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DEMOGRAPHY, SPATIAL DISTRIBUTION, AND GROWTH OF THREE ARBORESCENT PALM SPECIES IN A TROPICAL PREMONTANE RAIN FOREST IN COSTA RICA

Jürgen Homeier[1], Siegmar-W. Breckle[1], Helmut Dalitz[1], Claudia Leyers[1] & Rodolfo Ortiz[2]

[1]Abteilung Ökologie, Fakultät für Biologie, Universität Bielefeld, Universitätstr. 25, 33501 Bielefeld, Germany
[2]Sede de Occidente, Universidad de Costa Rica, San Ramón, Costa Rica

Resumen. La ecología de las tres palmas arborescentes *Cryosophila warscewiczii, Euterpe precatoria* e *Iriartea deltoidea* ha sido estudiada en el bosque lluvioso premontano de la Reserva Biológica Alberto Ml. Brenes" en el noroeste de Costa Rica. Estas tres especies presentan un número de individuos muy alto en el área y muestran una distribución con muchas plantas pequeñas y pocos adultos. La tasa de mortalidad mas alta se presenta en las plántulas de *Euterpe* e *Iriartea.* Las plántulas de las tres especies muestran una distribución acumulada. Durante el desarollo de plántulas a adultos cambia la distribución en razón de mortalidad y las palmas sobrevivientes de *Euterpe* e *Iriartea* presentan una distribución al azar, en contraposición los adultos de *Cryosophila* que muestran una distribución acumulada. Eso apoya la hipótesis que esta especie necesita claros para llegar a un tamaño reproductivo. Las tasas de crecimiento de *Euterpe* e *Iriartea* dependen de la altura. Con altura creciente las dos especies muestran tasas mas altas. Despues de llegar al tamaño adulto el incremento vertical es decreciente por causa de necesidades mas altas de energía tanto para la reproducción como para el matenimiento de la biomasa viva.

Abstract. The ecology of the three arborescent palm species *Cryosophila warscewiczii, Euterpe precatoria*, and *Iriartea deltoidea* was investigated in the premontane rain forest of the "Reserva Biológica Alberto Ml. Brenes" in north-west Costa Rica. All three species are common in the study area. They show pyramid-shaped size distributions with high numbers of seedlings and saplings and only a few adult individuals. Observed mortality rates were highest within the youngest seedlings of *Euterpe* and *Iriartea*. The seedlings of the three investigated species show a clumped distribution. During their growth they are thinned out, which leads to random distributions of the adult palms in *Euterpe* and *Iriartea*. In contrast, the mature *Cryosophila* palms display a clumped dispersion. This could strengthen the hypothesis that this species needs light gaps for growing of to reproductive size. Growth rates of *Euterpe* and *Iriartea* are height-dependent. With increasing height the two species display higher increment rates. After reaching adult size the vertical growth decreases because of the higher energy requirements for reproduction as well as maintenance of living biomass. *Accepted 17 September 2001.*

Key words: *Arecaceae*, Cryosophila, Euterpe, Iriartea, *demography, spatial distribution, growth.*

INTRODUCTION

Population processes of the larger plants strongly affect the productivity and the structure of the forest. Moreover the demography of their herbivores, pollinators, seed dispersers, and predators is affected (Clark 1994). Therefore population structure and growth of trees or arborescent palms are important factors for understanding the ecology of forests.

In the study area and many other rain forests, palms are numerically and structurally a substantial group (Kahn & De Granville 1992, Clark 1994, Lieberman *et al.* 1996). Their population processes have an important influence on many aspects of the forest ecosystem. This study deals with aspects of the population structure, spatial distribution, and growth of three arborescent palms in the Costa Rican premontane rain forest.

Palms are perfect objects for demographic studies because they are usually easy to recognize in the forest (Tomlinson 1990). The existence of just one apical meristem allows exact height growth measurements.

