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Allometric Relationships in *Psychotria suterella* Müll. Arg. (Rubiaceae) in a fragmented landscape of Atlantic Forest

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Abstract

The allometric relationship between diameter and height was studied in populations of *Psychotria suterella*, a common understory species of the Atlantic Forest of southeastern Brazil, in natural situations of different density and luminosity. Nine populations were sampled including three areas of continuous forest, three connected fragments and three isolated fragments, all within a fragmented Atlantic Forest landscape. In conditions of higher density and light availability, young individuals possessed a greater increase in height per unit of diameter than adult individuals. In all the varying conditions of light and density, the allometric pattern of young growth did not change. On the other hand, adult individuals exhibited a greater increase in height in high-density conditions. There were differences among allometric coefficients of some of the populations. In fragments where the canopy openness was greater, the population possessed individuals with greater height. On a smaller scale, light and density affected the allometric relationship of individuals. On a larger scale, populations with a low density of individuals, and which were subjected to greater luminosity, varied greatly in growth form.

Keywords: Allometry; Fragmented landscape; Light; *Psychotria suterella*; Tropical forest; Understory.

Introduction

Relationships of resource allocation in plants, or in other words the use of reserves in certain parts of a plant according to need such as growth and reproduction, may be related to life stage, the environmental situations that the plant is exposed to and the phenotypic characteristics of the species. The allometric specialization of plant species in tropical forests has been related to patterns of adaptation to obtain light (Kohyama 1987, King 1990).

Allometric studies of plants have focused on interspecific comparisons of species occupying different vertical strata of the forest (Aiba & Kohyama 1996, 1997, O'Brien *et al.* 1995, Kohyama 1987, 1991, Alves & Santos 2002, Batista et al. 2014) and levels of shade tolerance (King 1990, 1996, O'Brien *et al*. 1995, Claussen & Maycock 1995, Poorter & Werger 1999, Poorter *et al.* 2003, Batista et. al 2014). Studies indicate that understory species have a greater investment in horizontal expansion of the crown and a low mechanical stability factor, while canopy species exhibit greater investment in height growth, thus increasing light interception, and have a greater mechanical stability factor (Kohyama & Hotta 1990, Sterck & Bongers 1998, Haddad et al. 2016).

However, there is a great deal of variation in allometric patterns, which are related to the ontogeny or size of the individuals and competitive interactions with neighboring plants (Rich *et al.* 1986, Kohyama 1991, Weiner & Thomas 1992, Alvarez-Buylla & Martinez-Ramos 1992, Niklas 1995, Sterck & Bongers 1998, Poorter & Werger 1999, Sposito & Santos 2001, Alves & Santos 2002). Individuals growing in the understory are subjected to shading caused by canopy plants and their neighbors (Holbrook & Putz 1989, Kohyama 1991). Thus, the presence of neighbors can influence the growth trajectory of a plant by local changes in luminosity (Henry & Aarssen 1999). In situations of greater density, a greater allocation of biomass to the stem for height growth would be expected, which would minimize shading by other individuals and would maximize exposure to radiance (Holbrook & Putz 1989, Henry & Aarssen 1999).

Secondary and fragmented forests typically possess a low density of large trees and a significant reduction in canopy cover, which alters the luminosity and intensity of winds within these environments, and thus leads to structural modifications of the vegetation (Brown & Lugo 1990, Kapos 1989, Bierregaard *et al*. 1992, Oliveira-Filho *et al.* 1997). Fragmented habitats possess environmental conditions related to the frequency and intensity of external interventions and

edge effect (Bierregaard et al. 1992). The edge effect is characterized by increased radiation flux and greater wind intensity, which contribute to increased evapotranspiration and damage to nearby vegetation (Kapos 1989, Jules 1998). This alteration to the system, with increased luminosity and changes in the density of individuals, should alter the allometric relationships in populations isolated in forest fragments. According to the expectation that density and light availability alter the allometric relationships of individual plants, the effects would also be expected in populations of plants in fragmented forests.

The objective of this study was to describe the allometric relationships between height and diameter of a common understory species, *Psychotria suterella*, and to determine: (1) if the density of individuals and luminosity affect allometry; (2) if the relationships change with plant size; and (3) if there exists allometric differences among different populations of different forest fragments.

