ACTA
AMAZONICA

Allometry of the babassu palm growing on a slash-and-burn agroecosystem of the eastern periphery of Amazonia

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ABSTRACT

Babassu (*Attalea speciosa* C.Martius, Arecaceae) is a palm with extraordinary socioeconomic and ecologic importance in large areas of tropical Brazil, especially in frequently burned and degraded landscapes. Nevertheless, surprisingly little is known about this keystone species. This paper investigates the allometry of babassu, in order to improve understanding on palm architecture and to provide researchers with an efficient tool for aboveground biomass estimation of juvenile and adult palms. Juvenile leaf biomass can be accurately predicted with the easily measurable minimum diameter of rachis at 30 cm extension. Adult palm biomass can be estimated based on woody stem height, a variable fairly easily measurable on-field. Leaf biomass of adult palms was highly variable, averaged 31.7% of aboveground biomass and can be estimated only indirectly through the relationships between wood:leaf-ratio and total aboveground biomass. Carbon contents varied little in the babassu palm, without size- or growth-stage related differences, suggesting the general applicability of values (42.5% C for stems, 39.8% C for leaves). As a consequence of the limited secondary diameter growth inherent to palms, stem diameter of adult palms is unrelated to palm height and biomass. Stem tapering decreases with increasing palm height. This is partially compensated by increasing wood density in near cylindrical stems. Nevertheless, maximum babassu palm height of about 30 meters appears to be dictated by mechanical stability constraints. All allometric relationships of babassu described in this study are not affected by vegetation stand age, indicating the general applicability of these relationships.

KEYWORDS: *Attalea speciosa*; biomass estimation; carbon; plant architecture; wood density

Allometria da palmeira babaçu em um agroecossistema de derruba-e-queima na periferia este da Amazônia

RESUMO

A palmeira babaçu (*Attalea speciosa* C.Martius, Arecaceae) tem grande importância socioeconômica e ecológica em grande parte da área tropical brasileira, especialmente em áreas degradadas por queimadas freqüentes na Amazônia. No entanto, ainda pouco se sabe sobre as características ecológicas desta espécie-chave. Este estudo investiga a alometria do babaçu com o objetivo de estabelecer uma metodologia eficiente na estimativa da biomassa aérea de palmeiras juvenis e adultas e para um melhor entendimento da sua arquitetura. A biomassa de palmeiras juvenis pode ser estimada facilmente e com precisão com o diâmetro mínimo das ráquis das folhas a 30 cm de extensão. A biomassa de palmeiras adultas pode ser estimada com base na altura do tronco lenhoso, também relativamente de fácil medição em campo. A biomassa foliar das palmeiras adultas foi em media 31,7% da biomassa aérea, porém houve uma alta variação e, portanto, somente pode ser estimada indiretamente através da relação entre a razão madeira:folha e biomassa aérea total. Os teores de carbono no babaçu apresentaram baixa variação, sem diferenças sistemáticas em relação ao tamanho ou estágio de crescimento, o que aponta à aplicabilidade geral dos valores 42.5% C para troncos, 39.8% C para folhas. Em conseqüência do limitado crescimento secundário do diâmetro inerente de palmeiras, não houve relação do diâmetro de tronco com a altura e a biomassa das palmeiras adultas. Observou-se que o afilamento do caule diminui com o aumento da altura das palmeiras, o que é parcialmente compensado pelo incremento da densidade de madeira em troncos quase-cilíndricos. No entanto, a altura máxima do babaçu, de cerca de 30 metros, aparentemente está definida por limitações na estabilidade mecânica. Todas as relações alométricas aqui descritas são independentes da idade da vegetação, indicando a aplicabilidade geral das relações encontradas.

PALAVRAS-CHAVE: Arquitetura de planta; *Attalea speciosa*; carbono; densidade da madeira; estimativa de biomassa.