Most of the studies focusing on demography (Pinero *et al.* 1984, 1986; Svenning & Balslev 1997), spatial distribution (Vandermeer 1977, Sterner *et al.* 1986, Clark *et al.* 1995, Svenning & Balslev 1999), and growth (Van Valen 1975; Pinero *et al.* 1984, 1986; Lugo *et al.* 1987; Lieberman *et al.* 1988; Oyama 1990) of arborescent palms were conducted in the lowland tropics. But little is known about the height growth of Neotropical trees and arborescent palms especially in montane rain forests.

[1] e-mail: juergen.homeier@biologie.uni-bielefeld.de

STUDY AREA, STUDY SPECIES, AND METHODS

Study area. The field research for this study was carried out in the Reserva Biológica Alberto Manuel Brenes (RBAMB) which is located on the Caribbean slope of the Cordillera de Tilarán (10° 13′N, 84° 37′W). The RBAMB is part of the province Alajuela in north-central Costa Rica. Most of the protected area of 7800 ha is covered with primary forest.

The area shows a mountainous relief consisting of steep slopes and deep V-shaped valleys, with altitudes ranging between 800 m and 1500 m. The soils are of volcanic origin and can be classified as andosols according to Vargas (1991).

The mean annual rainfall reaches about 4095 mm without a real dry period during the year and the average monthly temperature varies from 18° to 21°C (data from a ten-year observation period). Following the life-zone system of Holdridge *et al.* (1971) the forest in the area is categorized as a tropical premontane rain forest, and according to Walter & Breckle (1985) the area is part of the zonobiome I.

The largest trees and least broken canopy, with heights of 30–40 m, occur in valleys or on gentle slopes below 1200 m. On wind-exposed ridges and steep slopes the canopy height is reduced to 15–25 m. Epiphytes are quite common and diverse, dense mats can be found especially on bigger trees. Numerous gaps within the different canopy layers permit a well developed understory.

At the study site, 94 tree species (436 stems without tree ferns) from 40 different plant families with a diameter of 10 cm or more at breast height (DBH) were counted per hectare (Wattenberg & Breckle 1995). The flora of the RBAMB displays a very high a-diversity; more than 1000 plant species were identified inside a one-kilometer radius around the biological station that has been investigated so far (Breckle 1998).

Study species. The three arborescent palm species *Cryosophila warscewiczii* (H.Wendl.) Bartlett, *Euterpe precatoria* (Mart.) Henderson, and *Iriartea deltoidea* Ruiz & Pav. are the commonest of more than 20 palm species identified so far in the RBAMB. Nomenclature for the palms follows Henderson *et al.* (1995). Hereafter the investigated species will be referred to by their genus name only.

According to Henderson *et al.* (1995), *Iriartea* is the only species in this genus. It has a distribution ranging from Nicaragua south to Bolivia and the western Amazon region in lowland and montane rain forest between 0 m and 1300 m elevation. The pinnate-leaved palm is the most frequent arborescent species (DBH ≥ 10 cm) in the RBAMB (Wattenberg & Breckle 1995). With heights exceeding 30 m it is a canopy species.

Euterpe ranges from Belize to northern South America (Henderson *et al.* 1995). It grows at elevations from sea level up to 2000 m and has pinnate leaves like *Iriartea*. In the RBAMB it reaches 25 m in height and is found mainly on ridges and steep slopes where the canopy is more open. Clark *et al.* (1995) found the same habitat preference for *Euterpe* in a tropical lowland forest in La Selva (Costa Rica).

The third species, *Cryosophila*, extends from the Caribbean side of Nicaragua to Panama at altitudes from sea level to 1200 m above sea level and reaches a maximum DBH of 10 cm. With maximum heights measured in the RBAMB below 8 m it is an understory species. Stems of this species are covered with root spines and the leaves are palmate.

Methods. To investigate the population structure of these important arborescent species one hectare of primary forest was selected and marked out in 1992. This plot is located on a flat mountain ridge just outside the southern border of the RBAMB at 1000–1040 m a.s.l.. It was divided into 100 quadratic subplots of 100 m^2.

