

# Growth and reproduction of the understory palm *Geonoma schottiana* Mart. in the gallery forest in Central Brazil<sup>1</sup>

MAURÍCIO BONESSO SAMPAIO<sup>2,5</sup> and ALDICIR SCARIOT<sup>3,4</sup>

(received: July 04, 2007; accepted: June 12, 2008)

**ABSTRACT** – (Growth and reproduction of the understory palm *Geonoma schottiana* Mart. in the gallery forest in Central Brazil). To understand the growth and reproduction of the palm *Geonoma schottiana* in the gallery forest of Central Brazil, two hypotheses were raised: (i) production of leaves and reproductive structures are concentrated in the period of the year with high light availability; (ii) leaf production and reproductive activity are related to plant length. However, it is expected that senility effects will cause fast reduction in growth and reproduction activities in higher plants. Growth and reproduction were concentrated in the dry season, when insolation is higher than in the wet season, suggesting that leaf and inflorescence production on *G. schottiana* in the gallery forest understory is more limited by light than by soil humidity. As the individual grows, leaf number and blade area increase, but reproduction activity is independent of plant length. Resources stored in the stem are important to growth, but exogenous factors, as canopy openness, should be more important to reproduction. Plant senescence seems to have a lesser effect on the production of vegetative and reproductive structures in *G. schottiana* than has been detected in congeneric species with greater clonal activity.

Key words - life stage, reproductive and vegetative phenology, seasonality, senescence

**RESUMO** – (Crescimento e reprodução da palmeira de sub-bosque *Geonoma schottiana* Mart. em mata de galeria no Brasil Central). Para compreender os fatores que influenciam o crescimento e a reprodução de *Geonoma schottiana* em mata de galeria no Brasil Central, foram levantadas duas hipóteses: (i) a produção de folhas e de estruturas reprodutivas está concentrada no período do ano de maior insolação; (ii) a produção de folhas e a atividade reprodutiva estão relacionadas ao comprimento do indivíduo. Entretanto, espera-se encontrar uma redução brusca nas atividades de crescimento e reprodução em indivíduos mais altos devido aos efeitos da senilidade. O crescimento e a reprodução ocorreram concentrados na estação seca, quando a insolação é maior do que na estação úmida. Assim, a produção de folhas e inflorescências de *G. schottiana* no sub-bosque de matas de galeria pode ser mais limitada pela luminosidade do que pela umidade do solo. Conforme o indivíduo cresce, o número de folhas e a área foliar aumentam, mas a atividade reprodutiva foi independente do comprimento do indivíduo. Os recursos armazenados no estipe são importantes para o crescimento, embora os fatores exógenos, como a abertura do dossel, possam ser mais importantes para a reprodução do que os carboidratos armazenados. A senilidade dos indivíduos parece ter um efeito menor na produção de estruturas vegetativas e reprodutivas ao contrário do que o tem sido detectado em espécies co-genéricas com maior atividade clonal.

Palavras-chave - estágio de vida, fenologia reprodutiva e vegetativa, sazonalidade, senilidade

## Introduction

Palm growth occurs by addition of new leaves into a single vertical stem, and leafing occurs continually, tending to be concentrated in a short period of the year

(Bullock 1980, De Steven *et al.* 1987, Voeks 2002). Many factors influence leafing seasonality (review in Fenner 1998), mainly climatic variables, such as precipitation (De Steven *et al.* 1987, Scariot *et al.* 1991, Voeks 2002, but see Ataroff & Schwarzkopf 1992), and irradiance (Wright & Van Schaik 1994). Where water is not a limiting factor, seasonal peaks of irradiance may play a predominant role in leaf production (Wright & Van Schaik 1994). These same climatic variables can affect reproduction seasonality. Flowering may be a physiological response to precipitation (Augsburger 1981, Voeks 2002), irradiance (Wright & Van Schaik 1994) or temperature (Ashton *et al.* 1988, Voeks 2002). In addition, competition for pollinators can influence flowering time of sympatric species reducing fitness of plants with synchronous flowering periods (Sakai 2001, Lobo *et al.* 2003). Alternatively, the flowering time of sympatric species

- 
1. Part of MSc thesis of the first author, developed at the Departamento de Ecologia, Universidade de Brasília, Brazil.
  2. Universidade Estadual de Campinas – Unicamp, Instituto de Biologia, Departamento de Botânica, Programa de Pós-Graduação em Biologia Vegetal, Caixa Postal 6109, 13083-970 Campinas, SP, Brazil.
  3. Embrapa Recursos Genéticos e Biotecnologia, Laboratório de Ecologia e Conservação, Parque Estação Biológica – PqEB – Av. W5 Norte (final), Caixa Postal 02372, 70770-900 Brasília, DF, Brazil.
  4. Programa das Nações Unidas para o Desenvolvimento, PNUD – ONU. EQSW 103/104, lote 01, Bloco D, 70670-350 Brasília, DF, Brazil.
  5. Corresponding author: mauriciobonesso@gmail.com

could be synchronous when occurs pollinators activity increase (Sakai 2001, Boulter *et al.* 2006).

Endogenous factors can also affect growth and reproduction. One of these factors is the life stage – the phase of development of an individual along its life cycle – which can affect the occurrence of vegetative and reproductive events of palms in three ways. First, the allocation of available resources among plant parts changes with individual size. In juveniles, sometimes resources are invested in the root system and in leaf production, while in adults they are allocated mainly to reproduction (Piñero *et al.* 1982, Osada *et al.* 2002). Reproductive palms can allocate about half of its annual dry weight increase to reproduction (Piñero *et al.* 1982), so it is expected that leaf production rate be reduced when reproductive activities along the life cycle increase. In adults, plant size can affect reproductive activity, bigger plants have more resources available than small ones, and carbohydrates stored in the stem can be used as a short-term buffer for the costs of reproduction (Cunningham 1997). Second, the environment that an individual experiences is influenced by plant size. Light availability increase as the individual reaches the upper stratum of the forest, this is particularly important to understory palms (Chazdon 1986b, Barot *et al.* 2005). Third, some palms exhibit senescence (Chazdon 1992, Enright 1992, Barot & Gignoux 1999, Souza *et al.* 2003), characterized by vegetative and/or reproductive activity reduction at the end of the life cycle. If senescence starts to occur in a specific time of the life cycle, then it is expected a non-linear relationship between growth and reproduction activities and the size of the individuals in a population. According to the senescence intensity, three groups of palms can be identified. In the first group, senescence can act heavily for a long period of the life cycle, beginning soon after the individual reaches sexual maturity. An example is *Borassus aethiopicum* Mart. adults which die when leaf number drops to half the number they had when they reached adulthood, and older reproductive individuals are less likely to reproduce than the younger (Barot & Gignoux 1999). In the second group, the older plants experience fast reduction in growth and reproduction activities at the end of the life cycle (Chazdon 1992, Souza *et al.* 2003). The third group includes the majority of palm species, which have growth and reproduction activities increasing linearly with plant size, during all life cycle (Piñero & Sarukhán 1982, Oyama 1990, Enright 1992, Mendoza & Franco 1998, Svenning 2000, Berry & Gorchov 2004). In this case, senescence may be expressed by the collapse of the tissues holding the stem (Crawley 1997) causing the mortality of the individual.