Material and methods

Study Area

The study took place among the municipalities of Cotia and Ibiúna, in the state of São Paulo, Brazil (23°35'S to 23°50'S; 46°45'W to 47°15'W), in a landscape characterized by continuous (Reserva Florestal do Morro Grande) and fragmented secondary forest. The altitude of the region varies from 850 m to 1,100 m. The climate is Cwa (Köppen 1948), temperate and rainy. The mean maximum and minimum temperatures are 27°C and 11°C, respectively (SABESP 1997). The average annual rainfall is approximately 1,400 mm, with cold and dry months from April to August. The vegetation of the region can be classified as “Low Montane Dense Ombrophylous Forest” (Oliveira-Filho & Fontes 2000), being a transition between Dense Ombrophylous Forest and Semideciduous Seasonal Forest. The 9,400 ha forest of Morro Grande is composed of a mosaic of forests in different stages of succession.

The study involved three isolated fragments, Teresa, Dito and Carmo Messias (Te, Dit and CM, respectively); three small fragments connected to larger fragments, Maria, Luíza and Alcides (Ma, Lu and Al); and three areas within the Reserva Florestal do Morro Grande (MGA, MGB and MGC). Both the areas sampled in the fragments and the areas sampled in the continuous forest are secondary forests, having experienced anthropic interventions between approximately 50 and 80 years ago (Pardini *et al*. 2005).

The studied species, *Psychotria suterella* Müll. Arg., (Rubiaceae), exhibits a shrub-tree habit, reaching 7 m in height, is typical of the understory and is frequently found in in great density in forest fragments in the region. The species performs vegetative propagation, with the production of clones being accomplished exclusively by stolons (pers. obs.).

Data Collection

Diameter at soil height (dsh cm) and height (m) were measured for all individual *P. suterella* greater than 10 cm in height present in 100 x 50 m plots located in the six fragments of Atlantic Forest (Te, Dit, CM, Ma, Lu and Al), and the three areas within the continuous forest (Reserva Florestal do Morro Grande). Measurements were made between September 2001 and February 2002. The plots were divided into 20 sub-plots of 10 x 25 m in order to calculate density. Hemispheric photos were taken in 2003 to characterize the light environment through quantifying canopy openness. These measurements were made at 1.5 m above ground at every 10 m from 5 m inside the edge of the plot for a total of 40 sampling points in each plot of 0.5 ha.

Data Analysis

Analysis of the hemispheric photos employed the Gap Light Analyzer 2.0 program (Frazer *et al*. 1999). The canopy openness (percentage) and density of individuals per plot were categorized as high, medium and low from the distribution of the data around the median. Values of canopy openness and plant density above the 75% percentile were considered high, those below 25% were considered low, and those in-between were considered medium.

Allometric relationships were established using simple linear regressions with the function: log (dsh) = a + b*log (alt)

Where *a* is the regression line intercept with the y-axis (*log dsh*), *b* is the slope of the line, *dsh* is the diameter above the soil (cm) and *alt* is height (m)

The Type II regression model was used following Henry & Aarssen (1999) and Niklas (2004). In Type II models, new values are calculated for the slope of the regression line (b_{II}) and for the intercept (a_{II}) where:

$$b_{II} = b/r \; ; \; a_{II} = y - b_{II} * x$$

With *y* = mean of the values of *log dsh*, and *x* = mean of the values of *log alt*

The regressions were compared using values of b_{II} and $a_{II,}$ considering overlapping, or not, of the standard errors obtained for the parameters of the simple linear regression (Sposito & Santos 2001).

Since it was not possible to determine characteristics for identifying ontogenetic stages, differences in allometric relationships were assessed among individuals of different sizes, using the following height classes: ≤ 100 cm; > 100 - ≤ 200 cm and > 200 cm.

Percentages of canopy openness were arcsine transformed while the densities of individuals were $\log_{10}$ transformed. The means of density and canopy openness were compared among areas using analysis of variance and Tukey *a posteriori* test (Zar 1996).

Results

The present study found that individuals of *P. suterella* did not exhibit differences in allometric coefficients (b_{II}) among different densities (Table 1, figures 1, 2a). However, there were differences in line intercepts (a_{II}) between individuals at high and medium densities and those at low densities (Table 1, Figure 3a). Heights in areas of lower density were greater than those in areas with higher density.

There were no differences in b_{II} among environments with different canopy openness (Table 1, Figure 2b). However, when intercepts (a_{II}) were compared, areas with greater canopy openness had higher values (Table 1, Figure 3b). This finding indicates that in conditions of a greater amount of light, compared to low or intermediate levels of light, individuals have lower heights.