In 1992 all individuals of the two species *Euterpe* and *Iriartea* within the plot were measured for height and DBH and their positions within the plot were determined. The height of a distinct palm was defined as the distance from the ground to the highest point of the leaf sheath of the youngest leaf. The height was measured to the nearest 5 cm for palms ≤1.3 m and to the nearest 10 cm for palms >1.3 m. DBH was measured to the nearest cm.

In 1996 the measurements and the determinations of the palm positions were repeated for the two species, and a new third species, *Cryosophila*, was added. The palms measured in 1992 were re-investigated, and their vertical growth was registered. All palms showing flowers, fruits, or old inflorescences were called adult palms.

The palm positions allowed us to calculate the spatial distribution of the three species within the plot. To investigate dispersion, the chi-square-test (Fowler & Cohen 1990, Sachs 1997) was used. This test compares the expected density with the real density of palms in the subplots. Three different forms of distribution are possible: uniform, random, and clumped.

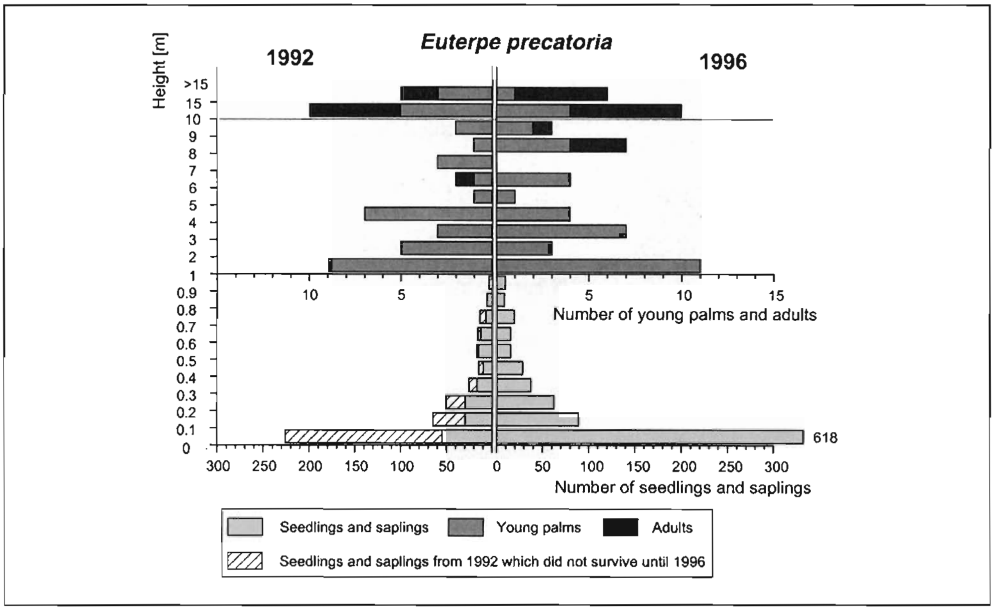

FIG. 1. Size classes of *Euterpe precatoria* with height given for three different life stages for 1992 (left) and 1996 (right) on the investigated one-hectare plot (note different ordination for the three height classes).

