

Leaf production, reproductive patterns, field germination and seedling survival in *Chamaedorea bartlingiana*, a dioecious understory palm

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Received August 11, 1991 / Accepted in revised form May 17, 1992

Summary. *Chamaedorea bartlingiana* is a dioecious palm that grows in the cloud forest understories of the Venezuelan Andes. Age and sexual differences in phenology and reproductive patterns were studied in labelled individuals of all age categories. This species has long-lived leaves and low leaf production, both characteristic of understory plants. Growth rates are lower in juveniles than in adults and in females than in males, as in other palms. Male and female individuals show different reproductive patterns. Male inflorescences are always produced at the same rate and the probability of surviving until anthesis is constant. Females produce reproductive buds at the same rate as males, but these buds have a 35% probability of becoming a ripe infructescence if the plant has infructescences already growing, and 70% if it does not. This pattern and the slow growth of inflorescences (1 year for males from bud to flowers, 2 years for females from bud to ripe fruits) cause a pluriannual reproductive pattern at the population level. Field germination does not follow this pattern, but shows one annual peak probably related to environmental conditions.

Key words: *Chamaedorea bartlingiana* – Dioecy – Vegetative phenology – Reproductive phenology – Seedlings

Forest understories present very particular environmental characteristics imposed by the canopy, especially light quantity and quality (Grubb and Whitmore 1966; Chazdon 1986a). Tropical mountain cloud forests have additional restrictions due to cloud cover and low temperatures all year round (Sarmiento et al. 1971; Huber 1986).

The understory microclimate has been considered to be fairly constant (Bentley 1979; Opler et al. 1980; Garwood 1983; Huber 1986; Kikuzawa 1989). In spite of this, in some cases understory phenological patterns are

affected by macroclimatic variables (De Steven et al. 1987). Understory species' responses to their microenvironment have motivated studies oriented towards the understanding of the relationship between environmental characteristics and: leaf production and longevity (Bentley 1979; Opler et al. 1980; Chazdon 1986a; Kikuzawa 1989); photosynthetic rates and carbon balance (Chazdon 1986a); leaf size and shape (Chazdon 1986b); population dynamics and seedling establishment (Garwood 1983; Chazdon 1986a), and reproductive activity (Opler et al. 1980; Huber 1986; Stratton 1989). The main purpose of this study is to analyze growth activities, reproductive activities and seedling dynamics of a successful understory species: *Chamaedorea bartlingiana*. Furthermore, since this is a dioecious species, we are also interested to know how the separation of sexes relates to phenology patterns and "reproductive cost".

Dioecy has received much attention at species and community levels related to its evolutionary advantages (Bawa 1980). The separation of individuals by sex may imply: a differentiation in physiological characteristics (Dawson and Bliss 1989); changes in the sex ratio as a function of the habitat, with the female individuals in the sites with the best water and nutrient conditions (Dawson and Bliss 1989; Krischik and Denno 1990a, b); differences in leaf growth and production (Clark and Clark 1988; Oyama 1990); and less injury due to herbivory in female individuals (Alliende 1989; Jing and Coley 1990; Krischik and Denno 1990b).

Study area

This study was carried out in a Venezuelan Andes cloud forest, in Monte Zerpa, 3 km north of Merida, at an altitude of 2150 m, and on the south slope of the main intramontane valley of the Sierra Nevada mountains. The nearest meteorological station (Santa Rosa, 1950 m) shows a mean annual temperature of 16.9° C and a bimodal water regime with two periods of low precipitation, the lower between January and February and

another in July, and two periods of high precipitation, the lower between March and June, and the higher between September and November. Mean total annual precipitation for 23 years is 2072 mm with a mean driest month of 68 mm. The high degree of cloud cover is shown in the mean sunshine of 5.3 h of sunshine/day with a minimum of 3.0 h/day in April and a maximum of 7.0 h/day in January.

