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Architecture of tree species of different strata developing in environments with the same light intensity in a semideciduous forest in southern Brazil

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ABSTRACT

We aimed to answer the following questions related to the architecture of individuals 0.5-3.0 m in height belonging to understory or canopy/emergent layer tree species: "Is there a difference between individuals belonging to different strata developing in environments with the same light intensity, in terms of their architecture?"; and "Given the same light intensity, do understory species exhibit less crown plasticity than do canopy/emergent layer species?" Thirteen architectural variables were evaluated in 80 individuals per species. We found that understory species showed greater increases in stem thickness and leaf number, as well as wider, deeper crowns, longer branches, greater self-shading and less crown plasticity. Stems and crowns were more slender in the canopy species than in the understory species. These differences might be due to the trade-off between vertical and lateral growth. Our results indicate that, regardless of the group to which they belong, species are best able to take advantage of light conditions in the understory of the forest. However, because they demand more light, canopy species showed a growth form that resulted in an architecture that is likely to enable better light capture in the understory.

Key words: resource allocation, canopy, allometric relationships, understory

Introduction

Tree architecture, which can be represented by allometric relationships, is defined as the overall shape of the tree and the spatial position of its components, expressing morphological aspects, such as plant height, stem diameter and crown characteristics (Poorter *et al.* 2003; Bohlman & O'Brien 2006). Tree height reflects the competitive ability related to light capture in the vertical gradient (Aiba & Kohyama 1996; Moles *et al.* 2009). Interspecific differences in crown architecture, in terms of size, shape, position and leaf area, might also have important implications for light capture (Kohyama 1991). However, stem diameter is associated with structural stability, mechanical strength and crown support (Sterck & Bongers 1998). Architectural descriptors, which characterize the plastic development of a plant (Weiner 2004), are influenced by habitat characteristics and the environmental pressures to which they are exposed (Parish *et al.* 2008; Vieilledent *et al.* 2010; Valladares *et al.* 2012), especially those related to light availability and intensity.

According to Poorter *et al.* (2003), light capture, which is dependent on plant architecture, is extremely important for the persistence of individual trees in the environment. Since light is a limiting resource, there might be positive selection for rapid vertical growth or maximization of leaf area in order to allow greater access to light. Within these limits, architecture varies widely among forest trees (Ackerly & Donoghue 1998; Poorter *et al.* 2006), a fact that becomes evident when understory, canopy and emergent layer species are compared.

Many studies have shown that architectural patterns vary among species belonging to different ecological groups (Kohyama *et al.* 2003; Poorter *et al.* 2003; Poorter *et al.* 2005; King *et al.* 2006; Poorter *et al.* 2006; Osunkoya *et al.* 2007; Parish *et al.* 2008; Iida *et al.* 2011). In particular, high crown plasticity has been reported among tree species of different ecological groups growing in the understory (King 1990, 1994, 1996; Aiba & Koyama 1997; Sterck *et al.* 1999; Poorter 1999; Sterck *et al.* 2001; Alves & Santos 2002; Poorter *et al.* 2003; Barker *et al.* 2006; Parish *et al.* 2008; Martínez-Sánchez *et al.* 2008). Some studies have suggested that, compared with canopy/emergent layer species, understory species have less crown plasticity (Martínez-Sánchez *et al.* 2008; Vicent & Harja 2008; Vieilledent *et al.* 2010). According to Vicent & Harja (2008), greater crown plasticity

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indicates that canopy/emergent layer species, while growing in the understory, are more flexible in allocating resources for vertical growth, horizontal growth and crown expansion than are true understory species, giving the former an adaptive advantage. In addition, by comparing distinct species, such studies have found a variety of relationships between crown architecture and light capture (Martínez-Sánchez *et al.* 2008; Vicent & Harja 2008; Vieilledent *et al.* 2010).

Kohyama & Hotta (1990) stated that comparisons of allometric relationships between species occurring in different environments are needed in order to understand the basic mechanisms defining the shape of tree species and the implications of this form in the niche they occupy. According to Condict (2006), the shape of species that belong to different strata varies in relation to the niche occupied, i.e., the way in which resources are used by each species. Some studies have demonstrated that the availability of light plays an important role in niche differentiation (Lusk 1996; Lusk *et al.* 2008; Valladares *et al.* 2012).

Although several studies have examined the architecture of species belonging to different ecological groups (Kohyama *et al.* 2003; Poorter *et al.* 2003, 2005, 2006; King *et al.* 2006; Osunkoya *et al.* 2007; Parish *et al.* 2008), the way in which young individuals of tree species of different strata live in the understory remains poorly understood. Canopy and emergent layer species probably reach the canopy, and even grow beyond it, in order to achieve reproductive success, possibly with less production of photoassimilates during ontogeny. In contrast, understory species probably remain below the canopy. Studies of this topic will also be able to address important questions about other ecological relationships other than those already described.

In view of the facts presented above, the present study aimed to compare individuals 0.5-3.0 m in height of six tree species from different ecological groups, in terms of their architecture. We raised the following questions: "Is there a difference between individuals belonging to different strata developing in environments with the same light intensity, in terms of their architecture?"; and "Given same light intensity, do understory species exhibit less crown plasticity than do canopy/emergent layer species?"

Material and methods

Study area

The study was conducted in Godoy Forest State Park (Torezan 2006), an area of 680 ha of semideciduous forest in the city of Londrina (23°27'S; 51°15'W, visitor center), which is in the state of Paraná, Brazil. We defined a sampling area of 5000 m^2. We were careful to choose an area away from the edge effect and without an overt presence of lianas and bamboos. The coverage ratio of the canopy in the studied sample area is greater than 90%. The canopy becomes more open in the winter and more closed in spring and summer, when there is increased precipitation (Bianchini *et al.* 2001).

According to the Köppen system of classification (1948), the climate of the region is type Cfa (humid subtropical), with an average annual rainfall of 1200-1600 mm, distributed unevenly throughout the year (IAPAR 2000). The main soil types are oxisols and eutroferric alfisols, in association with entisols, a soil of high fertility (EMBRAPA 1999; Vicente 2006).

Species

The species to be studied were selected on the basis of the importance values reported in a previous forest inventory (Soares-Silva & Barroso 1992). From among those with the highest values, we chose three understory species—*Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & de Boer (Moraceae); *Actinostemon concolor* (Spreng.) Müll. Arg.(Euphorbiaceae); and *Inga marginata* Kunth (Fabaceae)—and three canopy/emergent layer species—*Holocalyx balansae* Micheli (Fabaceae); *Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl. (Sapotaceae); and *Aspidosperma polyneuron* Müll.Arg. (Apocynaceae).