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INTRODUCTION

The babassu palm assumes an exceptional role throughout the eastern and eastern periphery of the Brazilian Amazon. The geographical range of this palm extends from Bolivia through eight states of Brazil to the Guianas, on an estimated total area of about 17 million hectares. In the transition-zone to the semi-arid north-eastern provinces of Brazil and to the inland savannas ('cerrado'), babassu dominates the human transformed landscape, both as the principal vegetation component and in terms of its unique socioeconomic importance (Pinheiro and Frazão 1995; Teixeira and Carvalho 2007). Babassu becomes dominant in frequently-burned degraded lands; the importance of babassu is therefore bound to increase even further in the course of continued colonization and degradation processes, calling for a better understanding of this extraordinary palm. The success story of babassu is due to two key characteristics, (1) its ruderal characteristics (tolerance of juvenile palms to slash-and-burn, vigorous resprouting dynamics, abundant seed production) resulting in sometimes extreme dominance in degraded lands, and (2) due to its socioeconomic value (extractivism of babassu oil and numerous side products sustaining an estimated 2 million people, making the babassu palm worldwide top-ranking among species relevant for extractivism) (Teixeira and Carvalho 2007).

In the human-transformed landscapes in which babassu predominates (slash-and-burn agriculture, extensive pastures, secondary forests), babassu population is typically divided into two distinct components, adult and juvenile palms. The adult component, here defined as palms with an aboveground woody stem, is decisive for extractivist palm oil and charcoal production. The stratum formed by adult babassu palms undergoes only small variations with time and forms a stable component in the dynamic landscape of productive (shifting cultivation fields, active pastures) and fallow phase (differently-aged spontaneous secondary regrowth of varying degrees of degradation). Adult palms are selectively spared of slashing and generally resist burning with little harm; only a few over-aged and unproductive palms are eliminated and substituted by emergent recruits from the juvenile component. By contrast, the juvenile component of stemless babassu palms (locally called 'pindovas') is characterized by the extreme robustness and vigorous resprouting dynamics after slash-burning of its aboveground components, by its rapid growth dynamics even on infertile soils and its astonishing degree of dominance in overexploited and degraded lands. Whereas adult palms are decisive in terms of biomass, carbon and nutrient stocks, juvenile palms are most important for carbon and nutrient accumulation, successional dynamics and between-plant competition.

Research needs to cover both adult and juvenile babassu palms, calling for allometric equations for biomass estimation of both distinct components of palm population. Sampling schemes of babassu palms likewise will need to differ for the two components, with adult palms best quantified in complete inventories, as opposed to juvenile palms which - due to their high abundance - require quantification in plots or transects. As is always the case, allometric equations need to be both sufficiently precise in their predictive power for biomass estimations, and at the same time easily and accurately measurable on-field, in order to be of practical relevance for field researchers.

The present study provides key allometric relationships of the babassu palm and allometric equations for biomass and carbon estimation of juvenile and adult babassu palms.

METHODS

Study sites

The study was carried out the so-called 'Zona dos Cocais', the center of distribution and dominance of babassu at the southeastern periphery, Ilha de São Luis, Maranhão State, Brazil (2º41'S, 44º16'W). Soils of the study sites are classified as Ultisol, Typic Paleustult, have a sandy texture and are acid and infertile. Climate is classified according to Köppen as sub-humid equatorial, with about 2000 mm annual precipitation largely concentrated in a 7-mo rainy season.

Field work was conducted on five sites covered by secondary forest fallow regrowth ranging in age from young (2-yr-old), mid-aged (15-yr-old) and old (>40-yr-old) and from 2 to about 25 meters main canopy height. Three of the five sites had suffered frequent previous slash-and-burn agriculture cycles. The three young sites had a distinct top stratum of adult babassu palms spared by farmers for extractivism of kernels. Adult palm density varied between 80 and 120 individuals per hectare.