This forest has a complex vertical structure with different strata with diffuse limits, and is rich in epiphytes (bryophytes, pteridophytes, Bromeliaceae, Orchidiaceae, Araceae). There are 30–80 tree species/ha (Sarmiento et al. 1971) with about 25 m canopy height. The understory has more than 30 species of angiosperms, mainly Solanaceae (20%), Rubiaceae (14%), Piperaceae (10%), Begoniaceae (7%) and Poaceae (7%). However, a palm species, *Chamaedorea bartlingiana*, dominates the undisturbed forest understory between 2000 and 2500 m, reaching its highest density (1 adult/m²) in the study area in soils with lower humidity and under a dense closed canopy (Schwarzkopf 1985).

Chamaedorea bartlingiana

C. bartlingiana is a dioecious solitary stem palm, growing up to 4 m in height. It has a thin stem of no more than 2 cm diameter and is very flexible. This characteristic enables it to grow even when the weight of branches falling from the canopy may frequently bend it down to the ground.

We have differentiated seven age categories according to stages of growth:

J: juveniles: from seedling emergence (germination), with small leaves usually only with a bifid blade, to the appearance of pinnate leaves with more than three leaflets.

P: pre-reproductives: from the appearance of the first pinnate leaf to the development of the first reproductive bud.

A: adults: from the moment when an axillary bud develops into a reproductive bud. From this moment on, all axillary buds become reproductive, leaving a scar in the nodes. This group is divided into five subcategories according to the number of nodes produced during their adult life: group A1, 1–20 reproductive nodes; A2, 21–40; A3, 41–60; A4, 61–80; and A5, 81 or more nodes. The oldest marked individual had produced 100 nodes (after reproduction) and it was still reproducing at the end of this study.

When they become adults, the individuals of both sexes produce one inflorescence per leaf, by differentiation of their axillary bud. This means that one plant may show different phenologic phases at the same time. We have distinguished 6 phenologic phases in reproduction: (1) bud (uniform inflorescence axis, flowers prefigured by an aureola); (2) flower bud (flower development, forming protuberances with sealed petals); (3) flower (anthesis period); (4) incipient fruit (fruit development and growth); (5) green fruit (fruits reach their final size but are still immature); and (6) ripe fruit (from the moment they turn a uniform orange color to the end of dispersal).

Methodology

Initially all rooted individuals were labelled in six plots at different sites in the forest, 1 m wide and 5, 7, 8, 11, 16 and 26 m long, respectively; a total of 73 m². Other randomly labelled individuals were chosen outside the plots to give a total of 100 juveniles (J), 50 prereproductives (P), 22 adults in the youngest group (A1), 50 in the intermediate group (A2), and 50 of the oldest ones (A3, A4 and A5).

Over 3.5 years (November 1985 – April 1989), leaf formation and inflorescence development were followed in all marked individuals by labelling each leaf and inflorescence produced. From October 1986 until April 1989, all new emergent seedlings were marked and followed in the four largest plots, with a total area of 61 m². Data were obtained monthly during the first 2 years and every 2 months during the rest of the study. Sunshine data comes from a standard meteorological station, measured by Campbell-Stokes sunshine recorder. Statistical analysis was conducted to test leaf production rate differences using ANOVA.

Results

Vegetative phenology

Throughout its life this species shows significant differences in leaf production rate (Fig. 1) (ANOVA, $F = 59.37$, $df = 978$, $P < 0.00001$). A leaf in the J group takes an average of 9 months to be produced, 1.5 months more than group P and 3 months more than the adults. Therefore, plant growth is slower at the beginning (as a juvenile), somewhat faster in the pre-reproductive stage (P), reaches its highest rate in the first three adult stages (A1, A2 and A3 belong to the same group, 95% confidence interval) and finally slows down in the oldest adult stages (A4 and A5 belong to the same group, 95% confidence interval).

Thus reproductive life of the species can be calculated: 30 years in its prime (A1, A2 and A3) and with a maximum of 54 years of reproductive activity.

