# Ontogeny, allometry and architecture of *Psychotria tenuinervis* (Rubiaceae)

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**ABSTRACT**

We evaluated the ontogeny of the understory shrub *Psychotria tenuinervis* Müll.Arg., considering morphological and morphometric characters. Four ontogenetic stages were identified: seedling, juvenile, immature and adult (vegetative and reproductive phases). Size measurements and allometric relationships of the stem and crown were compared between the immature and adult stages. Diameter and total height of the stem, as well as crown depth and width, increased throughout the ontogenetic stages and differed among immature, vegetative adult and reproductive adult individuals. The number of branches was lower in immature individuals than in vegetative and reproductive adult individuals but did not differ between the last two. The bifurcation ratio did not vary during ontogenetic development. In general, allometric relationships between the stem and the crown were similar among the ontogenetic stages. Although there was a progressive increase in size during ontogenetic development, there was no change in the allometric relationships between the size variables and architecture of *P. tenuinervis*, indicating that the form of individuals does not change over the course of ontogeny.

**Key words**: allometry, architecture, branching pattern, ontogenetic stages, understory

## Introduction

In population biology studies, age, developmental stage and size can be used, either separately or in combination, to categorize plants (Begon *et al.* 1996; Silvertown & Lovett-Doust 1993). The sequence of developmental phases of an individual is called ontogeny (Gatsuk *et al.* 1980). The average duration of the ontogenetic stages of each species is genetically fixed. However, given that environmental conditions can vary greatly, different individuals can reach certain ontogenetic stages at different times (Gatsuk *et al.* 1980). Therefore, the study of ontogenetic stages in plant populations supplies much more information with ecological meaning than does the study of age and the size of structures (Silvertown & Lovett-Doust 1993).

Structural differences during ontogenetic development in different plant groups involve the presence/absence of cotyledons, ramification patterns, stem type, stipe, reproductive structures, and the root system (Souza *et al.* 2000, 2003; Lienert & Fischer 2003; Logofet *et al.* 2006; Miranda-Melo *et al.* 2007; Bernacci *et al.* 2008; Fidelis *et al.* 2008; Schmucki & de Blois 2009). Morphological changes during ontogenetic development can be evaluated through the study of plant architecture (Bell 1991; Barthélémy & Caraglio

2007), which describes the inherited branching pattern of species, such as their characteristics related to the direction of growth, activity in time and destiny (Barthélémy & Caraglio 2007; León Enriquez *et al.* 2008).

Morphometric characteristics, such as stem and crown size, and allometry have been used to facilitate the characterization and delineation of ontogenetic stages (Souza *et al.* 2000; 2003). The allometric relationship between height and stem diameter indicates the amount of support that the plant requires within given environmental conditions (Claussen & Maycock 1995). Morphometric characteristics include total height; stem diameter; number and size of the leaves; rosette diameter; and number of branches (Souza *et al.* 2000, 2003; Lienert & Fischer 2003; Logofet *et al.* 2006; Miranda-Melo *et al.* 2007; Bernacci *et al.* 2008; Fidelis *et al.* 2008; Schmucki & de Blois 2009).

Plant ontogeny studies have been carried out with palms (Souza *et al.* 2000, 2003; Bernacci *et al.* 2008) and herbaceous species (Lienert & Fisher 2003; Logofet *et al.* 2006; Fidelis *et al.* 2008, Schmucki & de Blois 2009). However, there have been few studies on shrub and tree species (Gatsuk *et al.* 1980; Miranda-Melo *et al.* 2007). Due to its dominance in the tropical and subtropical forest understory, the genus *Psychotria* has been used as a model to infer

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patterns of speciation (Hamilton 1989); the specialization of habitats (Kinupp & Magnusson 2005); the association between crown architecture and light capture efficiency (Pearcy *et al.* 2004); and the plastic phenotypic response to light (Valladares *et al.* 2000).

