

Vegetative Growth in *Chamaedorea bartlingiana**

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ABSTRACT

Chamaedorea bartlingiana is a dioecious solitary palm, growing up to 4 m in height, that occurs as an understory species of some Andean cloud forests in Colombia and Venezuela. In this paper, we describe the main changes in vegetative morphology of *C. bartlingiana* from germination to the adult stage, and we estimate how long the plant lasts in each stage: juveniles 7 years, prereproductives 6 years, and more than 50 years as adults. Total life span is 60 to 66 years.

C. bartlingiana shows important morphological changes in leaf shape and size (from only a small bifid blade to a 53 cm paripinnate lamina), and in stem thickness and orientation (thin, horizontal and underground, to 2 cm in diameter, vertical and aerial), when plants change from juvenile to adult stages. There are no vegetative morphological differences between males and females.

Biomass allocation changes between stages: leaves and roots are more important in juveniles, stems and roots are more important in adults. There is no evidence that sexes have different storage organs or higher storage in some particular tissue.

Chamaedorea bartlingiana H. Wendl. is a dioecious solitary palm which grows up to 4 m in height (Fig. 1). It is found as an understory species in some Andean cloud forests in Colombia and Venezuela. In Mérida, Venezuela, this species is dominant in undisturbed understories between 2,000 and 2,500 m.

Individual palms have a flexible, thin stem with a diameter no greater than 2 cm, which continues to grow even when the weight of branches falling from the canopy bends the plants to the ground. The low rate of leaf production, long leaf life span, and different reproductive patterns in both sexes suggest a high adaptation of this species to understory environments (Ataroff and Schwarzkopf 1992).

In this article, the main changes in vegetative morphology of *C. bartlingiana* are described from germination to adult stage, with the absolute age of the plant estimated in each stage.

Study Area

This study was conducted in a cloud forest in the locality of Monte Zerpa, 3 km north of Mérida at 2,150 m. The nearest meteorological station, Santa Rosa (1,950 m), reports a mean annual temperature of 16.9° C and a bimodal water regime with two periods of low precipitation: the lower period between January and February and another in July; and two periods of high precipitation: the lower from March to June, and the higher from September to November. The mean total annual precipitation is 2,072 mm with a mean driest month of 68 mm. The high degree of cloud cover is seen by the mean sunshine of 5.3 hours of sunshine/day with a minimum of 3 hours of sunshine/day in April and a maximum of 7 hours of sunshine/day in January.

The complex vertical structure in this forest presents different strata with undefined limits. It is also rich in epiphytes (bryophytes, pteridophytes, Bromeliaceae, Orchidaceae, Araceae). There are between 30 and 80 tree species/ha (Sarmiento et al. 1971) with the canopy at approximately 25 m. The understory has more than 30 species of angiosperms, mainly Solanaceae, Rubiaceae, Piperaceae, Begoniaceae, and Poaceae. However, a single palm species, *Chamaedorea bartlingiana*, dominates the undisturbed forest understory, reaching its highest density (1 adult/m²) in the study area in well-drained soils and under a dense closed canopy (Schwarzkopf 1985).

Methodology

The growth data is derived from two sources: (1) 272 individuals were marked and followed as part of a sampling design for population dynamics and reproductive patterns studies (Ataroff and Schwarzkopf 1992). Morphological changes and leaf production of all marked individuals were monitored for 3½ years of study (November 1985–April 1989). The marked individuals were dis-

* Now *C. pinnatifrons*. See "Chamaedorea Palms" (Hodel 1992).



1. Adult of *Chamaedorea bartlingiana* (female).

tributed as follows: 100 juveniles (J), 50 prereproductive (P), 22 young adults (A_I), 50 intermediate adults (A_{II}) and 50 old adults (A_{III} , A_{IV} and A_V). (2) In order to establish a relationship between age, leaf production, and stem morphology, all new emergent seedlings in 61 plots of 1 m² were marked and followed from October 1986 until April 1989. Stem morphology was determined by dissection of several plants of different ages during the first years of the plants' lives. Data were taken monthly for the first two years and every two months for the remainder of the study.

In order to establish morphological information, 40 individuals, representative of different stages, were taken to the laboratory for study of the stem base morphology, node count, and inflorescence scar sequences.