Palm selection

We performed two separate allometric studies: the first one for juvenile palms based on the dimensions of individual leaves and the second one for adult palms based on the dimensions of the entire aboveground plants. For the former, we selected one leaf each of a total of 55 juvenile palms growing on the five study sites, and 25 entire adult palms from two (the youngest and the oldest) of these study sites. The length- and diameter-ranges of juvenile palm leaves and woody adult palms (Table 1) were designed to represent the entire size-range of these palms. Maximum leaf length of 8.8 meters confers to the maximum size of juvenile babassu palms (after which the palms start forming an aboveground woody stem). Adult palm sizes range from young adult palms emerging into the top stratum, to large and old palms with up to 27 meters height and 1.2 tons individual aboveground biomass. Babassu palms are always single-stem plants, which is in accordance with Kahn and de Castro (1985).

Juvenile and adult palm selection avoided obvious defects such as crown- or leaflet damage or partially charred trunks (a widespread phenomenon due to the high fire-frequency). We therefore assumed that this selection of 'perfect' palms likely causes a slight biomass-overestimation (see Nogueira *et al.* 2006).

Data of all variables of adult palms were normally distributed, whereas data of the juvenile leaflets were ln-normally distributed (Table 1). Size-distributions are in accordance with field reality, *i.e.* adult palms forming a quite evenly-sized top stratum, as opposed to juvenile palms within secondary regrowth with its typical uneven plant-size distribution with many small and a few large plant individuals (Gehring *et al.* 2005).

Measurements

For biomass prediction of juvenile palms, we measured the diameter of the pinnate leaf rachis and the leaf length. Since the cross-sectional areas of the rachis of babassu leaves is not circular, the diameter measurement procedure needs to unambiguously define the diameter measurement orientation. For this purpose, we defined 'diameter' as the 'minimum diameter'. We preferred the minimum diameter over the likewise possible maximum diameter. This decision was based on the observation that the minimum diameter is less prone to measurement errors than the maximum diameter. Diameter of leaf rachis was measured at 30 cm leaf stem extension, a measuring-standard introduced by Gehring *et al.* (2008) for small and mid-sized woody plants.

For biomass prediction of adult palms, we measured woody stem diameters at breast height (dbh) and at the crown base, stem height, wood density at breast height, mid-stem and crown base, and crown height and the number of leaves (Table 1). Since leaves of the babassu palm develop conically from the stem, a clear distinction between 'woody stem' and 'crown' is difficult. We therefore sub-divided vertical palm extension into 'woody stem', 'intermediate section' and 'crown'. The 'intermediate' section comprises an average 13.7% of palm height and 27.7% of aboveground biomass. Calculation of wood:leaf ratios excludes the intermediate palm section with its unknown proportions of wood and leaves.

Biomass of wood, intermediate and leaf components was measured by weighing total fresh weight with field balances and representative sub-sampling for dry-mass determination. Stems were dissected with a chainsaw into approximately 1-meter segments for weighing on the field balance (100 kg capacity, measurement precision ±50 g). We did not attempt to collect and weigh the chainsaw-dust, but quantities thus lost are likely very small. We determined the water content

Table 1 - Data structure of juvenile and adult palms used for allometric investigations.

a) Juvenile palms: $N = 55$ leaves					
	Mean	Median	Minimum	Maximum	Data distribution[a)]
Leaf rachis diameter (cm)	1.76	1.30	0.50	5.00	ln-normal
Leaf length (m)	2.88	1.86	0.55	8.77	ln-normal
Leaf biomass (kg)	0.66	0.18	0.01	3.80	ln-normal
b) Adult palms: $N = 25$ palms					
	Mean	Median	Minimum	Maximum	Data distribution[a)]
Stem diameter at breast height (dbh, in cm)	88.6	88.0	72.0	105.0	normal
Stem diameter at crown base (in cm)	86.3	89.0	66.0	106.0	normal
Woody stem height (m)	7.00	6.55	1.90	17.70	normal
Intermediate section height (m)[b)]	2.38	2.36	1.30	3.93	normal
Crown height (m)	8.55	8.40	5.86	11.65	normal
Total palm height (m)	17.93	17.11	12.20	27.05	normal
N° of leaves	23.8	23.0	17	36	normal
Wood biomass (kg)	203.9	147.1	26.5	948.0	normal
Intermediate section biomass (kg)	108.0	105.7	35.0	203.7	normal
Leaf biomass (kg)	130.8	134.0	43.9	261.1	normal
Total aboveground biomass (kg)	442.6	393.9	119.7	1273.6	normal
Wood:leaf-ratio[c)]	1.46	1.27	0.40	5.16	normal
Wood density at breast height (g / cm^3)[d)]	0.524	0.515	0.311	0.847	normal