Methods

Data were collected between July and December 2010. For each species, we selected 80 individuals of 0.5-3.0 m in height with no apparent damage. We avoided selecting individuals with very similar statures. To evaluate the architecture of individuals, we used 13 architectural descriptors related to light capture and mechanical support. Height was measured as the distance from the forest floor to the top of the individual (King 1990; O'Brien *et al.* 1995; King 1996; Aiba & Kohyama 1997; Alves & Santos 2002; Chave *et al.* 2005; Poorter *et al.* 2006; Osunkoya *et al.* 2007; Martínez-Sánchez *et al.* 2008; Vieilledent *et al.* 2010). Stem diameter was measured at 10 cm from the forest floor (King 1990; O'Brien *et al.* 1995; King 1996; Aiba & Kohyama 1997; Alves & Santos 2002; Chave *et al.* 2005; Poorter *et al.* 2006; Osunkoya *et al.* 2007; Martínez-Sánchez *et al.* 2008; Vieilledent *et al.* 2010). For the analysis of leaf number, only leaves with at least 50% expansion were considered, compared with the length of the smallest fully expanded leaf found for the species (Martínez-Sánchez *et al.* 2008). Horizontal crown area was estimated on the basis of the two cross-section diameters of the crown (D1 and D2) and calculated as an ellipse: $0.25\pi \times D1 \times D2$ (Bongers *et al.* 1988; Martínez-Sánchez *et al.* 2008). The vertical crown area was also estimated as an ellipse: $0.25\pi \times (D1+D2/2) \times CD$ (Crown depth) (Sterck *et al.* 2003; Martínez-Sánchez *et al.* 2008). Branch length was calculated as the average length of the two lateral branches along the main axis, leaves per branch was defined as the average number of leaves for those same two branches, and inter-branch distance was defined as the distance between two side branches along the main axis (Martínez-Sánchez *et al.* 2008). Crown depth was defined as the distance between the lower branch and the top of the individual (King 1996; Alves & Santos 2002; Poorter *et al.* 2006; Osunkoya *et al.* 2007; Martínez-Sánchez *et al.* 2008; Vieilledent *et al.* 2010). Stem slenderness, crown slenderness, the cost of leaf support, horizontal crown self-shading and vertical crown self-shading were calculated, respectively, as the following ratios (Martínez-Sánchez *et al.* 2008): height/diameter, horizontal crown area/crown depth, branch length/leaves per branch, leaf number/horizontal crown area and leaf number/vertical crown area.

Data analysis

For comparing the different architectural descriptors among species, we used ANOVA, and means were compared by Tukey's test at 5% probability. Initially, the Kolmogorov-Smirnov test ($\alpha = 0.05$) was used in order to verify the normality of the data. When normality was not observed, data were log transformed.

The allometric relationships were generally expressed by functions derived from linear regressions of log-transformed variables ($\log_{10}$). To express those relationships, we used the following equation:

$$y = ax^b \text{ or } \log y = \log a + b \log x$$

where *a* and *b* are the parameters obtained by linear regression (Sokal & Rohlf 1981; King 1990; Kohyama & Hotta 1990). When the growth form of individuals is compared among species, differences can occur either in *a* (y-intercept) or *b* (the slope). When the slope differs between species, the highest value of *b* will present a greater increase in *y* per increase in *x*. When the constant *a* differs but the slope does not, the species with a higher *a* value will present a higher value of *y* for any given value of *x* (Kohyama & Hotta 1990).

Analysis of covariance was used in order to test the differences between variables (Snedecor & Cochram 1967). Multiple comparisons among variables were performed by *a posteriori* Scheffé test, at a level of significance of $p<0.05$ (Huitema 1980; Zar 1984). The degree of significance for the correlation coefficient (r^2) was $p<0.001$, corresponding to an $r^2>0.11$. High values of r^2 indicate low variability in the architecture of individuals.

Results

Individuals in the population of *Actinostemon concolor* showed the highest quantity of leaves (Fig. 1). The leaf numbers for the other understory species (*Sorocea bonplandii* and *Inga marginata*) did not differ from those obtained for the canopy/emergent layer species, *I. marginata* and *Chrysophyllum gonocarpum* showing the lowest quantities of leaves. As can be seen in Fig. 1, two of the understory species (*S. bonplandii* and *A. concolor*) and one of the canopy species (*Holocalyx balansae*) made the greatest investments in horizontal crown area, vertical crown area, branch length, inter-branch distance and crown depth, showing a pattern similar to that of the other canopy/emergent layer species (*C. gonocarpum* and *Aspidosperma polyneuron*).

Stems and crowns were slenderest in *Holocalyx balansae* (Fig. 2). Individuals of the three understory species showed a pattern of stem slenderness and crown slenderness similar to that of the canopy/emergent layer species *Chrysophyllum gonocarpum* and *Aspidosperma polyneuron*. *Actinostemon concolor* showed the lowest cost of leaf support, as well as the highest horizontal crown self-shading and vertical crown self-shading (Fig. 2). However, the other two understory species (*Sorocea bonplandii* and *Inga marginata*) again did not differ from canopy/emergent layer species (Fig. 2).

Tab. 1 shows the results of the linear regressions between height and other architectural descriptors. Most of the regressions showed significant positive correlations for individuals of all of the species evaluated (r^2, $p<0.001$). Except for *Inga marginata*, the understory species (*Actinostemon concolor* and *Sorocea bonplandii*) showed higher values of the slope for height correlations with diameter, leaf number, horizontal crown area, vertical crown area, branch length and crown depth than did the canopy species *Chrysophyllum gonocarpum* and *Holocalyx balansae*. Therefore, for a given increase in height, the corresponding increase in stem thickness, leaf number, crown width, crown depth and branch length was greater in *A. concolor* and *S. bonplandii* than in *C. gonocarpum* and *H. balansae*. In the canopy species *C. gonocarpum*, taller individuals had slenderer stems, whereas this relationship did not differ between *Aspidosperma polyneuron* and *A. concolor* (Tab. 1).

Actinostemon concolor showed the greatest investment in horizontal crown self-shading per height increase (Tab. 1), whereas that relationship did not differ significantly between the other two understory species (*Sorocea bonplandii* and *Inga marginata*) and was comparable between *I. marginata* and *Aspidosperma polyneuron*. For the correlations between height and the cost of leaf support, between height and horizontal crown self-shading and between height and crown slenderness, the r^2 was not significant ($p<0.001$) in any of the species evaluated.