The aim of this study was to identify and describe the ontogenetic stages of the shrub *Psychotria tenuinervis* Müll. Arg. and evaluate changes in individual size, allometry and architecture during ontogenetic development. Because *P. tenuinervis* is a shade-tolerant shrub species, we expected differences during ontogenetic development, mainly related to architecture, given that species adapted to low-light conditions have a crown that is wide in order to intercept light over a large area and shallow in order to minimize self-shading (Givnish 1988).

## Materials and methods

### Study site and species

This study was carried out in the Serra de Palmital coastal mountain range, near the municipality of Saquarema, in southeastern Brazil. The study site (22°50'S; 42°28'W) comprised 1200 ha of Atlantic Forest at an elevation of 30-400 m. According to the Köppen system of classification, the climate is type Cwa (Veanello & Alvez 1991), defined as warm (up to 18°C) and semi-humid (with 4-6 dry months per year). In 2003, minimum and maximum monthly temperatures ranged from 12.6°C to 19.0°C and 23.8°C to 34.2°C respectively (Ramos & Santos 2006). The vegetation in the study area is evergreen forest, with 39 families and 132 morphospecies sampled in a 0.75 ha area (Ribeiro *et al.* 2009).

Rubiaceae has a pantropical distribution, comprising approximately 550 genera and 9000 species (Souza & Lorenzi 2005). *Psychotria* is the largest genus in Rubiaceae, with approximately 2000 species (Davis *et al.* 2001), and contains mainly shrubs and small trees, which are dominant in the tropical and subtropical forest understory (Hamilton 1990; Valladares *et al.* 2000). *Psychotria tenuinervis* is a shrub that reaches 1-5 m height, endemic to fragments of Atlantic Forest in the state of Rio de Janeiro, and common in the understory (Gomes *et al.* 1995). Flowers are produced within 1-3 months, whereas the fruiting lasts for 3-6 months per year (Ramos & Santos 2005). Vegetative growth has been observed for a few individuals of *P. tenuinervis*.

### Data collection

In order to characterize the ontogenetic stages of *Psychotria tenuinervis* individuals (Gatsuk *et al.* 1980), we registered the presence/absence of cotyledons, ramifications and reproductive structures, such as flowers and fruits. We also registered the total height and diameter at ground level of immature and adult individuals. To evaluate the architectural pattern of immature and adult individuals,

we measured the fork height, crown diameter (east-west and north-south cross sections), total number of branches, crown depth, crown width, and bifurcation ratio. Individuals were monitored for a period of 18 months.

Fork height was defined as the vertical distance between the stem base and lowest major branch, which itself is defined as a branch that is at least half as thick as the main stem at the same height (Osunkoya *et al.* 2007). Crown depth was calculated as the difference between total height and fork height (Osunkoya *et al.* 2007). Crown width was determined as the average diameter of the east-west and north-south cross sections of the crown (Poorter *et al.* 2003).

To evaluate the number of branches, the branches were ordered, with each terminal branch designated the first order (Strahler 1957, cited in Steingraeber *et al.* 1979, Sposito & Santos 2001a). Where two first-order branches met, the resulting segment was designated the second order. For the meeting of two branches of unequal order, the resulting branch retained the name of the class of the next-highest order. Therefore, the stem would be the class of higher order for the plant. The bifurcation ratio was calculated with the Motomura formula (Motomura 1947, cited in Steingraeber *et al.* 1979):

$$Br = (N - N_{max})/(N - N_1)$$

where $Br$ is the bifurcation ratio; $N$ is the total number of branches; $N_{max}$ is the number of higher-order branches, and $N_1$ is the number of first-order branches.

### Statistical analysis

After testing for normality and homoscedasticity (Zar 1996), we used ANOVA to compare morphometric characters among ontogenetic stages. Analyses were performed with the Systat program, version 10.2 (SPSS 2000).

For each ontogenetic stage, we compared the allometric relationships between total height and diameter at ground level using ANCOVA, in which the angular and linear coefficients of each regression analysis are compared. When the difference was significant, we used *post hoc* Scheffé tests through the program Ancova33 (Santos 1997).