a) Kolmogorov-Smirnov and Lilliefor's tests.
b) 'Intermediate' section of the adult babassu palms is composed of conically emerging leaves from the woody stem. Manual separation of wood and leaves in this palm section was deemed impossible.
c) For calculation of the wood:leaf ratio we omit the intermediate section with its unknown portions of wood and leaf material.
d) $N = 17$ adult palms.

in wood and leaf biomass in representative sub-samples from each palm. Wood sub-samples were composite samples of three slices (half- or quarter-discs) taken from stem-base, mid-stem and crown-base positions. Leaf sub-samples were composed of segments containing rachis and petioles taken from base, mid-leaf and leaf-tip positions of 2-3 leaves per palm. Sub-samples were dried at 70ºC for five days (leaves) and for ten days (wood) after which constant weight was attained. Sub-sample fresh and dry weights were determined with a digital balance (1 kg capacity, measurement precision ± 2 g). Mean dry weight percentages were 53.6% of fresh weight for leaves and 41.2% for wood. Wood dry matter percentage was positively related with woody stem height (R^2 = 0.34, P < 0.01), whereas leaf dry matter percentage was unrelated with rachis length. We assumed intermediate dry weight percentages (*i.e.*, 47.4%) for the 'intermediate' section of adult palms. All biomass values of this article are given as dry weight biomass estimates.

We also distinguished palm nuts (woody kernels). Though 48% of the adult palms had nuts, biomass shares of nutshells was small (*i.e.*, 2.9% of aboveground biomass), highly variable, and not related to palm size. We therefore added palm nuts to the woody biomass component.

Wood density was determined in 5-15 cm thick discs cut from the woody stem of 17 of the 25 adult palms at breast height, at mid-stem, and at crown base. Due to irregularities of disk geometry, calculation of disc volumes via disk dimensions was not possible. We therefore determined disc volume with the Archimedes Principle (displacement of volume by immersion in water) after previous impermeabilization of disc surfaces with paraffin in order to avoid water penetration.

We determined carbon content of babassu wood (seven palms) and leaf (nine palms) with the Walkley and Black method. Wood samples were composite samples of slices of stem-base and crown-base disks, guaranteeing a representative composition of wood within the stem. Leaf samples were composite samples of three mid-aged leaves per palm, each containing segments of rachis and petioles from leaf-base, mid-leaf and leaf-tip positions.

Data Analysis

Normality of data distribution was verified visually with histograms and statistically with Kolmogorov-Smirnov and Lilliefor's tests (see Table 1). We established regression equations for juvenile palms based on ln-transformed data, and for adult palms based on non-transformed data. Possible redundancy of independent variables was checked for visually by plotting residuals against predicted values, when residuals were normally distributed and no correlation between residuals and predicted values were apparent for any variable. In analogy with Nelson *et al.* (1999), we evaluate the goodness of fit of all regression equations reported here based on the following criteria: 1) r^2 of the simple regression (or R^2 of the multiple regression), which indicates the spread of the data in the y-direction about the regression line, relative to its spread about the average y value which is a horizontal line, 2) standard error for the intercept and for partial regression coefficients of the independent variables (multiple regressions only), 3) significance of t-values of the resulting equations, and 4) average or median unsigned deviation, also referred to as average error of estimate. This is an indicator of the accuracy in the estimation of individual palm or palm leaf biomass. For each palm or palm leaf used in a regression the difference between predicted and observed values was expressed both in relative and in absolute terms. We report on the unsigned median (juvenile palms) or mean (adult palms) values of all cases. Statistical analyses were conducted with Statistica 7.0 (StatSoft, 2004).

