003). Although ecosystem changes are not directly addressed in this study, determining differences in architectural/structural traits may address the mechanism of possible ecosystem consequences for species evolution.

In order to examine allometric relationships between architectural traits, I measured stem diameter, tree height, crown diameter, crown area, crown volume and the number of branch tips of savanna and forest congeneric species to determine if these relationships are

convergent by habitat for tree species across many lineages. Specifically, I hypothesized that after accounting for stem diameter, forest species would have greater crown area, a larger number of branch tips, and a greater density of leaves and branch tips per unit crown area than savanna species. These predictions are based on the expectation that forest trees are adapted to maintain high levels of light interception in a competitive light environment.

## **METHODS**

### *Study Site*

The Cerrado region of Brazil consists of habitats with a gradient of tree density from open grassland (campo limpo, near 0 % canopy cover) to dense woodlands (cerradão, up to 85% canopy cover), and riparian gallery forests (Eiten 1972, Oliveria-Filho and Ratter 2002). The vegetation is typically xeromorphic and semideciduous. The Cerrado contains a high diversity of tree species diversity – with as many as 150 species in a square hectare (Oliveria-Filho and Ratter 2002). Cerrado habitats are frequently affected by fire (Eiten 1972), and boundaries from grassland or woodland scrub to riparian gallery forests can be extremely abrupt, with light decreasing to less than 5 % of full sun within 10 meters of the forest boundary (Hoffmann et al 2009). The frequent establishment of forest-type species in fire-suppressed savanna environments allows the opportunity to study savanna- and forest-type species growing in a common savanna environment.

My study was located in sites that had approximately 50 % tree cover (cerrado *sensu stricto*) in central Brazil at the Reserva Ecológica do IBGE (Brazilian Institute of Geography and Statistics) approximately 30 km southwest of Brasília in the Federal District, Brazil, at an

elevation of approximately 1100 meters above sea level. Fire has been suppressed for more than 30 years, although there was a wildfire in 2005. I limited measurements to saplings that resprouted from the ground following the 2005 fire in order to provide a large sample of relatively small trees and to reduce the effect of age differences. The tree height and stem diameter of the resprouted saplings ranged from 0.2 m to 2.5 m and 12 mm to 40 mm, respectively. Measurements were made in the savanna habitat during the dry season from May to August 2008, and in June 2009.

### *Species selection*

I identified common tree species pairs of the same genus where one species was only found in savanna habitats, while the second was commonly found in both forest habitats and adjacent fire-suppressed savanna habitats. These species pairs typically exhibit morphological differences, for example savanna species tend to have thicker bark, thicker leaves and lower and more tortuous stature in comparison to forest species (Eiten 1972, Hoffmann et al 2009). The savanna-forest species pairs were chosen based on availability of comparably sized saplings at the study sites, and to encompass a broad taxonomic scale (the 15 genera covered 14 families; Table 1). The use of congeneric pairs reduces the bias from phylogenetic relatedness and ensures independence of any consistent differences between savanna or forest trees.

The complete architectural analysis included 30 species total with 3-5 individuals (median 4) per species that were all found in the savanna, often within 1 meter of other individuals. A total of 120 saplings were studied. For a subset of forest species in *Alibertia*,

*Aspidosperma*, and *Guapira*, I compared architectural traits of 4-5 individuals of the same species in two different light environments: the savanna and the shaded forest habitat within 20 meters of the savanna boundary.

Table 1. List of species used for architectural analysis in Cerrado habitat at IBGE Ecological Reserve in Brasilia, DF, Brazil.

| Savanna Species                | Forest Species          | Family        |
|--------------------------------|-------------------------|---------------|
| <i>Aegiphila lhotzkiana</i>    | <i>A. sellowiana</i>    | Verbenaceae   |
| <i>Alibertia sessilis</i>      | <i>A. elliptica</i>     | Rubiaceae     |
| <i>Aspidosperma tomentosum</i> | <i>A. subicanum</i>     | Apocynaceae   |
| <i>Brysonima crassa</i>        | <i>B. laxiflora</i>     | Malpighiaceae |
| <i>Diosypros burchellii</i>    | <i>D. hispida</i>       | Ebenaceae     |
| <i>Guapira noxia</i>           | <i>G. areolata</i>      | Nyctaginaceae |
| <i>Machaerium opacum</i>       | <i>M. acutifolium</i>   | Fabaceae      |
| <i>Myrcia rostrata</i>         | <i>M. tomentosa</i>     | Myrtaceae     |
| <i>Myrsine guianensis</i>      | <i>M. ferruginea</i>    | Myrsinaceae   |
| <i>Ouratea hexasperma</i>      | <i>O. castanarfolia</i> | Ochnaceae     |
| <i>Qualea parviflora</i>       | <i>Q. dichotoma</i>     | Vochysiaceae  |
| <i>Schefflera macrocarpum</i>  | <i>S. morototoni</i>    | Araliaceae    |
| <i>Styrax ferruginus</i>       | <i>S. camporum</i>      | Styracaceae   |
| <i>Symplocos lanceolata</i>    | <i>S. mosenii</i>       | Symplocaceae  |
| <i>Vochysia thyoidea</i>       | <i>V. tucanorum</i>     | Vochysiaceae  |

#### *Trait measurements*

For spatial measurements, a Patriot 3D digitizer (Polhemus, Colchester, VT, USA) was used with a tripod set-up for the electromagnetic source (origin) within 1 meter of the target sapling. This instrument records the three-dimensional Cartesian coordinates (x, y, z) of the stylus tip, relative to the source, as well as the direction, angle, and azimuth of the stylus relative to the plane of the electromagnetic source, with an accuracy of 0.01cm within

a 150 cm radius surrounding the source. The source was leveled manually and oriented to magnetic north with a compass (18° from true north). The location and orientation of each leaf was measured by positioning the stylus at the base of the petiole and oriented parallel to the major plane of the leaf. Position and orientation of branch tips (apical meristems) were recorded with the stylus flush to the branch. The number of branch tips and leaves was recorded digitally for each sapling, and the number of leaves per branch tip was calculated simply as the total number of leaves divided by the total number of branch tips.

Stem diameter was measured at 30cm above ground level with digital calipers accurate to 0.01mm. For the two genera with compound leaves (*Schefflera* and *Machaerium*), the leaflet was considered to be the unit of leaf display. Furthermore, saplings of these species often had only one apical meristem; so based on the unit of interest, the tip of the rachis (main petiole of the compound leaf) was recorded as the branch tip. Branch tips were counted manually on each sapling; additional individuals found in the sites were included in the architectural analysis for a total dataset of 288 saplings.

### *Data Analysis*

Tree height was taken from the highest leaf recorded for each tree, and crown diameter was calculated as the maximum horizontal distance between two leaves on the xy plane. Crown volume was calculated as the volume of the convex hull that encloses all leaf spatial points in three dimensions, using the *convulln* function (Barber et al., 1996) as implemented in the R package 'geometry' (Grasman and Gramacy, 2008). Crown area was calculated as the area of projection (the area of the smallest polygon enclosing all points on

the xy plane and ignoring the vertical [z] dimension) using the *areapl* function (Rowlingson and Diggle, 1993) in the R package ‘splancs’ (Bivand, 2008). Crown area was very highly correlated with crown volume ( $r=0.56$ ,  $P<0.0001$ ) and was derived from the same spatial data; as a result only crown volume was used in subsequent analyses. The R environment was used to process raw spatial data and aggregate the calculations above (R Core Development Team 2008).