In this study, seasonal variation and the influence of life stage in growth and reproduction of a population of *Geonoma schottiana* Mart. (Arecaceae) were evaluated in the understory of gallery forest of Central Brazil. Two hypotheses were raised: (i) the production of leaves and reproductive structures are concentrated in the period of the year with high light availability and not in the high soil humidity period, because gallery forests have patches of high soil humidity all over the year and light conditions are very limiting in the understory; (ii) leaf production and reproductive activity are related to plant length, since bigger plants have more stored resources available to growth and reproduction than small ones, and higher palms have more light availability than lower ones. However, a fast reduction in growth and reproduction in plants above a certain height may occur due to senility effects.

Throughout this study, the underlying factors influencing the growth and reproduction of an understory palm species can be understood and compared with congeneric species occurring in different habitats.

## Material and methods

**Area and study species** – The study was carried out in a gallery forest along the headwater of the Três Barras stream, in the plateau of the Contagem Chapada, in the National Park of Brasília (15°35' to 15°45' S and 47°53' to 48°05' W). The western portion of the valley is made of well-drained latosol, and the eastern portion of poorly drained organic soil (Ramos 1995).

The climate has two well-defined seasons (Aw, Köppen classification). In the dry season, from April to October, polar air masses bring low temperature and low relative humidity. In this season, there is a water deficit and the direct exposure to sun is longer than in the rainy season (figure 1). In the

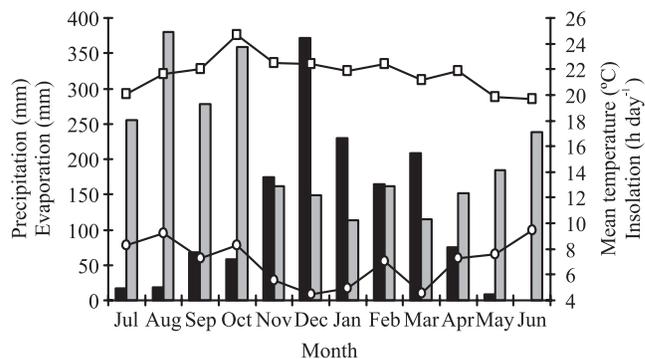


Figure 1. Monthly total precipitation (mm), evaporation (mm), mean temperature (°C) and average of insolation (h day<sup>-1</sup>) from July of 2002 to June of 2003. Source: Meteorological Station of INMET, 25 km of the study area. (■ = precipitation; □ = evaporation; □ = mean temperature; ○ = insolation).

rainy season, from November to March, cold fronts and tropical air masses promote more than 90% of the annual precipitation. The mean annual temperature is 21 °C and the mean annual precipitation is *ca.* 1600 mm (Nimer 1989).

*Geonoma schottiana* is monoecious and occurs in several regions of Brazil (Henderson *et al.* 1995); in the “Cerrado” biome it occurs only in the gallery forest. It is single-stemmed, rarely forming clumps. The stem is frequently tortuous, from 2 to 8 m long, 5 to 15 cm of diameter and has protuberant rings, the result of the leaf scars. Leaf development is similar to other palms (*e.g.* De Carvalho *et al.* 1999). Leaves are produced one at a time, in the center of the crown sheath. Initially the unexpanded leaf has the form of an arrow (arrow leaf), when the growth of the foliar sheet ceases, the arrow leaf starts to expand acropetally (from the top to the base). The expansion begins only after the complete expansion of the preceding leaf.

During life cycle, individuals undergo significant changes in morphology. Initially, the stem is underground and leaves are irregularly pinnatisect. In more advanced stages, the stem is aerial and the leaves are completely pinnate, except for the first and last leaflets, which are united in narrow groups (Martins 2000). Plants in this stage remain non-reproductive for some years. Reproduction is evidenced by the production of inflorescences which emerge from leaf axils, so the maximum rate of flowering is set by the rate of leaf production (Cunningham 1995).

Reproductive structures can be classified into four developmental phases, similar to those adopted by Ataroff & Schwarzkopf (1992) and by Martén & Quesada (2001): (i) inflorescence without fruits – this phase begins with the emergence of an inflorescence from the interior of the bract, includes the elongation of the rachis, rachillae and floral anthesis, and finishes with the abscission of the pistillate flowers and the emergence of developing fruits; (ii) infructescence with small fruits – the phase begins when the fruits are still small and bright green and ends when they reach nearly the size of ripe fruits, but while the color is still bright green; (iii) infructescence with green fruits – most fruits are similar in size to the ripe fruits, but are opaque green; (iv) infructescence with ripe fruits – almost all fruits are purple and black, although some still can be green. Reproduction is complete when the most of the fruits had been dispersed and rachis and rachillae become dry and brittle. Ripe fruits are globose, 0.7-1.0 cm long and 0.4-0.9 cm wide. The mesocarp is pulpy and the endocarp woody, with one seed per fruit (Martins 2000).

Leaf production – The choice of a variable that represents the life stage of an individual appropriately was of fundamental importance in this study. Some non-destructive variables as the stem diameter (Chazdon 1991, 1992); individual height, measured from the top of highest expanded leaf to the soil (Bullock 1980, Chazdon 1992); and individual length, measured along the stem, following its tortuosity (Chazdon 1992, Kimura & Simbolon 2002, Souza *et al.* 2003) have frequently been used in studies with palm trees.

The diameter of the stem, in palms, has little relation to the life stage, because the young stem grows more rapidly in diameter than it does in length. When the stem is aerial, its diameter scarcely increases in the remainder of the life cycle (Chazdon 1991, Kimura & Simbolon 2002). Plant height is also not a useful variable, because stems in *G. schottiana* frequently are leaning, tortuous or partially lying on the soil, similarly to other palms (Chazdon 1992, Kimura & Simbolon 2002, Souza *et al.* 2003, Watanabe *et al.* 2006). Plants with leaning stems can be shorter than younger individuals with straight stems and life stage has little relationship to plant height. Therefore, individual length, measured along the stem, following its tortuosity is the best choice to represent life stage.

