

Allometry of some woody plant species in a Brazilian savanna after two years of a dry season fire

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Received April 15, 2010 – Accepted July 20, 2010 – Distributed May 31, 2011

(With 1 figure)

Abstract

Studies of allometry are important in explaining effects of fire and herbivory, for estimating biomass in forests, and so on. There has been extensive research on plant allometry in temperate and tropical forests, showing that plant architecture often adjusts to the elastic similarity model, but not in Brazilian savannas (cerrado). We studied allometry of *Dalbergia miscolobium*, *Diospyros hispida*, *Erythroxylum suberosum*, *Miconia albicans*, *M. ligustrina*, *Schefflera vinosa*, and *Xylopia aromatica* in a cerrado *sensu stricto* area that was affected by a fire in August 2006. We expected that the study species would not adjust to any of the allometric models considered common for forest species (“constant stress”, “elastic similarity”, and “geometric growth”), and that there would be differences in allometry in burnt and unburnt patches. We sampled two species in 60 5 × 5 m contiguous plots placed in three transects, and five species in 100 5 × 5 m contiguous plots placed in five transects, where we measured the diameters at soil level (DSL) and the heights of all shoots. We used standardized major axis regressions on log-transformed data. The regression slope between the height and DSL was higher than 1.0 ($p < 0.05$) for four species, showing a greater height than would be expected under geometric growth, not predicted by theoretical models. We found significant differences ($p < 0.05$) in regression slopes and/or correlation coefficients between burnt and unburnt plots for five species, indicating that fire may influence plant allometry in the Brazilian cerrado, and that such a response is highly variable between species.

Keywords: cerrado, fire, geometric growth, reduced major axis.

Alometria de espécies lenhosas de cerrado dois anos após um incêndio

Resumo

Estudos de alometria são importantes para interpretar o efeito de fogo e da herbivoria, para estimar biomassa em florestas, entre outros. Há diversos estudos em florestas temperadas e tropicais, mostrando que as plantas desses ecossistemas frequentemente ajustam-se ao modelo de similaridade elástica; mas quase não há estudos realizados no cerrado. Estudamos a alometria de *Dalbergia miscolobium*, *Diospyros hispida*, *Erythroxylum suberosum*, *Miconia albicans*, *M. ligustrina*, *Schefflera vinosa* e *Xylopia aromatica* em um fragmento de cerrado *sensu stricto*, afetado de maneira heterogênea por um incêndio em agosto de 2006. Esperávamos que as espécies não se ajustassem a quaisquer dos modelos considerados comuns para espécies florestais (“estresse constante”, “similaridade elástica” e “crescimento geométrico”), e que haveria diferenças significativas entre manchas atingidas pelo fogo e as não atingidas. Amostramos duas espécies em 60 parcelas contíguas de 5 × 5 m dispostas em três transectos e cinco espécies em 100 parcelas contíguas de 5 × 5 m dispostas em cinco transectos, dentro das quais medimos o diâmetro à altura do solo (DAS) e a altura de todos os caules. Usamos regressões do tipo eixo principal reduzido sobre logaritmos dos dados. A inclinação da regressão foi maior do que 1,0 ($p < 0,05$) para quatro espécies, mostrando uma altura maior do que seria esperada sob crescimento geométrico. Esse padrão não é previsto por modelos teóricos. Encontramos diferenças significativas ($p < 0,05$) nos coeficientes de inclinação e/ou de correlação entre parcelas queimadas e não queimadas para cinco espécies; generalizamos que o fogo pode influenciar a alometria de plantas do cerrado, sendo que essa resposta pode variar entre espécies.

Palavras-chave: cerrado, fogo, crescimento geométrico, eixo principal reduzido.

1. Introduction

The study of allometric relationships may be relevant both for theory and practice, and has received much attention in different ecosystems (King, 1990; O'Brien et al., 1995; Rich, 1987; Archibald and Bond, 2003; Portela and Santos, 2003; Siqueira, 2006; Dean and Long, 1986; McMahon and Kronauer, 1976), in theoretical studies proposing physical explanations to allometric relationships (McMahon, 1973; McMahon and Kronauer, 1976; Dean and Long, 1986; Niklas and Spatz, 2006), and also in reviews (Niklas, 2004; Peltola, 2006). From the theoretical point of view, besides granting a better understanding of plant functioning, allometry studies indicate which factors operate in tree survivorship, such as compression or risk of buckling (McMahon, 1973; McMahon and Kronauer, 1976; Dean and Long, 1986). Regarding practice, plant allometry is important for biomass estimates, and therefore forest carbon assimilation (Nogueira et al., 2008), and also for understanding the impacts of factors such as fire and herbivory (Archibald and Bond, 2003).

Allometric relationships between height and diameter often follow one of three models, originally developed for cantilever beams but extended to tree structure (McMahon, 1973; McMahon and Kronauer, 1976; Dean and Long, 1986): elastic similarity, constant stress, and geometric growth, as shown in studies in forest physiognomies (Sposito and Santos, 2001; Osunkoya et al., 2007). All of these models follow the Equation 1:

$$H = b \cdot D^a \quad (1)$$

where H represents the tree height, D , the diameter, and a and b are constants (McMahon and Kronauer, 1976). The difference between them is the a value, which represents the proportionality between tree diameter and height. This parameter is equal to 1.0 for geometric growth, meaning that height is directly proportional to diameter; to 0.66 for the elastic similarity model, which presumes that diameter limits height due to the risk of tree buckling under its own weight (McMahon, 1973; McMahon and Kronauer, 1976); and to 0.5 in the constant stress or stress similarity model, which states that diameter varies with height, in such a way that stress resulting from wind action and/or from the tree's weight (Dean and Long, 1986) remains constant along the tree trunk (McMahon and Kronauer, 1976). It is important to note that the stress the model speaks of is the physical stress or strain applied to the fibers of the tree (McMahon and Kronauer, 1976), and is not to be confused with ecological stress such as fire, poor soil or disturbances.