Statistical analyses were completed using JMP 7.0 (SAS Institute, Cary, NC, USA). A mixed-model ANCOVA was used to compare slopes and intercepts for relationships between stem diameter and other variables of interest of forest and savanna species. All variables were  $\log_{10}$ -transformed prior to analysis. For analyses involving all species, genus was specified as a random factor. Regressions of crown traits against stem diameter were used to determine the slopes of the allometric relationships and to control for the effect of size differences among individuals. An ordinary least squares (OLS) regression is preferred for its predictive ability and because a previous study found that OLS effectively predicts the relationship between shoot number and the stem diameter (Pekka, 2003). Separate ANOVAs were also performed within genera to determine significant differences between each congeneric species pair.

The number of leaves per crown area (i.e. density of leaves, which was not correlated to stem diameter;  $r=0.028$ ,  $p=0.087$ ) was compared across savanna-forest species pairs and was analyzed in a mixed model ANOVA with species type and both genus and the genus by species type interaction as random factors. The log number of branch tips was regressed to mean leaf blade area to examine savanna and forest species differences. Finally, for the

comparison of the three forest species between savanna and forest habitats, the entire analysis was repeated using habitat as a factor instead of species type.

## RESULTS

Stem diameter was a significant predictor of tree height ( $r=0.172$ ,  $P<0.0001$ ), crown diameter ( $r=0.233$ ,  $P<0.0001$ ), crown volume ( $r=0.25$ ,  $P<0.0001$ ), and number of branch tips (apical meristems) ( $r=0.089$ ,  $P<0.0001$ , Figure 1). There was no difference between savanna and forest species in mean number of branch tips per crown area ( $77.4$  tips  $m^{-2}$  in forest type vs.  $54.7$  tips  $m^{-2}$  in savanna type;  $F_{1,12.6}= 1.7$ ,  $P=0.22$ ), mean number of leaves per branch tip ( $8.3$  leaves/tip in forest type vs.  $8.35$  leaves/tip in savanna type;  $F_{1,14.2}= 0.004$ ,  $P=0.95$ ) or mean number of leaves per crown area ( $553.75$  leaves/ $m^2$  in forest type vs.  $428.5$  leaves/ $m^2$  in savanna type;  $F_{1,12.68}= 0.83$ ,  $P=0.38$ ).

After accounting for stem diameter, forest species had more branch tips ( $F_{1,14.56}=11.3$ ,  $P=0.004$ , Figure 1) than savanna species. For nine of 15 genera sampled, forest trees had a significantly higher intercept for the relationship between number of branch tips and stem diameter than savanna trees (Figure 1), while only one genus (*Alibertia*) exhibited a significant difference in the opposite direction. For no genera did the value of the slope for this relationship differ significantly between savanna and forest species (Figure 1,  $0.03<F<4.22$ ,  $0.86>P>0.06$ ). There was no difference between forest and savanna species for five other genera (*Aegiphila*, *Ouratea*, *Qualea*, *Schefflera* and *Machaerium*). The latter two genera possess compound leaves and the number of “branch” tips was in fact considered the number of compound leaves. However, when true apical meristems were considered

rather than compound leaves, there continued to be no significant difference between savanna and forest species in either genus (data not shown).

The higher number of branch tips in forest species resulted from a greater crown volume ( $F_{1,13.32} = 10.4$ ,  $P=0.0065$ ), rather than a greater density of branch tips per unit volume. After accounting for stem diameter, forest trees had significantly greater crown volume than savanna trees in four out of 15 genera sampled, while an additional nine out of the remaining 11 genera showed a non-significant trend in the same direction (Figure 2a). This increase in crown volume is accounted for by both greater tree height ( $F_{1,12.48} = 20.09$ ,  $P=0.0007$ ) and crown diameter ( $F_{1,12.96} = 9.56$ ,  $P=0.009$ ) among forest species; there was no significant difference for the ratio of crown height to width between forest and savanna types ( $F_{1,13.74} = 0.24$ ,  $P=0.63$ ). When examined within genera, forest species had significantly greater crown diameter than savanna species for a given stem diameter in seven of 15 genera (Figure 2b). Also, forest species had a significantly greater tree height than savanna species for a given stem diameter in nine of 15 genera sampled (Figure 2c), while no genera exhibited the opposite trend.

There was also a significant difference in the intercept of the relationship between leaf area and the number of branch tips ( $F=10.35$ ,  $P=0.003$ , Figure 3), as forest species tended to have more branch tips for a given leaf area.

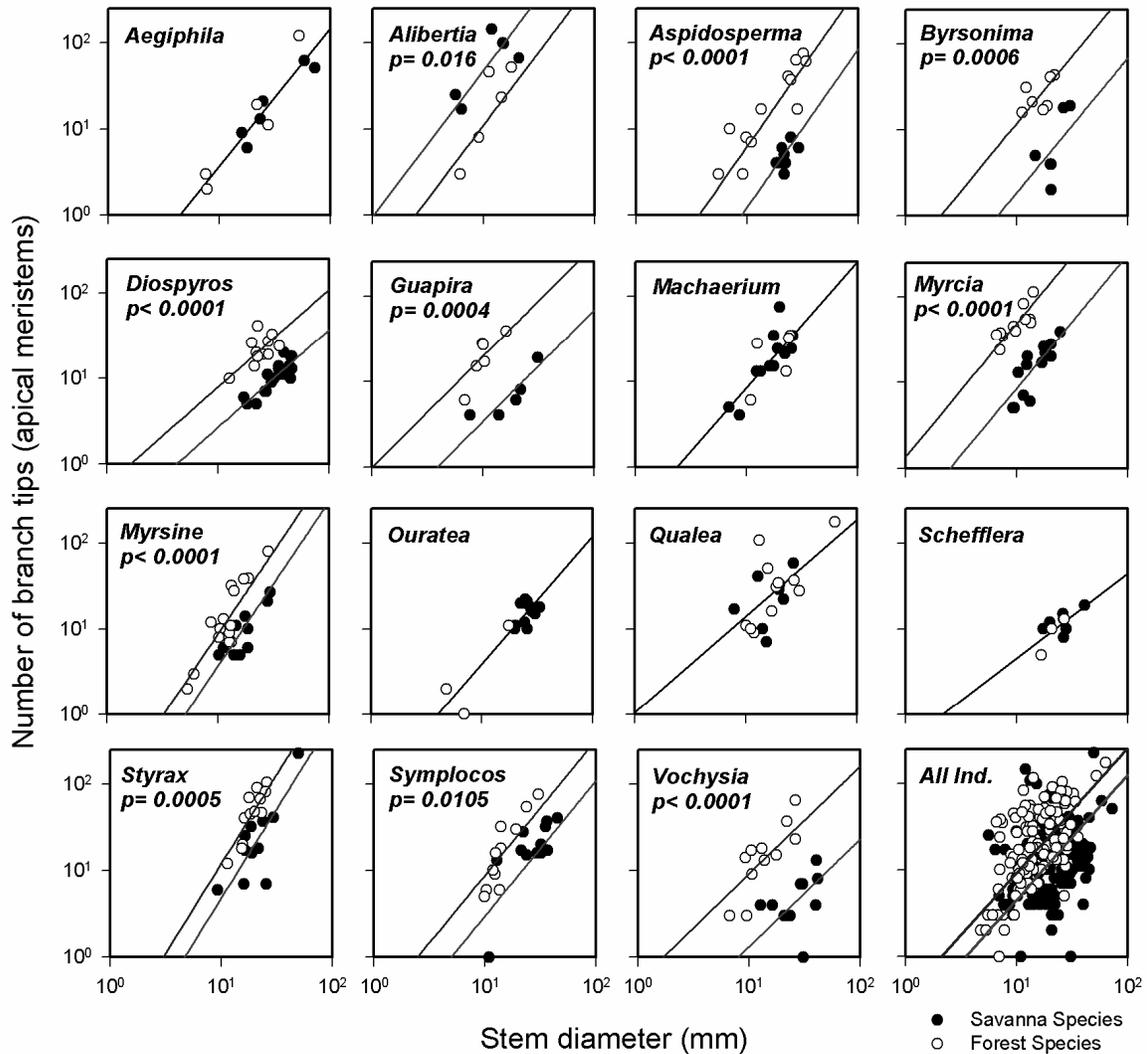


Figure 1. Allometric relationships between number of branch tips (apical meristems) and stem diameter for each forest-savanna species pair in this study. Two parallel regression lines are plotted for genera in which savanna and forest species had a significantly different intercept ( $P < 0.05$ ), while a single line is plotted for genera in which neither intercept nor slope differed between savanna and forest species. The bottom right plot with all individuals sampled contains data for 288 resprouted tree saplings found at IBGE Ecological Reserve in Brasilia, DF, Brazil.