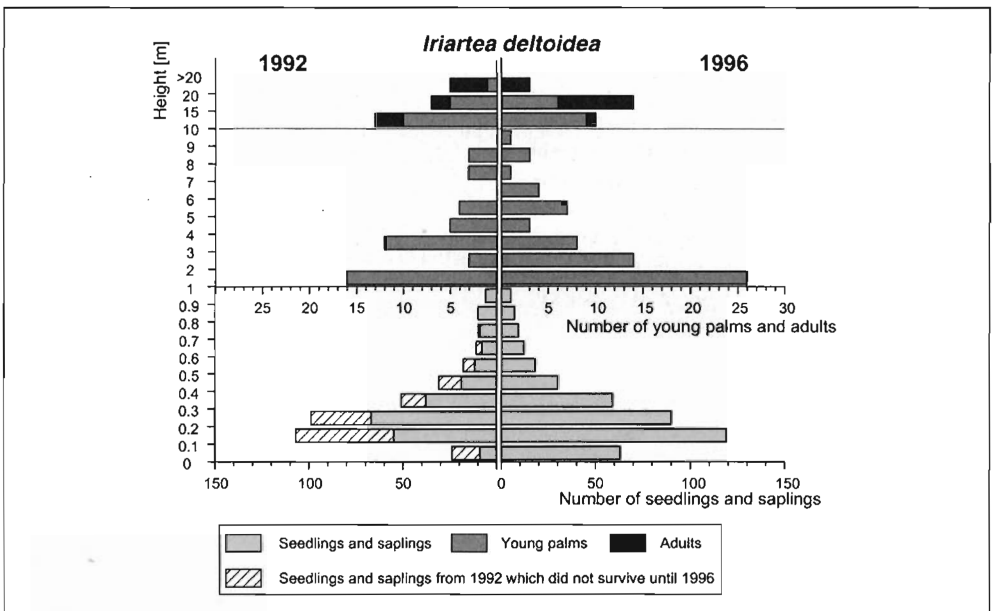

FIG. 2. Size classes of *Iriartea deltoidea* with height given for three different life stages for 1992 (left) and 1996 (right) on the investigated one-hectare plot (note different ordination for the three height classes).

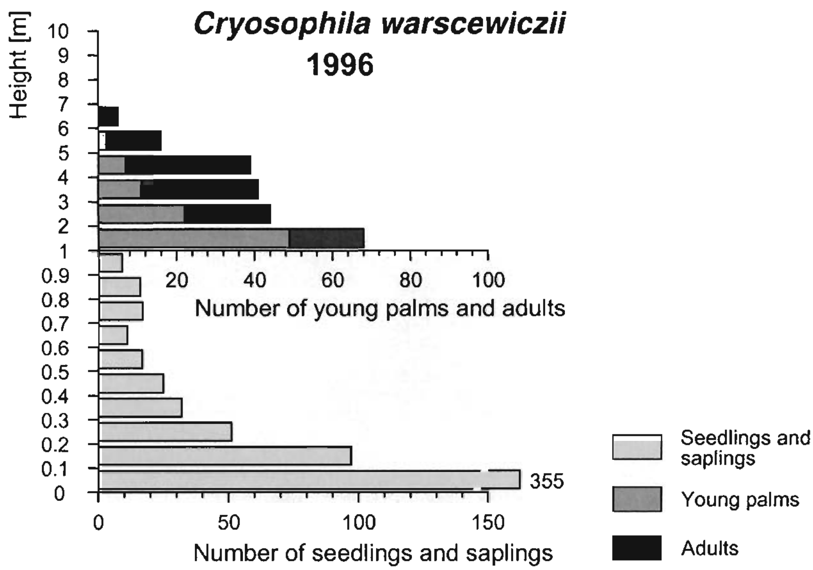

FIG. 3. Size classes of *Cryosophila warscewiczii* with height given for three different life stages for 1996 on the investigated one-hectare plot (note different ordination for the two height classes).

RESULTS

Demography. The palms of all three species showed pyramid-shaped distributions on the size-class graphs (Figs. 1–3), with many seedlings and saplings and only few adult individuals.

486 individuals of *Euterpe* and 439 individuals of *Iriartea* were found on the investigated one-hectare plot in 1992. In 1996 both palms showed higher numbers. This results especially from the higher number of *Euterpe* seedlings (more than twice as much as in 1992).

The two taller species showed high mortality rates within the seedlings and saplings (Figs. 1, 2). Only 42% of the *Euterpe* palms < 1 m and 63 % of the *Iriartea* palms < 1 m counted in 1992 survived until 1996.