RESULTS AND DISCUSSION

Allometry of juvenile palms

Leaf biomass of juvenile palms scales exponentially both with leaf height (Figure 1, top) and with the minimum diameter of leaf rachis (Figure 1, bottom). No systematic differences between the five study sites were detected (data not shown). Table 2 shows the resulting allometric equations for the estimation of juvenile palm leaf biomass, based on length, diameter and the combination of both.

The ln-transformed data of juvenile palm leaves scale linearly both with diameter of leaf rachis and with leaf height. Relationships are very close, palm leaf biomass can be predicted with high precision by either predictor variables (both r^2 = 0.91). Though combination of both predictor variables does further increase precision (R^2 = 0.96), such a procedure is also substantially more laborious and therefore presumably not worth the additional effort for most study purposes. In field reality, we recommend the minimum rachis diameter at 30 cm leaf extension as efficiently and precisely measurable single-input variable with a high predictive power for leaf biomass estimation of juvenile palms, the sum of leaves giving the aboveground biomass estimate of juvenile palms.

Adult palms: Allometric estimation of total biomass

Adult palm biomass can be predicted based on woody stem height (r^2 = 0.70, Figure 2). The allometric fit based on woody stem height is slightly better than that based on total palm height (r^2 = 0.64, data not shown). Due to the characteristic conical incision of palm leaves, the topward delimitation of 'woody stem' is well-defined and unambiguous in its application. Furthermore, woody stem height can be easily estimated with a measuring pole or via triangulation in most field situations. This is because adult palms often form an open top-canopy stratum with clear visibility, due to selective slash-burning by farmers or ranchers interested in babassu kernel production. We therefore recommend woody stem height as single predictor for the estimation of adult babassu palm biomass.

In contrast to results obtained for palm height, adult palm biomass is not related with stem diameter at breast height, at mid-stem or at crown height (data not shown). The lack of relationships of babassu stem diameter with palm biomass is to be expected for palms with their apical meristem, lacking primary and with limited secondary diameter-growth. This is also in line with all other palm allometric studies (Clark and Clark 2000; Brown 2002). In contrast to Cole and Ewel

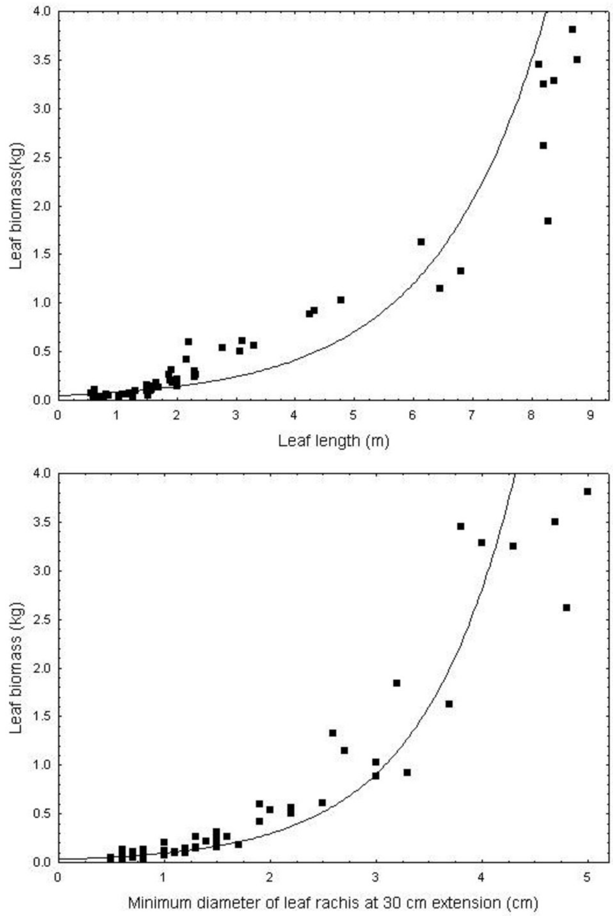


Figure 1 - Exponential relationship between leaf length and leaf biomass (top) and diameter of leaf rachis and leaf biomass (bottom) in juvenile babassu palms (N = 55 leaves).