## Results

### Ontogenetic stages

On the basis of the morphological and morphometric characteristics observed over the 18-month study period, we defined the four ontogenetic stages for *Psychotria tenuinervis*:

➢ Seedling (Fig. 1a)—In the seedling stage, the cotyledons are green or dry and are darker than are the other leaves. Some individuals exhibit cotyledons with a whitish color along the midrib. Some seedlings present one or more pairs of opposing primary leaves, without stem ramification. Growth is monopodial, and the stem can be lignified or not.

➢ Juvenile (Fig.1b)—In the juvenile stage, there are no cotyledons, growth is monopodial, and the stem has no branches. Some individuals present flexible, green stems, whereas others have woody stems, especially near the base.

➢ Immature (Fig. 1c)—In the immature stage, growth is sympodial and the stem is fully lignified, with orthotropic and plagiotropic branches. The total height is < 1 m.

➢ Adult (Fig. 1d and 1e)—In the adult stages, growth is sympodial and the stem has orthotropic and plagiotropic branches. The total height is ≥ 1 m. This stage was divided into two phases:

• Vegetative (Fig. 1d)—In the vegetative adult phase, individuals present no flowers or fruits.

• Reproductive (Fig. 1e and 1f)—In the vegetative adult phase, individuals present flowers, fruits or both.

Leaf shape was similar among the ontogenetic stages (Fig. 1). Analyses of morphometric data showed that total height, diameter at ground level, crown depth and crown width increased during ontogenetic development and differed among immature, vegetative adult and reproductive adult individuals (Tab. 1; Fig. 2). Individuals presented between 3 and 2020 first- to seventh-order branches. Although immature individuals showed fewer branches than did vegetative and reproductive adult individuals, there was no difference between vegetative and reproductive adults in terms of the number of branches (Tab. 1; Fig. 2). The bifurcation ratio did not vary during ontogenetic development (Tab. 1; Fig. 2).
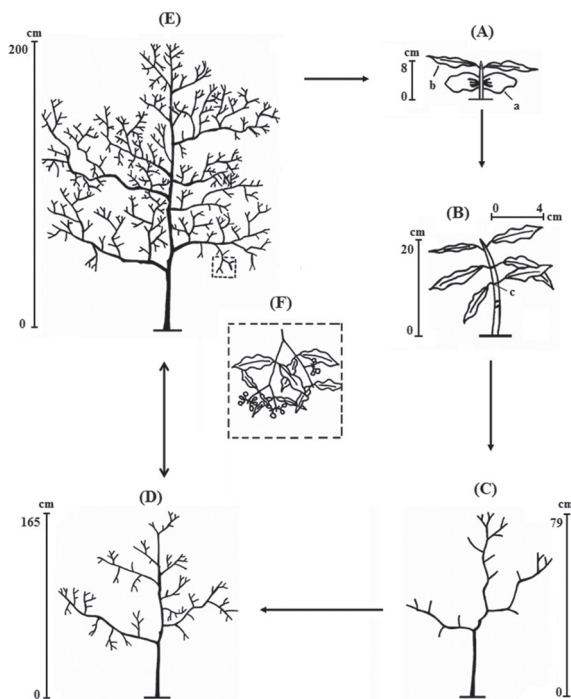


**Figure 1.** Schematic representation of the ontogenetic stages of *Psychotria tenuinervis* Müll.Arg.: (A) seedling; (B) juvenile; (C) immature; (D) adult (vegetative phase); and (E) adult (reproductive phase). In F, detail of branch with fruit. a – cotyledon; b – primary leaves; c – unbranched stem.

*Stem and crown relationships*

In general, the relationships between the stem and crown remain constant during ontogenetic development in *Psychotria tenuinervis*. Linear regression analyses revealed that nearly all of the associations between the crown and stem parameters were significant (p<0.001), the exception being the relationship between the number of branches and crown depth in reproductive adults (ANOVA: $F_{1,13}$=2.70, p=0.12).