Individuals of the understory species *Sorocea bonplandii* and *Actinostemon concolor* had the greatest increases in leaf number and horizontal crown area per increase in diameter, unlike what was observed for *Inga marginata* and for the three canopy/emergent layer species (Tab. 2). Only *A. concolor* showed greater increase in vertical crown area, crown depth and horizontal crown self-shading per increase in diameter, whereas the two other understory species (*S. bonplandii* and *I. marginata*) showed a pattern similar to those of canopy/emergent layer species, in terms of those descriptors (Tab. 2).

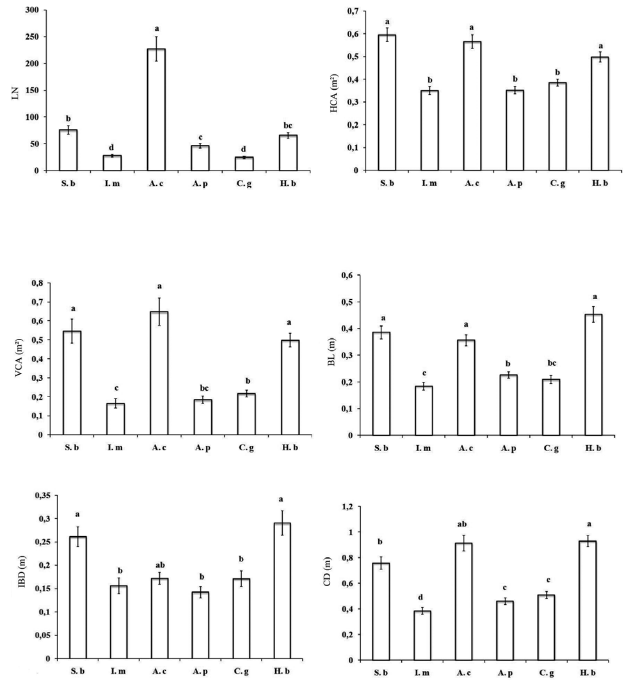

Figure 1. Architectural descriptors of individuals 0.5-3.0 m in height (n = 80 per species) of understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.
Means followed by the same letter do not differ at a 5% level of significance (Tukey's test).
LN – leaf number; HCA – horizontal crown area; VCA – vertical crown area; BL – branch length; IBD – inter-branch distance; CD – crown depth; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae.*

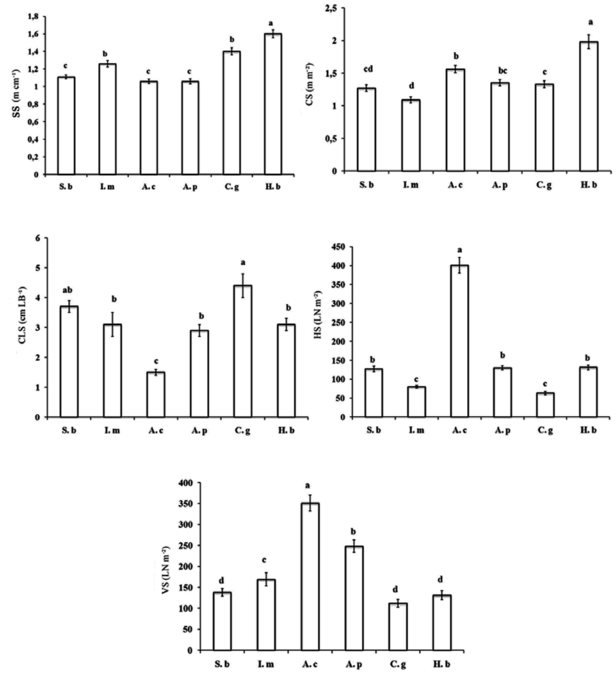

Figure 2. Architectural descriptors of individuals 0.5-3.0 m in height (n = 80 per species) of understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.
Means followed by the same letter do not differ at a 5% level of significance (Tukey's test).
SS – stem slenderness; CS – crown slenderness; CLS – cost of leaf support; HS – horizontal crown self-shading; VS – vertical crown self-shading; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae.*

Table 1. Estimation of the parameters of linear regressions (*a*, *b* and r²) of the correlations between height and other architectural descriptors ($\log y = a + b \log x$) in individuals 0.5-3.0 m in height (n = 80 per species) of understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.

Species	*a*	*b*	r²	*a*	*b*	r²	*a*	*b*	r²
		H per D			H per LN			H per HCA	
Understory									
S.b	0.096	0.838 a	0.859	−48.7	90.2 b	0.667	0.127	0.341 ab	0.700
I.m	0.188	0.625 bc	0.714	−12.7	39.4 c	0.638	0.061	0.281 bc	0.680
A.c	0.324	0.681 abc	0.784	−153	292 a	0.774	0.046	0.399 a	0.817
Canopy/emergent layer									
C.g	0.302	0.495 c	0.500	-	-	ns	0.141	0.190 c	0.373
H.b	0.126	0.577 c	0.607	8.01	33.7 c	0.176	0.199	0.176 c	0.296
A.p	0.158	0.796 ab	0.753	−5.03	50.6 bc	0.462	0.121	0.231 c	0.637
		H per VCA			H per BL			H per CD	
Understory									
S.b	−0.405	0.691 b	0. 637	0.039	0.253 a	0.616	0.009	0.543 b	0.655
I.m	−0.198	0.352 c	0.578	−0.044	0.221 ab	0.561	0.010	0.362 c	0.493
A.c	−0.623	0.974 a	0.885	0.011	0.264 a	0.795	−0.200	0.853 a	0.906
Canopy/emergent layer									
C.g	−0.103	0.249 c	0.392	−0.008	0.168 ab	0.295	0.115	0.305 c	0.303
H.b	−0.195	0.408 c	0.576	0.046	0.240 ab	0.315	−0.010	0.552 b	0.765
A.p	−0.079	0.262 c	0.537	0.084	0.142 b	0.455	0.145	0.313 c	0.447
		H per IBD			H per HS			H per SS	
Understory									
S.b	0.039 a	0.162	0.333	22.1	60.63 b	0.377	-	-	ns
I.m	−0.030 a	0.182	0.314	38.0	33.76 b	0.259	-	-	ns
A.c	-	-	ns	59.5	204 a	0.469	0.809	0.198 b	0.279
Canopy/emergent layer									
C.g	-	-	ns	-	-	ns	0.886	0.399 a	0.238
H.b	0.024 a	0.157	0.164	-	-	ns	-	-	ns
A.p	-	-	ns	78.9	40.63 b	0.158	0.879	0.184 b	0.126

r² – correlation coefficient; H – height; D – stem diameter; LN – leaf number; HCA – horizontal crown area; VCA – vertical crown area; BL – branch length; CD – crown depth; IBD – inter-branch distance; HS – horizontal crown self-shading; SS – stem slenderness; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae*; ns – not significant.
The same letters in the same column indicate that values do not differ significantly from each other at the significance levels of $p<0.05$ (analysis of covariance and Scheffé test) and $r^2>0.11$ ($p<0.001$; ANOVA).