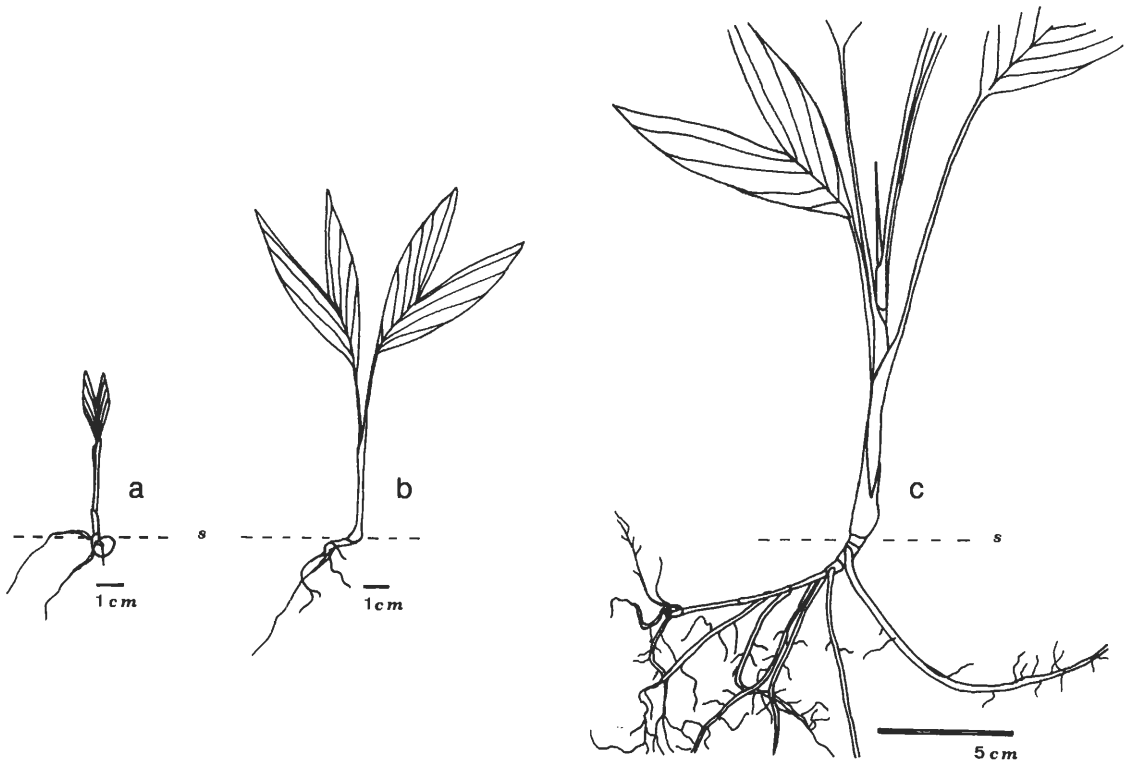
Age was estimated as follows: $D_i = N_i/L_i$ and

$A_i = A_{i-1} + D_i$, where i = development stage (from seedling to old adult), D_i = stage duration (years), N_i = leaves (nodes) produced during the stage "i", L_i = mean leaf production (leaves/year) during the stage "i", and A_i = age at the end of stage "i" (years).

Another set of individuals representative of different stages was taken to the laboratory and separated into seed (in the case of seedlings), roots, stem, stem apex (which includes sheath of live leaves), live leaves, inflorescence, peduncle of inflorescence, and necromass (dead leaves and reproductive parts attached to the plant). This material was oven-dried until constant weight was reached and weighed for the biomass study.

Results

Growth Stages. Shape and size of stem base and leaves change during the individual's life span.



2. Vegetative growth from germination to prereproductive stage. a) germination, seedling younger than 15 days old, b) 2 years old juvenile, c) beginning of prereproductive stage (4 of its 5 leaves are juvenile type). S: soil surface.

Based on these changes, three main stages are defined in a plant's life: juvenile, prereproductive, and adult. Figures 2, 3 and 4 show the most significant morphological changes.

I. Juvenile Stage: The juvenile stage starts with germination (Fig. 2a), which is adjacent-ligular (Uhl and Dransfield 1987). From the moment the second leaf appears, the stem base curves and becomes horizontal (Fig. 2b). During this stage, internode development occurs underground, directly under the surface, and the stem remains horizontal (Fig. 2).

The leaves are small and have a bifid blade (Figs. 2a, 2b, 4a). The last two or three leaves of this stage frequently have two or three little folioles. This stage ends when the node 10 ± 2 is formed.

It is difficult to distinguish a seedling stage from a general juvenile stage because stem and leaf morphology do not change. However, we can consider the life-span of the first two leaves as the first stage, since the seed remains attached to the plant in this period and leaves have a longer life-span: 20.9 months for the first leaf and 22.0 months for the second leaf compared to 17.5

months for the third leaf (Ataroff and Schwarzkopf 1992).