No significant differences were found among the immature and adult stages (vegetative and reproductive phases) in terms of the relationship between stem diameter and total height, neither for the angular coefficient (ANCOVA: $F_{2,72}$=0.15, p=0.86; Tab. 2) nor for the linear coefficient (intercept; ANCOVA: $_{F2,74}$=0.20, p=0.82; Tab. 2).

The relationship between total height and crown depth did not differ among immature, vegetative and reproductive adult individuals, for the angular coefficient (ANCOVA: $F_{2,74}$=3.69, p=0.03; Tab. 2), whereas the linear coefficient differed significantly between immature and reproductive adult individuals (ANCOVA: $F_{1,53}$=5.79, p=0.02; Tab. 2), but not between vegetative and reproductive adult individuals (ANCOVA: $F_{1,46}$=0.51, p=0.49; Tab. 2). This suggests that crown depth increases in parallel with the increase in total height during the immature stage. The relationship between total height and crown width did not differ between ontogenetic stages for the angular coefficient (ANCOVA: $F_{2,74}$=0.004, p=0.99, b=0.76; Tab. 2) or the linear coefficient (ANCOVA: $F_{2,76}$=0.008, p=0.98; a=−0.23; Tab. 2).

The relationship between total height and the number of branches did not differ during ontogenetic development, for the angular coefficient (ANCOVA: $F_{2,54}$=2.11, p=0.13, common b=2.18; Tab. 2) or the linear coefficient (ANCOVA: $F_{2,56}$=0.39, p=0.68, common a=1.96; Tab. 2)

The angular coefficient for the relationship between the number of branches and crown depth differed between immature and vegetative adult individuals (ANCOVA: $F_{2,54}$=14.37, p<0.001; Tab. 2). The angular coefficient for the relationship between the number of branches and crown width differed only between immature and vegetative adult individuals (ANCOVA: $F_{2,54}$=3.68, p=0.03; Tab. 2). The linear coefficient for that same relationship differed between immature and reproductive adult individuals (ANCOVA: $F_{1,42}$=0.66, p=0.43; Tab. 2) but not between vegetative and reproductive adults (ANCOVA: $F_{1,27}$=2.69, p=0.11; Tab. 2).

# Discussion

*Ontogenetic stages*

The overlap of some measurements of size and allometric relationships among immature, vegetative and reproductive adult individuals indicates that size does not always correspond to individual age. Hence, individuals of the same size may be at different ontogenetic stages and

**Table 1.** Morphometric characteristics of *Psychotria tenuinervis* Müll.Arg. (immature and adult individuals), in a fragment of Atlantic Forest in the Serra de Palmital coastal mountain range of southeastern Brazil.*

| Ontogenetic stage (m) | | Height (cm) | Diameter (m) | Crown depth (m) | Crown width | Number of branches | Bifurcation ratio |
|---|---|---|---|---|---|---|---|
| Immature | range | 0.16-0.99 | 0.08-1.29 | 0.01-0.99 | 0.13-0.71 | 3-200 | 2.00-4.00 |
| | mean | 0.51[a] | 0.53[a] | 0.37[a] | 0.35[a] | 36.33[a] | 3.05[a] |
| | n | 31 | 31 | 31 | 31 | 30 | 30 |
| Adult | | | | | | | |
| Vegetative phase | range | 1.13-3.05 | 0.94-3.98 | 0.67-2.48 | 0.53-2.00 | 38-1962 | 2.63-3.45 |
| | mean | 1.75[b] | 1.72[b] | 1.23[b] | 0.92[b] | 481.93[b] | 3.02[a] |
| | n | 24 | 24 | 24 | 24 | 15 | 15 |
| Reproductive phase | range | 1.05-4.40 | 0.85-4.46 | 0.69-4.22 | 0.58-2.15 | 126-2020 | 2.71-3.48 |
| | mean | 2.53[c] | 2.43[c] | 1.96[c] | 1.22[c] | 742.80[b] | 3.01[a] |
| | n | 25 | 23 | 25 | 25 | 15 | 15 |
| ANOVA | distribution | $F_{2,77}=91.41$ | $F_{2,75}=49.92$ | $F_{2,77}=57.98$ | $F_{2,77}=64.35$ | $F_{2,57}=16.59$ | $F_{2,57}=0.07$ |
| | p | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.932 |