In *Euterpe* particularly seedlings smaller than 10 cm were affected by mortality (67% of the palms of this size class died before 1996), while in *Iriartea* mortality was spread over the size classes up to 30 cm. In comparison with *Euterpe*, *Iriartea* showed a lower mortality rate. The two missing *Iriartea* palms from the tallest size class died between 1992 and 1996.

The 843 *Cryosophila* palms found on the one-hectare plot reached a DBH of 4-8 cm, more than 80% of the individuals taller than 1 m had a DBH of 6 or 7 cm. During an establishment phase in young palms of *Cryosophila* the number of leaves is increased and the stem reaches its final diameter. After this the palm starts its vertical growth with a sufficient diameter to support its maximum height.

The two taller species reached DBH values up to 21 cm (*Euterpe*) and 26 cm (*Iriartea*). Both species start growing with a slender stem and show a limited diameter increment by sustained cell expansion during their development. Throughout height growth, stem strength and stiffness are increased (Rich 1987).

The relation of height to DBH shows different growth strategies for *Euterpe* and *Iriartea*. *Euterpe* palms grow regularly in height and in DBH (Fig. 4).

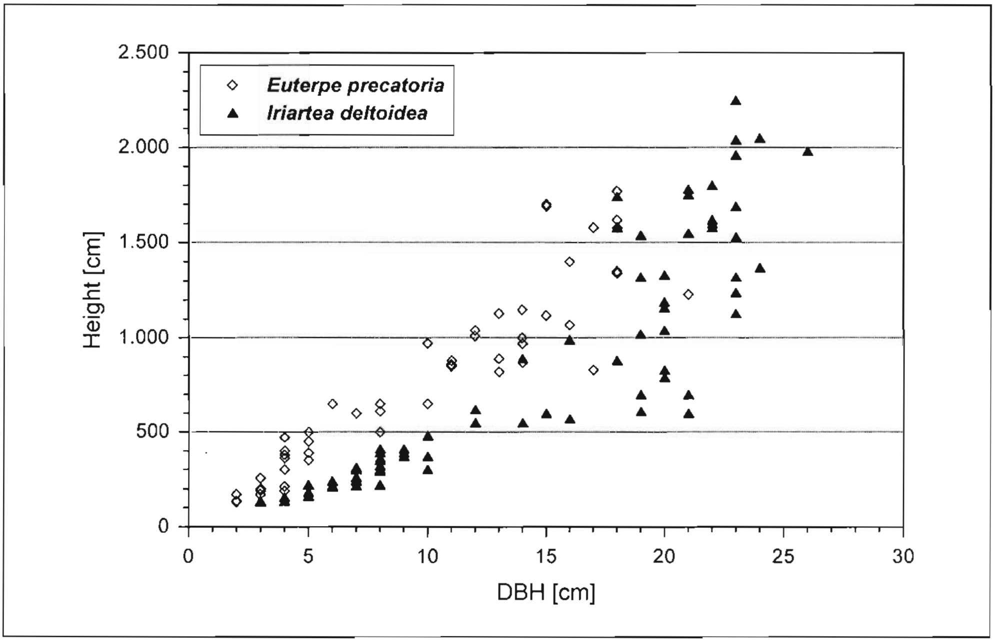

FIG. 4. Height-DBH relationship of *Euterpe* and *Iriartea* taller than 1 m on the investigated one-hectare plot in 1996.

In *Iriartea* palms, first diameter growth is prioritized up to a DBH of about 20 cm. After almost reaching their final diameter they then grow mainly vertically.

Phenology. In the study area, *Euterpe* and *Iriartea* show flowering and fruiting throughout the entire year. A main flowering period could not be recognized.

The height of the smallest adult *Euterpe* was 8.2 m, the smallest flowering *Iriartea* was 11.3 m. Numbers of adult individuals are given in Table 1. *Cryosophila* showed a synchronized flowering period in June/July and a fruiting period during the driest season in February/March. Mature palms of this species were found as small as 1.3 m.

Spatial distribution. The spatial distribution of the three species within the plot was calculated by using the palm positions.