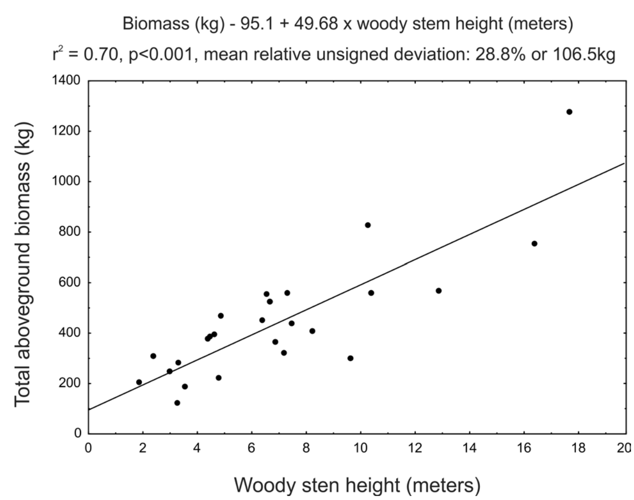


Figure 2 - Linear relationship between adult babassu palm woody stem height and aboveground biomass (N = 25 palms).

Table 2 - Allometric models, coefficients of parameters and goodness of fit for the estimation of juvenile palm leaf biomass.

Parameter	Coefficient	SE	P
Model: ln (leaf biomass) = c + α * ln (length). N = 55, adjusted r^2 = 0.91, median relative unsigned deviation = 16.1% or 0.034 kg, significance level of t-value < 0.001			
intercept	-2.804	0.085	<0.001
ln (height)	1.797	0.079	<0.001
Model: ln (leaf biomass) = c + α * ln (diameter). N = 55, adjusted r^2 = 0.91, median relative unsigned deviation = 28.0% or 0.053 kg, significance level of t-value < 0.001			
intercept	-2.220	0.067	<0.001
ln (diameter)	2.138	0.090	<0.001
Model: ln (leaf biomass) = c + α * ln (length) + α x ln (diameter). N = 55, adjusted R^2 = 0.96, median relative unsigned deviation = 17.8% or 0.030 kg, significance level of t-value < 0.001			
intercept	-2.554	0.065	<0.001
ln (height)	0.911	0.123	<0.001
ln (diameter)	1.165	0.146	<0.001

(2006) and Claussen and Maycock (1995), we did not detect any relationships between diameter and total or stem height. No differences in allometric relationships were apparent between the two (youngest and oldest) study sites (data not shown).

Leaf biomass of adult palms

Leaves of adult babassu palms accounted for an average of 31.7% of total aboveground biomass or an average 130.8 kg dry mass per palm. Direct allometric estimation of this component is problematic, since no relationships were found with leaf number, stem diameters or crown height (data not shown) and only a weak relationship with total palm height: leaf biomass (kg) = 16.2 + 6.39 x palm height (meters); $R^2 = 0.23$, $P < 0.05$.

Babassu palm leaf biomass can be estimated indirectly based on previous total aboveground biomass estimates, since the wood:leaf ratio increases linearly with increasing plant size (Figure 3). Estimation nevertheless remains problematic due to error potentiating inherent to such a two-step estimation procedure. Validity of our equation becomes doubtful for the (rather seldom) very large palms, *i.e.* > 600 kg aboveground biomass.