*Means sharing the same letter within a column do not differ significantly (ANOVA and Tukey's test).
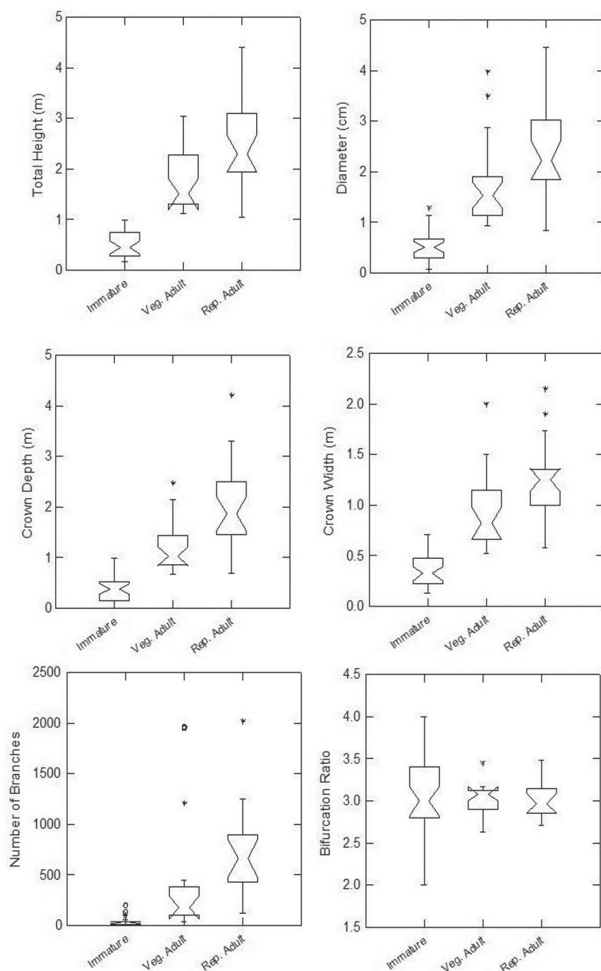


**Figure 2.** Box-plot of morphometric characters for the ontogenetic stages of *Psychotria tenuinervis* Müll.Arg. The length of each box encompasses the two central quartiles (50% of the central values), in which the narrowest part of the box represents the median and the narrowing region is the confidence interval (McGill *et al.* 1978). Asterisks and circles are outliers. Where confidence intervals overlap, the median is equal between the stages.
A-vp – Adult-vegetative phase; A-rp – Adult-reproductive phase.

may differ in terms of their use of environmental resources at a given time and in a given space (Gatsuk, *et al.* 1980). The identification and characterization of the ontogenetic stages of *Psychotria tenuinervis* is partly consistent with the classification system devised by Gatsuk *et al.* (1980): seed, seedling, juvenile, immature, virginile, reproductive (young, mature, old), subsenile and senile.

Seedlings have cotyledons, characteristically with partial heterotrophic nutrition showing vestiges of embryonic structures (Gatsuk *et al.* 1980). We found that, during the 18 months of our study period, *Psychotria tenuinervis* seedlings showed low density in comparison with the subsequent stages (Rosseto *et al.*, unpublished data). In a study of eight *Psychotria* species, Paz & Martínez-Ramos (2003) found that, at two months after emergence, individuals no longer presented cotyledons and developed a pair of true leaves, indicating that the seedling stage is ephemeral in this genus.