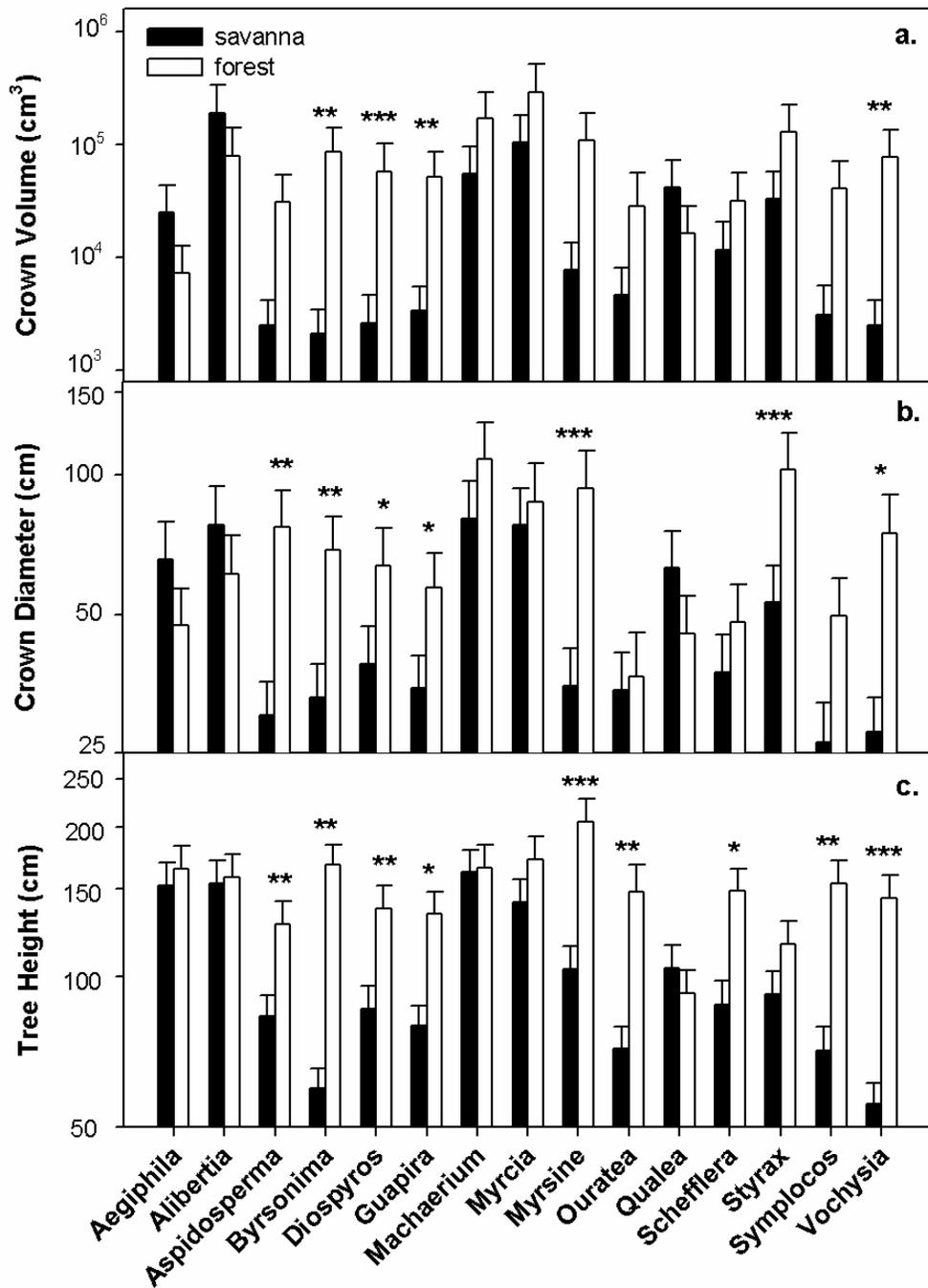


Figure 2a-c. Least squared means of crown volume (a), crown diameter (b), and tree height (c) between savanna and forest species across 15 genera, showing average values at a standard stem diameter for tree species found at IBGE Ecological Reserve in Brasilia, DF, Brazil. Error bars represent the standard error of the means. Symbols indicate significantly different means between habitat types (\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ).

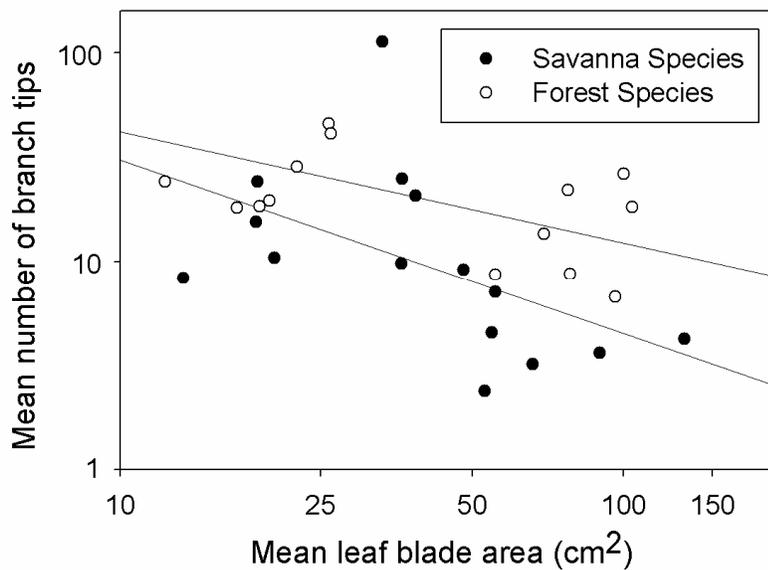


Figure 3. Correlation between mean leaf blade area (Hoffmann, unpublished data) to least squared mean number of branch tips (apical meristems) in 26 tropical tree species at the IBGE Ecological Research in Brasilia, DF, Brazil. Open circles are forest species, closed circles are savanna species. The lines represent the logarithmic-linear regression between the two factors by habitat type; there was a significant difference between forest and savanna types ( $F=10.35$ ,  $P=0.003$ ).

The high light environment of the savanna habitat did not influence allometric relationships for the genera examined in this study. For the subset of forest species (*A. sessilis*, *A. subicanum*, *G. noxia*) that were compared between savanna and forest environments, I found that there was no difference in many allometric relationships of the architectural traits sampled (stem diameter vs. number of branch tips, crown volume, area, and diameter;  $0.09 < P < 0.75$ ) of individuals of the same forest species in two different light environments. However, individuals of forest species growing in shaded forest habitat had a greater tree height than those growing in the savanna after accounting for stem diameter ( $F_{1,2.029} = 190.739$ ,  $P=0.0049$ ).