Growth differences between female and male individuals are also interesting (Fig. 1): females are consistent-

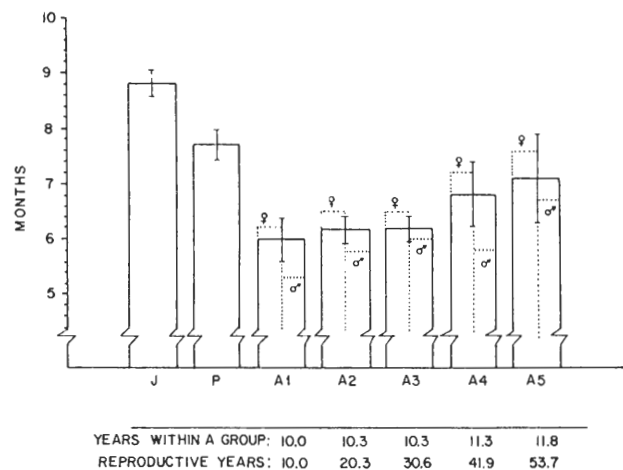


Fig. 1. Leaf production (months between the unfolding of one leaf and the following) in seven age groups of *Chamaedorea bartlingiana*, and mean number of years that a plant belongs to each adult group. Different rates in the two sexes shown by dotted line. Standard errors surround means (ANOVA, $P < 0.00001$).

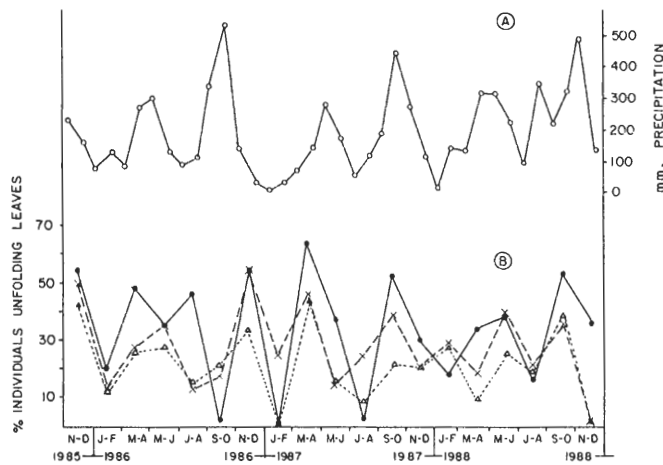


Fig. 2. A Monthly precipitation (mm) for the nearest meteorological station (Santa Rosa, 1950 m) during the study period. B Proportion of *C. bartlingiana* individuals which unfold a new leaf: ○ adults, × pre-reproductive, △ juveniles

ly slower than males, with a difference in the time of leaf production ranging from 0.5 to 1.5 months (ANOVA; for A1 $F=5.52$, $df=59$, $P=0.022$; for A2 $F=9.60$, $df=207$, $P=0.002$; for A3 $F=12.26$, $df=240$, $P=0.0006$; for A4 $F=4.44$, $df=37$, $P=0.024$; A5 did not show differences probably because of the low number of individuals).

Leaves are long-lived, lasting in juveniles an average of 22 months after unfolding, 27 months in pre-reproductives and between 25 to 29 months in adults.

Leaf production of each individual is continuous with an average of 2.5 leaves at any given time in juvenile crowns, 3.5 leaves in pre-reproductives and between 3.9 and 4.3 leaves in adults. At a population level, peaks in the rate of leaf unfolding do not fit statistically with the two annual precipitation peaks (correlation analysis with and without time delay) (Fig. 2.)

Reproductive phenology

Females and males did not show any differences with respect to vegetative structures, showing a similar sex ratio (51% F / 49% M). Most adults reproduced during the study period: 75% A1 ($n=20$), 95% A2 ($n=41$), 98% A3 ($n=49$), 100% A4 ($n=8$), 83% A5 ($n=6$).