The seedlings and saplings of all three species show a clumped dispersion (Table 1). In *Euterpe* and *Iriartea* the clumped seedlings are thinned out during their growth which leads to a random dispersion of the adults. By contrast mature *Cryosophila* palms exhibit a clumped distribution, although juveniles taller than 0.5 m show a random distribution. In all three species the distances to the nearest palm within the same height-class increase from the seedling stage to the mature palms.

Height growth of Euterpe *and* Iriartea. By comparing the height measurements from 1992 for *Euterpe* and *Iriartea*, the vertical growth over a period of four years was calculated. Only palms bigger than 20 cm in 1992 were taken into account, because smaller plants could have been replaced between 1992 and 1996 by new seedlings in the same spot.

The growth rates show variations between 0.01 m/yr and 1.3m/yr for *Euterpe* and between 0.01 m/yr and 1.5 m/yr for *Iriartea.*

Small palms (palms ≤ 1 m) of both species grow slowly, forming a kind of seedlings bank. With increasing height the palms show immense vertical growth. Maximum rates were reached at 8–10 m by *Euterpe* and at 10–12 m by *Iriartea* at the time when the palms reach reproductive age.

TABLE 1. Number of individuals in the different size classes and their dispersion (χ^2-test) in the one-hectare plot. 73,37 < χ^2 < 128,41 gives the 95 % confidence zone of random dispersal.

species and size class	number of palms inside the one-hectare plot in 1996	χ^2	dispersion
Cryosophila			
all palms	843	215,72	clumped
< 0.5 m	544	225,49	clumped
0.5-1.3 m	112	102,29	random
juveniles ≥ 1.3 m	65	93,46	random
adults	122	176,36	clumped
Euterpe			
all palms	956	795,67	clumped
< 0.5 m	822	770,39	clumped
0.5–1.3 m	81	208,91	clumped
juveniles ≥ 1.3 m	38	156,74	clumped
adults	15	111,67	random
Iriartea			
all palms	506	169,89	clumped
< 0.5 m	344	149,02	clumped
0.5–1.3 m	86	151,21	clumped
juveniles ≥ 1.3 m	64	120,38	random
adults	12	104,67	random

From the growth data, mean growth functions were calculated for the two species (Figs. 5, 6). The increments of the larger palms are highly variable and we had few data from taller individuals. For this reason the right-hand parts of the two graphlines are dotted. The fits shown, which display decreasing growth rates, were the best of a variety of fits tested.

For *Euterpe* the results indicate that a small palm of 20 cm needs about 40 years to reach a height of 10 m. *Iriartea* grows faster than *Euterpe*, a young *Iriartea* of 20 cm reaching 10m in approximately 30 years.

DISCUSSION

Demography. The assumption is made that the size of an individual plant reflects its age and therefore the pyramid-shaped size-distributions, with many seedlings and saplings and few adult palms, indicate a regular regeneration in all three palm species.

According to Hartshorn (1978) and Whitmore (1984) this is typical for shade-tolerant primary forest species.

The three palm species represent a stable portion of the investigated forest. In contrast, more than a third of the 94 tree species found by Wattenberg & Breckle (1995) on the one-hectare plot in the RBAMB are rare species represented by only one individual (DBH ≥ 10 cm).

It seems that the period between 1992 and 1996 was favorable for the regeneration and development of the *Euterpe* and *Iriartea* populations because in 1996 we found many new individuals of both species.

The seeds of *Euterpe* have diameters of 0.9–1.3 cm and those of *Iriartea* 2.0–2.5 cm. Therefore the *Iriartea* seedlings have a better nutrient supply and better starting conditions. In the investigation area *Euterpe* produced many more seedlings than *Iriartea*, but they were subject to a higher mortality compared with *Iriartea*. Consequently, within the one-hectare plot *Iriartea* is in the majority among the palms bigger than 1 m. The different seed sizes and frequencies of seedlings and saplings lead to the conclusion that *Euterpe* and *Iriartea* follow different regeneration strategies.

