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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Received: 16 February, 2013. Accepted: 13 September, 2013

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 & Kohyama 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...
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 m². 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 gonoarpum (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: 0.25π × D1 × D2 (Bongers et al. 1988; Martínez-Sánchez et al. 2008). The vertical crown area was also estimated as an ellipse: 0.25π × (D1+D2/2) × 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 (Martinez-Sanchez 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; Martinez-Sanchez 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 (Martinez-Sanchez 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 (α = 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 y). 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 & Cochran 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 (r²) was p<0.001, corresponding to an r²>0.11. High values of r² 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).

Table 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 (r², 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 r² 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).
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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 $r^2$) 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 | $a$   | $b$   | $r^2$ | $a$   | $b$   | $r^2$ | $a$   | $b$   | $r^2$ |
|---------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|         | 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 |   -   |   -   |   -   | 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    |       |       | 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 |

$r^2$ – 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 $r^2$ 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 $r^2$ 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.
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Table 2. Estimation of the parameters of linear regressions (a, b and r²) 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      | r²   | a      | b      | r²   |
|--------------------------|--------|--------|------|--------|--------|------|
|                          | 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               | D per VCA | D per CD |
| 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   | D per VCA | D per CD |
| 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               | D per BL | D per HS |
| 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   | D per BL | D per HS |
| 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 r²>0.11 (p<0.001; ANOVA).

cost of leaf support, the r² 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 r² 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 r² 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 r²) 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      | r²   | a      | b      | r²   |
|---------|--------|--------|------|--------|--------|------|
|         | 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  | -0.03 2 | 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 c | 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 r²>0.11 (p<0.001; ANOVA).
Architecture of tree species of different strata developing in environments with the same light intensity in a semideciduous forest in southern Brazil

Table 4. Estimation of the parameters of linear regressions \((a, b \text{ and } r^2)\) 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 \((n = 80 \text{ per species})\) of understory species \((Sorocea bonplandii, Inga marginata \text{ and } Actinostemon concolor)\) and canopy/emergent layer species \((Aspidosperma polyneuron, Chrysophyllum gonocarpum \text{ and } Holocalyx balansae)\) in Godoy Forest State Park, city of Londrina, state of Paraná, Brazil.

| Species          | IBD per CD | IBD per CS | IBD per VS | CD per LN | CD per HS | CD per VS | BL per CD | BL per LN | BL per VS | CLS per HS | CLS per VS | HS per VS |
|------------------|------------|------------|------------|-----------|-----------|-----------|-----------|-----------|-----------|------------|------------|-----------|
| **Understory**   |            |            |            |           |           |           |           |           |           |            |            |           |
| S.b              | 0.358      | 1.52 a     | 0.408      | 1.05 b    | 0.83      | 0.125     | -         | -         | ns        | -          | -          | ns        |
| I.m              | 0.214      | 1.08 ab    | 0.465      | 0.93 b    | 1.04      | 0.141     | 296 a     | -357      | 0.152     | -357       | 0.152      |           |
| A.c              | -          | -          | ns         | -         | 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        | -         | -9       | 0.317     |           |            |            |           |
| A.p              | 0.339      | 0.853 ab   | 0.158      | 1.10 a    | 1.64      | 0.178     | -         | -         | ns        | -          | -          | ns        |
| **Understory**   |            |            |            |           |           |           |           |           |           |            |            |           |
| S.b              | -14.0      | 118 b      | 0.517      | 42.9      | 87.0 b    | 0.337     | -         | -         | ns        | -          | -          | 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     |           |            |           |
| **Understory**   |            |            |            |           |           |           |           |           |           |            |            |           |
| S.b              | 0.132      | 1.61 b     | 0.601      | -28.3     | 268 b     | 0.613     | -         | -         | ns        | -          | -          | 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        |           |            |           |
| **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 b    | 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 \(r^2>0.11\) \((p<0.001; \text{ ANOVA})\).
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

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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 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.

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