Individuals of *Aspidosperma polyneuron* showed the smallest increase in branch length per increase in diameter (lowest value of *b*). That relationship did not differ significantly among the remaining species (Tab. 2). For the correlations between diameter and inter-branch distance, between diameter and crown slenderness, between diameter and the cost of leaf support and between diameter and vertical crown self-shading, the r² was not significant ($p<0.001$) in any of the species evaluated.

Individuals of the understory species *Sorocea bonplandii* and *Actinostemon concolor* showed a greater increase in horizontal crown area per increase in vertical crown area than did any of the other four species studied (Tab. 3). In addition, *A. concolor* showed the greatest investment in leaf number per increase in horizontal crown area.

Actinostemon concolor showed the greatest investments in leaf number and horizontal crown area per increase in vertical crown area, whereas this relationship did not differ between the other understory species (*Sorocea bonplandii* and *Inga marginata*) and the canopy/emergent layer species. However, the increase in branch length per increase in vertical crown area was significantly greater in all three of the canopy/emergent layer species and in the understory species *I. marginata* than in the other two understory species (Tab. 3). None of the species showed r² significant ($p <0.001$) For the correlations between horizontal crown area and inter-branch distance, between horizontal crown area and stem slenderness, between vertical crown area and stem slenderness and between vertical crown area and the

Table 2. Estimation of the parameters of linear regressions (*a*, *b* and r^2) of the correlations between stem diameter and other architectural descriptors ($\log y = a + b \log x$) in individuals 0.5-3.0 m in height (n = 80 per species) of understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.

Species	*a*	*b*	r^2	*a*	*b*	r^2
		D per LN			D per HCA	
Understory						
S.b	−58.5	107 b	0.772	0.108	0.390 ab	0.750
I.m	−11.7	47.69 c	0.510	0.061	0.349 bc	0.574
A.c	−194	348 a	0.651	−0.035	0.496 a	0.748
Canopy/emergent layer						
C.g	−1.39	27.4 c	0.212	0.126	0.276 bc	0.387
H.b	16.32	44.3 c	0.167	0.210	0.261 c	0.356
A.p	−6.90	55.11 c	0.460	0.126	0.236 c	0.563
		D per VCA			D per CD	
Understory						
S.b	−0.429	0.780 b	0.664	0.033	0.579 b	0.608
I.m	−0.215	0.456 cd	0.531	−0.023	0.489 bc	0.491
A.c	−0.792	1.18 a	0.777	−0.282	0.986 a	0.714
Canopy/emergent layer						
C.g	−0.098	0.336 cd	0.351	0.131	0.401 bc	0.257
H.b	−0.091	0.532 c	0.539	0.267	0.598 b	0.493
A.p	−0.076	0.272 d	0.488	0.162	0.311 c	0.371
		D per BL			D per HS	
Understory						
S.b	0.050	0.270 a	0.574	15.9	71.7 b	0.432
I.m	−0.062	0.295 a	0.549	39.3	40.1 b	0.201
A.c	−0.026	0.315 a	0.668	47.8	230 a	0.350
Canopy/emergent layer						
C.g	−0.015	0.238 ab	0.289	-	-	ns
H.b	0.074	0.343 a	0.355	-	-	ns
A.p	0.099	0.133 b	0.337	78.5	43.0 b	0.150

D – stem diameter; LN – leaf number; HCA – horizontal crown area; VCA – vertical crown area; CD – crown depth; BL – branch length; HS – horizontal crown self-shading; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae*; ns – not significant.
The same letters in the same column indicate that values do not differ significantly from each other at the significance levels of $p<0.05$ (analysis of covariance and Scheffé test) and $r^2>0.11$ ($p<0.001$; ANOVA).

cost of leaf support, the r^2 was not significant ($p<0.001$) in any of the species evaluated.

Evaluating the correlation between inter-branch distance and crown depth (Tab. 4), we found that *Sorocea bonplandii* showed the greatest increase in crown depth per increase in inter-branch distance. For that relationship, *Inga marginata* did not differ from canopy/emergent layer species *Holocalyx balansae* and *Aspidosperma polyneuron*. For any given inter-branch distance, *Actinostemon concolor* showed a greater investment in crown slenderness than did the other two understory species (*S. bonplandii* and *I. marginata*). *A. concolor* showed the greatest investment in leaf number and crown self-shading per increase in crown depth. The other understory species (*S. bonplandii* and *I. marginata*) showed the same pattern as the canopy/emergent layer species (Tab. 4). None of the species showed r^2 significant ($p <0.001$) For the correlations between inter-branch distance and stem slenderness, between inter-branch distance and horizontal crown self-shading, between crown depth and stem slenderness and between crown depth and the cost of leaf support, the r^2 was not significant ($p<0.001$) in any of the species evaluated.

Individuals of the species *Actinostemon concolor* showed the greatest increases in crown depth and leaf number per increase in branch length, whereas *Sorocea bonplandii* and *Inga marginata* exhibited a pattern similar to that observed for the canopy/emergent layer species (Tab. 4). For any given branch length, the increase in vertical crown self-shading was greatest in *A. concolor*, whereas it was lowest in *Chryso-*

Table 3. Estimation of the parameters of linear regressions (*a*, *b* and r^2) of the correlations that horizontal crown area and vertical crown area present with other architectural descriptors ($\log y = a + b \log x$) in individuals 0.5-3.0 m in height (n = 80 per species) of understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.