In individuals with an aerial stem, plant length as the sum of the length of the stem plus the vertical length of the crown sheath was calculated. Stem length from the soil to the insertion of the sheath of the lowest leaf was measured using a flexible tape, following the tortuosity of the stem. The vertical length of the crown sheath was measured from the insertion of the sheath of the lowest leaf to the highest point reached by a leaf completely expanded. For individuals with underground stem, it is not possible to measure the stem length by non-destructive means, thus only the vertical length of the crown sheath was used.

In May 2002, 40 individuals were randomly marked, 20 with aerial stem in a 1.5 km trail along the headwater of the stream, and 20 individuals with an underground stem in a 400 m<sup>2</sup> plot. Although the population abundance in the study area is high (245 ± 1.4 reproductive ha<sup>-1</sup>) (Sampaio 2006), the tallest individuals which could not be bent using the hands, were not included in the sampling because it was needed to mark each leaf in the plant crown with aluminum tags. Notwithstanding some straight and tall individuals (up to 8 m of length) had flexible stem and were included in the sampling. Each stem (ramet) in a clump (genet) was treated as an individual and used only a ramet of each randomly selected genet. Genets of *G. schottiana* are not connected and are easily distinguished in the field. For all tagged plants, individual length, leaf number, and length width<sup>-1</sup> ratio of the five youngest fully expanded leaves were measured.

To estimate leaf area by non-destructive way, the following equation was used:

$$(A)^{0.5} = 2.75 + 0.66 \times (L \times W)^{0.5},$$

where *A* is the leaf area (cm<sup>2</sup>), *L* is the length (cm) and *W* is the width (cm) of the leaf. The fit of this equation ( $F_{1,46} = 1.339$ ;  $P < 0.0001$ ;  $r^2 = 0.97$ ) was made with measurements of 48 leaves from 48 individuals, selected randomly among all plant sizes. Length and width of each leaf were measured and leaf area was estimated using a CI202 leaf meter (CID, Inc., Camas, Washington). The total leaf area of each plant crown sheath was estimated by calculating the average leaf area of the five measured leaves and multiplying it with the number of leaves that each individual had in May 2002.

Leaf production rate was estimated and the influence of climatic variation was assessed during the year on leaf

emergence; taking leaf samples at three-month intervals for 24 months, until May 2004. This sampling interval was chosen because other species of *Geonoma* produce from 0.18 to 0.39 leaves month<sup>-1</sup> (Chazdon 1992, Souza *et al.* 2003). In each sample, the numbered leaves of the 40 individuals was classified according to their condition (green, dry or absent) and numbered the new ones.

Production of reproductive structures – The phenology in 20 reproductive individuals randomly selected was evaluated at the same trail (above). In August 2002, every reproductive structure was tagged and numbered, classified in one of the four developmental phases and inspected monthly for 12 months, until August 2003. At each visit, new inflorescences were numbered and the reproductive structures were classified again according to their new developmental phase. The mean number of fruits was obtained per infructescence from nine infructescences with ripe fruits of nine individuals.

Climatic variables data (precipitation, evaporation, temperature and insolation) were obtained from a National Institute of Meteorology (INMET) meteorological station located ca. 25 km from the study area.

Data analysis – To test the hypothesis (i), the Rayleigh's Z statistics from circular analysis was used. This statistics was employed to investigate the concentration of vegetative and reproductive structures production in a time of the year (Zar 1999). This analysis uses the representation of the frequency of phenology events in angular scale and tests the uniformity of the distribution through the time. To evaluate the concentration of an event in a given period, the value of  $r$  (Zar 1999), which varies from zero (when the data are so dispersed that a mean angle cannot be calculated) to the unity, (when all occurrences of the event are concentrated in a single period) was calculated. The mean angle of the frequency distribution was estimated, when  $r$  was different from zero, with January 1<sup>st</sup> considered 0°. Two-year data of the production of vegetative structures were grouped for the circular analyses. The assumption that the events had no bimodal distribution was valid for all tests (Zar 1999).

To assess the hypothesis (ii), the relationships between the productions rates of reproductive and vegetative structures and individual length were tested using regression analysis. For these analyses, plant length was used as the independent variable, and as the dependent variables it was used the average rate of leaf production during the two years; number of leaves; mean leaf length; width length<sup>-1</sup> leaf ratio; total leaf area; annual productions of inflorescences without fruit, and of inflorescence with ripe fruit. Shapiro-Wilk's test was used to assess the assumption of normal distribution, and when necessary, transformed to logarithm or square root (Zar 1999). Transformed data that did not meet analysis assumptions was ordered, because this is a non-parametric alternative to fit a linear relationship between variables without normal distribution (Zar 1999) and removed outliers following Tabachnick and Fidell (2001). Analysis of residues was used to test the assumptions of homogeneity of the variances and of linearity among the variables (Tabachnick & Fidell 2001).

## Results

Climatic seasons – Emergence of the arrow leaf ( $Z = 8.38$ ;  $P < 0.001$ ), expansion of the leaf blade ( $Z = 25.98$ ;  $P < 0.001$ ) and the abscission of leaves ( $Z = 14.91$ ;  $P < 0.001$ ) in *Geonoma schottiana* were slightly concentrated ( $r = 0.19$ ;  $r = 0.32$  and  $r = 0.23$ , respectively) at the end of the dry season (August-October). These three events occurred during the whole year, but they were less frequent during the period of highest precipitation (December to March).

The emergence of inflorescences without fruits were concentrated in May (figure 2a; table 1), end of the wet period (figure 1). These structures can remain in this phase for more than six and a half months (table 1), when the rachis and rachillae elongate, anthesis and the abscission of the staminate and pistillate flowers occur. The infructescence with small fruit phase was characterized

Table 1. Time of the year in which the production of reproductive structures is concentrated, results of the Rayleigh test (Z) and the concentration measure ( $r$ ) of the event. Time of duration (months) and average rate of annual production of reproductive phases of *Geonoma schottiana* in gallery forest in Central Brazil. (IWF = inflorescence without fruits; ISF = infructescence with small fruits; IGF = infructescence with green fruits; IRF = infructescence with ripe fruits).