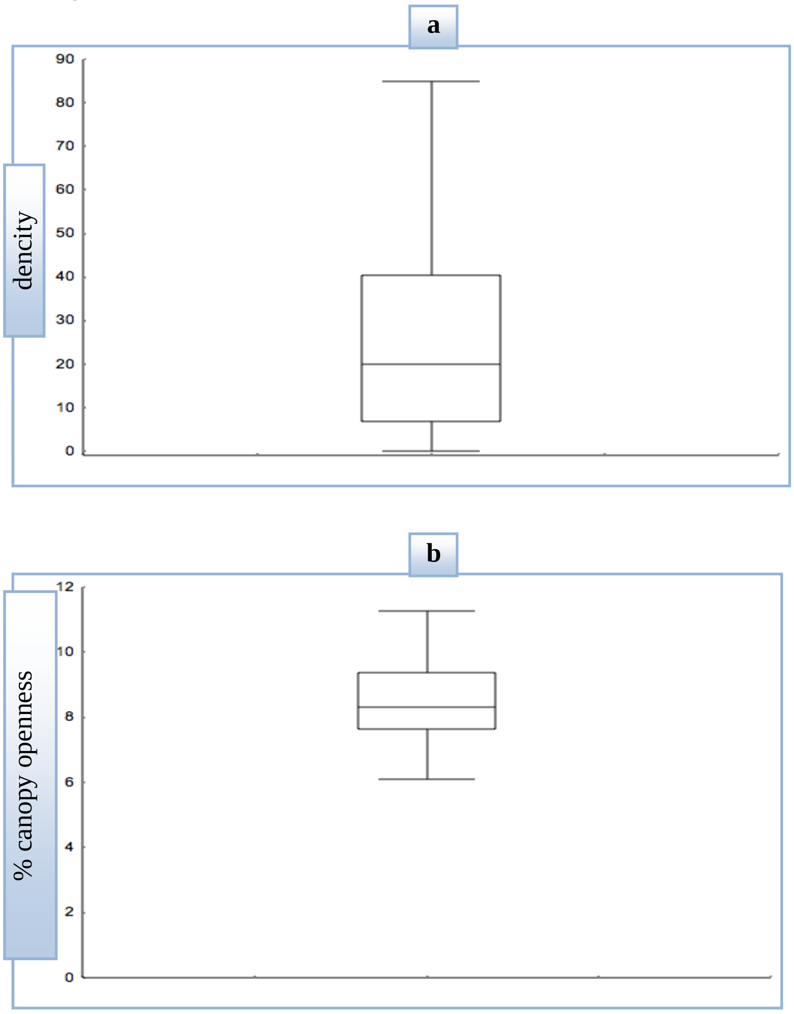

Figure 1 – Variation in the density of individuals (a) and the canopy openness (b). Horizontal line inside boxes = median; boundaries of the boxes = percentiles (25%); horizontal lines = minimum and maximum values.

Table 1 – Comparison of the coefficients of linear regression (Model Type II) and deviations of the allometric relationship between log of dsh (cm) and log of height (cm) in different situations of density and % canopy openness; n = number of individuals, r^2 = coefficient of determination, b_{II} = slope of the adjusted regression line, a_{II} = adjusted intercept, SE b = standard error of b and SE a = standard error of a. For all of the regression analyses $p < 0.01$; equal letters indicate equal values.

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	n	r^2	b_{II}	SE b	a_{II}	SE a
density						
low	1359	0.773	1.104	± 0.029	-0.200^a	± 0.011
medium	2360	0.784	1.079	± 0.021	-0.180^b	± 0.008
high	1314	0.807	1.067	± 0.026	-0.167^b	± 0.011
% canopy op.						
low	1274	0.805	1.106	± 0.027	-0.204^a	± 0.010
medium	2483	0.830	1.084	± 0.018	-0.186^b	± 0.007
high	1276	0.826	1.113	± 0.026	-0.150^c	± 0.009

