Leaf Ecology of Pre-reproductive Ontogenetic Stages of the Palm Tree *Euterpe edulis* Mart. (Arecaceae)

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We studied leaves of 208 seedlings (S), infants (I) and juveniles (J) of *Euterpe edulis*, randomly selected from plants in 1 ha of swampy forest in SE Brazil. Each new leaf began extending after the complete development of the preceding leaf. The sequence steps of leaf growth were emergence, linear growth while closed, opening of segments and logarithmic growth of the petiole. Average leaf production rate (2·21 leaves per plant year^{-1}) did not vary among ontogenetic stages, conforming to a plastochronic rhythm. Average linear growth rate of the closed leaf was directly related to average area of the open lamina. Herbivores attacked 33·0% of all leaves giving rise to up to 10% loss of area and included damping-off-inducing suckers (7·1%), ordinary suckers (9·8%), chewers (5·4%), miners (2·7%) and multiple attacks (8·0%). These attacks varied among stages (S = 22·4%, I = 38·1%, J = 33·3%), as did leaf mortality rates (S = 26·5%, I = 14·3% and J = 0·0%). Unknown factors were the main cause of leaf mortality (S = 14·3%, I = 7·1%). Not losing a leaf while a seedling and attaining a minimum leaf area in the infant stage were critical events for survival. Plants gained leaf area by not losing leaves while a seedling, by producing larger leaves with greater growth rates, and by accumulating leaves with longer lifespans. The petiole can simulate an energetically cheaper branch, delimit a vital space around the stem, favourably position the leaf lamina and substitute provisionally for stem growth in height.

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Key words: Arecaceae, *Euterpe edulis*, herbivory, leaf ecology, leaf growth, leaf production, semideciduous forest, southeastern Brazil.

INTRODUCTION

Studies on plant demography have greatly increased our understanding of population dynamics in many species (Harper and White, 1974). Yet, there is a gap in our knowledge of how specific traits of individuals are related to changes in plant numbers (Jurik and Pleasants, 1990). How forest trees survive through the sapling stage and grow into adult trees is a crucial problem (Kohyama and Hotta, 1990).

The growth of a plant is determined in part by the dynamics and longevity of its leaves (Givnish, 1984), since they are the carbon-gaining organs of plants (Chabot and Hicks, 1982). Concepts such as leaf area index and net assimilation rate have contributed to the understanding of how a photosynthetic surface contributes to determining the growth rate of plants (Harper, 1989*a*). Notwithstanding its importance, there are relatively few data concerning leaf population dynamics (Jurik and Chabot, 1986; Escudero and del Arco, 1987; Costa and Seeliger, 1988*a*, *b*; Hegarty, 1990; Costa, Seeliger and Cordazzo, 1991; Cavelier *et al.*, 1992; Clark, Clark and Grayum, 1992; Lowman, 1992; Aide, 1993; Telenius, 1993).

Leaf demography is affected by several environmental factors. Herbivory is considered an important selective force in plant evolution (Marquis, 1987) and plays a significant role in leaf dynamics. Intraspecific variation in

damage by herbivory affects the success of individual plants. However, the extent of variation of damage by herbivory among individuals in natural populations is not well documented (Coley, 1983).

Euterpe edulis Mart. is a common palm in rain- and seasonal forests in southeastern Brazil (Uhl and Dransfield, 1987), and it is one of the main species from which heart of palm is commercially produced. As the palm tree is always sacrificed to remove the palm heart, natural populations are being drastically reduced (Hodge, 1965; Johnson, 1982; Silva, 1992). The main problems in plantations are the slow growth and high mortality of seedlings, both in the glasshouse and field (Bovi, Godoy and Saes, 1987*a*).

This study focuses on the following questions for the palm *Euterpe edulis*: (1) how does the leaf grow; (2) what are the leaf production and leaf growth rates at different ontogenetic stages of the plant; (3) are there differences in growth rates during leaf development; (4) what is the leaf surface area lost to herbivory; and (5) does herbivory affect plant survival?

MATERIALS AND METHODS

The study site

The study was carried out in a swampy area at Santa Genebra Reserve, municipality of Campinas (22°49′ S, 47°06′ W, 575–585 m a.s.l.), state of São Paulo, southeastern Brazil. Santa Genebra Reserve is a 250 ha fragment of

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subtropical moist forest (*sensu* Holdridge, 1967) or tropical semideciduous forest (*sensu* Longman and Jeník, 1987). The forest was fragmented in the 1950s, and the remnant area is surrounded by corn and soybean plantations and more recently by human habitations. Mean annual rainfall is 1371 mm, and the year can be divided into wet (November–February), dry (May–August), and transitional (March–April and September–October) seasons (Galetti, 1993). *Euterpe edulis* is one of the most abundant species in the swampy area in Santa Genebra Reserve (Morellato, 1991), with 249 adult individuals ha^{-1} in the study site (Alves, 1994).

Procedure in the field

Silva (1992) numbered all the individual palms in 100 random plots of 25 m² over 1 ha, and determined four ontogenetic stages for the population (seedling, juvenile, immature and adult). Plants used in the present study were chosen by random numbers from the previously numbered palms. Observations were made in two periods. The first period included observations on herbivory conducted fortnightly from August to December 1991 for 112 young plants. The second period included observations conducted monthly from December 1992 to December 1993 on leaf production and survival, and leaf and petiole growth for 96 other young plants. Complementary non-systematic observations were also made during this second period of study.