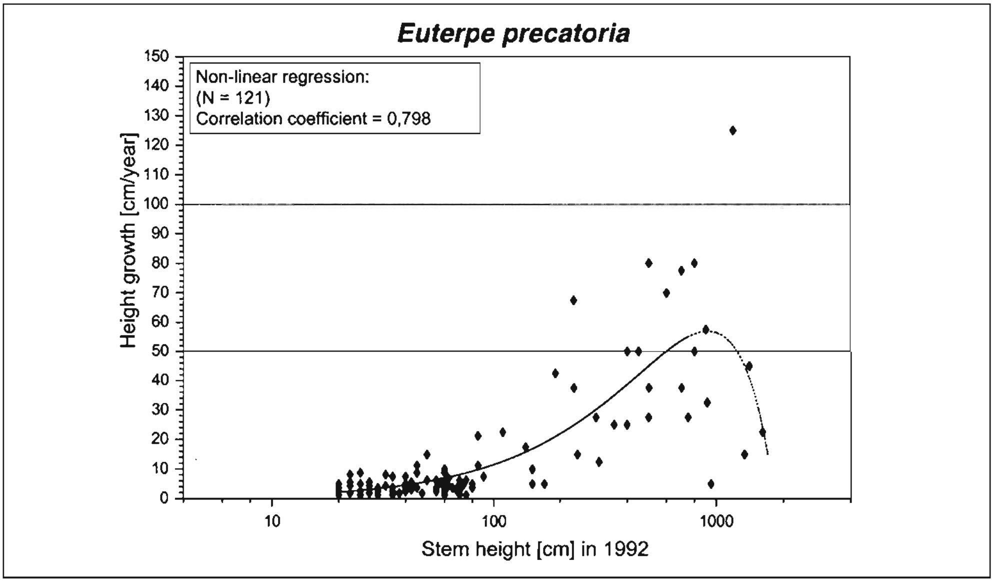

FIG. 5. Semi-logarithmic graph [$y = -3182{,}4 + 3239{,}3^{-((x-914{,}9)/6860{,}1)^2}$] for the height growth of *Euterpe precatoria* calculated from the height increment of 121 palms over a period of 4 years (1992–1996). The right-hand part of the graphline is dotted because of the few data for the greater palm heights.