## DISCUSSION

Savanna and forest species exhibited different allometric relationships between architectural traits, consistent with my hypothesis that there is convergence in these traits with respect to adaptation in high and low light environments. For several architectural traits of trees for each species type within one common habitat, savanna (*cerrado sensu stricto*), congeneric forest-savanna species pairs exhibited divergent allometric relationships. Forest species had more branch tips per stem diameter for more than half of the genera sampled across many tree families (Figure 1). Forest species also have larger crown volumes (Figure 2a), crown diameter (Figure 2b), and greater height (Figure 2c) relative to savanna species for a given stem diameter. These differences demonstrate that forest species exhibit adaptive traits related to light competition. Other traits that influence patterns of light interception also differed, with savanna species exhibiting more convoluted leaf blades and shorter petioles (Chapter 3). Overall, differences in the number of branch tips between congeneric species pairs (Figure 1) largely agreed with differences in crown diameter, with the exception of *Myrcia* and *Symplocos* (Figure 2b). These results suggest that forest species allocate more carbon to structures for light interception.

Plant traits can have a large effect on ecosystem properties when the number and quality of leaves grown influences rates of production and nutrient cycling. These traits also have consequences for rates of canopy closure and consequently ecosystem flammability (Schwilk 2003). Since forest species have high rates of growth in stem diameter, the greater relative tree height and crown dimensions make forest species strong competitors in acquiring light resources. Savanna trees maintain small crown sizes relative to stem diameter

and allow more light interception by grasses. As light interception decreases for grasses in the cerrado, the amount of grass biomass is likely to decrease which causes fire frequency to decrease (Hoffmann et al 2003). Fire is an important factor in maintaining open environments, and exclusion of fire has been shown to allow colonization of savanna habitat by forest tree species (King et al 1997) and to subsequently decrease the amount of light that reaches the ground layer in savanna habitats.

The architectural differences can be explained based on adaptation to different light environments. The combination of greater tree height, larger crown diameter, larger crown area, and larger crown volume in forest species compared to their savanna congeners indicates that forest species are investing in increased interception of light resources. A likely explanation for the atypical significance pattern in the number of branch tips of *Alibertia* was that the savanna species of *Alibertia* had smaller leaves than the forest species and small-leaved species generally have with more branch tips, while species with larger leaves tend to be supported on fewer branches (Figure 3). Species may also compensate for having fewer branch tips by producing larger leaves, while having smaller leaves would require more branch tips in order to display a comparable amount of leaf area. In tropical rain forest trees, leaf size is correlated to architectural traits such as branching height and crown diameter, such that trees with larger leaves often have greater demand for light (King 1998).

Adaptive evolution of architectural traits may determine ecosystem properties, if the larger canopies of forest species reduces light penetration to the understory and excludes grasses, potentially facilitating fire suppression and the further expansion of forest tree species. Differences in allometric relationships between the savanna-forest congeners are

consistent with predictions that forest trees have a greater demand for light resources: forest species have leaves with higher nutrient content while savanna species tend to have higher water use efficiency after accounting for specific leaf area (Hoffmann et al., 2005). Based on these considerations, I suggest that adaptation to one factor (i.e., light) has indirect consequences for ecosystem properties and vegetation-fire feedbacks.

In relation to other environments, architectural differences between savanna and forest species may be analogous to differences between pioneer and understory species. Pioneer trees exploit available light as they are adapted to high competition environments (Osada, 2006; Poorter et al., 2006), much like forest species that establish in savannas. In the savanna, these trees are not likely to be overtopped and may become the dominant vegetation if the ecosystem is not disturbed or nutrient limited (Eiten, 1972; King et al., 1997; Jeltsch, 2000). The structure of woody vegetation determines ecosystem properties in the Cerrado partly by regulating the amount of light that reaches the understory.

### *Conclusion*

In the Brazilian Cerrado, allometric relationships among tree architectural traits are convergent by habitat type across many families, providing evidence of divergent natural selection. In addition to the differences associated with habitat, differences among genera indicate that evolutionary history partly explains the allometric relationships seen today. Forest trees able to colonize the savanna may be competitively superior and displace savanna trees. Species traits associated with adaptation to habitat are likely to affect many of those factors that govern the expansion of gallery forests and generally determine the distribution

of species in the Cerrado (Hoffmann et al., 2003; Wright et al., 2007). Understanding the types of architectural traits present in the Cerrado will likely increase our understanding of processes that govern ecosystem properties and ultimately lead to experiments to directly test for ecosystem-level consequences of tree architecture.

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## CHAPTER III

### Differences in Leaf Traits of Savanna-Forest Congeneric Species in the Brazilian Cerrado

#### INTRODUCTION

Leaf traits play an important role in determining plant function (Reich 2003, Wright et al 2007). The longevity and photosynthetic rate of a plant's leaves determine its carbon assimilation potential (Ackerly and Bazzaz 1995) and the display angles of leaves relative to the horizontal largely determine the amount of sunlight intercepted throughout the day (Percy and Yang 1996, Utsugi 1999, Percy et al 2005). The angular distribution of leaves on a tree determines light interception by the canopy, because it determines the extinction coefficient for the crown – the projected leaf area on the plane perpendicular to the direction of a light source (Wang et al 2007).

Plants in high light environments exhibit many characteristics that are believed to optimize their growth and survival. The display angle of leaves is variable both among species and among layers within a single crown, and may be a response to light environment (Utsugi 1999, Faster and Westoby 2003). The display of individual leaves at steeper angles (i.e. more vertical) often reduces their exposure to direct light at midday (Percy et al 2005), reducing midday heat-loads (King 1997) and decreasing water-use with respect to daily carbon gain (Cowan 1982). Conversely, the benefits of horizontal leaf display is that each leaf has high light interception potential and helping to maintain the necessary carbon balance for survival in low light environments (Sterck et al. 2001, Baltzer and Thomas 2007). In general, understory trees have leaves arranged horizontally and with minimal overlap

(Pearcy et al 2005). A study of Australian savanna trees found that mean leaf angle was not related to leaf size or plant height, indicating that this trait modifies plant architecture independently of plant size (Falster and Westoby 2003).

Undulations (i.e., waviness) of leaf surfaces also affect light interception in an analogous way by creating a distribution of angles within individual leaves. Three dimensional leaf shapes can vary from flat with no obvious features, to concave margins that create a boat-shaped leaf, or spiraling edges for a corkscrew shaped leaf. Leaf waviness is one of many traits that affect the amount and intensity of sunlight that can be absorbed over the surface area (Fleck et al 2003). The shape of leaves likely influences boundary layer dynamics by sheltering against wind to reduce transpiration (Meinzer et al 1995, Pachepsky et al 1999).

Plants have diverse structural adaptations that allow them to tolerate intense sunlight. Petiole length of leaves is likely to be another adaptive trait that determines the shape of tree crowns. Generally, longer petioles reduce shading among leaves on the same branch (Pearcy et al 2005) and increase the potential crown size as the leaf is extended further from the stem bearing it and from other leaves on the same stem. Long petioles may also effectively replace the function of long stem internodes that require considerable costs in carbon allocation to structural tissue (Pearcy et al 2005).

In the Cerrado, the savanna biome in central Brazil, two functional types of trees dominate the landscape: species that are only found in high light savanna environments (savanna type) and species that are native to forest habitats but can also be found in savannas that undergo fire suppression (forest type). Following the expansion of tropical savannas in

the Miocene (Beerling and Osborne 2006), trees from many ancestral forest type lineages appear to have repeatedly crossed forest-savanna boundaries and thrived in savanna conditions. Savanna species tend to have thicker leaves and greater water use efficiency than forest species (Hoffmann et al 2005a). Forest trees have more leaves per unit of crown area (Hoffmann et al 2005b), which makes them strong competitors for light in the cerrado. Leaf traits that affect light interception at a smaller, but more pervasive scale may also show significant differences in forest and savanna species in the cerrado. Micro-scale differences in leaf morphology between forest and savanna tree species are poorly understood. And, there has been no empirical data collected to date that addresses potential differences in leaf orientation and leaf shape between these closely related species in the cerrado.