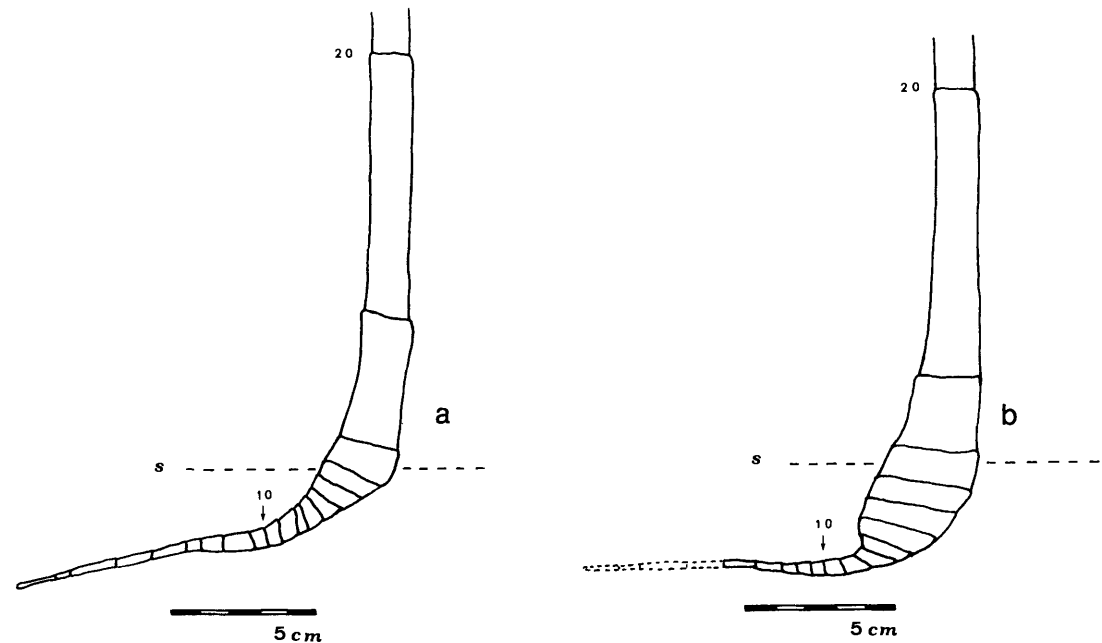
II. Prereproductive Stage: The prereproductive stage begins at the end of horizontal stem growth. New internodes elongate causing the stem to curve upward, or vertically. All internodes are curved, forming the future stem base of the adult plant (Figs. 2c, 3a). This stem base swells during the prereproductive stage until it reaches its definitive diameter.

Simultaneously, leaves change to paripinnate with 3 to 10 leaflets (Fig. 4b) with each leaf growing larger than its precedent.

This stage ends with the formation of two long, above ground and vertical internodes (nodes 18 to 20). Their diameter is the maximum diameter reached during stem growth (Figs. 3a, 3b).

III. Adult Stage: Adult stage begins when an axillary bud, corresponding to node 17 to 20, differentiates into a reproductive bud. From this moment on, all axillary buds become reproductive, leaving a marked scar over each node.

During this stage, the stem grows above ground and vertically. As the weight of branches falling



3. Adult stem base and underground parts, without roots. a) beginning of adult stage (individual with 23 nodes, apex bud at 70 cm), b) adult (individual with 31 nodes, apex bud at 120 cm, 1st reproductive bud at node 22). Nodes 10 and 20 are indicated; S: soil surface.

from the canopy bends the stem to the ground, new internodes curve to attain a vertical position. This decumbent form is accidental. The stem base diameter remains the same as reached in the preceding stage. The oldest part of the stem, corresponding to the first underground nodes, decomposes and disappears (Fig. 3b).

Leaves remain paripinnate, but they are bigger than in prereproductive, 68.3 cm including lamina and petiole, with 7 to 14 wider leaflets (Fig. 4c).