Inflorescence development is slow (Table 1): 1 year for male and 2 years for female inflorescences. Common phenophases between male and female inflorescences (bud, flower bud and flowers) have the same duration. The "flower" phase is shorter than the sampling periods and therefore we were not able to measure it. The duration of each phenophase is variable, as may be observed from the high dispersion and widely spread extreme values (Table 1). No pattern was observed in this variability: it arises from individual and population differences. More than half the female inflorescences produced ripe fruits (58%). However, this relation changed with time (Fig. 3); not all buds finish their development and this

Table 1. Duration (months) of inflorescence phenophases in females and males of *Chamaedorea bartlingiana*

	Female inflorescences					Male inflorescences	
	Bud	Flower bud	Incipient fruit	Green fruit	Ripe fruit	Bud	Flower bud
\bar{x}	9.0	2.1	4.3	3.0	7.1	9.3	3.3
σ_{n-1}	2.7	0.9	1.3	1.2	4.2	3.1	1.2
max	17.0	4.0	7.4	7.3	20.6	18.3	9.2
min	2.3	0.9	1.0	1.0	0.7	2.5	1.2
n	189	103	92	167	148	163	49

n : number of inflorescences

max, min: maximum and minimum duration

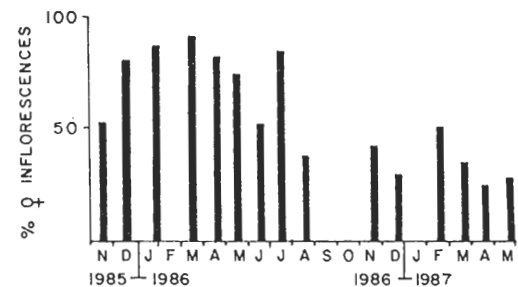


Fig. 3. Female inflorescences (%) which complete their development, in *C. bartlingiana*. Time of emergence for each bud cohort is indicated on abscissa (those which emerged after March 1987 did not have time to completely develop before the end of the study)

depends on the time of bud development, as will be shown later.

The unavoidable relation of "1 leaf – 1 inflorescence" *a priori* implies that individuals must reproduce with the same regularity as leaves are produced. However, this is true only for males, which during the study period produced inflorescences at the same rate as leaves: one leaf every 6 months. Since the inflorescence lasts a year, there is an overlap where an individual may have more than one inflorescence at any one moment. There is an average of 1.74 inflorescence/individual, a value that does not vary much throughout the year (Fig. 4A).

On the other hand, females show a population peak (Fig. 4A); a period with greater inflorescence overlap. This behavior cannot be explained by differences in leaf production since leaves were produced continuously, but is due to individual internal adjustments in the reproductive pattern. If we analyze each individual inflorescence sequence there were periods in which the plant did not reproduce, even though bud emergence rate was the same as for males (2.1 buds/year). Furthermore, female bud production did not show population peaks that could explain the ripe fruit peak (Fig. 4B, C). Greater probability of bud mortality seems to be the reason: 22% for females compared to 7% for males, in addition to 36% inflorescence mortality before reaching a "ripe fruit". Female inflorescence mortality was not random but depended on plant conditions: when an individual produced fruits (green or ripe) new emergent buds had a 35%