In order to address this knowledge gap, I measured leaf angle, leaf waviness, petiole length, and leaf length to determine if these traits are convergent by habitat for tree species across many genera. Specifically, after accounting for effects of leaf size, I hypothesized that forest species would have longer petioles that theoretically increase light interception while savanna species would have a more undulating leaf morphology which reduces light interception. Also, I hypothesized that savanna species would display leaves at steeper angles. This orientation would avoid direct sunlight, but there may be higher overall variation in leaf angles as there would also be less pressure to optimize leaf orientation for light interception. These expected differences between savanna and forest species have consequences not only for determining plant success under contrasting light environments, but also on ecosystem structure and productivity.

## **METHODS**

### *Study Site*

The Cerrado region of Brazil consists of a range of habitats across a gradient of tree density, from open grassland (campo limpo) to dense woodlands (cerradão) and riparian gallery forests (Oliveria-Filho and Ratter 2002). These savanna and forest habitats contain a high diversity of tree species, many of which are restricted to one habitat type. However, the recent establishment of forest species in fire-suppressed savanna environments allows us to study savanna and forest species growing in a common savanna environment.

Our study site was located in areas with approximately 50 % tree cover (cerrado *sensu stricto*) in central Brazil at the Reserva Ecológica do IBGE (Brazilian Institute of Geography and Statistics) approximately 30 km southwest of Brasília, DF. Fire suppression has been implemented for 35 years, though there was one wildfire in 2005. I limited measurements to saplings that resprouted following the 2005 fire in order to provide a large sample of relatively small trees and to ensure that all trees were measured at similar age. Measurements were made in cerrado habitat during the dry season from May to August 2008.

### *Species selection*

The use of congeneric pairs reduces bias of phylogenetic similarity in comparisons. Savanna-forest species pairs in 22 genera (Appendix Table 1) were chosen based on availability of comparably sized saplings at the study sites; these pairs of congeners were distributed across 20 families. Only trees growing in savanna habitats were measured for these analyses. Functional types (forest or savanna trees) were identified based on consistent

morphological differences, with savanna species having thicker bark and leaves and lower and more tortuous stature (Silva and Santos 2005, Hoffmann et al 2009). The leaf angle analysis included 30 species (representing 15 of the 22 studied genera, see Table 1 in Chapter 2) with three to five individuals (median 4) per species, for a total of 120 individual saplings. Leaf length, petiole length, and leaf complexity (waviness) were measured in 44 species (representing all 22 genera, see Appendix) with three to five individuals and one to three (median 3) replicate leaves measured from each tree, for a total of 565 leaves.

#### *Trait measurements and calculations*

For spatial measurements, a Patriot 3D tracker (Polhemus, Colchester, VT, USA) on a tripod was set up to provide the electromagnetic source (origin) within 1 meter of the target sapling. This instrument records the three-dimensional Cartesian coordinates (x, y, z) of the stylus tip, relative to the source, as well as the direction, angle, and azimuth of the stylus relative to the plane of the electromagnetic source, with an accuracy of 0.01cm within 150 centimeter radius surrounding the source. The source was leveled manually and was oriented to magnetic north with a compass. Location and orientation of each leaf were measured by positioning the stylus at the petiole base, oriented parallel to the major plane of the leaf. Leaf angles of were recorded from 124 individual saplings. Mean leaf angle and standard deviation of leaf angle was calculated from 10 to 534 leaves (median 101) for each individual.

Determining the angular distribution of a plant's photosynthetic area is difficult because of two factors that affect light interception: display angle and leaf shape. Leaf shape

was represented by digitizing the edges of each leaf as well as bisecting lines to incorporate the relief of the interior. There is no commonly accepted method to characterize leaf shape (McLellan and Endler 1998), but it seems likely that the amount of variation at Cartesian coordinate axes (x,y,z) would supply a good metric (Figure 2a). To quantify leaf waviness, the standard deviation of digitized points in the vertical [z] axis perpendicular to the ground was calculated (hereafter referred to as “sd[z]”). Sd[z] was divided by leaf length to produce an index of waviness (hereafter simply “leaf waviness”) that is independent of leaf size ( $R^2=0.007$ ,  $P=0.25$ ). Flat leaves lying on a horizontal plane will have lower waviness values than more complex leaves, such as folded or spiraling leaves. High waviness values may be due to large undulations or folding within a leaf. As an alternate metric for leaf shape, “leaf ratio” was calculated from leaf volume of the digital trace (Figure 2a, example plot) divided by leaf length to the third power in order to better account for undulating leaves. Leaf ratio was calculated for 16 congeneric pairs. The R environment was used to process and aggregate the data above (R Core Development Team 2008).

### *Data Analysis*

All analyses were completed using JMP 7.0 (SAS Institute, Cary NC, USA). Leaf length and petiole length were  $\log_{10}$  transformed and a mixed model ANOVA was used to test for differences in slopes and intercepts between the forest-savanna species types with genus as a random factor. Separate ANOVAs were performed to determine whether the forest and savanna species differed significantly within each congeneric species pair. Variance components estimates, the percentage of total interspecific variance explained by an

independent factor, were recorded from an ANOVA with random effects for each trait in this study to determine the magnitude of phylogenetic (genus) and functional (habitat) effects.

## RESULTS

Leaf length was highly variable among genera (Table 1). There was no overall difference in leaf length between savanna and forest species ( $F_{1,21}=0.43$ ,  $P=0.52$ ), but there were significant species differences for leaf length for 16 out of 22 genera. Traits related to leaf shape were dependent on the size of leaves; differences in leaf shape between savanna and forest congeners may be confounded by differences in leaf size among genera.

Forest species had significantly greater petiole lengths than savanna species ( $F_{1,21.043}=6.28$ ,  $P=0.02$ ). Within genera, forest species had longer petioles than savanna species in 13 out of 22 genera (*Aegiphila*, *Alibertia*, *Aspidosperma*, *Brysonima*, *Eriotheca*, *Hymenaea*, *Miconia*, *Myrcia*, *Mysine*, *Ouratea*, *Pouteria*, *Qualea*, *Styrax*;  $P < 0.05$ , Table 1), while no genera demonstrated a significant trend in the opposite direction. Savanna-forest species differences were also present when petiole length was regressed against leaf length ( $F = 44.3$ ,  $P=0.0045$ ). Differences among genera accounted for more than half of the variation in petiole length (Table 2). Furthermore, when savanna leaves were (on average) similarly sized or larger than their forest congeners, there was often little difference in petiole length (Table 1). However, when forest leaves were (on average) longer than their savanna congeners, then those forest species also tended to have longer petioles compared to savanna species.

The means and variances of leaf angle were not often significantly different between savanna and forest types (data not shown). Within genera, there were a few cases where savanna trees displayed leaves at a significantly higher (i.e. steeper) mean leaf angle (*Guapira* and *Styrax*, Figure 1a), while no genera demonstrated a significant trend in the opposite direction. Standard deviations of leaf angles were often more similar within genera, but there were significant differences between five pairs of forest and savanna congeners (see following, Figure 1b). For *Aegiphila*, *Aspidosperma*, and *Styrax*, leaves of savanna species were displayed at more variable angles, relative to the horizontal, than the forest species. In one case, the leaves of savanna *Aspidosperma* were held in a rosette-like pattern at the end of each branch tip. For *Alibertia* and *Myrsine*, leaves of forest species were displayed at more variable angles than savanna species, but savanna species also tended to be more shrub-like than their forest congeners with many small leaves that were densely packed and often pointed downwards. Differences among genera accounted for about 25 % of variation in mean leaf angle values while differences between functional types accounted for only 3 % of variation in the trait. Neither genus nor type accounted for much variation in standard deviation of leaf angle (Table 2).