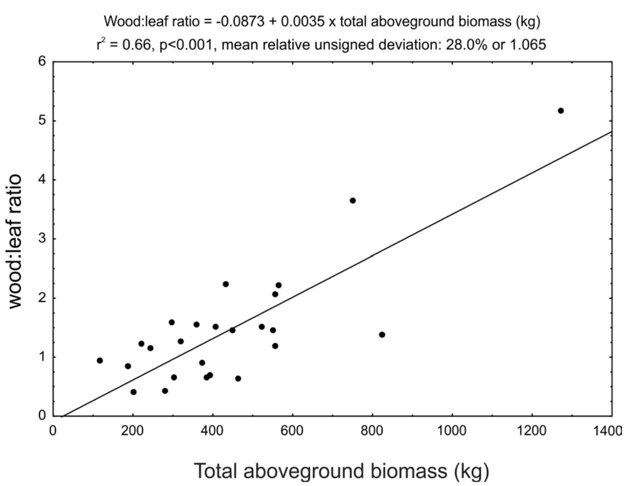


Figure 3 - Linear increase of wood:leaf ratio with increasing palm biomass (N = 25 adult palms).

Stem architecture of adult palms

Adult palm diameter at breast height is unrelated to total or stem height (data not shown), a result also found by Rich *et al.* (1986) for arborescent palm species in Costa Rica.

Stem diameter is more variable at breast height than at crown base. Both diameter-measures are reasonably well linearly related with one another (Figure 4). Diameter at crown base was significantly and on average 16.5% smaller than the diameter at stem base. Diameter reduction with increasing stem height is called 'tapering' (Brown 1997). Here, we investigated the diameter-reduction between breast height and crown base. Figure 5 (top) relates babassu stem tapering with woody stem height. Tapering decreases with increasing height and results in a near cylindrical form in tall palms (*i.e.*, >11 meters stem height or >20 meters total height). Although most palms are capable of some diffuse secondary diameter growth (Raven *et al.* 1992), the lack of a lateral cambium impedes stem diameter growth by cell division (Tomlinson 1979), thus posing mechanical stability constraints which could limit maximum palm height (Rich *et al.* 1986). Therefore, maximum babassu palm height of 27 meters may be dictated by the approach to the 'theoretical buckling limit' of this palm.

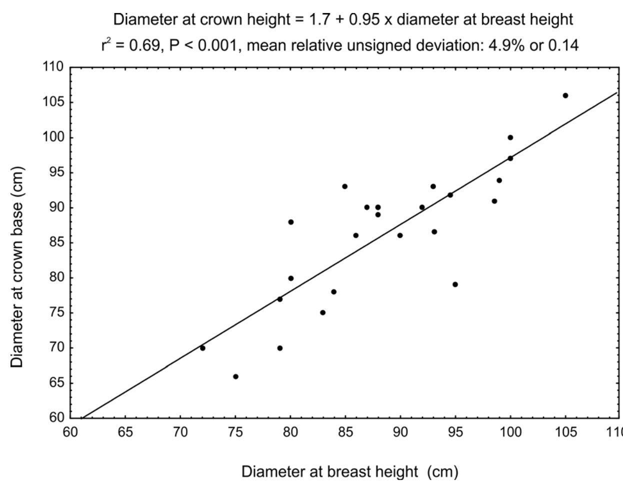
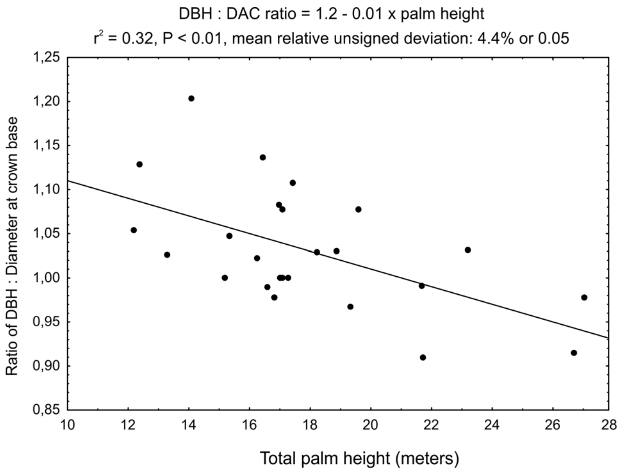


Figure 4 - Linear relationship between diameters at breast height and at crown base (N = 25 adult palms).