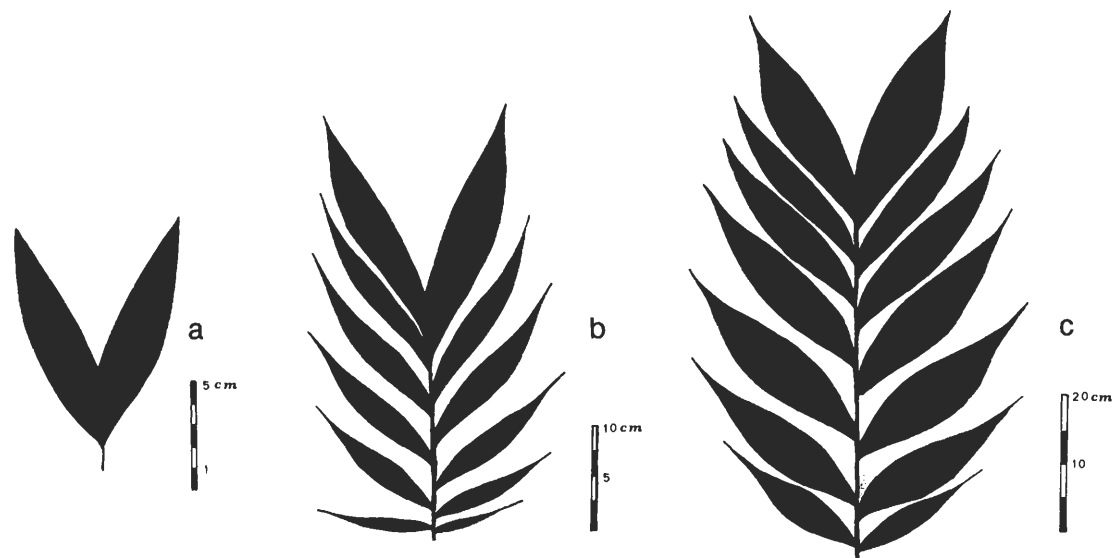
Stage Duration. The number of nodes produced during life span and all nodes that have produced inflorescence are easy to count since nodes form strong rings around the stem and inflorescences leave conspicuous scars. Only one leaf and one inflorescence are produced per node in adults of this species. The only way to grow is by leaf or node production. The knowledge of total nodes and rate of leaf production per stage (Ataroff and Schwarzkopf 1992) allows a correlation between stages and absolute age of plants (Table 1). Juvenile and prereproductive stages are long-lived, 7 ± 1 years and 6 ± 1 years respectively; it takes nearly 13 years for plants to become reproductive. This species is reproductive for the duration of the adult stage, which lasts more than 50 years $\frac{1}{2}$ of the plant's life. A population dynam-

ics study would be necessary to evaluate the contributions of each stage to the population growth.

Leaf Growth. Between germination and the adult stage, each new leaf is bigger than the preceding one (Fig. 5). During the juvenile stage, there is slow growth at a rate of 1.5 cm per new leaf lamina. During the prereproductive stage, the lamina mean growth rate increases to 3.5 cm. In adults, leaf lamina size remains around the mean, 53 cm. The leaf lamina size ranges from 7.5 cm, in the first juvenile leaf, to 53 cm in adults (Table 2).

The petiole length increases from the first leaf in the juvenile stage (3.1 cm) to the mean juvenile length (6.5 cm) and continues to grow in the prereproductive stage (25.8 cm) (Table 2). The maximum length is reached in the prereproductive stage and then declines in the adult stage (15.8 cm). Although the petiole growth pattern is distinct, the growth of the entire leaf is similar to that seen in lamina growth in Figure 5.

Leaf life span values of *C. bartlingiana* (Table 3) corresponds to long-lived leaves, common to understory plants (Bentley 1979, Kikuzawa 1989), but they are surprisingly low compared to other understory palms: *Rhapidophyllum hystrix* 5.9 years (Clancy and Sullivan 1990), *Podococcus*



4. Leaf types (lamina): a) juvenile leaf, b) prereproductive leaf and c) adult leaf.

barteri 5 years (Bullock 1980), 3 years *Geonoma congesta* (Chazdon 1992), and other values reported by Corner (1966) and Tomlinson (1990): *Elacis guineensis* 3.5 years, *Cocos nucifera* 5 years, *Nypa fruticans* 5.5 years, *Rhopalostylis sapida* 7 years and *Lodoicea maldivica* 18 years.

Biomass Allocation. The biomass distribution to each big structural part of the plant changes during its life span. During the juvenile stage, leaves are 35% to 45% of the total biomass, while the rest is divided more or less equally between stem and roots (Fig. 6, Table 4). During the prere-

productive stage, the stem apex (the future stem base) swells, concentrating resources and becoming the largest part of plant (Fig. 6, Table 4).