These models seem to apply largely to tree growth in neotropical and temperate forests, and also to trees of the temperate zone growing in more open conditions (McMahon and Kronauer, 1976; Dean and Long, 1986; O'Brien et al., 1995; Niklas, 1995). Models based on wind-induced stress state that drag forces are proportional to stem mass, which in turn is correlated with stem height (Niklas and Spatz, 2006). While this probably holds true

for straight-growth trees (McMahon, 1973; Dean and Long, 1986; O'Brien et al., 1995), savanna trees are often twisted and they may have a complex branching structure, with at least some branches arising from close to the ground, especially in resprouts (Gottberger and Silberbauer-Gottberger, 2006). In such cases, wind drag may have more influence on tree architecture as a whole than its height; or, alternatively, tree height may also be limited by other factors, such as poor soil or fires (Ribeiro and Walter, 2008).

It must also be considered that the three models presented above take into account that one single factor is the most important in determining plant allometry (Niklas, 1995). Phenotypic plasticity, environmental conditions (Holbrook and Putz, 1989; Coomes and Grubb, 1998; Archibald and Bond, 2003) and disturbances such as fire (Gignoux et al., 1997) may also affect plant allometry. Trees in African savannas, for example, subject to frequent fire events, present characteristics associated with rapid height gain (smaller canopies, more elongated shoots, narrower stems and others) when compared to trees of the same species in arid shrubland and forest, where fire is less frequent (Archibald and Bond, 2003). In the Brazilian cerrado, the probability of topkill (death of the above-ground biomass) decreases with increasing stem diameter (Hoffmann and Solbrig, 2003), and, therefore, individuals with larger diameters may be favoured during fire events. Individual growth rate and presence of thick bark is also affected by fire events (Gignoux et al., 1997). Considering this, the Brazilian cerrado is a savanna-like ecosystem of interest as it is considered a natural vegetation type commonly affected by fire, in terms of its physiognomy (Ribeiro and Walter, 2008), reproduction of some species (Hoffmann, 1998), and composition (Moreira, 2000). Most of the cerrado woody species presents a sympodial mode of growth with twisted and winding form of trunks and branches, as a consequence of fire impact on their growth form (Gottberger and Silberbauer-Gottberger, 2006).

We conducted a study on the allometry of seven cerrado woody species in burnt and unburnt patches two years after a dry season fire. Considering that fire may reduce the mean population size in cerrado ecosystems (Silva et al., 2008), and that cerrado plants are often twisted and have diverse adaptations to fire, such as thick bark (Gottberger and Silberbauer-Gottberger, 2006) and larger development of underground structures (Hoffmann and Franco, 2003) than forest species, we expect that the three models (constant stress, elastic similarity and geometric growth) will not apply to these species. Therefore, we proposed that an alternative model could explain their allometric relationship. We also expect to find differences between allometric coefficients of plants in burnt and unburnt patches, due to probability of topkill (Hoffmann and Solbrig, 2003), and because higher trees may be more resistant to fire (Archibald and Bond, 2003).

2. Material and Methods

2.1. Study species

The following woody cerrado species, all frequently sampled in floristic surveys in São Paulo State, Southeastern Brazil (Durigan et al., 2003), were chosen for this study: *Dalbergia miscolobium* Benth. (Fabaceae), *Diospyros hispida* A. DC. (Ebenaceae), *Erythroxylum suberosum* A. St.-Hil. (Erythroxylaceae), *Miconia albicans* (Sw.) Steud. (Melastomataceae), *Miconia ligustroides* Naudin. (Melastomataceae), *Schefflera vinosa* (Cham & Schlehd.) Frodin & Fiaschi (Araliaceae), and *Xylopia aromatica* (Lam.) Mart. (Annonaceae). They were chosen in such a way as to encompass different degrees of deciduousness (deciduous or evergreen), sizes (shrubs or trees), and fire resistance strategies, with some species being able to withstand a fire due to their thick bark and other species suffering topkill and resprouting after the fire. Their names have followed IPNI (2009).

D. miscolobium is a tree, typical of open savanna (*campo cerrado*), closed savanna (*cerrado sensu stricto*), and dry forest (*cerradão*); its trunk and branches are twisted, and it has thick bark with irregular sulks (Durigan et al., 2004). *D. hispida* may be either a tree or a shrub, with thick bark, and occurs from field physiognomies to *cerradão* (Durigan et al., 2004). *E. suberosum* is a shrub, it has thick suberous bark (Durigan et al., 2004), and occurs in open physiognomies and in *cerrado sensu stricto*. *M. albicans* is a shrub or small tree, with thin bark, and occurs from open physiognomies to the *cerradão* understory. (Durigan et al., 2004). It is more common in areas protected from fire (Moreira, 2000). *M. ligustroides* is an evergreen small tree with thin smooth bark, and occurs mostly in the *cerradão*, but also in *cerrado sensu stricto* (Durigan et al., 2004). *S. vinosa* may be either a shrub or a tree (Durigan et al., 2004), with thin bark. *X. aromatica* is a small tree with a straight trunk and relatively thin bark (Durigan et al., 2004); it occurs in *cerrado sensu stricto* and in the *cerradão* (Almeida et al., 1998).

2.2. Study area

This study was carried out at a *cerrado sensu stricto* area (*sensu* Coutinho, 1978), part of São Carlos Federal University *campus*, São Paulo State, Southeastern Brazil (21° 58' to 22° 00' S and 47° 51' to 47° 52' W), between February and October 2008. The area occupied by the *cerrado* has about 124.8 ha; altitude varies from 815 m to 895 m; the soil is deep and characterized by a sandy texture (LAPA, 2005). This area is surrounded by *Eucalyptus* spp. plantations and University buildings. The climate is warm with a wet summer and dry winter - Cwa in Köppen's classification (Tolentino, 1967); dry season extends from April to September, while rainy season extends from October to March. Mean yearly temperature varies from 20.8 to 21.7 °C; mean annual precipitation is of 1506 ± 26 mm (Tolentino, 1967). The area was partially burnt in an accidental fire in August 2006. This fire affected about

80% of the entire area, but it was not burnt homogeneously, leaving burnt and unburnt patches.