Leaf waviness was used as a standardized measure of leaf shape by taking the standard deviation in the vertical axis of a leaf divided by the leaf length to produce a size independent variable. Savanna species had marginally greater leaf waviness than forest species ( $F_{1,21.08}=3.45$ ,  $P=0.08$ ). However, there was no consistent pattern for differences in leaf waviness between savanna and forest species; savanna species had greater leaf waviness than forest species in only four out of the 22 genera while forest species had greater leaf

waviness in six other genera (Figure 2b). *Hymenaea* species have leaves with two flat leaflets, as indicated by very low leaf waviness values but are arranged in a “V” with one leaflet almost perpendicular to the other. *Machaerium* species are also compound leaved but with multiple opposite leaflets that are typically folded over with the concave side down. Savanna leaves in *Erthroxylum*, *Machaerium*, *Piptocarpha*, and *Tabebuia* were often extremely wavy or folded and had mean leaf waviness greater than 0.06. These species likely drove the general trend for savanna species to have marginally greater leaf waviness than forest species, as species differences accounted for almost 40 % of the variance in leaf waviness (Table 2).

Patterns within genera differed when leaf waviness was compared to leaf ratio (leaf volume divided by leaf length<sup>3</sup>), which measures the volume an undulating leaf occupies relative to its size. For *Aegiphila*, *Aspidosperma*, *Brysonima*, and *Vochysia*, savanna leaves had greater leaf volume relative to leaf size (data not shown), but only *Vochysia* showed the corresponding pattern in leaf waviness. Also, despite large differences in leaf waviness found between savanna and forest *Piptocarpha* species, there was no difference in leaf ratio, as the amount of leaf volume relative to leaf size was similar for the congeneric species.

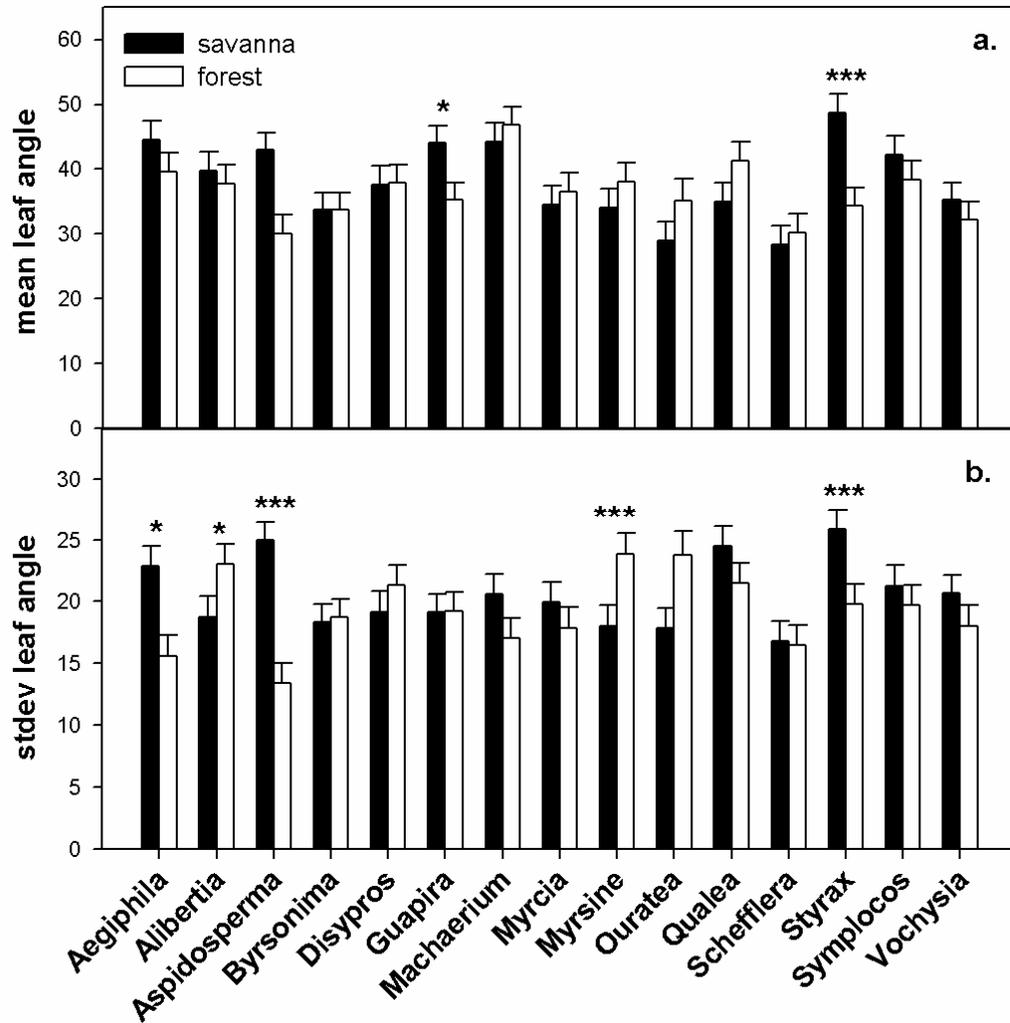


Figure 1. Mean leaf angle (a) and standard deviation of leaf angles (b) between savanna and forest species across 15 genera at IBGE Ecological Reserve in Brasilia, DF, Brazil. Error bars represent the standard error of the means. Symbols indicate significantly different means between types (\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ).