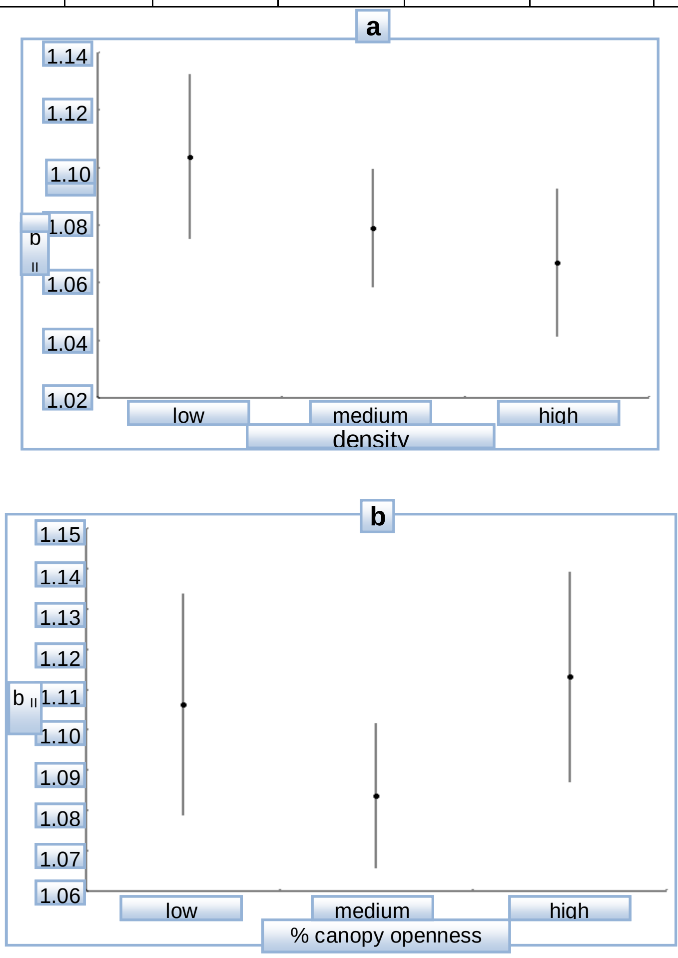

Figure 2 – Slope of the regression lines (Model Type II) and respective standard deviations of the regressions of *Psychotria suterella* at different densities of individuals (a) and canopy openness (b).

There were no differences in b_{II} among environments with different canopy openness (Table 1, Figure 2b). However, when intercepts (a_{II}) were compared, areas with greater canopy openness had higher values (Table 1, Figure 3b). This finding indicates that in conditions of a greater amount of light, compared to low or intermediate levels of light, individuals have lower heights.

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There were allometric differences among size classes in the different light and density conditions (Table 2). In situations of intermediate density and light, r^2 values were very low, which indicates a great deal of variation in the relationship between diameter and height. Comparing the values of b_{II} for different conditions of density and light, found that individuals of ≤ 100 cm in height had lower values than individuals > 200 cm, except in the case of intermediate canopy openness, in which the values of b_{II} did not differ among size classes. In general, larger individuals had higher allometric coefficients (b) than smaller individuals (Table 2). This indicates that larger individuals had a relatively greater increase in diameter than height, compared to smaller individuals.