At the beginning of the adult stage, leaves reach their maximum size. They remain unchanged for the rest of the plant's life (Fig. 5). Stem and roots continue growing, so their biomass increase with age in relation to the rest of the plant (Fig. 6, Table 4). Leaves, reproductive parts, and necromass have approximately equivalent relative biomass proportions.

The root system is strongly attached to soil and

Table 1. Growth characteristics and age of stages. Adult stage has been subdivided into 5 categories each comprising the production of 20 new nodes (since this is an arbitrary division error of ± 2 or ± 1 comes from former stages).

Stage	Final Leaf (or Node)	Mean Leaf Production (Leaves/ Year)	Stage Duration (Years)	Final Age (Years)
Juvenile	10 \pm 2	1.5	7 \pm 1	7 \pm 1
Prereproductive	20 \pm 2	1.7	6 \pm 1	13 \pm 1
Adult I	40 \pm 2	2.1	10 \pm 1	23 \pm 1
♀		2.4	8 \pm 1	22 \pm 1
♂		2.0	10 \pm 1	33 \pm 1
Adult II	60 \pm 2	2.2	9 \pm 1	31 \pm 1
♀		1.9	11 \pm 1	44 \pm 1
♂		2.1	10 \pm 1	41 \pm 1
Adult III	80 \pm 2	1.8	11 \pm 1	55 \pm 1
♀		2.2	9 \pm 1	50 \pm 1
♂		1.8	11 \pm 1	66 \pm 1
Adult IV	100 \pm 2	1.8	11 \pm 1	66 \pm 1
♀		1.8	11 \pm 1	61 \pm 1
♂				

Table 2. Mean leaf length in cm ($\bar{X} \pm s$).

	Juvenile Stage	Prereproductive Stage	Adult Stage
Lamina length	11.35 \pm 0.8	33.19 \pm 2.4	52.70 \pm 1.2
Petiole length	6.49 \pm 0.8	25.84 \pm 2.1	15.80 \pm 0.8
Total leaf length	17.57 \pm 1.6	56.29 \pm 4.5	68.31 \pm 1.6

mixed with the roots of other species, particularly in adults. Because of this, biomass is underestimated even with careful root collection. Total biomass of two nearly 30 year old individuals, approximately 2 m high, differ greatly with values of 410.6 g and 240.0 g (Table 4). This difference is not necessarily due to sex, since the means of total male individuals and female individuals show different biomass distribution, for example, in reproductive parts, stem apex, and necromass (Table 4).

Vegetative Characters vs Sexes. There are no differences between male and female vegetative morphologies. Therefore, juveniles and prereproductives cannot be typed according to gender. In the study area, male-female ratio in adults was

equivalent (51% F/49% M). The same has been reported for other dioecious palms (Clancy and Sullivan 1990).

Leaf production rate is consistently slower in females, with a significant difference in leaf production time, 0.5 to 1.5 months (ANOVA $P < 0.024$) (Ataroff and Schwarzkopf 1992) and total leaf production, 1.97 leaves/year compared to 2.20 leaves/year for the male individuals (ANOVA $P < 0.0001$).

Except for youngest adults, the mean crown size is slightly larger in females, but differences are not statistically significant. Crown size and leaf production rates allow estimation of leaf life-span since, under normal conditions, a new leaf unfolds as the oldest dies (Table 3). Average leaf life-span