Juveniles presented monopodial growth and stems without embryonic structures, although the leaf shape remained similar in the subsequent stages. In *Psychotria tenuinervis*, the change from monopodial to sympodial growth occurs at the immature stage and is likely associated with greater lignification of the stem, resulting in improved resistance. The immature stage can be characterized by considerable growth, in terms of the total height and the crown parameters, especially crown depth.

It was necessary to use a size descriptor in order to differentiate between the pre-reproductive and reproductive stages in *Psychotria tenuinervis*, because of the lack of visible macro-morphological markers. In addition, because no permanent reproductive markers were found, it was necessary to adapt the classification of Gatsuk *et al.* (1980) by creating an adult ontogenetic stage (vegetative and reproductive phases). The vegetative adult phase includes the pre-reproductive, reproductive and post-reproductive periods because it includes individuals who did not reproduce, individuals who already have reproduced, and senile

**Table 2.** Linear regressions ($\log_{10}$) and statistical parameters for morphometric characteristics of *Psychotria tenuinervis* Müll.Arg. (immature and adult individuals), in a fragment of Atlantic Forest in the Serra de Palmital coastal mountain range of southeastern Brazil.*

| Comparison<br>Ontogenetic stage | b | SE1 | a | SE2 | $r^2$ | N |
|---|---|---|---|---|---|---|
| **Height vs. Diameter** | | | | | | |
| Immature | 1.01[a] | ±0.12 | −0.01[b] | ±0.05 | 0.71 | 31 |
| Adult | | | | | | |
| Vegetative phase | 1.03[a] | ±0.19 | −0.03[b] | ±0.05 | 0.58 | 24 |
| Reproductive phase | 1.14[a] | ±0.17 | −0.06[b] | ±0.07 | 0.68 | 23 |
| **Height vs. Crown Depth** | | | | | | |
| Immature | 1.79[a] | ±0.24 | 0.01[a] | ±0.10 | 0.66 | 31 |
| Adult | | | | | | |
| Vegetative phase | 0.98[a] | ±0.12 | −0.16[b] | ±0.03 | 0.74 | 24 |
| Reproductive phase | 1.14[a] | ±0.15 | −0.18[b] | ±0.06 | 0.72 | 25 |
| **Height vs. Crown Width** | | | | | | |
| Immature | 0.77[a] | ±0.08 | −0.23[b] | ±0.04 | 0.74 | 31 |
| Adult | | | | | | |
| Vegetative phase | 0.76[a] | ±0.16 | −0.23[b] | ±0.04 | 0.51 | 24 |
| Reproductive phase | 0.76[a] | ±0.10 | −0.22[b] | ±0.04 | 0.70 | 25 |
| **Height vs. Number of Branches** | | | | | | |
| Immature | 2.01[a] | ±0.20 | 1.96[b] | ±0.08 | 0.77 | 30 |
| Adult | | | | | | |
| Vegetative phase | 3.10[a] | ±0.58 | 1.71[b] | ±0.14 | 0.69 | 15 |
| Reproductive phase | 2.13[a] | ±0.56 | 1.93[b] | ±0.23 | 0.53 | 15 |
| **Number of Branches vs. Crown Depth** | | | | | | |
| Immature | 0.86[a] | ±0.10 | −1.71 | ±0.14 | 0.73 | 30 |
| Adult | | | | | | |
| Vegetative phase | 0.19[b] | ±0.06 | −0.39 | ±0.15 | 0.44 | 15 |
| Reproductive phase | 0.21[a] | ±0.13 | −0.32 | ±0.36 | 0.17 | 15 |
| **Number of Branches vs. Crown Width** | | | | | | |
| Immature | 0.36[a] | ±0.03 | −0.96[a] | ±0.04 | 0.86 | 30 |
| Adult | | | | | | |
| Vegetative phase | 0.22[b] | ±0.06 | −0.60[b] | ±0.13 | 0.54 | 15 |
| Reproductive phase | 0.29[ab] | ±0.07 | −0.73[ab] | ±0.20 | 0.56 | 15 |

*Means sharing the same letter within a column/comparison do not differ significantly (ANCOVA and Scheffé test, p=0.05).
b – angular coefficient; SE1 – standard error (angular coefficient); a – linear coefficient; SE2 – standard error (linear coefficient); $r^2$ – coefficient of determination; N – sample size.

individuals. The reproductive adult phase includes the reproductive and post-reproductive periods. In the adult stage, sexual maturation occurs and there is an increase in the size of the organs, although this does not change the growth pattern in comparison with the pre-reproductive period.