Species	*a*	*b*	r^2	*a*	*b*	r^2
		HCA per VCA			HCA per LN	
Understory						
S.b	−0.592	1.90 a	0.808	−60.4	228 b	0.708
I.m	−0.246	1.17 b	0.742	−15.5	123 bc	0.729
A.c	−0.571	2.15 a	0.840	−146.9	660 a	0.772
Canopy/emergent layer						
C.g	−0.201	1.08 b	0.721	2.24	57.4 c	0.183
H.b	−0.220	1.44 b	0.756	−18.5	168 bc	0.461
A.p	−0.187	1.05 b	0.728	−32.3	222 b	0.740
		HCA per VS			HCA per CLS	
Understory						
S.b	-	-	ns	0.056	−0.032 b	0.210
I.m	-	-	ns	-	-	ns
A.c	-	-	ns	0.024	−0.016 a	0.260
Canopy/emergent layer						
C.g	235 b	−256	0.176	-	-	ns
H.b	252 a	−184	0.138	-	-	ns
A.p	-	-	ns	-	-	ns
		VCA per LN			VCA per BL	
Understory						
S.b	21.2	99.5 b	0.608	0.220	0.305 c	0.674
I.m	14.3	82.4 b	0.598	0.093	0.550 ab	0.746
A.c	42.2	285 a	0.796	0.192	0.253 c	0.782
Canopy/emergent layer						
C.g	13.1	51.7 b	0.243	0.073	0.627 ab	0.643
H.b	19.4	92.1 b	0.379	0.138	0.632 a	0.635
A.p	14.7	168.4 b	0.653	0.155	0.388 bc	0.437
		VCA per HS			VCA per IBD	
Understory						
S.b	73.8	64.2 b	0.305	0.160	0.187 b	0.332
I.m	64.0	53.2 b	0.139	0.081	0.458 a	0.429
A.c	206.9	184 a	0.410	-	-	ns
Canopy/emergent layer						
C.g	-	-	ns	-	-	ns
H.b	-	-	ns	0.143	0.294 ab	0.167
A.p	92.6	146 ab	0.264	-	-	ns

HCA – horizontal crown area; VCA – vertical crown area; LN – leaf number; VS – vertical crown self-shading; CLS – cost of leaf support; LN – leaf number; BL – branch length; HS – horizontal crown self-shading; IBD – inter-branch distance; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae*; ns – not significant.
The same letters in the same column indicate that values do not differ significantly from each other at the significance levels of $p<0.05$ (analysis of covariance and Scheffé test) and $r^2>0.11$ ($p<0.001$; ANOVA).

Table 4. Estimation of the parameters of linear regressions (*a*, *b* and r^2) of the correlations that inter-branch distance, crown depth, branch length, the cost of leaf support, horizontal crown self-shading and vertical crown self-shading present with other architectural descriptors ($\log y = a + b \log x$) in individuals 0.5-3.0 m in height (n = 80 per species) of understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.

Species	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2
	IBD per CD			IBD per CS			IBD per VS		
Understory									
S.b	0.358	1.52 a	0.408	1.05 b	0.83	0.125	-	-	ns
I.m	0.214	1.08 ab	0.465	0.93 b	1.04	0.141	296 a	−357	0.152
A.c	-	-	ns	-	-	ns	-	-	ns
Canopy/emergent layer									
C.g	-	-	ns	-	-	ns	175 b	−223	0.159
H.b	0.689	0.829 b	0.258	-	-	ns	-	-	ns
A.p	0.339	0.853 ab	0.158	1.10 a	1.64	0.178	-	-	ns
	CD per LN			CD per HS			CD per VS		
Understory									
S.b	−14.0	118 b	0.517	42.9	87.0 b	0.337	-	-	ns
I.m	3.22	64.4 bc	0.452	-	-	ns	365	−323 b	0.317
A.c	−66.0	321 a	0.753	120	226 a	0.459	535	−133 a	0.186
Canopy/emergent layer									
C.g	2.54	42.9 c	0.326	-	-	ns	-	-	ns
H.b	20.0	48.8 c	0.147	-	-	ns	298	−148 a	0.336
A.p	−2.53	105 bc	0.438	72.3	103 b	0.223	405	−251 ab	0.195
	BL per CD			BL per LN			BL per VS		
Understory									
S.b	0.132	1.61 b	0.601	−28.3	268 b	0.613	-	-	ns
I.m	0.126	1.40 bc	0.646	4.40	128 b	0.585	311 b	−386	0.148
A.c	−0.022	2.62 a	0.753	−111	950 a	0.721	535 a	−342	0.133
Canopy/emergent layer									
C.g	0.241	1.27 bc	0.510	13.8	50.2 c	0.140	195 c	−280	0.210
H.b	0.542	0.853 c	0.332	24.3	90.5 c	0.231	227 b	−147	0.153
A.p	0.175	1.26 bc	0.320	−11.8	255 bc	0.517	-	-	ns
	CLS per HS			CLS per VS			HS per VS		
Understory									
S.b	193	−2294 b	0.414	241	−2247 ab	0.254	91.8	0.614 b	0.241
I.m	83.4	−333 a	0.130	-	-	ns	118	1.68 a	0.141
A.c	514	−12488 c	0.355	-	-	ns	-	-	ns
Canopy/emergent layer									
C.g	84.9	−498 a	0.170	200	−1421 a	0.355	57.1	1.27 ab	0.417
H.b	190	−1996 ab	0.244	289	−4082 b	0.362	83.0	0.600 b	0.131
A.p	157	−1265 ab	0.189	394	−3545 b	0.217	156	1.10 ab	0.179

IBD – inter-branch distance; CD – crown depth; CS – crown slenderness; VS – vertical crown self-shading; LN – leaf number; HS – horizontal crown self-shading; BL – branch length; CLS – cost of leaf support; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae*; ns – not significant.
The same letters in the same column indicate that values do not differ significantly from each other at the significance levels of $p<0.05$ (analysis of covariance and Scheffé test) and $r^2>0.11$ ($p<0.001$; ANOVA).

phyllum gonocarpum. For this parameter, *I. marginata* did not differ significantly from *Holocalyx balansae*.

For any given increase in the cost of leaf support, *Actinostemon concolor* showed the lowest investment in horizontal crown self-shading. *Chrysophyllum gonocarpum* showed the greatest increase in vertical crown self-shading per increase in the cost of leaf support. None of the other species showed any differences in either of those parameters. The investment in vertical crown self-shading per increase in horizontal crown self-shading was greatest in *Inga marginata*, whereas there were no differences among the remaining species (Tab. 4). For the correlations between stem slenderness and crown slenderness, between stem slenderness and leaf number, between stem slenderness and horizontal crown self-shading, between stem slenderness and vertical crown self-shading, between crown slenderness and leaf number, between crown slenderness and the cost of leaf support, between crown slenderness and horizontal crown self-shading and between crown slenderness and vertical crown self-shading, the r^2 was not significant ($p<0.001$) in any of the species evaluated.

In general, the understory species showed less variability in the architectural descriptors analyzed than did the canopy/emergent layer species. This can be inferred by the fact that the correlation coefficients (r^2, $p<0.05$) were higher for the former than for the latter (Fig. 3).