Developmental phase <sup>a</sup>	Time of the year			Duration (month)			Production <sup>b</sup>	
	Month	Z	$r$	Mean	$s$	$n$	Mean	$s$
IWF	May	12.51 <sup>***</sup>	0.48	6.64	0.67	11	2.75	1.33
ISF	December	11.13 <sup>***</sup>	0.59	2.36	0.62	28	1.60	1.60
IGF	February	10.26 <sup>***</sup>	0.61	4.50	2.43	6	1.40	1.10
IRF	–	1.97 <sup>ns</sup>	–	2.62	0.87	13	0.80	1.11

<sup>a</sup> see description of developmental phases in the material and methods section; <sup>b</sup> mean number of structures produced by year for each developmental phase ( $n = 20$ ); <sup>ns</sup> non significant at  $P > 0.05$ ; <sup>\*\*\*</sup> significant at  $P < 0.001$ .

by fruit development initiation, concentrated in December (figure 2b; table 1), in the rainy season (figure 1). In this phase, reproductive structures can hold growing fruits for two months (table 1). Inflorescences with green fruits were present in the population mainly from December to March (figure 2c), being concentrated in February (table 1). These inflorescences can stay in this phase for more than four months (table 1), which had the highest

development time variability (1 to 7 months) among developmental phases. Fruit ripening occurred throughout the year (table 1), although almost absent in February, April and July (figure 2d). An inflorescence can disperse fruits for more than two months (table 1). Based on the mean time of each developmental phase (table 1), it took an average of 16 months since a reproductive structure emerges from the bract until it disperses all its fruits.

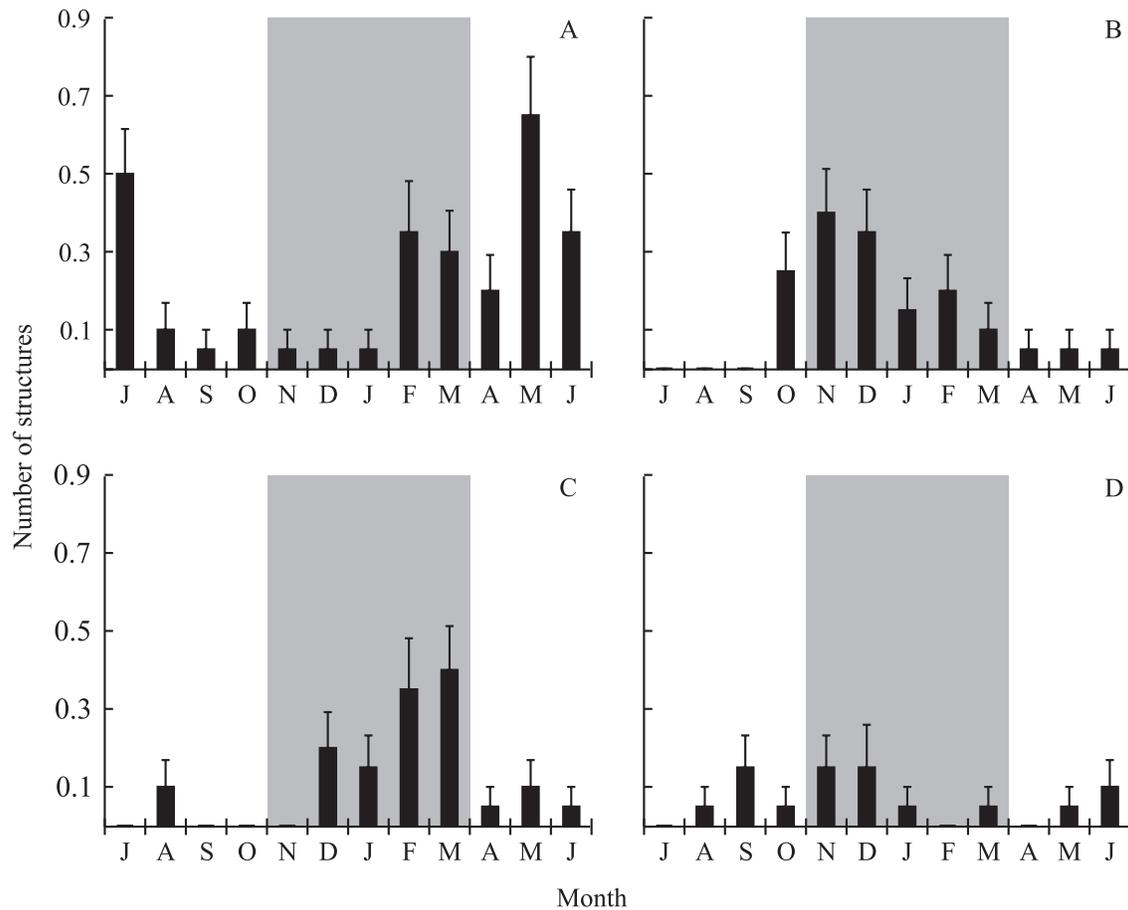


Figure 2. Mean number (1 SE) of reproductive structures produced by individuals of *Geonoma schottiana* ( $n = 20$ ), from July 2002 to June 2003, in a gallery forest of Central Brazil. (A = inflorescence without fruits; B = infructescence with small fruits; C = infructescence with green fruits; D = infructescence with ripe fruits). The shaded area represents the wet season.

**Life stage** – The leaf production rate increased linearly with individual length ( $F_{1,37} = 74.76$ ;  $P < 0.001$ ;  $r^2 = 0.66$ ; figure 3a), but the relationship was not significant when only plants with aerial stem ( $F_{1,18} = 1.62$ ;  $P = 0.22$ ;  $r^2 = 0.03$ ) or with underground stem ( $F_{1,17} = 1.06$ ;  $P = 0.32$ ;  $r^2 = 0.003$ ) were analyzed separately. Plants with aerial stem produced on average 4.6 (SE = 0.31;  $n = 20$ ) leaves  $\text{yr}^{-1}$ , while those with underground stem produced 2.0 (SE = 0.1;  $n = 19$ ) leaves  $\text{yr}^{-1}$ . The number of leaves ( $F_{1,36} = 158.45$ ;  $P < 0.001$ ;  $r^2 = 0.81$ ; figure 3b) and the

mean leaf length ( $F_{1,36} = 252.79$ ;  $P < 0.001$ ;  $r^2 = 0.87$ ; figure 3c) also increased linearly with individual size. The width length<sup>-1</sup> ratio of leaves decreased exponentially as individuals increased in length ( $F_{1,37} = 62.15$ ;  $P < 0.001$ ;  $r^2 = 0.77$ ; figure 3d) and leaf area increased linearly with plant length ( $F_{1,35} = 322.0$ ;  $P < 0.001$ ;  $r^2 = 0.90$ ; figure 3e).