Adult babassu palm wood density over all three stem positions (at breast height, at mid-stem and at crown base) averaged 0.49 g / cm^3 (±0.014 SE), well above the average wood density value given for Amazonian palms (0.31 g / cm^3 in Baker *et al.* 2004). Wood density is known to vary within woody plants with height (Swenson and Enquist 2008). Wood density in adult palms tended to vary with woody stem height and was non-significantly (on average 11.8%) lower at crown base than at breast height. Wood density at different stem positions was interrelated, and relative (percentage) wood density reduction along the stem position was dependent from wood density at breast height ($R^2 = 0.41$, $P<0.01$).

Wood density was unrelated with stem diameter or palm height (all $R^2 < 0.08$ and non-significant). This is in accordance with results of the data compilation of Baker *et al.* (2004) for the wood density of Amazonian trees. Wood density was, however, negatively related with stem tapering (Figure 5 bottom), supporting the hypothesis of a tradeoff strategy between these two stability-relevant stem characteristics, *i.e.* a compensation of lower tapering by increased wood density.



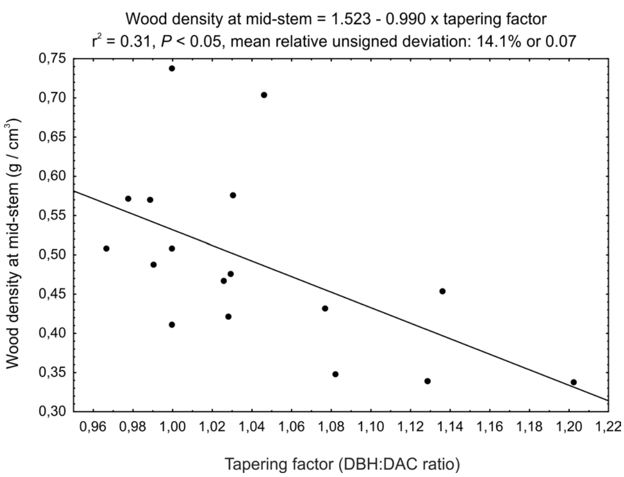


Figure 5 - Top: Reduction of tapering (*i.e.*, the ratio of diameters at breast height (DBH) and at crown base (DAC)) with increasing palm height (N = 25 adult palms). Bottom: Decreasing wood density with decreasing stem tapering (ratio between diameters at breast height (DBH) and at crown base (DAC)) (N = 17 adult palms).

Allometry of other palms

This paper fills in a knowledge gap and rounds up the collection of palm allometric equations already existent for other important palm species such as *Attalea phalerata* (Salis *et al.* 2009), *Astrocaryum mexicanum* (Hughes *et al.* 1999), *Bactris gasipaes* (Ares *et al.* 2002), and *Euterpe edulis* (Brown *et al.* 1989; Alves *et al.* 2004). Although both methods and size-ranges vary, stem height as single palm allometric biomass predictor is a common feature in these studies.

Babassu carbon content

Babassu carbon content was 42.5% (±1.5% SE) and 39.8% (±0.9% SE) for wood and leaves, respectively. No relationships of these concentrations was apparent with study site, or with trunk, crown or total palm dimensions or biomass estimates (all $R^2 < 0.10$ and non-significant). These values can thus be securely applied for in carbon inventories involving the babassu palm.

ACKNOWLEDGEMENTS

We gratefully acknowledge financial support by the Brazilian Research Council CNPq (CT-Agronegócio Nº. 39/2007).

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Recebido em 08/12/2009
Aceito em 18/03/2010