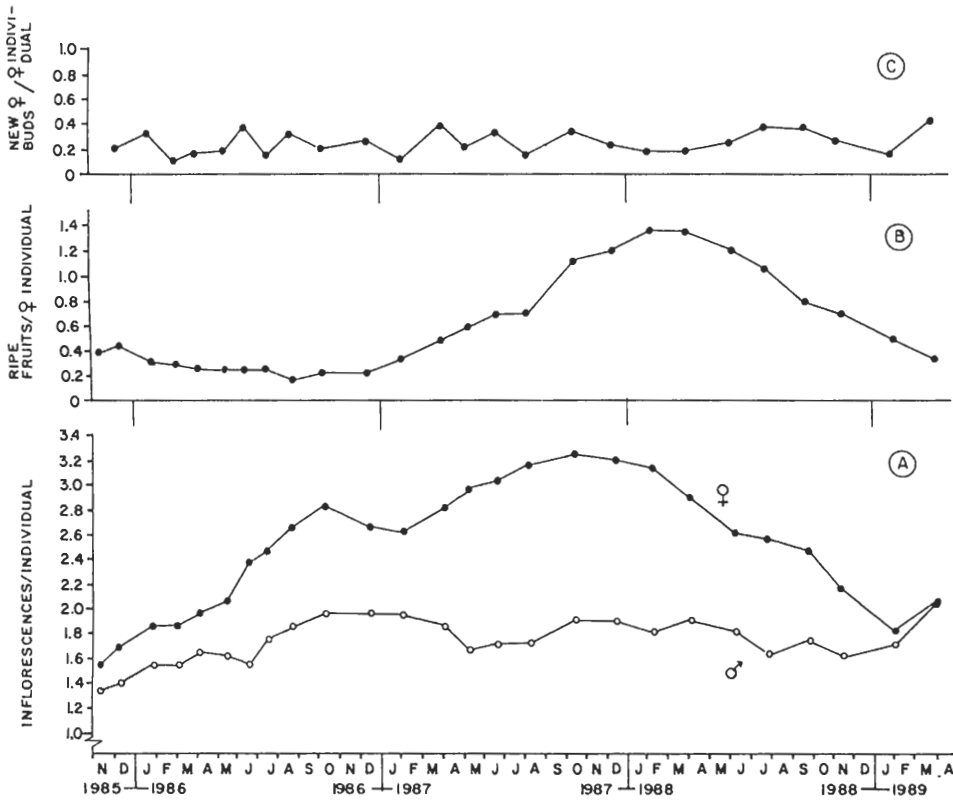


Fig. 4A-C. Reproductive activity of *C. bartlingiana* during the study period. A Mean of inflorescences per individual in both sexes: ● females, ○ males. B Mean of ripe infructescences per female. C Mean of female reproductive buds emerging

probability of completely developing, whereas the probability was 70% if the plant did not have any inflorescences or the inflorescence was in the stages of bud, flower bud, flower or incipient fruit.

This behavior results in a pattern of reproductive cycles in females, of which a model is presented in Fig. 5. The cycle starts with the consecutive production of buds which complete their development; the following four buds do not develop, and a new cycle starts with the eighth bud. The whole cycle lasts approximately 36 months. For the population under study, 75% of the 60 reproducing females showed this pattern, completing a cycle with a mean duration of 33 months; 25% had a non-reproductive period (successive mortality of several buds) which lasted 2–20 months.

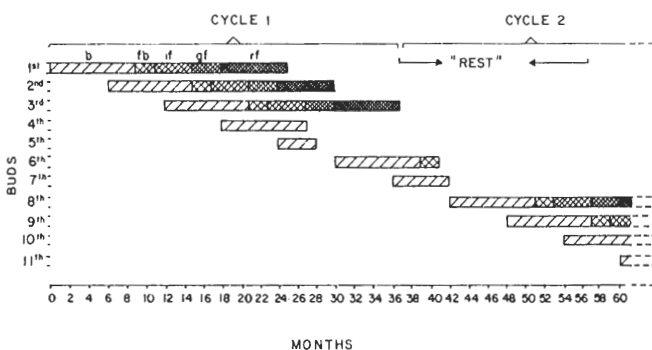


Fig. 5. Model for individual reproductive cycles in *C. bartlingiana* females, showing bud emerging sequence and its destiny, and period without fruits ("rest"). b: bud; fb: flower bud; if: incipient fruit; gf: green fruit; rf: ripe fruit

This pattern provides for a constant and low production of ripe fruits in the population which peaks every 3 years.

Seedling emergence and development

Seedling emergence (Fig. 6A) follows a different pattern to that of ripe fruit production (Fig. 4B). Emergence peaks occur at the end of major rains (Figs. 2A and 6A). During the 3 years of the study a peak was detected each year from September to December, and its magnitude was related to dispersal magnitude for the same year: low in 1986, higher in 1987 and highest in 1988 (Figs. 4B and 6A).

During the first 8 months individuals only produce one leaf (Table 2) which remains attached to the rest of the seed, suggesting its dependence until second leaf formation. Unfolding of the third leaf takes the longest, probably because it is the first leaf produced by its own resources.