2.3. Sampling

In order to sample both burnt and unburnt patches by the 2006 fire, during 2008 we delimited 20 5 × 5 m contiguous plots along five 100 m parallel transects, separated 20 m from each other. From a total of 100 plots, we had 53 burnt interspersed with 47 unburnt plots. We sampled these 100 plots systematically: *D. hispida*, *E. suberosum*, *M. albicans*, *M. ligustroides* and *S. vinosa* were sampled in all 100 plots, while *X. aromatica* and *D. miscolobium* were sampled in 60 plots (33 burnt and 27 unburnt plots) located in three of the five transects.

In all the plots, we measured the diameters at soil level (DSL) and height of all the individuals of the study species. DSL was measured with a vernier caliper, and the height was measured using a measurement pole. For some individuals, we observed if they were already standing before the fire or if they originated after the fire. We classified the individuals that were already standing before the fire as "adults", and differentiated plants that originated after the fire into resprouts and seedlings. *M. albicans*, *S. vinosa* and *X. aromatica* resprouts and seedlings, unlike adult plants, presented a flexible, pubescent stem without bark, and this could be still seen in the 2008 census. Resprouts and seedlings have a similar stem texture, and we considered a young shoot to be a resprout if it was connected or adjacent to a live adult or to a burnt stem. If this stem was not found, the shoot was considered a seedling. We did not differentiate adults from large resprouts and resprouts from seedlings of *M. ligustroides*, *E. suberosum* and *D. hispida*.

2.4. Analysis

We analyzed the allometric relationship between height (H) and diameter at soil level (DSL) using Standardized Major Axis (SMA) regressions on log-transformed data, using the software Past 1.91 (Hammer et al., 2001). Standardized major axis, also known as reduced major axis or "geometric mean functional relationship" (Warton et al., 2006), should be used when there is no clearly independent variable (when the relationship is symmetric) and/or when both variables are subject to equation error (Warton et al., 2006; McArdle, 2003). Equation error, as opposed to measurement error, means that, even if the measurements were made with complete accuracy, the sampling points would not necessarily lie on the predicted line because of intrinsic variation or natural heterogeneity between them (McArdle, 2003). This analysis is widely used in allometry (Niklas, 2004; Warton et al., 2006), and it is also recommended when we intend to verify the relationship between two variables instead of predicting one variable from another through line-fitting (Warton et al. 2006).

We performed separate analyses for the burnt and unburnt plants for each species, obtaining their slope and intercept, as well as determination (r^2) coefficient. We obtained 95% confidence intervals for slopes by bootstrapping, and the number of resample boots was equal to the number of

individuals (Hammer, 2010). Bootstrapping is a robust technique for estimating confidence intervals and does not assume normality (Manly, 1998). We used confidence intervals instead of a Student's *t*-test or ANCOVA because some of the assumptions of the latter were violated in our data. Student's *t*-test for comparing regression slopes is based on the residual mean square (Zar, 1984), which is calculated from the sum of squares of residuals or deviations between expected and observed values (Lowry, 2010). Similar to a regular Student's *t*-test requiring normality of values (Zar, 1984), a *t*-test to compare regression slopes would require normality of residuals (personal communication from Oyvind Hammer), which was not the case. The same would apply to ANCOVA (Zar, 1984). Another reason for not using the Student's *t*-test or ANCOVA is that the data was not balanced having a different numbers of individuals in burnt and unburnt plots (Zar, 1984).

Since results of a regression analysis can only be applied to the range of values for which the regression was made (Zar, 1984), in order to make meaningful comparisons between burnt and unburnt individuals, we used the same range of DSL values for individuals of each species, from burnt and unburnt plots (shown in Table 1). We excluded from the analysis burnt plants whose DSL was outside the range of DSL values presented by unburnt plants and vice-versa. Therefore, the DSL range used in the analysis did not encompass the whole DSL range the species sampled in the study area.

The slopes (*a*) of each regression were compared, using their 95% confidence intervals, with three allometric models (*a* = 1 for geometric growth, *a* = 0.66 for elastic similarity, *a* = 0.5 for stress similarity). In order to observe

the fire effects on allometry, we used the 95% confidence intervals to compare the slopes in burnt and unburnt plots. This percentage shows where the regression slopes would lie if the entire population had been sampled. Therefore, two slopes were considered significantly different when their confidence intervals did not overlap. We also compared the correlation coefficients obtained for plants in burnt and unburnt plots using Fisher's Z-transform and Z-test (Zar, 1984; Phonetic Sciences, 2010).

3. Results

As shown in Table 1, our first hypothesis corroborated with all species except *X. aromatica* and *M. ligustroides*, which adjusted to the geometric similarity model. All other species presented a regression slope larger than 1.0, indicating a greater height that would be expected in geometric growth. Regression slopes of burnt and unburnt individuals were significantly different for only two species, *S. vinosa* and *X. aromatica*. However, correlation coefficients in burnt and unburnt patches were different for all species except *E. suberosum*, thus showing that fire may have effects on plant allometry and corroborating our second hypothesis.

All regression coefficients were significantly different from zero ($p < 0.05$), except for *D. miscolobium* (Figure 1e) in unburnt plots ($p = 0.98$, $r^2 = 1.06 \times 10^{-5}$, $N = 75$). For *D. miscolobium* in burnt plots (Figure 1e) there was a significant relationship, but the r^2 was too small ($p = 0.004$, $r^2 = 0.009$, $N = 1029$). In other words, even though the regression was statistically significant for the individuals of this species that we examined, plant height and diameter

Table 1. Number of individuals (N), median (M), Quantiles 25-75% (Q 25%-75%), lower limit (LL) and upper limit (UL) for diameter of soil level (DSL) and height (H) of the seven woody species used in the study, located in burnt (B) and unburnt (U) plots in a cerrado *sensu stricto* area. DSL was measured using analogical or digital Vernier calipers; H was measured with a measurement rod. Medians and quantiles were used instead of means and standard deviations because all data presented non-normal distribution (Shapiro-Wilk test, $p < 0.001$).