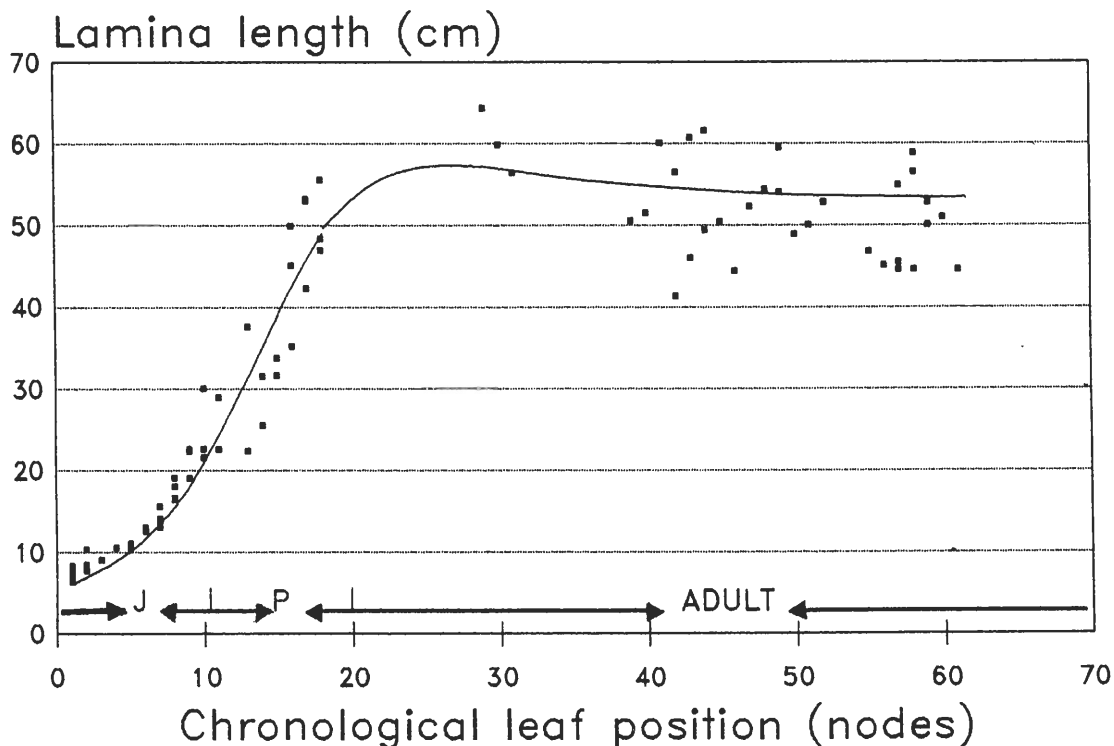


Table 3. Vegetative growth parameters in young individuals, and in adults of both sexes.

Stage	Mean Crown Size (Leaves/Crown)	Mean Leaf Production (Leaves/Year)	Mean Leaf Life-span (Years)
Juvenile	2.5 ± 0.09	1.5 ± 0.03	1.8 ± 0.03
Prereproductive	3.5 ± 0.16	1.7 ± 0.04	2.3 ± 0.05
Adult I ♀	5.0 ± 0.00	2.1 ± 0.12	2.6 ± 0.11
♂	5.3 ± 0.42	2.4 ± 0.13	2.3 ± 0.12
Adult II ♀	4.3 ± 0.20	2.0 ± 0.07	2.3 ± 0.06
♂	4.4 ± 0.24	2.2 ± 0.08	2.1 ± 0.05
Adult III ♀	4.7 ± 0.22	1.9 ± 0.04	2.6 ± 0.05
♂	4.4 ± 0.15	2.1 ± 0.05	2.2 ± 0.04
Adult IV ♀	4.1 ± 0.14	1.8 ± 0.08	2.4 ± 0.11
♂	4.0 ± 0.58	2.2 ± 0.29	1.9 ± 0.15

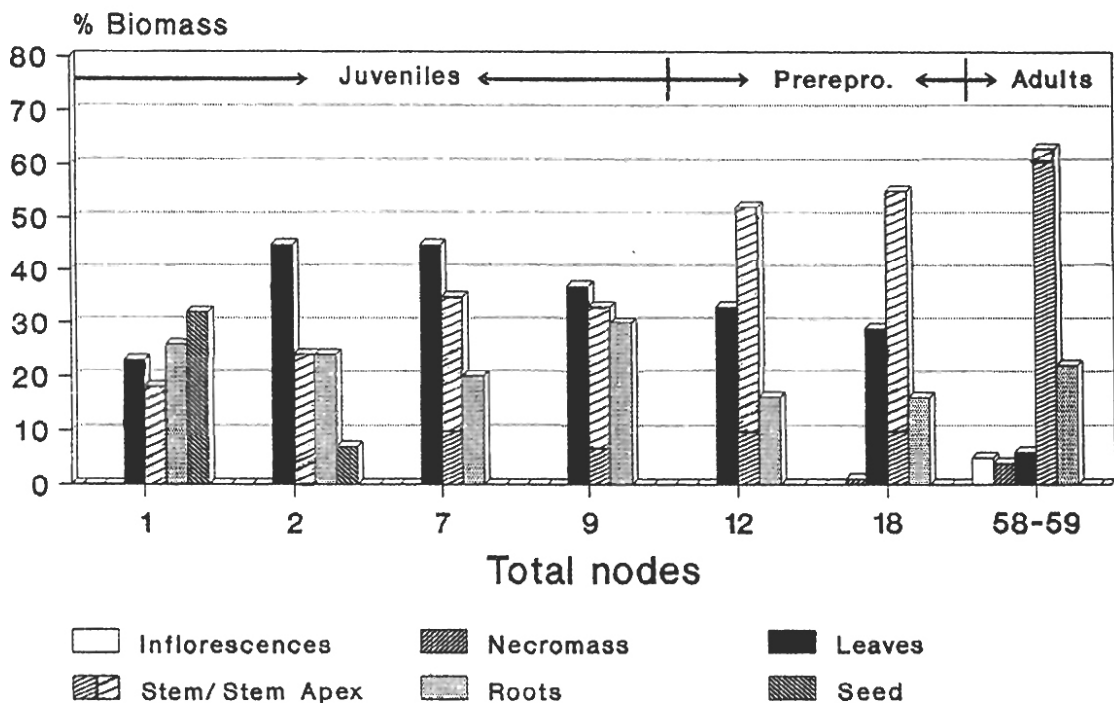
is significant at 2.5 years for females and 2.2 years for males (ANOVA $P < 0.0001$).