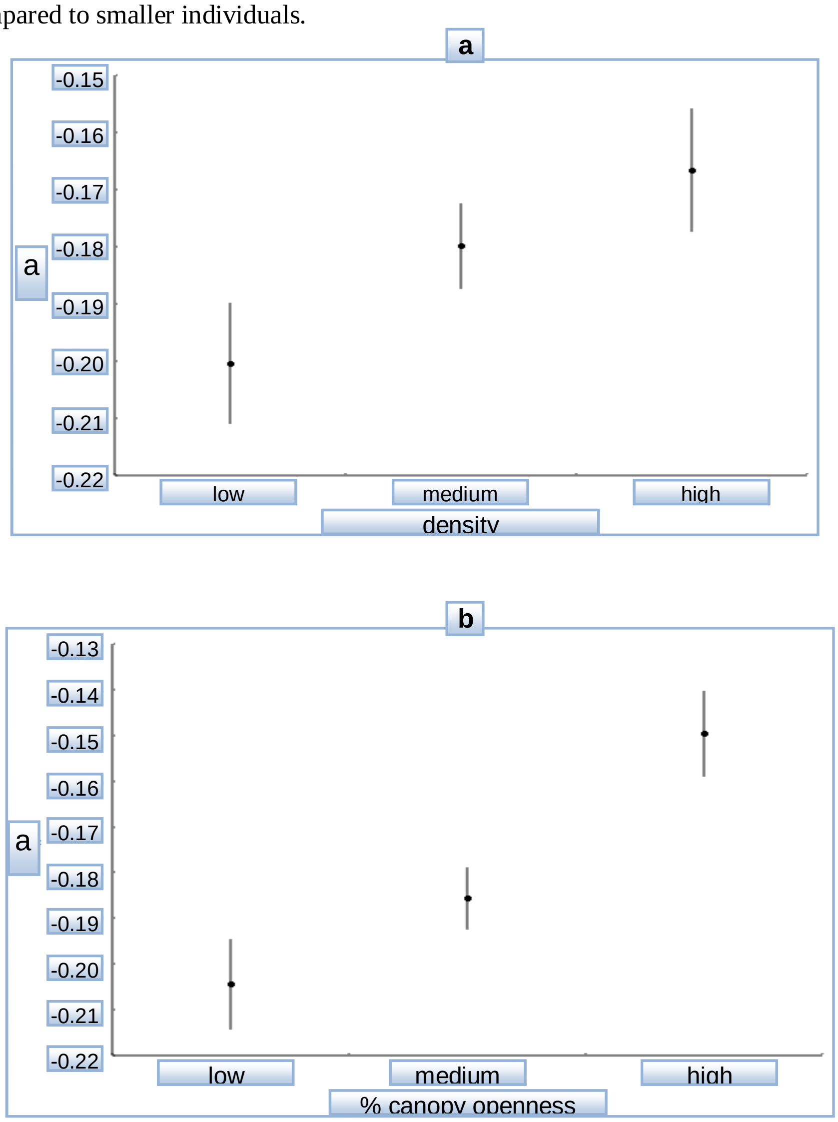

Figure 3 – Intercepts of the regression lines (Model Type II) and respective standard deviations of the regressions of individuals of *Psychotria suterella* in different densities of individuals (a) and canopy openness (b).

For individuals ≤ 100 cm, variation in light and density do not seem to interfere with their allometric characteristics (Table 2). Over all, the b_{II} ratios varied from 1.29 to 1.37. For individuals greater than 200 cm, the values of b_{II} decreased with increasing density and canopy openness (Table 2). Thus, in situations of greater canopy openness and increased density, larger individuals had thinner trunks and increased height.

Table 2 – Comparison of the coefficients of linear regression (Model Type II) and deviations of the allometric relationship between log of dsh (cm) and log of height (cm) in different situations of density and % canopy openness, for different classes of height of individuals; n = number of individuals, r^2 = coefficient of determination, b_{II} = slope of the adjusted regression line, a_{II} = adjusted intercept. The allometric relationships among individuals with r^2 less than 30 were not considered.For all of the regression analyses $p < 0.01$; equal letters indicate equal values.

Classes	N	r^2	r	b_{II}	b+	b-	a_{II}	a+	a-
Density									
Low									
< 100 cm	539	0.523	0.722	1.371 [a]	1.452	1.289	-0.119	0.183	-0.421
101-200 cm	411	0.177	0.421	1.944 [b]	2.119	1.770	-0.039	-0.007	-0.072
> 201 cm	410	0.324	0.569	1.762 [b]	1.905	1.618	-0.008	0.059	-0.074
medium									
< 100 cm	1105	0.522	0.723	1.360 [a]	1.416	1.303	-0.306	-0.286	-0.327
101-200 cm	673	0.253	0.503	1.876 [b]	2.002	1.751	-0.451	-0.428	-0.474
> 201 cm	584	0.415	0.644	1.564 [c]	1.663	1.465	-0.350	-0.305	-0.396
High									
< 100 cm	752	0.573	0.757	1.311 [a]	1.373	1.248	-0.370	-0.344	-0.397
101-200 cm	275	0.324	0.569	1.899 [b]	2.088	1.710	-0.715	-0.679	-0.750
> 201 cm	288	0.524	0.724	1.475 [a]	1.595	1.354	-0.443	-0.383	-0.503
% canopy openness									
Low									
< 100 cm	569	0.542	0.736	1.372 [a]	1.451	1.294	-0.138	-0.108	-0.168
101-200 cm	364	0.145	0.381	2.026 [b]	2.223	1.829	-0.015	0.022	-0.053
> 201 cm	351	0.381	0.617	1.730 [b]	1.876	1.585	-0.008	0.061	-0.076
medium									
< 100 cm	1128	0.538	0.734	1.355 [a]	1.410	1.300	-0.300	-0.278	-0.321
101-200 cm	660	0.276	0.526	1.844 [b]	1.966	1.722	-0.476	-0.453	-0.499
> 201 cm	697	0.381	0.618	1.483 [a]	1.571	1.394	-0.276	-0.235	-0.318
High									
< 100 cm	708	0.563	0.751	1.289 [a]	1.353	1.225	-0.364	-0.339	-0.388
101-200 cm	556	0.309	0.556	1.818 [b]	1.984	1.652	-0.658	-0.628	-0.688
> 201 cm	234	0.528	0.727	1.636 [b]	1.784	1.488	-0.557	-0.485	-0.628

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The allometric data analyzed above are for a set of populations located in nine different areas. These areas differ in the density of *P. suterella* and in the openness of the canopy (Figures 4 and 5). Differences in intercept values and similarity of slopes of the regression lines, found for areas of high density and high canopy openness, would be expected to correspond to the characteristics of the fragments. The slopes of the regression lines differed among some of the fragments (Table 3, Figure 6). The populations of areas MGA and MGC exhibited greater diameters with increasing height, than did the MMGB population, and individuals of the Al population had smaller diameters with increasing height than the MGC population (Figure 6).