Species	Status	N	DSL (cm)			H (cm)		
			MED	Q 25%-75%	LL-UL	MED	Q 25%-75%	LL-UL
<i>Schefflera vinosa</i>	B	589	1.50	0.80-2.10	0.20-4.30	130	60-180	5-400
<i>Schefflera vinosa</i>	U	390	1.28	0.60-2.00	0.20-4.30	119.5	40-190	7-350
<i>Miconia ligustroides</i>	B	1067	0.80	0.57-1.08	0.01-7.29	82	60-108	4-260
<i>Miconia ligustroides</i>	U	583	0.81	0.52-1.36	0.01-7.29	80	47-115	1-310
<i>Miconia albicans</i>	B	3153	0.50	0.40-0.80	0.30-6.70	50	32-75	1-310
<i>Miconia albicans</i>	U	409	1.60	1.10-2.40	0.30-6.70	94	60-156	10-350
<i>Diospyros hispida</i>	B	76	1.38	0.91-1.98	0.38-7.70	41	24-70	8-150
<i>Diospyros hispida</i>	U	38	1.41	0.84-2.81	0.38-7.70	43	21-83	4-220
<i>Dalbergia miscolobium</i>	B	1029	0.16	0.12-0.16	0.03-0.21	23.5	11-37	1-50
<i>Dalbergia miscolobium</i>	U	75	0.14	0.12-0.16	0.03-0.21	33.5	14-83	3-10
<i>Erythroxylum suberosum</i>	B	114	1.09	0.55-1.82	0.17-8.89	17	9-31	2-300
<i>Erythroxylum suberosum</i>	U	96	0.86	0.48-1.33	0.17-8.89	23	12-53	1-300
<i>Xylopia aromatica</i>	B	493	0.30	0.17-0.60	0.07-12.32	6	5-7	2-401
<i>Xylopia aromatica</i>	U	135	0.52	0.24-1.18	0.07-12.32	6	5-7	3-453

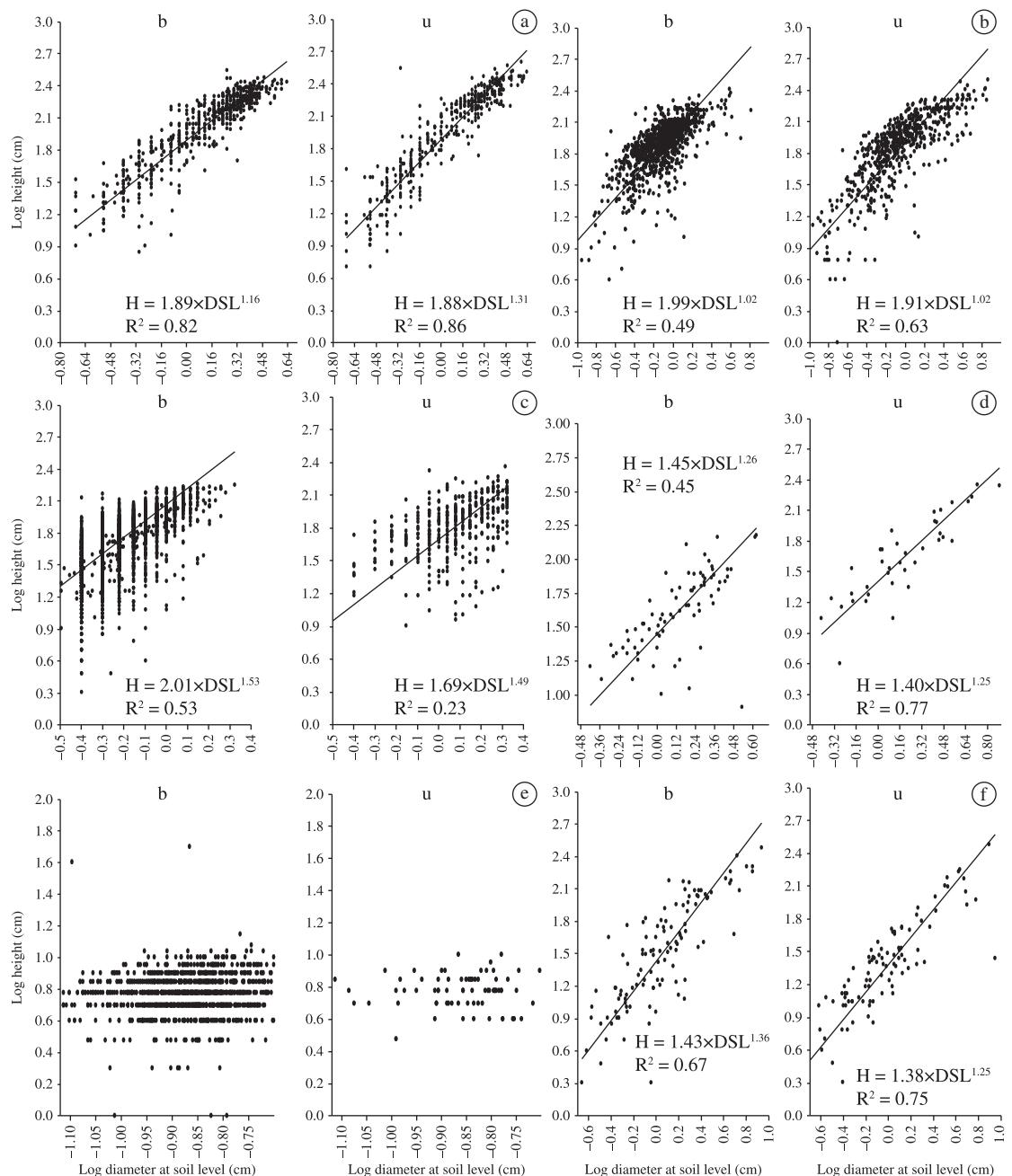
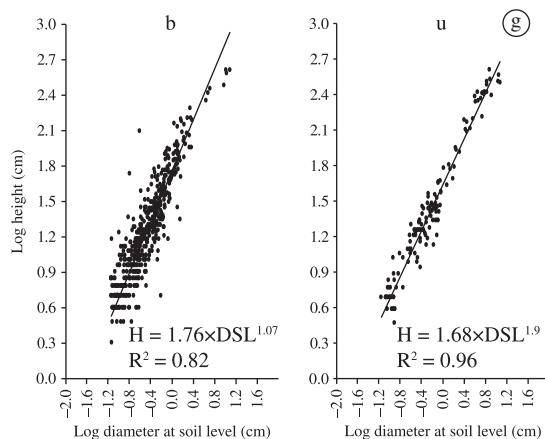