Seedling survival and time of emergence are related (Fig. 6A, B): those that emerge in the first wet season have a 50% probability of survival for more than 4 months (Fig. 6B), until the season of highest precipitation; while those that emerge at any other time have a probability greater than 70% of surviving 4 months, 8 months (before unfolding of second leaf) or 16 months (before unfolding of third leaf) (Figs. 6A and B, and Table 2). Since the seedlings emerging during the first wet season represent a very small proportion, their higher mortality was not noticeable in the population as a whole (Fig. 7).

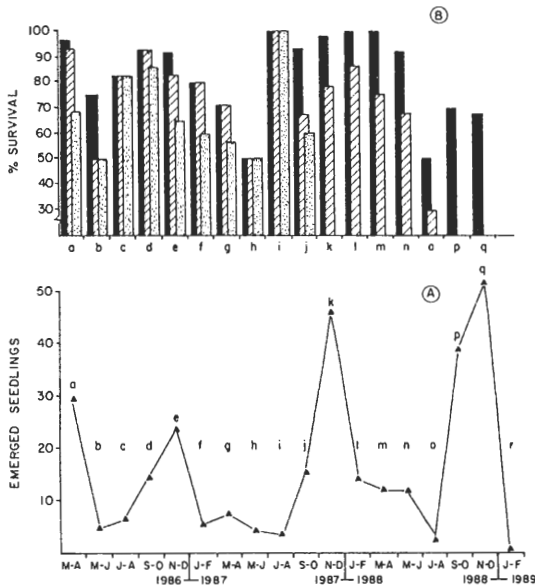


Fig. 6A, B. *C. bartlingiana* seedling dynamics. **A** Number of seedlings emerged in total area (61 m²) during the study period, each cohort identified by "a" through "q". **B** Survival of each cohort (identified as in A), where: ■: survival to the first four months; ▨: survival before unfolding of second leaf; ▩: survival before unfolding of third leaf (cohorts "k" to "q" had not unfolded second leaf by the end of the study)

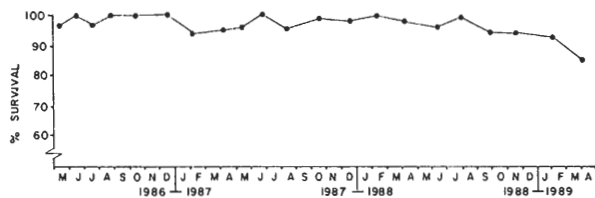


Fig. 7. Seedling survival (%) of *C. bartlingiana* throughout the study period. Each value indicates the proportion of survivors in relation to total seedlings in the preceding sample

Table 2. Leaf production (months between the unfolding of one leaf and the following) in *C. bartlingiana* seedlings, from germination to fourth leaf

	Leaves		
	1st to 2nd	2 nd to 3rd	3rd to 4th
\bar{x}	8.4	10.2	8.8
σ_{n-1}	3.8	2.8	2.4
max	30.1	17.5	17.0
min	2.6	6.0	5.5
n	121	57	27

n: number of seedlings
max: min: maximum and minimum duration

Monthly seedling mortality was low throughout the three years, approximately 3%, with no seasonal variation (Fig. 7).

Mortality rates during the first 2 years of life are low and constant (80% and 75% survival for the first and second year, respectively); however, third-year survival is reduced to 50% (Fig. 8). Mean life span of first, second