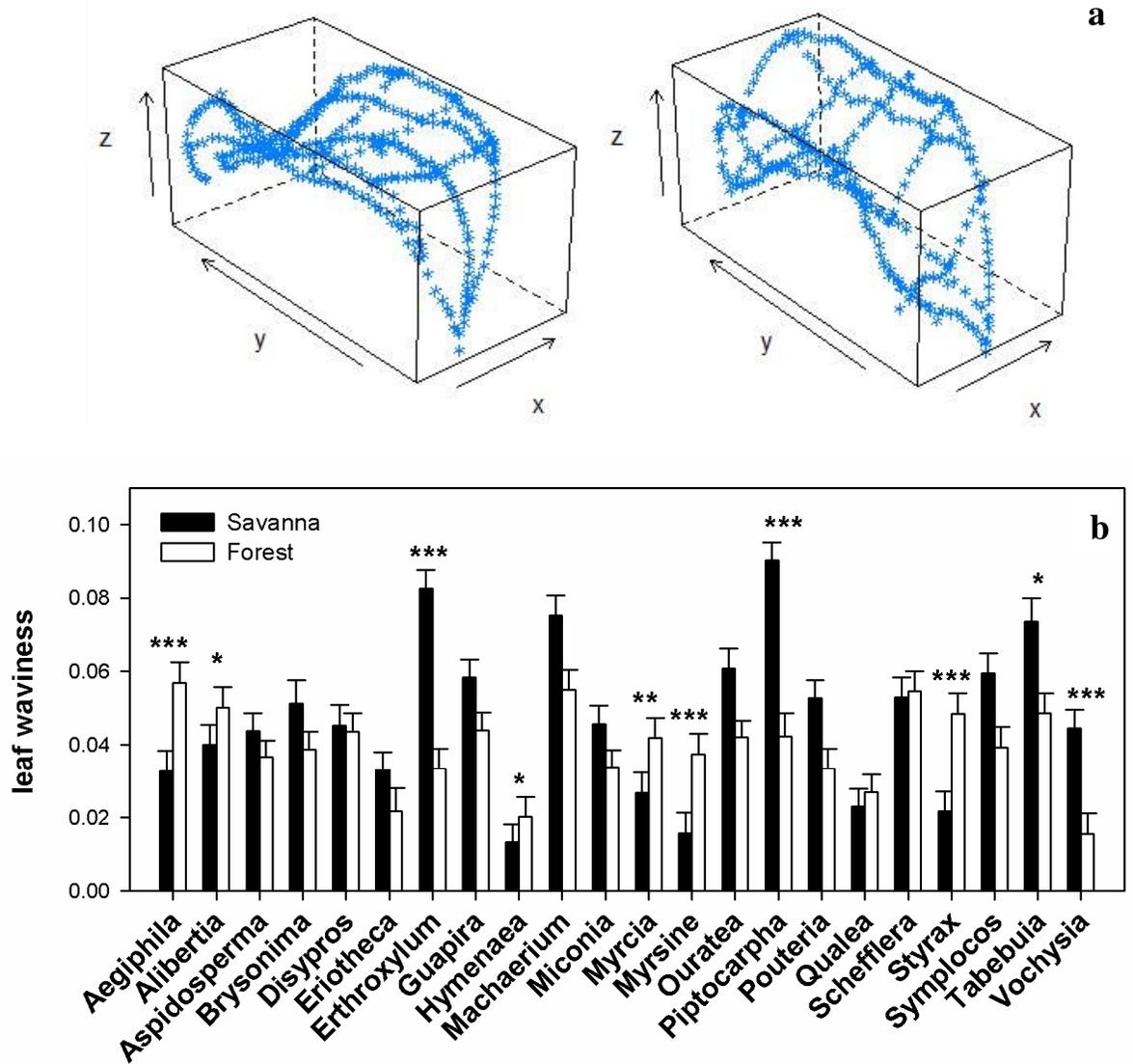


Figure 2. (a) Digital leaf traces of two *Qualea dichotoma* leaves with an exaggerated [z] vertical axis. (b) Means of leaf waviness between savanna and forest species across 22 genera. Error bars represent the standard error of the means. Symbols indicate significantly different means between types (\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ).

Table 1. Average values of leaf length and petiole length in 22 savanna-forest species pairs at IBGE Ecological Reserve in Brasilia, DF, Brazil. Standard Errors (SE) are recorded and bold face denotes a significant difference between savanna and forest species ( $P \leq 0.05$ ).

| Genus               | average leaf length (cm) |               |              |               | average petiole length (mm) |               |              |               |
|---------------------|--------------------------|---------------|--------------|---------------|-----------------------------|---------------|--------------|---------------|
|                     | savanna                  | SE            | forest       | SE            | savanna                     | SE            | forest       | SE            |
| <i>Aegiphila</i>    | <b>11.90</b>             | ± <b>0.76</b> | <b>14.71</b> | ± <b>0.76</b> | <b>3.46</b>                 | ± <b>1.34</b> | <b>9.19</b>  | ± <b>1.34</b> |
| <i>Alibertia</i>    | <b>7.57</b>              | ± <b>0.76</b> | <b>12.16</b> | ± <b>0.76</b> | <b>5.23</b>                 | ± <b>1.34</b> | <b>7.46</b>  | ± <b>1.34</b> |
| <i>Aspidosperma</i> | 14.78                    | ± 0.68        | 16.76        | ± 0.62        | <b>1.18</b>                 | ± <b>1.20</b> | <b>8.21</b>  | ± <b>1.09</b> |
| <i>Brysonima</i>    | <b>18.91</b>             | ± <b>0.88</b> | <b>9.54</b>  | ± <b>0.68</b> | <b>3.33</b>                 | ± <b>1.55</b> | <b>5.25</b>  | ± <b>1.20</b> |
| <i>Diosypros</i>    | <b>19.20</b>             | ± <b>0.76</b> | <b>13.91</b> | ± <b>0.68</b> | 8.05                        | ± 1.34        | 7.04         | ± 1.20        |
| <i>Eriotheca</i>    | <b>11.20</b>             | ± <b>0.68</b> | <b>4.19</b>  | ± <b>0.88</b> | <b>3.18</b>                 | ± <b>1.20</b> | <b>1.40</b>  | ± <b>1.55</b> |
| <i>Erthroxylum</i>  | 8.83                     | ± 0.68        | 6.58         | ± 0.76        | 4.33                        | ± 1.20        | 3.50         | ± 1.34        |
| <i>Guapira</i>      | <b>13.87</b>             | ± <b>0.68</b> | <b>9.91</b>  | ± <b>0.68</b> | 10.05                       | ± 1.20        | 9.20         | ± 1.20        |
| <i>Hymenaea</i>     | <b>6.24</b>              | ± <b>0.68</b> | <b>9.65</b>  | ± <b>0.76</b> | <b>4.15</b>                 | ± <b>1.20</b> | <b>5.32</b>  | ± <b>1.34</b> |
| <i>Machaerium</i>   | <b>6.98</b>              | ± <b>0.76</b> | <b>5.27</b>  | ± <b>0.76</b> | 3.18                        | ± 1.34        | 2.82         | ± 1.34        |
| <i>Miconia</i>      | 8.79                     | ± 0.68        | 8.51         | ± 0.62        | <b>5.50</b>                 | ± <b>1.20</b> | <b>4.35</b>  | ± <b>1.09</b> |
| <i>Myrcia</i>       | <b>6.80</b>              | ± <b>0.76</b> | <b>10.81</b> | ± <b>0.76</b> | <b>3.64</b>                 | ± <b>1.34</b> | <b>8.43</b>  | ± <b>1.34</b> |
| <i>Myrsine</i>      | 10.99                    | ± 0.76        | 10.33        | ± 0.76        | <b>3.52</b>                 | ± <b>1.34</b> | <b>9.53</b>  | ± <b>1.34</b> |
| <i>Ouratea</i>      | <b>12.00</b>             | ± <b>0.76</b> | <b>16.02</b> | ± <b>0.62</b> | <b>4.78</b>                 | ± <b>1.34</b> | <b>9.74</b>  | ± <b>1.09</b> |
| <i>Piptocarpha</i>  | <b>8.55</b>              | ± <b>0.68</b> | <b>15.32</b> | ± <b>0.88</b> | 24.31                       | ± 1.20        | 23.67        | ± 1.55        |
| <i>Pouteria</i>     | <b>12.63</b>             | ± <b>0.68</b> | <b>20.88</b> | ± <b>0.76</b> | <b>11.65</b>                | ± <b>1.20</b> | <b>19.86</b> | ± <b>1.34</b> |
| <i>Qualea</i>       | <b>7.77</b>              | ± <b>0.68</b> | <b>11.01</b> | ± <b>0.68</b> | <b>2.90</b>                 | ± <b>1.20</b> | <b>7.90</b>  | ± <b>1.20</b> |
| <i>Schefflera</i>   | 16.13                    | ± 0.76        | 16.60        | ± 0.76        | 41.13                       | ± 1.34        | 49.14        | ± 1.34        |
| <i>Styrax</i>       | <b>8.68</b>              | ± <b>0.76</b> | <b>12.79</b> | ± <b>0.76</b> | <b>6.15</b>                 | ± <b>1.34</b> | <b>11.69</b> | ± <b>1.34</b> |
| <i>Symplocos</i>    | 7.38                     | ± 0.76        | 8.76         | ± 0.76        | 5.39                        | ± 1.34        | 6.42         | ± 1.34        |
| <i>Tabebuia</i>     | <b>9.16</b>              | ± <b>0.88</b> | <b>13.65</b> | ± <b>0.76</b> | 27.73                       | ± 1.55        | 33.43        | ± 1.34        |
| <i>Vochysia</i>     | <b>16.18</b>             | ± <b>0.68</b> | <b>11.04</b> | ± <b>0.76</b> | 6.69                        | ± 1.20        | 5.45         | ± 1.34        |