Figure 1. Allometric relationship between log height (H) and log diameter at soil level (DSL) for seven woody species in a cerrado *sensu stricto* area, in burnt (b) and unburnt (u) plots. a) *Schefflera vinoso*, b) *Miconia ligustroides*, c) *Miconia albicans*, d) *Diospyros hispida*, e) *Dalbergia miscolobium*, f) *Erythroxylum suberosum*, g) *Xilopia aromatica*. The lines and equations represent the fit of the Standardized Major Axis regression. Regression was not significant for burnt *D. miscolobium* and had a very small R^2 , of 0.009, for unburnt *D. miscolobium*, and therefore regression lines and equations for this species are not presented.

**Figure 1.** Continued...

are not very related. However, all of the individuals of this species that we examined were seedlings, the r^2 would probably be larger if both seedlings and adult plants had been present in burnt and unburnt plots. For the other coefficients, r^2 varied from 0.23 for burnt *M. albicans* to 0.96 for unburnt *X. aromaticata*, the only coefficient larger than 0.90, showing that, as expected, the plant height and diameter are related. In spite of intraspecific variation shown by the r^2 , all regression coefficients were either close to or larger than 1.0, that is, they represent either geometric growth, with the plant growing proportionally in height and in diameter, or a disproportional growth, in which height is larger than would be expected in the geometric growth model (Table 2).

Regression for *S. vinosa* (Figure 1a), in burnt plots, had a slope of 1.1, slightly larger than that expected for the geometric model (yet this difference was significant), while in unburnt plots the slope was much higher, of 1.3 (Table 2); most of the *S. vinosa* plants in burnt plots were resprouts, and seedlings represented less than 10% of them. The determination coefficient r^2 was also marginally larger ($p = 0.046$) in unburnt plots ($r^2 = 0.86$) than in burnt plots ($r^2 = 0.82$), which may show that the variability in unburnt plots is smaller.

X. aromaticata also presented differences between burnt and unburnt plots (Figure 1g). The slope for burnt plots was 1.07, and for unburnt plots was 0.99. Therefore, although the 95% confidence intervals did not overlap (Table 2), individuals in burnt patches are very close to the geometric growth model and unburnt patches adjust to this model. Determination coefficients were significantly different ($p < 0.001$), but very high for both burnt ($r^2 = 0.82$) and unburnt ($r^2 = 0.96$) plots.

E. suberosum (Figure 1f) had a regression slope higher than 1.0 in both burnt and unburnt plots. There was a large overlap in the 95% confidence intervals, showing no significant differences in the allometry of plants in burnt and unburnt plots. We also found no significant differences between the correlation coefficients ($p = 0.21$).

M. ligustroides (Figure 1b) in both burnt and unburnt plots adjusted to the geometric similarity model, and r^2 was higher ($p < 0.001$) for unburnt ($r^2 = 0.63$) than burnt ($r^2 = 0.49$) individuals. These results show that although fire apparently did not influence the mean height: DSL ratio, it may still influence its scatter, with burnt plants – mostly resprouts – presenting more architectural variability than unburnt individuals. *M. albicans* presented the opposite

Table 2. Allometric coefficients for the seven study species in burnt (B) and unburnt (U) plots. Regression slope was obtained by reduced (standardized) major axis regression; the 95% confidence intervals were obtained by bootstrapping. b: intercept; r^2 : determination coefficient; N: number of individuals employed in the analysis.

Species	Status	Regression slope	95% confidence intervals for slope	Regression intercept	r^2	N
<i>Schefflera vinosa</i>	B	1.16	1.12-1.22	1.89	0.82	588
<i>Schefflera vinosa</i>	U	1.31	1.25-1.36	1.88	0.86	390
<i>Miconia ligustroides</i>	B	1.02	0.95-1.08	1.99	0.49	1067
<i>Miconia ligustroides</i>	U	1.02	0.95-1.10	1.91	0.63	409
<i>Miconia albicans</i>	B	1.53	1.49-1.56	2.06	0.53	3994
<i>Miconia albicans</i>	U	1.49	1.34-1.65	1.69	0.23	409
<i>Diospyros hispida</i>	B	1.26	1.10-1.46	1.45	0.45	76
<i>Diospyros hispida</i>	U	1.25	1.06-1.48	1.40	0.77	38
<i>Dalbergia miscolobium</i>	B	1.52	1.38-1.68	2.09	0.01	1029
<i>Dalbergia miscolobium</i>	U	1.13	-1.34-1.41	1.74	1.06×10^{-5}	75
<i>Erythroxylum suberosum</i>	B	1.36	1.24-1.52	1.43	0.67	114
<i>Erythroxylum suberosum</i>	U	1.25	1.09-1.41	1.38	0.75	96
<i>Xylopia aromaticata</i>	B	1.07	1.03-1.11	1.76	0.82	493
<i>Xylopia aromaticata</i>	U	0.99	0.96-1.02	1.68	0.96	135

effect (Figure 1c), with r^2 higher for burnt plants (0.53 for burnt plants, 0.23 for unburnt plants; $p < 0.001$). *M. albicans*, plants in burnt plots, were significantly smaller than those found in unburnt plots ($t = 15.561$, $p < 0.001$). Most of the *M. albicans* plants in burnt plots were resprouts, and less than 10% of them were seedlings. This pattern was not observed for *M. ligustroides* ($t = 1.08$, $p = 0.28$). For *D. hispida* (Figure 1d), both burnt and unburnt plants had a regression slope close to 1.25, higher than expected for geometric growth; no significant differences were observed between them. Burnt individuals ($r^2 = 0.45$) had significantly lower ($p = 0.006$) determination coefficient than the unburnt ones ($r^2 = 0.77$).