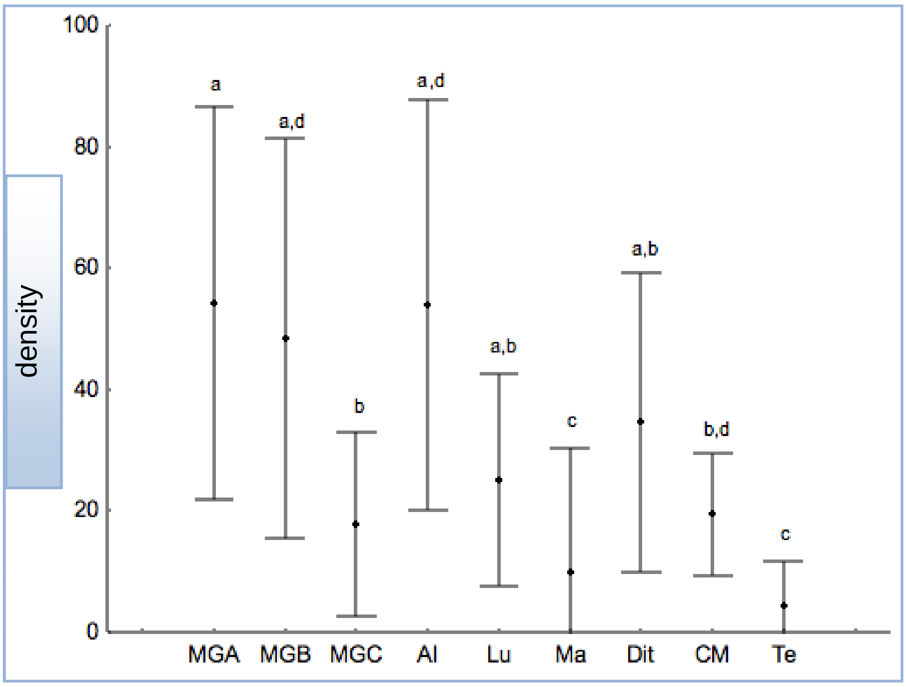

Figure 4 – Variation in density of the populations of *Psychotria suterella*. Filled circles represent mean density and the lines represent the standard deviation. Letters above the lines indicate equality in the distribution of density among the populations (Tukey test, p< 0.05).

The values of a_{II} for areas with the same slope differed among some areas (Table 3, Figure 7). A very similar pattern was observed among the fragments relative to canopy openness and the amplitude of te a_{II} values in each population (Figures 5 and 7). In fragments where canopy openness was greater, the populations had individuals with greater height yet with the same diameter.