Reproductive individuals, on average, produced 2.75 inflorescences without fruits per year (table 1), this rate not being related to plant length ( $F_{1,18} = 0.102$ ;

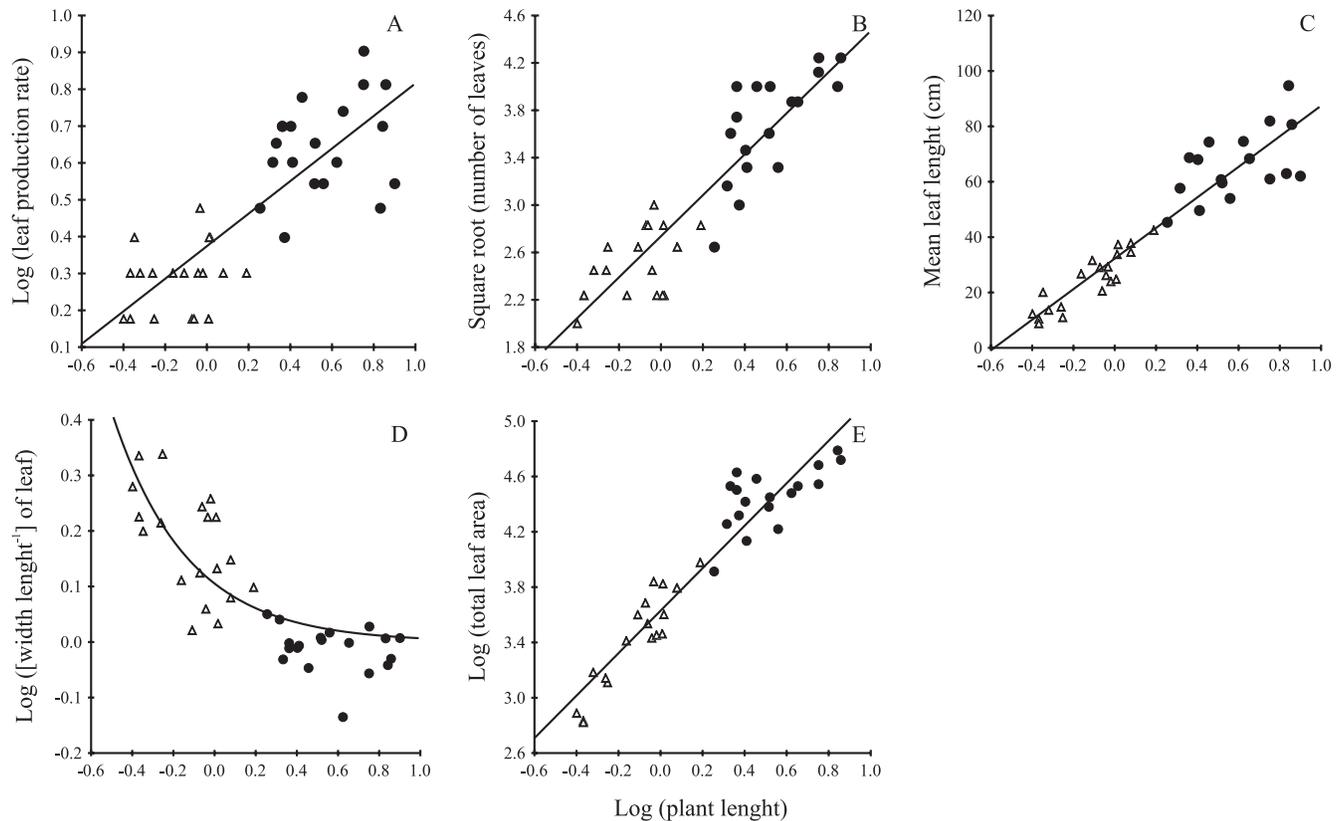


Figure 3. Association between plant length and: A) annual leaf production rate ( $r^2 = 0.66$ ;  $n = 39$ ;  $P < 0.001$ ); B) number of leaves in the crown ( $r^2 = 0.81$ ;  $n = 37$ ;  $P < 0.001$ ); C) mean leaf length (cm;  $r^2 = 0.97$ ;  $n = 36$ ;  $P < 0.001$ ); D) leaf width length<sup>-1</sup> mean ratio [ $r^2 = 0.67$ ;  $n = 38$ ;  $P < 0.001$ ;  $Y = 0.105 * \exp(-2.739 * X)$ ] and; E) total leaf area (cm<sup>2</sup>;  $r^2 = 0.90$ ;  $n = 37$ ;  $P < 0.001$ ) in a population of *Geonoma schottiana* in gallery forest in Central Brazil. Triangles represent individuals with underground stem and circles represent those with aerial stem.

$P = 0.752$ ;  $r^2 = 0.005$ ). The shortest reproductive individual found had 2.1 m of length and the tallest had 8.5 m. Of the inflorescences emerging from bracts, 22% did not persist due to herbivory or unknown causes. Among infructescences with small fruits, 11% did not reach to the next phase. Thus, in reproductive plants, on average, only 0.8 infructescences per plant succeeded in producing ripe fruits in a year (table 1), this rate being independent of the plant length ( $F_{1,18} = 3.02$ ;  $P = 0.099$ ;  $r^2 = 0.096$ ). An infructescence with ripe fruits produced, on average, 310 fruits (SE = 57.4;  $n = 9$ ), resulting in 248 ripe fruits produced per reproductive individual per year.

**Senescence** – If individuals do not become senile, they can have a linear increase in growth and reproduction activities during all the life cycle. If they become senile, the growth and reproduction activities decrease in the end of life cycle, then it is expected a non-linear relationship between the length of individuals and activities of growth and reproduction. Inflorescence production of *G. schottiana*

was not related to plant length. Growth parameters (e.g. leaf production rate, number of leaves at the crown) had a linear relationship with individual length (figure 3), indicating lack of senescence evidences in the life cycle of *G. schottiana*. Although the width length<sup>-1</sup> ratio of leaves had an exponential reduction with plant length (figure 3d), this relationship cannot be attributed to the senescence because leaves become narrower and longer as the plant grows. Initially the leaf is bifid and is wider than long, as the life cycle progresses they become pinnate and leaf blade length increases more than the width. Among individuals of more advanced life stages (immatures and reproductives), leaf shape tends to stabilize with leaves becoming completely pinnate (figure 3d).