4. Discussion

Our results show that species from the cerrado are expected to present more variable allometric patterns than plants from other tropical forests and savannas. There was a large variation in the scatter of data around the regression line for the studied species. The scatter of data was higher than that observed for *Acacia karroo* in the African savanna, shrubland and forest, where Archibald and Bond (2003) found all r^2 between the height and diameter to be above 0.90. It was also larger than that observed by O'Brien et al. (1995) for eight tree species in a semideciduous moist tropical forest in Panama, where all r^2 varied from 0.88 to 0.97. Sterck and Bongers (1998) also found larger r^2 , ranging from 0.85 to 0.86, for three rainforest trees in French Guiana. Scattered data means that the observed values do not lie on the regression line, and one of the reasons for this is intrinsic variability among the individuals, due to genetic variation and other factors (McArdle. 2003).

Plants from the cerrado normally have a twisted form: their trunk is not straight, and branching may start close to the ground in some species, including *M. albicans* and *M. ligustroides* (Gottsberger and Silberbauer-Gottsberger, 2006), while thick bark such as that of *E. suberosum* and *D. hispida* (Durigan et al., 2004) may explain part of this variation. The extremely small r^2 obtained for *D. miscolobium* may have resulted from the fact that most *D. miscolobium* were seedlings, from the cohort that germinated after the fire.

When compared to other studies, we found that the allometry of some of our tree species is different from those commonly observed in other ecosystems. The studied species either adjusted to the geometric model, which states that height and diameter increase at the same rate, or presented a slope larger than one, with a larger height than would be expected under geometric growth. In a neotropical forest, the elastic similarity model is more common (O'Brien et al., 1995). In contrast, the lack of adjustment to any of the three allometric models has been observed for *Cecropia glaziou* and *C. hololeuca* in a Brazilian Atlantic Rain Forest (Santos, 2000), *Cecropia obtusifolia* in a Mexican tropical rain forest (Alvarez-Buylla and Martinez-Ramos, 1992), and *Alphitonia petrii* and

Polyscias australiana in a tropical rain forest in Australia (Claussen and Maycock, 1995). Regression slopes lying between elastic and geometric similarity have been found by King (1990) for saplings and understory trees in a Panamanian forest.

This shows that, even though elastic similarity, constant stress, or geometric similarity models have a sound theoretical basis (McMahon, 1973; McMahon and Kronauer, 1976), they do not apply to all species from different environments. Two of our species adjusted to the geometric growth model, as has also been observed by Niklas (1995) for small and young trees. However, none of the studies mentioned above found regression slopes higher than one, observed for four of our species, which suggest that the allometry of some tree species in the cerrado will be better described by a new model, based on different premises than constant stress, elastic similarity or geometric growth models.

Differences between burnt and unburnt plots, as has been observed for most species in our study, indicate that burnt plot plants are still recovering from the fire, corroborating the fact that fire is a causal factor of changes in plant growth. Nearly all adult stems of *S. vinoso* experienced topkill during the fire. Therefore, we believe that these allometric differences indicate that resprouts need more than two years to assume their pre-fire allometric pattern. The difference observed for *X. aromatica* was very small, probably as a result of the partial topkill: while the smaller individuals suffered topkill due to fire, larger plants were able to withstand it without death of the above-ground biomass. Differences in slope may have resulted from the presence of both resprouts and adult plants in burnt plots. For the five species whose allometric coefficients did not differ between burnt and unburnt patches, the determination coefficients differed between burnt and unburnt plots, indicating that fire changed their allometry. This effect was variable between species, showing that fire plays different roles in the allometry of plants from the cerrado.

The determination coefficient of *M. albicans* was higher in burnt plots, but for all other species it was higher in unburnt plots. It seems, therefore, that fire reduces intraspecific variation in *M. albicans*, but increases it in the other species. A possible explanation for this is that adult individuals of *M. albicans* have a highly twisted structure, and thus present much variability in the relationship between height and diameter at soil level. However, they experience complete topkill in a fire (Hoffmann and Solbrig, 2003), and our study shows that resprouts are more similar among each other than adult plants. For other species that experience topkill, such as *S. vinoso* and probably *M. ligustroides*, the opposite may be observed, with resprouts being more variable among them than adult plants. For other species, fire reduced height and/or diameter of some, but not all individuals, thus bringing an additional source of variation. We observed that *Diospyros hispida* and *E. suberosum* lost part of their branches during and after the fire as a consequence of it, reducing their height but not the diameter at soil level. Differences between savanna species with

regards to fire-related strategies have also been noted by Hoffmann (1998) and by Gignoux et al. (1997).

It is known that high temperatures during a fire in a cerrado ecosystem are able to damage, as well as kill leaves up to 160 cm high (Miranda et al., 1993, 1996). In the event of the fire in 2006, in our study area, we observed damage on the canopy of trees up to a height of 7.0 m. Therefore, the thick bark of some species (Gottsberger and Silberbauer-Gottsberger, 2006), as well as the ability of other species to resprout after fire (Hoffmann and Solbrig, 2003), may have contributed to their recovery after a two-year interval, or, alternatively, fire may not have caused such damage which has influenced plant allometry of some species.