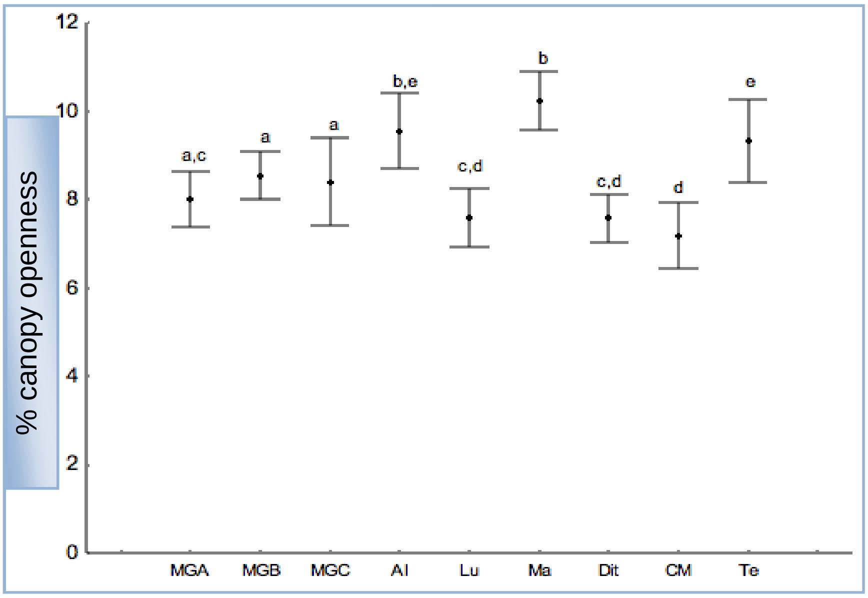

Figure 5 – Variation in the percentage canopy openness in sampled areas (Mean = filled circles, standard deviation = vertical lines).Different letters indicate significant differences in the canopy openness among areas (Tukey test, p< 0.05).

Table 3 – Comparison of the coefficients of linear regression (Model Type II) and deviations of the allometric relationship between log of dsh (cm) and log of height (m) among populations; n = number of individuals, r^2 = coefficient of determination, b_{II} = slope of the adjusted regression line, a_{II} = adjusted intercept, SE b = standard error of b and SE a = standard error of a. For all regression analyses $p < 0.01$

Populations	N	r^2	r	b_{II}	SE b	a_{II}	SE a
MGA	1077	0.780	0.883	1.141	0.016	-0.181	0.006
Al	1074	0.861	0.928	1.089	0.013	-0.154	0.005
MGB	952	0.840	0.916	1.066	0.014	-0.183	0.005
MGC	347	0.819	0.908	1.175	0.028	-0.165	0.009
CM	376	0.766	0.875	1.151	0.030	-0.235	0.012
Dit	679	0.761	0.873	1.117	0.022	-0.220	0.008
Lu	488	0.804	0.896	1.083	0.023	-0.210	0.009
Ma	191	0.724	0.851	1.140	0.045	-0.144	0.019
Te	81	0.737	0.859	1.218	0.073	-0.042	0.033

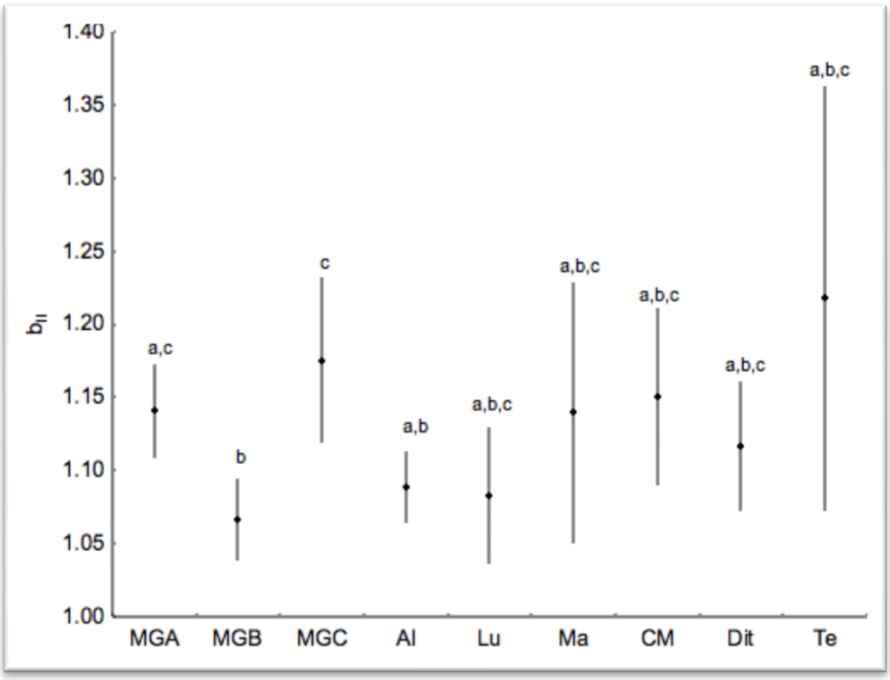

Figure 6 – Comparison of the slopes of the regression lines (Model Type II) and respective deviations of the regressions of individuals of *Psychotria suterella* in different populations.