Individuals of the species *Sorocea bonplandii* and *Actinostemon concolor* showed the most uniform architectural patterns (r^2 of 29.8% and 33.4%, respectively). In contrast, the r^2 values for *Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae* were lower than 19.9%, which suggests that individuals of these species showed the greatest variability in their architecture (Fig. 3).

Discussion

We observed differences between the two different forest strata evaluated, in terms of the architecture of individual trees. Except for *Inga marginata*, the understory species (*Actinostemon concolor* and *Sorocea bonplandii*) exhibited greater increases in stem thickness and leaf number, as well as wider crowns, deeper crowns and longer branches, thereby achieving greater self-shading, than did the canopy species *Chrysophyllum gonocarpum* and *Holocalyx balansae*. Other studies have also demonstrated that understory species show a greater investment in stem thickness than do canopy species of similar height (King 1996; Bongers & Sterck 1998; Sterck *et al*. 2001; Kohyama *et al*. 2003; Poorter *et al*. 2003, 2006; King *et al*. 2006). These observations are consistent with suggestions that the relationship between height and diameter can vary greatly among species (King *et al*. 2006; Poorter *et al*. 2006; Osunkoya *et al*. 2007). Thicker stems can be extremely important for supporting heavier crowns and to withstand the impact of branches falling from taller trees (Martínez-Sánchez *et al*. 2008), and understory species spend more of their life cycle subjected to this adversity.

In a forest in Panama, King (1990) found that understory species individuals typically had larger crowns than did the young individuals of canopy species of similar height. The authors interpreted these results as indicating that understory species have adapted in order to intercept more of the limited quantity of light that typically reaches the understory. As observed in the present study for the understory species *Actinostemon concolor* and *Sorocea bonplandii*, species of the understory tend to invest more resources in leaf area or leaf number, thereby maximizing

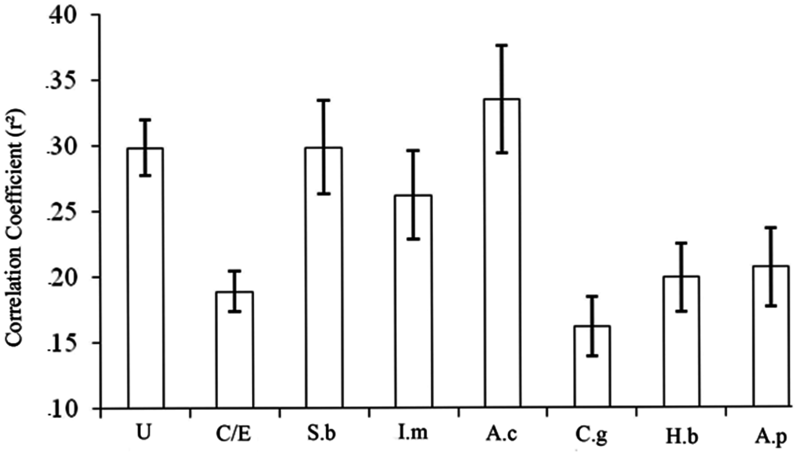

Figure 3. Variability in the architectural descriptors analyzed for understory species (*Sorocea bonplandii*, *Inga marginata* and *Actinostemon concolor*) and canopy/emergent layer species (*Aspidosperma polyneuron*, *Chrysophyllum gonocarpum* and *Holocalyx balansae*), as well as for understory species collectively and for canopy/emergent layer species collectively, in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.
Results presented as correlation coefficients ± standard error.
U – understory; C/E – canopy/emergent; S.b – *Sorocea bonplandii*; I.m – *Inga marginata*; A.c – *Actinostemon concolor*; A.p – *Aspidosperma polyneuron*; C.g – *Chrysophyllum gonocarpum*; H.b – *Holocalyx balansae*.

light capture (Osunkoya *et al*. 2007; Valladares & Niinemets 2010). According to Abe & Yamada (2008) and Vieilledent *et al*. (2010), species adapted to low light levels show, as a result of their evolution, wider, yet shallower, crowns (unlike what we observed for *S. bonplandii* and *A. concolor*), thereby reducing the level of self-shading. However, the correlation between crown depth and light capture might be weaker than previously thought. Light capture is affected not only by the number of leaf layers but also by the efficiency of the distribution and geometry of the foliage (Poorter *et al*. 2003). Changes in the shape, size and orientation of leaves can compensate for the negative effect of self-shading caused by the greater crown depth. Shade-tolerant species such as *A. concolor* and *S. bonplandii* have, in general, a light compensation point lower than that of the more light-demanding species (Ackerly 1996; Poorter *et al*. 2003, 2006). Although the shaded leaves contribute to the net carbon gain from the tree, these leaves are extremely important because the have a positive influence on growth and survival (Sterck *et al*. 2003). A deep, highly branched crown can effectively increase light capture for individuals in the understory, especially in places where there is more lateral light than vertical light (McMahon 1973; Parish *et al*. 2008).

In the present study, individuals of the canopy species *Chrysophyllum gonocarpum* and *Holocalyx balansae*, showed slenderer stems and crowns than did those of the understory species. Shukla & Ramakrishnan (1986), King (1990; 1996), Poorter & Werger (1999), Sterck (1999), Sposito & Santos (2001), Sterck & Bongers (2001), Sterck *et al*. (2001), Alves & Santos (2002) and Poorter *et al*. (2003, 2005, 2006) correlated crown size with the height of individuals. All of those authors found that, in the initial stages of development, canopy species show slenderer crowns than do understory species. This architectural pattern allows canopy species to achieve greater heights, rising above the dark understory, at a relatively low cost, considering their lower energy investment for the expansion of the crown, resulting in individuals crowns that are not as lush as are those of understory species (Kohyama 1987; King 1990, 1996; Chave *et al*. 2005; Parish *et al*. 2008).

For many of the descriptors evaluated, we observed that, unlike the other understory species, *Inga marginata* often showed a pattern similar to that of the canopy species. In addition, the canopy species *Aspidosperma polyneuron* showed a pattern similar to that of the understory species. The requirements in the various ontogenetic stages can change over time. This architectural pattern observed for *I. marginata* might enable it to occupy different niches, allowing it to coexist within the community studied.

Similar to what we observed for the understory species, we found that the canopy species *Aspidosperma polyneuron* showed a greater investment in diameter and a greater increase in height than did the other canopy/emergent layer species. According to Bohlman & O'Brien (2006) and Osunkoya *et al*. (2007), understory and canopy species do not differ, in terms of their height-diameter relationships, in the immature ontogenetic stage. Individuals of *A. polyneuron* are slow-growing and can remain in the understory for a long time. It is possible that more robust stems are needed in order to increase physical stability necessary, allowing such individuals to persist in the understory before being recruited to the higher strata when the conditions become appropriate (Kohyama *et al*. 2003; King *et al*. 2006; Osunkoya *et al*. 2007; Martínez-Sánchez *et al*. 2008).