Discussion

C. bartlingiana exhibits important morphological changes in leaf shape, leaf size, stem thickness, and stem orientation as the plants develop. There are no vegetative morphological differences between sexes. Therefore, it is not possible to

distinguish sex in non-reproductive individuals. The main vegetative differences between sexes are leaf life-span and leaf production rates.

Leaf production rates vary at different stages and between sexes (Ataroff and Schwarzkopf 1992), lower in juveniles and prereproductives compared to adults, and lower in females. Similar variances have been reported for other palms (De Steven et al. 1987, Oyama 1990) and other dioecious species (Lloyd and Webb 1977).



6. Biomass allocation: distribution of total biomass (%) between different parts of a plant, in individuals with 1, 2, 7, 9, 12, 18, 58 and 59 nodes.

Table 4. Biomass in dry weight (g) distributed into different structural plant parts, in plants of different age and sex.

	Total nodes:	1 *	2 *	7	9	11 **	18 *	58 ♀	59 ♂	Adults x̄	Adults x̄
Age (years)		0.5	1	5	6	8	11	31	28		
Stem apex		0.03	0.2	0.5	1.1	5.4	16.1	10.7	9.5	8.2	15.9
Single lamina		0.04	0.19	0.18	0.32	0.84	2.22	5.85	4.5	4.0	4.2
Peduncle		—	—	—	—	—	—	5.4	5.8	3.9	4.1
Inflorescence		—	—	—	—	—	—	11.0	11.2	6.2	8.4
Total reproductive		—	—	—	—	—	—	16.4	17.0	10.1	12.5
Necromass		—	—	—	—	—	0.3	15.2	13.3	4.8	6.6
Leaves		0.04	0.37	0.9	1.6	3.6	10.5	23.4	13.5	18.6	22.4
Total stem		0.03	0.2	0.7	1.4	6.4	19.7	251.9	159.5	—	—
Roots		0.05	0.2	0.4	1.3	2.1	5.7	103.7	36.7	—	—
Seed		0.05	0.06	—	—	—	—	—	—	—	—
Total plant		0.17	0.8	2.0	4.3	12.1	36.2	410.6	240.0	—	—

*: the mean of 3 plants.

** : the mean of 2 plants.

x̄: the mean of 4 plants, with 31, 44, 52 and 58 nodes (16, 23, 27 and 28 years respectively).

x̄: the mean of 2 plants, with 49 and 59 nodes (23 and 28 years respectively).

Total reproductive: sum of reproductive parts (peduncle and inflorescence).

Total stem: sum of stem apex and the rest of the stem.

Total plant: sum of total reproductive, necromass, leaves, total stem, roots and seed.

The lower leaf production rates in females have been interpreted as a consequence of a higher reproductive cost (Hoffman and Allende 1984, Lloyd and Webb 1977, Silvertown 1987, Clark and Clark 1988). In addition to the fact that females produce fewer leaves/year and leaves are more long-lived, the main feature of *C. bartlingiana* is a female reproductive pattern with rest periods which allows them to meet the energetic cost of fruit production (Ataroff and Schwarzkopf 1992).

It would be interesting to prove that females have a higher energy expenditure than males during the life-cycle. Since females have a higher inflorescence abortion rate, we hypothesize that the total cost of reproduction for females is not significantly higher than that for males. If this is the case, it would differ from reports of other dioecious species (Hoffman and Allende 1984, Lloyd and Webb 1977, Silvertown 1987, Clark and Clark 1988, Maze and Whalley 1990, Oyama and Dirzo 1991).