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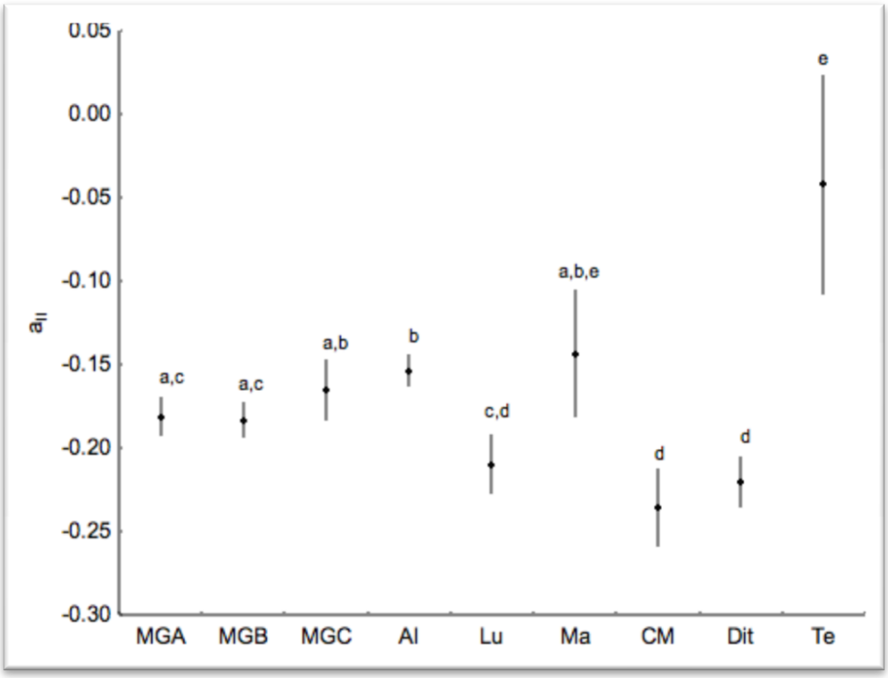

Figure 7 – Comparison among the intercepts of regression lines (Model Type II) and respective deviations of the regressions of individuals of *Psychotria suterella* in different populations.

Discussion

Individual plants of *Psychotria suterella* in conditions of high intraspecific density and light availability (1.5 m above the ground) were shorter than those of the same diameter in different conditions. Allometric coefficients varied between 1.07 and 1.11, which are values very close to the geometric similarity model, have also been found in other studies of understory and canopy species (King 1990, 1996). When individuals were separated into height classes, both density and canopy openness were related to alterations in growth pattern. Individuals >200 cm had coefficients greater than individuals ≤ 100 cm. The lower allometric coefficient of individuals of smaller size may indicate greater investment in crown or height, in order to better capture light, to the detriment of stem resistance (Sterck & Borgers 1998). This pattern has also been reported in other studies that included size dependence in analyses of allometric variation, and which found that with an increase in individual size there was a change in coefficients, from a geometric similarity model (b = 1), to a elastic similarity model (b=1.5, Rich *et al*. 1986, Niklas 1995).

In all of the various conditions of light and density of the present study, the allometric pattern of growth of young plants did not change, which seems to indicate the absence of intraspecific competition among individuals of this size class.

Variation in density and canopy openness led to differences in allometric coefficients for adult individuals. The allometric coefficients went from 1.76 in conditions of low density, to 1.48 in conditions of high density. Thus, larger individuals in high-density conditions were thinner than those in low-density conditions. In a high-density situation, biomass allocation to the stem for height would be expected because it minimizes shading by neighbors and maximizes exposure to radiance (Rich *et al*. 1986). Variation in the availability of light also led to allometric differences in adults, although related to situations of intermediate light. Both, in conditions of high and low canopy openness, the values of the allometric coefficients were higher than 1.5, while in intermediate light conditions they were lower. Thus, density in adults seems to be a more important factor in determining allometric ratios for this size class than canopy openness.

On a local scale, light and density indeed had an affect on allometric relationships. However, on a larger scale, a greater complexity of factors were involved with altering the allometry of the studied populations. It would be expected, according to the results of the regressions of different density and light conditions, that populations in areas with higher densities and a greater amounts of light would differ from others, but this was not found. The processes that influence allometric relationships on a larger scale should be related to other factors, such as population dynamics and interspecific relationships. In areas with extremely low density and high canopy openness, deviations from the allometric coefficients of the populations had large amplitudes, being twice that of the areas with greater densities of individuals. This indicates a wide variation in the form of individuals in reduced populations.

Variation in light among areas seems to be an important factor in the height of individuals, since the pattern of light variation among fragments corresponded to the pattern of variation in the intercepts observed for the populations.

Thus, to a lesser extent, light and intraspecific density were determinants in the growth pattern of individuals, and young and adult individuals responded differently to these factors. On a larger scale, the populations presented a more complex response to variation in light and density, and populations with low density of individuals and subjected to greater luminosity varied greatly in growth form.

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