Care must be taken when comparing slopes obtained by ordinary least sum of squares regression (OLS) (King, 1990; O'Brien et al., 1995), and by standardized major axis regression (SMA), such as in this study and in King (1990), because SMA usually results in a steeper slope (King, 1990). Still, our work shows that allometry in the cerrado, and possibly in savannas in general, is quite different from the allometry in forests, where either elastic similarity (O'Brien et al., 1995) or values between elastic and geometric similarity (King, 1990) are more common. It is known that allometry is influenced by fire and by many other factors, such as plant life time, stem density, and environmental variables (Claussen and Maycock, 1995). As had been previously shown for African savannas (Archibald and Bond, 2003), our results indicate that fire has an effect on the allometry of plants in the Brazilian cerrado and should, therefore, be taken into account when studying allometry and population structure. It also shows that its influence is highly variable and species-dependent, and any generalizations must be avoided. Therefore, both our initial expectations were confirmed for most species: cerrado plants seem not to adjust to the allometric models commonly observed in forest species; and fire affects their allometry, with plants in burnt and unburnt patches, presenting different allometric patterns.

Acknowledgements – We would like to thank the São Paulo State Foundation for the Support of Research (FAPESP), the National Council of Scientific and Technological Development (CNPq), and the Coordination of Improvement of Higher Level Personnel (CAPES) for the student scholarships conceded to P. D., I. C. L., and M. B. L. respectively. We are also very grateful to the people who helped us in the field, especially Ademir de Paula, Carolina S. Gonçalves, Carolina S. Souza, Carolina B. Zanelli, Fernanda C. S. Tibério, Maristela Imatomi, Rafael O. Xavier, Raquel C. Miato, and Talita Sampaio; to Yasemin Tulu for proofreading an earlier version of this manuscript; and to two anonymous referees for insightful comments on an earlier version of this paper.

References

- ALMEIDA, SP., PROENÇA, CEB., SANO, SM. and RIBEIRO, JF., 1998. *Cerrado: espécies vegetais úteis*. Planaltina: Embrapa. 464 p.
- ALVAREZ-BUYLLA, ER. and MARTINEZ-RAMOS, M., 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree – an evaluation of the climax-pioneer paradigm for tropical rain forests. *Journal of Ecology*, vol. 80, no. 2, p. 275-290. doi:10.2307/2261011
- ARCHIBALD, S. and BOND, WJ., 2003. Growing tall vs growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos*, vol. 102, no. 01, p. 3-14. doi:10.1034/j.1600-0706.2003.12181.x
- CLAUSSEN, JW. and MAYCOCK, CR., 1995. Stem allometry in a North Queensland Tropical Rainforest. *Biotropica*, vol. 27, no. 4, p. 421-426. doi:10.2307/2388953
- COOMES, DA. and GRUBB, PJ., 1998. A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Functional Ecology*, vol. 12, no. 3, p. 426–435. doi:10.1046/j.1365-2435.1998.00211.x
- COUTINHO, LM., 1978. O conceito de cerrado. *Revista Brasileira de Botânica*, vol 1, p. 17-23.
- DEAN, TJ., and LONG, JN., 1986. Validity of constant-stress and elastic-instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Annals of botany*, vol. 58, no. 6, p. 833-840.
- DURIGAN, G., SIQUEIRA, MF., FRANCO, GADC., BRIDGEWATER, G. and RATTER, JA., 2003. The vegetation of priority areas for Cerrado conservation in the São Paulo State, Brazil. *Edinburgh Journal of Botany*, vol. 60, no. 2, p. 217-241. doi:10.1017/S0960428603000155
- DURIGAN, G., BAITELLO, JB., FRANCO, GADC. and SIQUEIRA, MF., 2004. *Plantas do Cerrado Paulista: Imagem de uma paisagem ameaçada*. São Paulo: Páginas e Letra.
- GIGNOUX, J., CLOBERT, J. and MENAUT, JC., 1997. Alternative fire resistance strategies in savanna trees. *Oecologia*, vol. 110, no. 4, p. 576-583. doi:10.1007/s004420050198
- GOTTSBERGER, G. and SILBERBAUER-GOTTSBERGER, I., 2006. *Life in the Cerrado: a South American Tropical Seasonal Ecosystem. Vol I: Origin, Structure, Dynamics and Plant Use*. Ulm: Reta Verlag. 277 p.
- HAMMER, Ø., 2010. PAST – PAleontological STAtistics – Version 2.01 – Reference manual. Available from: <<http://folk.uio.no/ohammer/past/doc1.html>>.
- HAMMER, Ø., HARPER, DAT. and RYAN, PD., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, vol. 4, p. 9. Available from: <http://paleo-electronica.org/2001_1/past/issue1_01.htm>.
- HOFFMANN, WA., 1998. Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology*, vol. 35, no. 3, p. 422-433. doi:10.1046/j.1365-2664.1998.00321.x
- HOFFMANN, WA. and FRANCO, AC., 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology*, vol. 91, p. 475-484. doi:10.1046/j.1365-2745.2003.00777.x
- HOFMANN, WA. and SOLBRIG, OT., 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management*, vol. 180, no. 1, p. 273-286. doi:10.1016/S0378-1127(02)00566-2
- HOLBROOK, NM. and PUTZ, FE., 1989. Influence of neighbors on tree form - effects of lateral shade and prevention of sway on the allometry of liquidambar-styraciflua (sweet gum). *American Journal of Botany*, vol. 76, p. 1740-1749. doi:10.2307/2444473