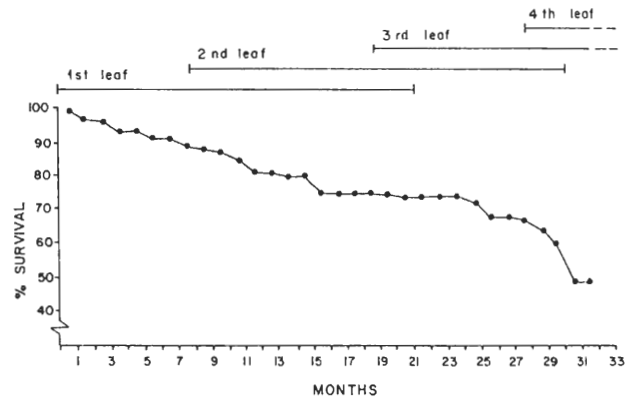


Fig. 8. Seedling survival (%) of *C. bartlingiana* according to age (months). Upper bars indicate mean life span of first and second leaves and first months of third and fourth leaves

and third leaves is 20.9 (n=60), 22.0 (n=36) and 17.5 (n=23) months, respectively (Fig. 8). This means that after the 30th month of seedling life, probability of maintenance of first two leaves (probably produced by seed resources) is very low and we can hypothesize that the energy stored and provided by the third leaf is not enough for seedling survival.

Discussion

Leaf production and growth

Leaf production rate for *C. bartlingiana* at both individual and population level is continuous and slow. Leaves are also long-lived: all common characteristics of understory species. It has been suggested that long-lived leaves are an advantage in understory and high mountain environments (Bentley 1979; Kikuzawa 1989), as an adaptation to light restriction and low temperatures, respectively. It has been hypothesized that leaf longevity is greater when production costs increase and even more if photosynthetic rates are low since more time would be required to develop a positive cost-benefit relation (Chabot and Hicks 1982; Kikuzawa 1989).

Some understory plants in Barro Colorado, Panamá (De Stevens et al. 1987) and La Selva, Costa Rica (Clark and Clark 1988) show correlation between leaf production and precipitation pattern. In the case of *C. bartlingiana* leaf production peaks do not fit statistically with the two annual precipitation peaks.

Leaf production rates vary significantly throughout the plant's life, which implies different growth rates depending on age. As in the case of other palms (De Steven et al. 1987), juveniles have lower rates than adults. Differences between female and male individuals are also significant, with slower rates for the females, as was also shown for *Chamaedorea tepejilote* (Oyama 1990).

Reproductive pattern and dioecy

Energetic restrictions also seem to condition the reproductive patterns. With the possible development of a

reproductive bud for each leaf produced, complete growth of each bud implies a cost which can be assumed by males, as is shown by the regular parallel sequence of inflorescence and leaf production. This is not the case for females. Our results show that both male and female inflorescence development up to the flower bud stage is equivalent, both in duration and shape, and probably in costs. But fruit development (growth and ripeness) implies a load for which the plant must allocate larger quantities of energy. The results suggest that females cope with this problem by the following strategies: (1) leaf production decreases; (2) a proportion of the new buds are atrophied to favor developed inflorescences. As a consequence of bud abortion, the plant creates an out-of-phase postfructification period, in which the plant has a minimum of inflorescences and therefore a "rest" period. This provides better conditions for fruit development in the following reproductive cycle. (3) some individuals may not have any kind of reproductive activity for a few months.

In this case dioecy is a great advantage. The separation of sexes seems to solve an energetic problem, allowing "labor sharing" by sexes. The reproductive patterns described show great differences between males and females with regard to reproductive rhythm and duration, and especially its cost. It has been hypothesized in other dioecious species that this cost is compensated for in different ways: in *Spinifex sericeus* by an increase in the number of leaves annexed to the reproductive apparatus, which will increase its photosynthetic capacity (Maze and Whalley 1990); in *Zamia skinneri* by an increase in leaves during the prereproductive period and a halving of leaf production during the postreproductive period (Clark and Clark 1988).

Dioecy has been related to dispersal systems: the majority of dioecious species have fleshy fruits, energetically costly, but considered as "the price to pay" for animal dispersal, which guarantees a much greater success rate (Bawa 1980; Givnish 1980). *C. bartlingiana* has, in fact, fleshy and very colorful, orange to red fruits and their existence throughout the year constitutes a common pattern in understory zoochore species which give a continuous food supply to the disperser and thereby assure the latter's survival (Soriano 1983).