Plant size is an important component of plant fitness, having consequences for survival and fecundity (Harper & Bell 1979; Weiner & Thomas 1986). Size is related to fecundity because plants flower and fruit only after reaching a certain size (Harper & White 1974). A size difference between vegetative and reproductive adults would indicate that energy accumulation is necessary before reproducing, and that this accumulation could only be achieved by an increase in size.

### Stem and crown relationships

Various studies have demonstrated significant differences among ontogenetic stages in terms of stem diameter-height relationships (Niklas 1993; Claussen & Maycock 1995; O'Brien *et al.* 1995; Sterck & Bongers 1998; Sposito & Santos 2001b; Alves & Santos 2002; Bohlman & O'Brien

2006; Osunkoya *et al.* 2007). For small-sized understory species, the increase in stem diameter provides the improved mechanical stability needed to survive in the lower strata (Kohyama *et al.* 2003). However, for *Psychotria tenuinervis*, no change was observed between immature and adult individuals in terms of the stem diameter-height relationships. This indicates that there is an isometric relationship between those variables, meaning that structures of different sizes have the same shape (Rich *et al.* 1986). That might be associated with the fact that understory species are less exposed to lateral wind, so that, with a minimal biomass investment in branches, stem diameter is proportional to height (Norberg 1988; Osunkoya *et al.* 2007).

Some authors have shown that understory tree species have more horizontal expansion of the crown than do other successional groups (King 1990, 1996; Kohyama & Hotta 1990; Aiba & Kohyama 1996; Sterck & Bongers 1998), although others have found the opposite or even no difference (Poorter *et al.* 2003; Osunkoya *et al.* 2007). Although *Psychotria tenuinervis* exhibited a continuous increase in crown parameters (crown depth, crown width and number of branches) during ontogenetic development, we observed no variation among ontogenetic stages in terms of the relationships between height and crown parameters. The relationship between crown depth and crown width remained similar across stages, indicating a symmetrical pattern of crown development. The bifurcation ratio did not change during ontogenetic development, indicating that the addition of new branches follows a branching pattern that apparently remains constant over the life history of *P. tenuinervis*.

In the understory, light availability is highly heterogeneous (Poorter & Arets 2003, Valladares & Niinemets 2008). At the study site, canopy openness ranged from 4.0% to 18.9%, depending on the season (Ramos & Santos 2006). Strategies of survival, growth and establishment in light gradient among understory species are related to plant size, leaf geometry, crown architecture and position, as well as physiological factors (Valladares *et al.* 2000; Poorter *et al.* 2003; Pearcy *et al.* 2004; Osunkoya *et al.* 2007). In tropical rainforests of Central America, *Psychotria* species have less physiological plasticity and lower efficiency of light absorption in canopy gaps and in the understory than do understory species of different taxa (Valladares *et al.* 2000; Pearcy *et al.* 2004). The low growth rate, photosynthesis and nutrient absorption seen in *Psychotria* genus might be a mechanism of tolerance to light stress (Kitajima 1994, Valladares *et al.* 2000, Valladares & Niinemets 2008).

In *Psychotria tenuinervis*, we observed little morphological or allometric variation between ontogenetic stages, indicating that the form of individuals does not change during ontogenetic development. Over the course of ontogenetic development, there was a progressive increase in size, although there was no change in the allometric relationships between size variables and architecture in this species. The persistence of *P. tenuinervis* in the understory might be associated with the minimal structural variations during ontogenetic development, which could be an energy-saving strategy.

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