- Internation Plant Name Index - IPNI, 2009. Available from: <<http://www.ipni.org>>. Access in: 01 jul. 2009.
- KING, DA., 1990. Allometry of saplings and understorey trees of a Panamanian forest. *Functional Ecology*, vol. 4, no. 1, p. 27-32. doi:10.2307/2389648
- Laboratório de Análise e Planejamento Ambiental - LAPA, 2005. Available from: <<http://www.lapa.ufscar.br>>. Access in: 15 nov. 2005.
- LOWRY, R., 2010. *Concepts and applications of inferential statistics*. Available from: <<http://faculty.vassar.edu/lowry/webtext.html>>. Access in: 23 jun. 2010.
- MANLY, BJF. 1998. Randomization, bootstrap and Monte Carlo methods in biology. 2nd ed. London: Chapman & Hall.
- McARDLE, BH., 2003. Lines, models, and errors: Regression in the field. Resultados da pesquisa. *Limnology and Oceanography*, vol. 48, no. 3, p. 1363-1366.
- McMAHON, T., 1973. Size and shape in biology. *Science*, vol. 179, no. 4079, p. 1201-1204. PMID:4689015. doi:10.1126/science.179.4079.1201
- McMAHON, TA. and KRONAUER, RE., 1976. Tree structures: deducing the principles of mechanical design. *Journal of Theoretical Biology*, vol. 59, no. 2, p. 443-466.
- MIRANDA, AC., MIRANDA, HS., DIAS, IO. and DIAS, BF., 1993. Soil and air temperatures during prescribed Cerrado fires in central Brazil. *Journal of Tropical Ecology*, vol. 9, no. 03, p. 313-320.
- MIRANDA, HS., ROCHA, E., SILVA, EP. and MIRANDA, AC., 1996. Comportamento do fogo em queimadas de campo sujo. In MIRANDA, HS., DIAS, BFS., SAITO, CH. (Org.). *Impacto de Queimadas em Área de Cerrado e Restinga*. Brasília: ECL/Universidade de Brasília. p. 1-10.
- MOREIRA, AG., 2000. Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography*, vol. 27, no. 4, p. 1021-1029. doi:10.1046/j.1365-2699.2000.00422.x
- NIKLAS, KJ., 1995. Size-dependent allometry of tree height, diameter and trunk taper. *Annals of Botany*, vol. 75, no. 3, p. 217-227. doi:10.1006/anbo.1995.1015
- , 2004. Plant allometry: is there a grand unifying theory? *Biological Reviews*, vol. 79, no. 4, p. 871-889. PMID:15682874. doi:10.1017/S1464793104006499
- NIKLAS, KJ. and SPATZ, HC., 2006. Allometric theory and the mechanical stability of large trees: proof and conjecture. *American Journal of Botany*, vol. 93, no. 6, p. 824-828. doi:10.3732/ajb.93.6.824
- NOGUEIRA, EM., NELSON, BW., FEARNSIDE, PM., FRANÇA, MB. and OLIVEIRA, AC., 2008. Tree height in Brazil's 'arc of deforestation': shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecology and Management*, vol. 255, no. 7, p. 2963-2972. doi:10.1016/j.foreco.2008.02.002
- O'BRIEN, ST., HUBBEL, SP., SPIRO, P., CONDIT, R. and FOSTER, RB., 1995. Diameter, height, crown, and age relationship in eight neotropical tree species. *Ecology*, vol. 76, no. 06, p. 1926-1939. doi:10.2307/1940724
- OSUNKOYA, OO., SHENG, TK., MAHMUD, NA. and DAMIT, N., 2007. Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island. *Austral Ecology*, vol. 32, no. 2, p. 191-201. doi:10.1111/j.1442-9993.2007.01678.x
- PELTOLA, HM., 2006. Mechanical stability of trees under static loads. *American Journal of Botany*, vol. 93, no. , p. 1501-1511.
- Phonetic Sciences, 2010. *Two correlation coefficients*. Available from: <http://www.fon.hum.uva.nl/Service/Statistics/Two_Correlations.html>. Access in: 6 jul. 2010.
- PORTELA, RCQ. and SANTOS, FAM., 2003. Alometria de plântulas e jovens de espécies arbóreas: copa x altura. *Biota Neotropica*, vol. 3, no. 2, p. 5.
- RIBEIRO, JF. and WALTER, BMT., 2008. As principais fisionomias do Bioma Cerrado. In SANO, SM., ALMEIDA, SP. and RIBEIRO, JF. (Ed.) *Cerrado: Ecologia e Flora*. Embrapa Informação Tecnológica. Brasília.
- RICH, PM., 1987. Mechanical structure of the stem of arborescent palms. *Botanical Gazette*, vol.148, no. 1, p. 42-50. doi:10.1086/337626
- SANTOS, FAM., 2000. Growth and leaf demography of two Cecropia species. *Revista Brasileira de Botânica*, vol. 2, no. 22, p. 133-141.
- SILVA, IA., VALENTI, MW. and SILVA-MATOS, DM., 2008. Fire effects on the population structure of *Zanthoxylum rhoifolium* Lam. (Rutaceae) in a Brazilian savanna. *Brazilian Journal of Biology*, vol. 69, p. 813-818.
- SIQUEIRA, AS., 2006. Alometria de *Caryocar brasiliense* (Caryocaraceae) em diferentes fisionomias do Parque Estadual da Serra de Caldas Novas. GO. *Biota Neotropica*, vol. 06, no. 03, p. 01-06.
- SPOSITO, TC. and SANTOS, FAM., 2001. Scaling of stem and crown in eight Cecropia (Cecropiaceae) species of Brazil. *American Journal of Botany*, vol. 88, no. 5, p. 939-949. doi:10.2307/2657047
- STERCK, FJ. and BONGERS, F., 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *American Journal of Botany*, vol. 85, no. 2, p. 266-272. doi:10.2307/2446315
- TOLENTINO, M., 1967. *Estudo crítico sobre o clima da região de São Carlos*. São Carlos: Prefeitura Municipal.
- WARTON, DI., WRIGHT, IJ., FALSTER, DS. and WESTOBY, M., 2006. Bivariate line-fitting methods for allometry. *Biological Reviews*, vol. 81, no. 2, p. 259-291.
- ZAR, JH., 1984. *Biostatistical analysis*. 2nd ed. New Jersey: Prentice-Hall International. 718 p.