We observed high variability among individuals of the same species, as evidenced by the low correlation coefficient values obtained for many of the allometric relationships. This suggests high heterogeneity of the environment in the horizontal space, as well as in the vertical space. However, in general, understory species showed less architectural variability than did the canopy/emergent layer species. Therefore, individuals of understory species have less crown plasticity than do those of canopy/emergent layer species, as has been previously reported (Valladares *et al*. 2002; Portsmuth & Niinemets 2007; Martínez-Sánchez *et al*. 2008; Vicent & Harja 2008; Vieilledent *et al*. 2010). Higher crown plasticity indicates that the canopy/emergent layer species, when developing in the understory of the forest, can be more flexible in allocating resources for growth in height, diameter and crown expansion than can understory species, giving the former important adaptive advantages (Vicent & Harja, 2008). As observed in this and other studies, canopy/emergent layer species make a greater investment in vertical growth, which favors their access to the canopy in order to achieve their reproductive size (Poorter *et al*. 2006). According to King (1990) competition for light is the primary factor responsible for the evolution and maintenance of the shape of individual trees and even a small advantage in light capture can significantly increase carbon absorption (Bohlman & O'Brien 2006; Valladares & Niinemets 2008). Therefore, greater crown plasticity is an important feature for competition and survival under a closed canopy (Alves & Santos, 2002).

In the present study, by comparing the architecture of individuals (height between 0.5 to 3 m) of tree species in a semideciduous forest, we observed significant differences between species of different ecological groups, in terms of the growth forms of individuals. These differences might be due to a trade-off between vertical and lateral growth. Our results indicate that, in a forest environment, where light is the most limiting resource, although understory species show less crown plasticity, all six species evaluated (understory and canopy/emergent layer species alike) are better able to exploit the light conditions in the understory of the forest. However, because they are more light-demanding, canopy species showed a growth form that probably allows greater light capture in the understory. The architectural variations observed in the growth stage studied here, in individuals of populations of plants belonging to different forest strata, are probably crucial to the survival of these individuals, contributing greatly to the reproductive success of the species. Our results also indicate that, as observed empirically in the field, the understory of a semideciduous forest is heterogeneous. It is likely that, within this ecosystem, even in the understory, the availability of light and water is sufficient for the growth and development of many species of different strata, which occupy slightly different niches. This adaptation to different niches can be evidenced indirectly by architectural variations, which result in high biodiversity in the understory.

Overall, we found that species of the same stratum did not show a pattern. Our results indicate that there is a need to expand the measures of other species in each stratum, as a way of trying to identify a more consistent pattern.

References

Aiba, S. & Kohyama, T. 1996. Tree species stratification in relation to allometry and demography in a warm-temperate rain forest. **Journal of Ecology 2**: 207-218.

Aiba, S. & Kohyama, T. 1997. Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. **Journal of Ecology 5**: 611-624.

Abe, N. & Yamada, T. 2008. Variation in allometry and tree architecture among *Symplocos* species in a Japanese warm-temperate forest. **Journal Plant Research 121**: 155-16.

Alves, L.F. & Santos, F.A.M. 2002. Tree allometry and crown shape of four tree species in Atlantic rain forest, south-east Brazil. **Journal Tropical Ecology 18**: 245-260.

Ackerly, D.D. 1996. Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. Pages 619-658 in S. S. Mulkey, R. L. Chazdon & A. P. Smith, editors. Tropical forest plant physiology. **Chapman and Hall**, London.

Ackerly, D.D. & Donoghue, M.A. 1998. Leaf size, sapling allometry and Corners rules: A phylogenetic study of correlated evolution of maples (Acer). **American Naturalist**, de 1998.

Barker, M. G.; Pinard, M. & Nilus, R. 2006. Allometry and shade tolerance in pole-sized trees of two contrasting dipterocarp species in Sabah, Malaysia. **Biotropica 28**: 437-440.

Bianchini, E.; Pimenta, J. A. & Santos, F.A.M. 2001. Spatial and Temporal Variation in the Canopy Cover in a Tropical Semi-Deciduous Forest. Brazilian **Archives of Biology and Technology 44**: 269-276.

Bohlman, S.A. & O'Brien, S.T. 2006 Allometry, adult stature and regeneration requirements of 65 tree species on Barro Colorado Island, Panama. **Journal of Tropical Ecology 22**: 123-136.

Bongers, F.; Popma, J.; Meque Del Castillo, J.; Carabias, J. 1988. Structure and floristic composition of the low-land rain forest of Los Tuxtlas, Mexico. **Vegetatio 74**: 55-80.

Chave, J.; Andalo, C.; Brown, S.; Cairns, M.A.; Chambers, J.Q.; Eamus, D.; Folster, H.; Fromard, F.; Higuchi, N.; Kira, T.; Lescure, J.P.; Nelson, B.W.; Ogawa, H.; Puig, H.; Riera, B. & Yamakura, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. **Oecologia 145**: 87-99.

Condict, R. 2006. The importance of demographic niches to tree diversity. **Science 313**: 98-101.

Dahle, G.A. & Grabosky, J. C. 2009. Review of literature on the function and allometric relationships of tree stems and branches. **Arboriculture & Urban Forestry 35**: 311-320.

EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária. 1999. **Sistema Brasileiro de Classificação de Solos**. Rio de Janeiro: EMBRAPA Solos,.

Huitema, B. E. 1980. **The analysis of covariance and alternatives**. New York, John Wiley & Sons.

IAPAR - Instituto Agronômico do Paraná. 2000. **Cartas climáticas do estado do Paraná**. Londrina, Fundação Instituto Agronômico do Paraná.

Iida, Y.; Kohyama, T.S.; Kubo, T.; Kassim, A.R.; Poorter, L.; Sterck, F. & Potts, D. 2011. Tree architecture and life-history strategies across 200 co-occurring tropical tree species. **Functional Ecology 25**: 1-9.

King, D.A. 1990. Allometry of saplings and understorey trees of a Panamanian forest. **Functional Ecology 4**: 27-32.

King, D.A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. **American Journal of Botany 81**: 948-957.

King, D.A. 1996 Allometry and life history of tropical trees. **Journal of Tropical Ecology 12**: 25-44.

King, D.A.;Wright, S.J & Connell, J.H. 2006. The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. **Journal of Tropical Ecology 22**: 11-24.