## Discussion

**Climatic seasons** – The hypothesis (i) raised in this study was accepted because leaf production and reproductive activity were concentrated in the period of the year with

high light availability (April to October) and not in the period of high soil humidity (November to March). Several biotic and/or abiotic selective forces can affect time growth and reproduction synchronicity among individuals in a population (Fenner 1998). The emergence and expansion of new leaves of *Geonoma schottiana* were lower in the rainy season, probably a consequence of lower average hours of daily insolation in the rainy season compared to the dry season (figure 1). Light availability has been pointed out as a decisive factor for leaf production in tropical trees (Wright & Van Schaik 1994, Barone 1998), principally in forests where the water is not a limiting factor (Wright & Van Schaik 1994). Gallery forests occur associated with streams, and can suffer periodic overflow and have superficial water table influenced by topography, principally in micro-habitats nearest to the stream (Schiavini 1997, Cardoso & Schiavini 2002). In semideciduous lowland forests, where the rainfall is strongly seasonal and the water can be a limiting factor, 6 of the 11 palm species tested have decreased leaf expansion during the dry season (De Steven *et al.* 1987). Luminosity should be still more important for species occupying the understory of tropical forests, where light conditions are very restricted (Chazdon & Fetcher 1984, Chazdon 1986b, Montgomery 2004).

Leaf production can influence the reproductive activity in palms, because reproductive structures emerge from buds in leaf axils. Consequently the maximum flowering rate is set by leaf production rate (Ataroff & Schwarzkopf 1992, Cunningham 1995). Leaf production in reproductive individuals of *G. schottiana* (4.6 leaves year<sup>-1</sup>) was at least 1.5 times higher than inflorescence production (2.75 infl year<sup>-1</sup>). As a result, inflorescence production is not generally at the maximum level set by availability of inflorescence buds, similar to results from *Chamaedorea bartlingiana* H. Wendl. female inflorescences (Ataroff & Schwarzkopf 1992). In addition, the leaf production of *G. schottiana* is 2.5 times less concentrated in a period of the year ( $r = 0.19$ ) than inflorescence production ( $r = 0.48$ ). Therefore, inflorescence production was detached of leaf production, and consequently, other factor could constrain the amount of inflorescences produced in a year and affect reproductive activity time in *G. schottiana*.

Factors related to climatic seasons affecting reproduction time have been discussed (Fenner 1998, Sakai 2001). In tropical forests, the flowering of palm trees communities can be affected by variation in climate during the year, being concentrated in the rainy (De Steven *et al.* 1987) or in the dry season (Ibarra-Manríquez 1992). In some plant communities, even with pronounced

dry season, palm trees can bloom during the whole year (Henderson *et al.* 2000), but at the species or genus level, individuals tend to bloom in a specific climatic season (Henderson *et al.* 2000). In seasonal tropical forests, 20% of the *Geonoma* species whose reproductive phenology is known ( $n = 10$ ), bloom in the dry season, 40% in the rainy period and 40% have an irregular flowering pattern (De Steven *et al.* 1987, Listabarth 1993, Henderson *et al.* 2000). In *G. schottiana*, the inflorescences emerge from the bracts in the beginning of the dry season and develop over the next six months, period of the year with higher average hours of daily insolation. Moreover, the concentration of the reproductive activity in this period may also have occurred because flowering time of sympatric species is synchronous, time when occurs increase of pollinators activity (Sakai 2001, Boulter *et al.* 2006). The floral anthesis of *G. schottiana* probably occurs at the end of the dry period and beginning of the wet period (figure 2a, b). The period of floral anthesis of *G. schottiana* is similar to the majority of the arboreal community species of gallery forests (Gouveia & Felfili 1998, Antunes & Ribeiro 1999, Oliveira & Paula 2001, Funch *et al.* 2002). *Geonoma* species are pollinated by insects, mainly of the orders Hymenoptera, Diptera and Coleoptera (Listabarth 1993, Martén & Quesada 2001, Borchsenius 2002, Henderson *et al.* 2000), it could also be true for *G. schottiana*, as is for the majority of arboreal species of gallery forests (Oliveira & Paula 2001). The flowering of the palm *Rhopalostylis sapida* H. Wendl. & Drude occurs when the pollinators are more abundant, too (Enright 1992), the same, probably occurs to *Euterpe edulis* Mart. (Silva Matos & Watkinson 1998).

Seed germination time is another factor influencing the reproductive activity period that should be a selective constraint on the flowering and fruiting period for the majority of tropical plants (Garwood 1983). *G. schottiana* produces seeds throughout the year (figure 2d), which are dormant and maintain the viability in the soil for more than four years (Sampaio 2006), not fitting the findings above, probably because the understory of gallery forests is a mesic environment, with patches of high soil humidity all over the year.

Life stage – The hypothesis (ii) was partially confirmed since leaf production relates to plant length, but not to reproductive activity. During their life cycle, the palm trees increase leaf production, number of leaves, leaf length and total leaf crown area (Chazdon 1986a, De Carvalho *et al.* 1999, Kimura & Simbolon 2002). This also occurs to *Geonoma schottiana*, probably because bigger individuals have more available resources to growth

than smaller ones (Cunningham 1997). Nevertheless, leaf production increase during life cycle in *G. schottiana* was significant only when all individuals – with and without aerial stem – were evaluated simultaneously, but not when separately analyzed (figure 3a).

Seed number in an inflorescence probably is not related to plant length, and although not quantified for *G. schottiana*, it has been detected in *Astrocaryum mexicanum* Liebm. and *Chamaedorea radicalis* Mart. (Piñero & Sarukhán 1982, Berry & Gorchov 2004). In *A. mexicanum*, when resources fail to reach a reproductive threshold, instead of producing a smaller inflorescence, it produce none at all (Piñero *et al.* 1982), so the reproductive effort could be estimated by the number of inflorescence produced annually. In *G. schottiana* no significant relationship between inflorescence production rate and individual length was detected, contrasting with *Geonoma brevispatha* Barb. Rodr. whose inflorescence production rate initially increases as the individual grows, reaches a production peak in plants of intermediate size and declines soon afterwards in towards senescence (Souza *et al.* 2003). In other palm species the sexual fecundity is positively related to individual length (Oyama 1990, Scariot *et al.* 1995, Cunningham 1997, Svenning 2000). The variability in inflorescence production among *G. schottiana* plants could be more influenced by extrinsic factors, as canopy openness (Enright 1992, Barot *et al.* 2005), than by individual length.