Since there are no vegetative differences in morphology or biomass allocation between sexes, there is no proof of different storing organs or higher storage in particular tissues. However, weight data is not always conclusive and nutrient content analysis is convenient (Bullock 1984, Ashman 1992). A particular case has been reported for *Chamaedorea tepejilote* showing no differences in nutritional and secondary compounds of leaf tissues between sexes (Oyama and Dirzo 1991). In the same context, *Chamaedorea tepejilote*, a well studied understory dioecious palm, also shows no significant differences between sexes in response to disturbances such as leaf tissue loss and net height gains in a four year study (Oyama 1990). Defoliated male and female plants had significantly more new leaves than control plants (Oyama and Mendoza 1990).

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LITERATURE CITED

- ASHMAN, T. L. 1992. Indirect cost of seed production within and between seasons in a gynodioecious species. *Oecologia* 92: 266-272.
- ATAROFF, M. AND T. SCHWARZKOPF. 1992. Leaf production, reproductive patterns, field germination and seedling survival in *Chamaedorea bartlingiana*, a dioecious understory palm. *Oecologia* 92: 250-256.
- BENTLEY, B. L. 1979. Longevity of individual leaves in a tropical rain forest understory. *Annals of Botany* 43: 119-121.
- BULLOCK, S. H. 1980. Demography of an undergrowth palm in littoral Cameroon. *Biotropica* 12: 247-255.
- . 1984. Biomass and nutrient allocation in a tropical dioecious palm. *Oecologia* 63: 426-428.
- CHAZDON, R. L. 1992. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica* 24: 43-51.
- CLANCY, K. E. AND M. J. SULLIVAN. 1990. Demography of the needle palm, *Rhaphidophyllum hystrix*, in Mississippi and Alabama. *Principes* 34(2): 64-78.
- CLARK, D. B. AND D. A. CLARK. 1988. Leaf production and the cost of reproduction in the neotropical rain forest Cycad, *Zamia skinneri*. *Journal of Ecology* 76: 1153-1163.
- CORNER, E. J. H. 1966. The natural history of palms. University of California Press, Berkeley, 393 pp.
- DE STEVEN, D., D. M. WINDSOR, F. E. PUTZ, AND B. DE LEON. 1987. Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica* 19: 342-356.
- HOFFMAN, A. J. AND M. C. ALLIENDE. 1984. Interactions in the patterns of vegetative growth and reproduction in woody dioecious plants. *Oecologia* 61: 109-114.
- KIKUZAWA, K. 1989. Ecology and evolution of phenological pattern, leaf longevity and leaf habit. *Evolutionary Trends in Plants* 3(2): 105-110.
- LLOYD, D. G. AND C. J. WEBB. 1977. Secondary sex characters in seed plants. *Botanical Review* 43: 177-216.
- MAZE, K. M. AND R. D. B. WHALLEY. 1990. Resource allocation patterns in *Spinifex sericeus* R. Br. a dioecious perennial grass of coastal sand dunes. *Australian Journal of Ecology* 15: 145-153.
- OYAMA, K. 1990. Variation in growth and reproduction in the neotropical dioecious palm *Chamaedorea tepejilote*. *Journal of Ecology* 78: 648-663.
- AND R. DIRZO. 1991. Ecological aspects of the interaction between *Chamaedorea tepejilote*, a dioecious palm and *Calyptocephala marginipennis*, a herbivorous beetle, in a Mexican rain forest. *Principes* 35: 86-93.
- AND A. MENDOZA. 1990. Effects of defoliation on growth, reproduction, and survival of a neotropical dioecious palm, *Chamaedorea tepejilote*. *Biotropica* 22: 119-123.
- SARMIENTO, G., M. MONASTERIO, A. AZOCAR, E. CASTELLANO, AND J. F. SILVA. 1971. Vegetación natural. Estudio integral de la Cuenca de los Ríos Chama y Capazón. Facultad de Ciencias Forestales, Universidad de Los Andes, Mérida, Venezuela, 63 pp.
- SCHWARZKOPF, T. 1985. Patrones de distribución en plantas del Sotobosque de una Selva Nublada. Tesis de Grado. Universidad de Los Andes, Mérida, Venezuela, 117 pp.
- SILVERTOWN, J. 1987. Possible sexual dimorphism in the double coconut: reinterpretation of the data of Savage and Ashton. *Biotropica* 19: 282-283.
- TOMLINSON, P. B. 1990. The structural biology of palms. Clarendon Press, Oxford, 447 pp.
- UHL, N. W. AND J. DRANSFIELD. 1987. Genera Palmarum. Allen Press, Lawrence.