Table 2. Percent of total interspecific variance that is explained by phylogeny (genus) and by functional type. These estimates were based on equating mean squares to expected value calculated from an ANOVA with random effects.

| Trait                   | Genus | Type  |
|-------------------------|-------|-------|
| mean leaf angle         | 24.75 | 3.06  |
| stdev leaf angle        | 3.31  | 3.68  |
| log10 (leaf length)     | 55.02 | 0.424 |
| log 10 (petiole length) | 68.03 | 8.93  |
| leaf waviness           | 39.32 | 7.58  |
| leaf ratio              | 16.32 | 2.31  |

## DISCUSSION

Savanna and forest species exhibited differences in petiole length, consistent with my hypothesis that there is evolutionary convergence with respect to high and low light environments. Although savanna leaves were bigger about half of the time, petiole length was strongly correlated with leaf length, suggesting that these traits act in combination to increase distance from the crown and thus light interception. Despite substantial variability in petiole length among genera, there was a strong habitat effect; forest species had petioles up to six times longer than their savanna congeners (Table 1, example *Aspidosperma*). In general, compound leaved species have the longest true petioles which may aid in avoiding carbon allocation to longer stems and internodes to receive the same benefit of increasing light interception (Pearcy et al 2005).

Contrary to expectations, there were no significant differences in leaf angle (Figure 1) and only marginal differences in leaf waviness (Figure 2) between savanna and forest species. For *Alibertia* and *Myrsine*, more shrub-like habit in savanna species likely

contributed to decreased variation in leaf angles as leaves were packed more tightly; so the expected difference in standard deviations of leaf display angle between savanna and forest species was reversed, as differences in growth form may have confounded this trait. There was support for the hypothesis that savanna species display leaves at steeper and more variable angles for two genera (*Guapira* and *Styrax*), and weak opposing evidence from other genera. These results indicate that closely related species (i.e. congeners) had traits more similar to each other than to other species in the community. The strong genus effect and weak habitat effect suggest strong conservatism for these traits (refer to Table 2), in contrast to our prediction of convergent adaption to habitat type. There are multiple possible explanations for the apparent lack of adaptive evolution in these traits, including weak or absent selective pressures associated with habitat, or genetic and structural constraints on trait values (Ackerly 2004).

Savanna species are hypothesized to have greater leaf waviness than forest species because more self shading and larger leaf-boundary layer of wavier leaves may allow for greater water use efficiency with less water loss from transpiration (Meinzer et al 1995). The leaf waviness metric quantified variance independent of size to separately test for differences in leaf size and shape. Within genera, there was evidence that some savanna species have leaves that are up to two times wavier (e.g. spiral-shaped savanna leaves of *Erthroxylum* and *Piptocarpha*) than forest species. There were no obvious reasons to expect leaves of forest species to have greater waviness, but savanna species in a few genera (e.g. *Myrcia*, *Mysine*, and *Styrax*) tended to be very flat with low leaf waviness values. These flat savanna leaves are often small and so leaf waviness may have been underestimated due to the influence of

scale, and ultimately leaves of forest species seem comparatively wavier. Leaf waviness and display angle may represent alternate pathways to increase self shading, as some species (e.g. *Styrax*) appeared to display flat leaves at steep angles.

There were slightly different patterns within genera for our second metric for quantifying three-dimensional leaf shape – leaf ratio – which measures the volume occupied by the leaf relative to its size. This method was an effort to distinguish undulating leaves from folded leaves and further refine our analysis of three dimensional leaf shapes.

Disagreements between leaf waviness and leaf ratio occurred in *Aegiphila*, which has concave boat-shaped leaves and had high leaf waviness in the forest species but low leaf ratio, and in *Piptocarpha* with large spiral-shaped leaves that had high leaf waviness in the savanna species but did not differ from forest leaves in leaf ratio. In general, undulating leaves can be expected to occupy a greater volume relative to leaf size than flat leaves, but this fairly rough measure of leaf shape may require additional refinement to adequately characterize subtle differences in leaf form.

Leaf traits have large consequences for plant function (Wright et al 2007). Some characteristics are consistently associated with habitat and effectively distinguish functional groups (Reich et al 2003, Hoffmann et al 2005a). Leaf petiole length may be another useful indicator of plant function due to the habitat-associated variability detected in this study. Leaf angle and leaf waviness are more complex traits that may together determine the amount of light intercepted, but our understanding of the causes and consequences of variability in these traits remains incomplete. This study provides a wealth of detailed three-dimensional data for future modeling of light interception of different leaf arrangements (Percy et al 2005).

The leaf characteristics examined, combined with changes in architectural relationships like crown diameter and tree height (Chapter 2), likely explain the physiological differences between forest and savanna species. These differences in leaf and allometric traits determine light transmission through the canopy, which influences the light environment and microclimate of the understory. Consequently, these abiotic changes influence grass productivity and likely affect the density and composition of savanna communities.

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## APPENDIX

## APPENDIX

Table 1. List of species in leaf trait analysis in Cerrado habitat at IBGE Ecological Reserve in Brasilia, DF, Brazil.

| Savanna Species                 | Forest Species          | Family          |
|---------------------------------|-------------------------|-----------------|
| <i>Aegiphila lhotzkiana</i>     | <i>A. sellowiana</i>    | Verbenaceae     |
| <i>Alibertia sessilis</i>       | <i>A. elliptica</i>     | Rubiaceae       |
| <i>Aspidosperma tomentosum</i>  | <i>A. subicanum</i>     | Apocynaceae     |
| <i>Brysonima crassa</i>         | <i>B. laxiflora</i>     | Malpighiaceae   |
| <i>Diosypros burchellii</i>     | <i>D. hispida</i>       | Ebenaceae       |
| <i>Eriotheca pubescens</i>      | <i>E. gracilipes</i>    | Bombacaceae     |
| <i>Erthroxylum suberosum</i>    | <i>E. daphnites</i>     | Erythroxylaceae |
| <i>Guapira noxia</i>            | <i>G. areolata</i>      | Nyctaginaceae   |
| <i>Hymenaea stignocarpa</i>     | <i>H. courbaril</i>     | Fabaceae        |
| <i>Machaerium opacum</i>        | <i>M. acutifolium</i>   | Fabaceae        |
| <i>Miconia pohliana</i>         | <i>M cuspidata</i>      | Melastomataceae |
| <i>Myrcia rostrata</i>          | <i>M. tomentosa</i>     | Myrtaceae       |
| <i>Myrsine guianensis</i>       | <i>M. ferruginea</i>    | Myrsinaceae     |
| <i>Ouratea hexasperma</i>       | <i>O. castanarfolia</i> | Ochnaceae       |
| <i>Piptocarpha rotundifolia</i> | <i>P. macropoda</i>     | Asteraceae      |
| <i>Pouteria ramiflora</i>       | <i>Pouteria sp.</i>     | Sapotaceae      |
| <i>Qualea parviflora</i>        | <i>Q. dichotoma</i>     | Vochysiaceae    |
| <i>Schefflera macrocarpum</i>   | <i>S. morototoni</i>    | Araliaceae      |
| <i>Styrax ferruginus</i>        | <i>S. camporum</i>      | Styracaceae     |
| <i>Symplocos lanceolata</i>     | <i>S. mosenii</i>       | Symplocaceae    |
| <i>Tabebuia ochracea</i>        | <i>T. roseo-alba</i>    | Bignoniaceae    |
| <i>Vochysia thyoidea</i>        | <i>V. tucanorum</i>     | Vochysiaceae    |