Kohyama, T. 1987 Significance of architecture and allometry in saplings. **Functional Ecology 1**: 399-404.

Kohyama, T. 1991. Simulating stationary size distribution of trees in rain forests. **Annals of Botany 62**: 173-180.

Kohyama, T. & Hotta, M. 1990. Significance of allometry in tropical samplings. **Functional Ecology 4**: 515-521.

Kohyama, T.; Suzuki, K.; Partomihardjo, T.; Yamada, T. & Kubo, T. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. **Journal of Ecology 91**: 797-806.

Köppen, W. 1948. **Climatología:** con un estudio de los climas de la tierra. México D.F., Fondo de Cultura Económica.

Lusk, C. H. 1996. Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile. **Revista Chilena de História Natural 69**: 401-11.

Lusk, C. H.; Falster, D. S.; Jara-Vergara, C. K.; Jimenez-Castillo M. & Saldaña, A. 2008 Ontogenetic variation in light requirements of juvenile rainforest evergreens. **Functional Ecology 22**: 454-459.

Martínez-Sánchez, J.L.; Meave, J.A. & Bongers, F. 2008. Light-related variation in sapling architecture of three shade-tolerant tree species of the Mexican rain Forest. **Revista Chilena de História Nacional 81**: 361-371.

McMahon, T.A. 1973. Size and shape in biology. **Science 179**: 1201-1204.

Moles, A.T.; Warton, D.I.; Warman, L.; Swenson, N.G.; Laffan, S.W.; Zanne, A.E.; Pitman, A.; Hemmings, F.A. & Leishman, M.R. 2009. Global patterns in plant height. **Journal of Ecology 97**: 923-932.

O'Brien, S.T.; Hubbell, S.P.; Spiro, P.; Condit, R. & Foster, R.B. 1995. Diameter, height, crown, and age relationships in eight neotropical tree species. **Ecology 76**: 1926-1939.

Osunkoya, O.O.; Omar-Ali, K.; Amit, N.; Dayan, J.; Daud, D.S. & Sheng, T.K. 2007. Comparative height crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. **American Journal of Botany 94**: 1951-1962.

Parish, R.; Nigh, G.D. & Antos, J.A. 2008. Allometry and size structure of trees in two ancient snow forests in coastal British Columbia. **Canadian Journal of Forest Research 38**: 278-288.

Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. **Functional Ecology 13**: 396-410.

Poorter, L. & Werger, M.J.A. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. **American Journal of Botany 86**: 1464-1473.

Poorter, L.; Bongers, L. & Bongers, F. 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. **Ecology 87**: 1289-1301.

Poorter, L.; Bongers, F.; Sterck, F.J. & Wöll, H. 2003. Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. **Ecology 84**: 602-608.

Poorter, L.; Bongers, F.; Sterck, F.J. & Wöll, H. 2005. Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. **Journal of Ecology 93**: 256-267.

Portsmuth, A. & Niinemets, U. 2007. Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. **Functional Ecology 21**: 61-77.

Shukla, R.P. & Ramakrishnan, P.S. 1986. Architecture and growth strategies of tropical trees in relation to successional status. **Journal of Ecology 74**: 33-46.

Soares-Silva, L.H. & Barroso, G. M. 1992. Fitossociologia do estrato arbóreo da floresta na porção norte do Parque Estadual Mata dos Godoy, Londrina, PR, Brasil. Pp. 101-112. In: **Congresso da Sociedade Botânica de São Paulo**, 8, Campinas. Anais do VIII Congresso da Sociedade Botânica de São Paulo, Campinas.

Sokal, R.R. & Rohlf, F.J. 1981. **Biometry**. San Francisco, W.H. Freeman.

Snedecor, G.W. & Cochram, W.G. **Statistical methods**. Ames: Iowa State University Press, 1967.

Sposito, T.C. & Santos, F.A.M. 2001. Scaling of stem and crown in eight *Cecropia* (Cecropiaceae) species of Brazil. **American Journal of Botany 88**: 939-949.

Sterck, F.J. 1999. Crown development in tropical rain forest trees in gaps and understorey. **Plant Ecology 143**: 89-98.

Sterck, F.J. & Bongers, F. 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. **American Journal of Botany 85**: 266-272.

Sterck, F.J. & Bongers, F. 2001. Crown development in tropical rain forest trees: patterns with tree height and light availability. **Ecology** 89: 1-13.

Sterck, F.J.; Bongers, F. & Newbery, D.M. 2001. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. **Plant Ecology 153**: 279-292.

Sterck, F.J.; Clark, D.B.; Clark, D.A. & Bongers, F. 1999. Light fluctuations, crown traits, and response delays for tree saplings in a Costa Rican lowland rain forest. **Journal of Tropical Ecology 15**: 83-95.

Sterck, F.J.; Martínez-Ramos, M.; Dyer-Leal, M.G.; Rodríguez-Velázquez, J. & Poorter, L. 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. **Functional Ecology 17**: 194-200.

Torezan, J.M.D. 2006. **Ecologia do Parque Estadual Mata dos Godoy**. Londrina, Itedes.

Valladares, F. & Niinemets, Ü. 2008 Shade tolerance, a key plant feature of complex nature and consequences. **Annual Review of Ecology, Evolution, and Systematics 39**: 237-57.

Valladares, F. & Niinemets, U. 2010. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annual Review of Ecology, Evolution, and Systematics 39: 237-259.

Valladares, F.; Saldaña, A. & Gianoli, E. 2012. Costs versus risks: Architectural changes with changing light quantity and quality in saplings of temperate rainforest trees of different shade tolerance. **Austral Ecololy 36**: 1-9.

Valladares, F.; Skillman, J. B. & Pearcy, R. W. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: a case of morphological compensation. **American Journal of Botany 89**: 1275-1284.

Vieilledent, G.; Courbaud, B.; Kunstler, G.; Dhôte, J.F. & Clark, J.S. 2010. Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. **Oecologia 163**: 759-773.

Vincent, G. & Harja, D. 2008. Exploring Ecological Significance of Tree Crown Plasticity through Three-dimensional Modelling. **Annals of Botany 101**: 1221-1231.

Vicente, R.F. O Parque Estadual Mata dos Godoy. In: Torezan, J.M.D. (Ed), **Ecologia do Parque Estadual Mata dos Godoy**. Londrina, Itedes, 2006.

Weiner, J. 2004. Allocation, plasticity and allometry in plants. **Perspectives in Plant Ecology, Evolution and Systematics 6**: 207-215.

Zar, J.H. **Biostatistical analysis**. 2nd ed. New Jersey, Prentice Hall. 1984.