Senescence – Growth rate and reproduction increases until a certain point in the life cycle. After that individuals become more susceptible to senescence effects in some species, as was detected in later life stages of the clonal palms, *Geonoma congesta* H. Wendl. ex Spruce (Chazdon 1992) and *G. brevispatha* (Souza *et al.* 2003). In these species, the vegetative reproduction begins before sexual maturity, and near the end of the life cycle of a ramet, resources can be drained intensely by the youngest ramet produced at that point (Chazdon 1992). In this stage, the senile ramet reduces leaf production, leaves become smaller, reproductive activity decreases and the plant becomes more susceptible to mechanical instability, increasing the probability of stem leaning caused by fall of canopy trunks and branches (Chazdon 1992, Souza *et al.* 2003). In species with intense clonal activity, the maintenance of an older ramet is less important for genet survival, because pre-reproductive ramets could behave as a meristem bank (Souza & Martins 2006). Despite the short period of study (12 to 24 months), *G. schottiana* had no signal of senescence in the leaf production rate, number of leaves in the crown, leaf area, width length<sup>-1</sup>

ratio of leaves or production of reproductive structures (figure 3). Probably this happened because *G. schottiana* has a low investment in clonal growth in comparison with congeneric species and along its whole life cycle, resources are destined preferentially for the maintenance of the single apical shoot, growth and to sexual reproduction. Several non-clonal palms do not reduce growth and reproduction when they get old (Piñero & Sarukhán 1982, Oyama 1990, Cunningham 1997, Svenning 2000, but see Ataroff & Schwarzkopf 1992, Enright 1992). If so, the senescence to these species can be only expressed by the collapse of the tissues holding the stem (Crawley 1997) and occur at the end of life cycle.

Conclusion – *Geonoma schottiana* growth and reproduction are affected by the availability of resources, since both events are concentrated in the period of the year with higher light availability. The soil humidity probably is not a limiting factor, but light conditions are very restricted in the understory of gallery forests. The resources stored in the stem influence the growth of this palm, as evidenced by the positive relationship of leaf size and production to plant length. However, reproduction is not affected by plant length, probably this activity is more influenced by extrinsic than endogenous resources. Most of the patterns found here concur with findings described for other *Geonoma* species. Some discordant aspects can be attributed to environmental conditions, or to the life history of this species, as the absence of senescence expression, possible explained by low clonal activity compared with other congeneric species. However, the cause of other discordant aspects remains unknown.

Acknowledgments – We thank M. W. Pacheco and W. Hoffmann for their comments on the manuscript. Our field assistants Bernardo Bianchetti, Brunno S. de Andrade, Gustavo de O. Lopes, Hugo A. H. Schaedler, Ísis M. Medri, João M. de Rezende, Juarez P. do Amaral, Leandro de S. Lima and Nilton F. Barbosa, and the staff of the National Park of Brasília and Ibama. Capes and CNPq awarded a fellowship to M.B. Sampaio. Ecology and Conservation Laboratory of Embrapa Recursos Genéticos e Biotecnologia provided resources for fieldwork.

## References

- ANTUNES, N.B. & RIBEIRO, J.F. 1999. Aspectos fenológicos de seis espécies vegetais em matas de galeria do Distrito Federal. *Pesquisa Agropecuária Brasileira* 34:1517-1527.
- ASHTON, P.S., GIVNISH, T.J. & APPANAH, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132:44-66.

- ATAROFF, M. & SCHWARZKOPF, T. 1992. Leaf production, reproductive patterns, field germination and seedling survival in *Chamaedorea bartlingiana*, a dioecious understory palm. *Oecologia* 92:250-256.
- AUGSPURGER, C.K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62:775-788.
- BARONE, J.A. 1998. Effects of light availability and rainfall on leaf production in a moist tropical forest in central Panama. *Journal of Tropical Ecology* 14:309-321.
- BAROT, S. & GIGNOUX, J. 1999. Population structure and life cycle of *Borassus aethiopum* Mart.: evidence of early senescence in a palm tree. *Biotropica* 31:439-448.
- BAROT, S., MITJA, D., MIRANDA, I., MEIJA, G.D. & GRIMALDI, M. 2005. Reproductive plasticity in an Amazonian palm. *Evolutionary Ecology Research* 7: 1051-1065.
- BERRY, E.J. & GORCHOV, D.L. 2004. Reproductive biology of the dioecious understory palm *Chamaedorea radicalis* in a Mexican cloud forest: pollination vector, flowering phenology and female fecundity. *Journal of Tropical Ecology* 20:369-376.
- BORCHSENIUS, F. 2002. Staggered flowering in four sympatric varieties of *Geonoma cuneata* (Palmae). *Biotropica* 34:603-606.
- BOULTER, S.L., KITCHING, R.L. & HOWLETT, B.G. 2006. Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology* 94:369-382.
- BULLOCK, S.H. 1980. Demography of an undergrowth palm in littoral Cameroon. *Biotropica* 12:247-255.
- CARDOSO, E. & SCHIAVINI, I. 2002. Relação entre distribuição de espécies arbóreas e topografia em um gradiente florestal na Estação Ecológica do Panga (Uberlândia, MG). *Revista Brasileira de Botânica* 25: 277-289.
- CHAZDON, R.L. 1986a. The costs of leaf support in understory palms – economy versus safety. *American Naturalist* 127:9-30.
- CHAZDON, R.L. 1986b. Light variation and carbon gain in rain forest understory palms. *Journal of Ecology* 74: 995-1012.
- CHAZDON, R.L. 1991. Plant size and form in the understory palm genus *Geonoma*. Are species variations on a theme? *American Journal of Botany* 78:680-694.
- CHAZDON, R.L. 1992. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica* 24:43-51.
- CHAZDON, R.L. & FETCHER, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72:553-564.
- CRAWLEY, M.J. 1997. Life history and environment. *In* Plant ecology (M.J. Crawley, eds.). Blackwell Science, Oxford, p.73-131.
- CUNNINGHAM, S.A. 1995. Ecological constraints on fruit initiation by *Calyptrogyne ghiesbreghtiana* (Arecaceae): floral herbivory, pollen availability, and visitation by pollinating bats. *American Journal of Botany* 82:1527-1536.
- CUNNINGHAM, S.A. 1997. The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understory palm. *Oecologia* 111:36-44.
- DE CARVALHO, R.M., MARTINS, F.R. & SANTOS, F. A.M. 1999. Leaf ecology of pre-reproductive ontogenetic stages of the palm tree *Euterpe edulis* Mart. (Arecaceae). *Annals of Botany* 83:225-233.
- DE STEVEN, D., WINDSOR, D., PUTZ, F. & DE LEON, B. 1987. Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica* 19:342-356.
- ENRIGHT, N.J. 1992. Factors affecting reproductive behavior in the New Zealand nikau palm, *Rhopalostylis sapida* Wendl. et Drude. *New Zealand Journal of Botany* 30:69-80.
- FENNER, M. 1998. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 1:78-91.
- FUNCH, L.S., FUNCH, R. & BARROSO, G.M. 2002. Phenology of gallery and montane forest in the Chapada Diamantina, Bahia, Brazil. *Biotropica* 34:40-50.
- GARWOOD, N.C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53:159-181.
- GOUVEIA, G.P. & FELFILI, J.M. 1998. Fenologia de comunidades de cerrado e de mata de galeria no Brasil Central. *Revista Árvore* 22:443-450.
- HENDERSON, A., FISCHER, B., SCARIOT, A., PACHECO, M.A.W. & PARDINI, R. 2000. Flowering phenology of a palm community in a central Amazon forest. *Brittonia* 52:149-159.
- HENDERSON, A., GALEANO, G. & BERNAL, R. 1995. Field guide to the palms of the Americas. Princeton University Press, New Jersey.
- IBARRA-MANRÍQUEZ, G. 1992. Fenología de las palmas de una selva cálida húmeda de México. *Bulletin de l'Institut Français d'Etudes Andines* 21:669-683.
- KIMURA, M. & SIMBOLON, H. 2002. Allometry and life history of a forest understory palm *Pinanga coronata* (Arecaceae) on Mount Halimun, West Java. *Ecological Research* 17:323-338.
- LISTABARTH, C. 1993. Pollination in *Geonoma macrostachys* and three congeners, *G. acaulis*, *G. gracilis*, and *G. interrupta*. *Botanica Acta* 106:496-506.
- LOBO, J.A., QUESADA, M., STONER, K.E., FUCHS, E.J., HERRERIAS-DIEGO, Y., ROJAS, J. & SABORIO, G. 2003. Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. *American Journal of Botany* 90:1054-1063.
- MARTÉN, S. & QUESADA, M. 2001. Phenology, sexual expression, and reproductive success of the rare neotropical palm *Geonoma petiolata*. *Biotropica* 33:596-605.