At a population level reproductive activity is continuous. The majority of females have more or less simultaneous reproductive cycles, which means there are peaks in propagule dispersal which should be repeated every 3 years if the model is correct.

Seedling dynamics Vs. reproductive pattern

Peaks of fruit dispersal are not reflected in seedling emergence, as the latter seems to be influenced to a greater extent by environmental conditions. The highest precipitation, at the end of October, is immediately followed by the largest germination peak. However, the other, smaller, peak of precipitation between April and May does not have the same effect. We hypothesize that the greater germination response in the first case may be due

to a combination of higher soil humidity (due to the recent high precipitation) and incoming radiation: December has the greatest sunshine value for the area and comes at the end of a period of high rainfall, while April–May has half the sunshine (3.5 h/day) and marks the beginning of rains after 3 months of minimum precipitation. Experiments on germination responses to different light and soil humidity conditions are needed to confirm this.

Seedlings emerging in months other than November–December are few and have a 20% lower probability of surviving to the next year. From these results we may infer that in dry years there might be very low germination.

Germination, in general, may be controlled by (a) dormancy, (b) time of dispersal and/or (c) a more convenient time for some subsequent developmental stage more critical than the seedling stage (Garwood 1983, 1986). In the case of *C. bartlingiana* case (c) can be excluded because seedlings are long-lived (in the seedling stage) and survival is almost the same throughout the year (except for seedlings emerging in May–June). Case (b) can be discarded because there is no correspondence between the time of propagule dispersal, which should occur massively every 3 years, and germination, which shows annual peaks. We know that seed dispersal occurs continuously, therefore the existence of germination peaks suggests that seeds are dormant, and that dormancy may be broken by exogenous factors; in fact, this dormancy has been detected in laboratory tests (Jimenez, unpublished data).

The magnitude of germination peaks is related to dispersal magnitude (but not dispersal time); in this way, although there is a germination peak each year, every 3 years the peak will be greater.

Seedling growth is slow. Individually, survival probability slowly decreases during the first 2 years, and strongly decreases at the beginning of the third year. But from the population point of view, mortality is very low (approximately 3%) which means that population growth is very high in the first age group. This low seedling mortality, frequent in species adapted to the understory, has been explained by Garwood (1983) as a consequence of low competition with other seedlings, most of which have a very hard time establishing themselves in dark environments. In the case of *C. bartlingiana* we would add that, during the study period, herbivore attack was negligible and the most important mortality factor observed in seedlings was that they were frequently uprooted maybe due to movement of terrestrial animals. However, this is not sufficient to slow down increase in the seedling population which must respond to factors occurring on a much greater time scale and which we have not been able to detect.

Significance of a pluriannual pattern

Pluriannual reproductive patterns have not been frequently described in the literature on tropical forests. However, we feel the species under study is not a special or unique case. Rather, we believe that longer reproduc-

tive cycles are the answer to an energetic problem for plants that produce very costly fruits.

The pattern described here is one apparently successful strategy that may develop in environments with energetic restrictions and low seasonality: (a) energy shortage is counteracted by more time investment in reproductive and vegetative development, while buds that would be too costly to develop are atrophied; and (b) low seasonality does not impose time restrictions on the plant since environmental factors will not change sufficiently to make it expend its energy on other urgent functions. This pattern not only allows for production of costly fruits, but also gives other advantages: (a) it does not affect the continuous resource offer (an advantage from the disperser's point of view) since it does not enforce a strict population synchronization, and (b) the production of seeds is not affected by the best time for germination since they have dormancy mechanisms. Finally, lack of strict synchronization between females does not affect their fertilization capacity, since males are continuously producing flowers. For male individuals energy does not need to be saved, which means continuous new bud development, and as a consequence, all of them have the same probability of developing.

Acknowledgements. We are grateful to Pedro Jiménez and M. Josune Canales for their field work assistance, to Herbario de la Facultad de Ciencias Forestales, Universidad de Los Andes, for species identification, to Mario Fariñas and Juan Silva for helpful comments, to Fermin Rada, Ian Woodwar and Gerardo Piñeiro for their help.

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