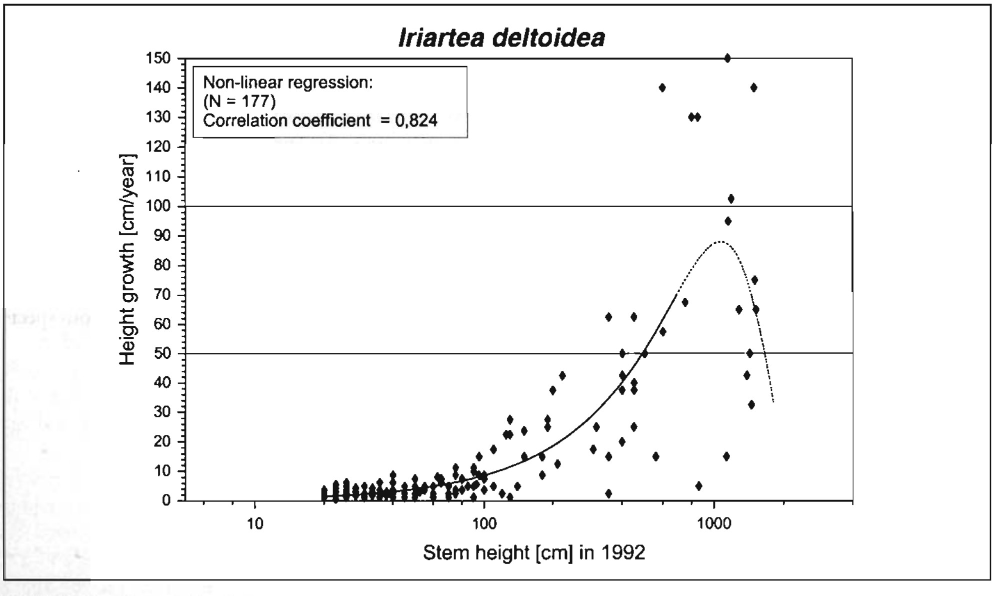

FIG. 6. Semi-logarithmic graph [$y = -36{,}4 + 124{,}4^{-((x-1068{,}9)/962{,}1)^2}$] for the height growth of *Iriartea deltoidea* calculated from the height increment of 177 palms over a period of 4 years (1992–1996). The right-hand part of the graphline is dotted because of the few data for the greater palm heights.

Van Valen (1975), for *Prestoea acuminata,* and Pinero *et al.* (1986), for *Astrocaryum mexicanum,* found that mortality was highest within the smallest seedlings, as found here for *Euterpe* and *Iriartea.*

Spatial distribution. Most studies of the distribution of trees in tropical forests found clumped or random distributions for adult trees (Lang *et al.* 1971, Hubbell 1979, Hubbell & Foster 1983, Sterner *et al.* 1986, Lieberman & Lieberman 1994).

If the distribution of size classes was compared the adults were almost always less clumped than the young individuals (Lang *et al.* 1971, Sterner *et al.* 1986, Lieberman & Lieberman 1994). *Euterpe* and *Iriartea* showed the same distribution pattern in this study. Sterner *et al.* (1986) found clumped distribution for *Iriartea* in La Selva (Costa Rica) for palms with DBH < 10 cm and random distribution for palms with DBH ≥ 10 cm.

Factors effecting the thinning out of clumped seedlings to randomly dispersed adults have been reported to be influences from pathogens (Augspurger & Kelly 1984), falling trees, branches or palm leaves (Vandermeer 1977), and root or canopy competition (Lieberman & Lieberman 1994). Svenning & Balslev (1999) showed for *Iriartea* that mortality is dependent on variation in microhabitat.

A possible interpretation of the clumped dispersion of the adult Cryosophila palms could be that this species needs sufficient light to mature and therefore adults can only be found in previous gaps. Young, stemless palms are "waiting" for a gap event because trunk growth in this species appears to be restricted to times when the overstory canopy is open, and thus the sapling bank is activated.

Williamson (1983) found for *Cryosophila guagara* that clumps of this species mature in gaps and that these groups of adults can be spotted years later under the already closed overstory canopy, thus being indicators of former gap-positions.

Height growth of Euterpe *and* Iriartea. The results of this study indicate that the growth rates of the two species are highly variable, depending on life stage and microhabitat heterogeneity even inside a relatively small investigation area.

This variance is caused by diverse factors such as influences of herbivores, inter- and intraspecific competition, climatic and topographic factors, all of which have an effect on the development of palms during different life stages.

The height increments which Lieberman *et al.* (1988) determined for the palm species *Welfia georgia* in Costa Rican lowland rain forest were highly variable too, ranging from 0.3 to 9.9 m over a 10-year period.

Euterpe and *Iriartea* show the highest increments when reaching reproductive heights. At that time the growth rates are quite variable depending on the particular situation of the individual within the stand (e.g., light conditions, water and nutrient supply).

The fits shown illustrate that growth rates decrease after growing to adult size. This appears plausible because the palms need more energy for the production of flowers and fruits, as well as for the supply and maintenance of the living biomass (Van Valen 1975). Moreover at this time the palms cease to increase leaf surface for reasons of statics.

We calculated that for an *Iriartea* palm of average growth to reach maturity needs about 30 years plus the time to grow up to 20 cm. By comparison, Svenning & Balslev (1997) found that *Iriartea* palms in Ecuadorian Amazonian forest need approximately 57 years to reach reproductive age with a mean height of 14 m (by estimating the age of palms from leaf scars). This is nearly twice the time needed to reach adult size, indicating to what extent vertical growth of this species depends on its habitat.

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