- MARTINS, R.C. 2000. Arecaceae (Palmae) no Distrito Federal, Brasil. Dissertação de mestrado, Universidade de Brasília, Brasília.
- MENDOZA, A. & FRANCO, M. 1998. Sexual reproduction and clonal growth in *Reinhardtia gracilis* (Palmae), an understory tropical palm. *American Journal of Botany* 85:521-527.
- MONTGOMERY, R.A. 2004. Effects of understory foliage on patterns of light attenuation near the forest floor. *Biotropica* 36:33-39.
- NIMER, E. 1989. Climatologia do Brasil. IBGE, Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro.
- OLIVEIRA, P.E. & PAULA, F.R. 2001. Fenologia e biologia reprodutiva de plantas de matas de galeria. In *Cerrado: caracterização e recuperação de matas de galeria* (J.F. Ribeiro, C.E.L. Fonseca & J.C. Sousa-Silva, eds.). Embrapa Cerrados, Planaltina, DF, p.303-334.
- OSADA, N., TAKEDA, H., FURUKAWA, A. & AWANG, M. 2002. Ontogenetic changes in leaf phenology of a canopy species, *Elateriospermum tapos* (Euphorbiaceae), in a Malaysian rain forest. *Journal of Tropical Ecology* 18:91-105.
- OYAMA, K. 1990. Variation in growth and reproduction in the neotropical dioecious palm *Chamaedorea tepejilote*. *Journal of Ecology* 78:648-663.
- PIÑERO, D. & SARUKHÁN, J. 1982. Reproductive behavior and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* 70:461-472.
- PIÑERO, D., SARUKHAN, J. & ALBERDI, P. 1982. The costs of reproduction in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* 70:473-481.
- RAMOS, P.C.M. 1995. Vegetation communities and soils in the National Park of Brasília. Ph.D. Thesis, University of Edinburgh, Edinburgh.
- SAKAI, S. 2001. Phenological diversity in tropical forests. *Population Ecology* 43:77-86.
- SAMPAIO, M.B. 2006. Ecologia populacional da palmeira *Geonoma schottiana* Mart. em mata de galeria no Brasil Central. Dissertação de mestrado, Universidade de Brasília, Brasília.
- SCARIOT, A., LLERAS, E. & HAY, J.D. 1991. Reproductive biology of the palm *Acrocomia aculeata* in Central Brazil. *Biotropica* 23:12-22.
- SCARIOT, A., LLERAS, E. & HAY, J.D. 1995. Flowering and fruiting phenologies of the palm *Acrocomia aculeata*: patterns and consequences. *Biotropica* 27:168-173.
- SCHIAVINI, I. 1997. Environmental characterization and groups of species in gallery forests. In *International symposium on assessment and monitoring of forests in tropical dry regions with special reference to gallery forests* (J. Imaña-Encinas & C. Kleinn, eds.). Universidade de Brasília, Brasília, p.107-113.
- SILVA MATOS, D.M. & WATKINSON, A.R. 1998. The fecundity, seed, and seedling ecology of the edible palm *Euterpe edulis* in southeastern Brazil. *Biotropica* 30:595-603.
- SOUZA, A.F. & MARTINS, F.R. 2006. Demography of the clonal palm *Geonoma brevispatha* in a Neotropical swamp forest. *Austral Ecology* 31:869-881.
- SOUZA, A.F., MARTINS, F.R. & BERNACCI, L.C. 2003. Clonal growth and reproductive strategies of the understory tropical palm *Geonoma brevispatha*: an ontogenetic approach. *Canadian Journal of Botany* 81: 101-112.
- SVENNING, J.C. 2000. Growth strategies of clonal palms (Arecaceae) in a neotropical rainforest, Yasuni, Ecuador. *Australian Journal of Botany* 48:167-178.
- TABACHNICK, B.G. & FIDELL, L.S. 2001. Using multivariate statistics. Allyn & Bacon, Boston.
- VOEKS, R.A. 2002. Reproductive ecology of the piassava palm (*Attalea funifera*) of Bahia, Brazil. *Journal of Tropical Ecology* 18:121-136.
- WATANABE, N.M., MIYAMOTO, J. & SUZUKI, E. 2006. Growth strategy of the stoloniferous rattan *Calamus javensis* in Mt. Halimun, Java. *Ecological Research* 21:238-245.
- WRIGHT, S.J. & VAN SCHAIK, C.P. 1994. Light and the phenology of tropical trees. *American Naturalist* 143: 192-199.
- ZAR, J.H. 1999. Biostatistical analysis. Prentice Hall, Inc., New Jersey.