Ontogenetic stages

Carvalho (1995) established infant as an intermediate ontogenetic stage between seedling and juvenile, according to morphological features (Gatsuk *et al.*, 1980). These three ontogenetic stages were considered in this study. Seedlings are individuals with embryonic structures up to only three primary fan-shaped leaves (Silva, 1992). Infants are individuals that have already produced the fourth leaf (of an intermediate shape between fan and feather), and whose feather-shaped leaves have up to 18 segments. Juvenile individuals have feather-shaped leaves with more than 18 segments, a minimum height of 17 cm and a maximum diameter of 52 mm at the stem base (Carvalho, 1995). During this study some individuals progressed from one ontogenetic stage to the next. Each individual was assigned to the ontogenetic stage in which it was at the time of measurement. This resulted in different sample sizes for each statistical analysis. Death of some individuals during this study also contributed to different sample sizes.

Leaf area

A simple formula (Ross, 1981) was used to estimate leaf area (*A*) non-destructively (Norman and Campbell, 1989) through the arithmetic averages of length (*L*) and width (*W*) of segments and the number of segments (*N*) in a leaf, using a coefficient $K = 2/3$, as below:

$$A = K(LWN) \qquad (1)$$

Measurements for each plant were taken from one to five leaves, chosen from the youngest, fully expanded, healthy ones in the second period of study. For 31 seedlings the largest and smallest leaf segments were measured. For 30 infants the same procedure was adopted when the leaf had up to eight segments (leaves with intermediate shape). When the leaf had more than eight segments (feather-shaped), three segments (basal, central and terminal) along the rachis were chosen. This procedure was followed for infants and the 30 juveniles.

Leaf production

The time interval for the production of two consecutive leaves was estimated in months. The differences among mean values of different stages were tested by ANOVA and the Tukey test (Zar, 1984).

Leaf and petiole growth

The first measurement of leaf length was made when a leaf appeared (time 0 for leaf growth) as a small, vertical arrow-like structure in the centre of the plant crown. The first measurement of petiole length was recorded when the petiole was distinguishable from the leaf lamina, always after the lamina had opened (time 0 for petiole growth). Each leaf was labelled when it appeared on each numbered individual, and was monitored until the end of the study period. Thus, each leaf was monitored for different lengths of time. Mean monthly growth rates in each stage (G_s) were calculated by the formula (Zar, 1984):

$$G_s = \left[\sum_{j=1}^{N} 30(L_{t+i} - L_t)_j (i^{-1}) \right] N^{-1}$$

where *L* is the length of the leaf lamina (or petiole), *t* is the first time of two consecutive measures, *i* is the interval of time between two consecutive measurements (which varied from 26 to 34 d) and *N* is the number of leaves included in each measurement.

The minimum *N* for the calculation of G_s in each measurement was 4. The Kruskal-Wallis test was used to evaluate differences in growth rate among measurements because of data heteroscedasticity (Zar, 1984).

Herbivory

Leaf damage was classified as: no herbivory, one herbivore agent, more than one agent. According to the pattern of damage left on leaves, herbivores were classified as suckers (small hole of dead tissue in the leaf lamina), chewers (slice of leaf surface missing), necrosis-inducers (petiole-suckers inducing necrosis that cut off the leaf lamina, which was always found intact lying beside the plant, i.e. damping-off) or miners (internal trails in mesophyll). Leaves damaged by more than one agent were classified as 'multiple attack', and not recorded under the individual agents. The leaf area lost to herbivory was estimated in six classes (Morrow, 1984).

RESULTS

Leaf area

Juveniles showed the greatest leaf area, followed by infants and seedlings (Table 1). Seedling and infant leaves showed a similar number of segments and total area, infants and juveniles showed similar numbers of leaves per individual plant, and all three stages differed with respect to the size of leaf segment (Tukey test, $P < 0.05$).

Leaf production

Leaves are produced one at time, each leaf beginning its expansion after the complete expansion of the preceding one. The 96 plants studied during the second period produced 212 new leaves in 12 months (annual mean production of 2·21 leaves per individual plant). The monthly leaf production rate (average $\pm$ s.d.) of seedlings (0·18 $\pm$ 0·08), infants (0·21 $\pm$ 0·05) and juveniles (0·17 $\pm$ 0·06) did not differ ($F_{2,93} = 2.943$, $P = 0.058$). The mean time (in months) to produce a new leaf did not differ ($F_{2,116} = 1.808$, $P = 0.169$) among seedlings (5·32 $\pm$ 1·47), infants (5·57 $\pm$ 2·08) and juveniles (6·19 $\pm$ 2·35). The statistical distributions of the time to produce a new leaf (Fig. 1) showed overlap of the confidence intervals, indicating no difference in the central tendency of the data among the stages (SYSTAT, 1992). The time to produce a new leaf showed a tendency to be more variable as the ontogenetic stage advanced (Fig. 1).

Leaf lamina growth

The appearance, growth and opening of a leaf were the events studied visually in its macroscopical development. The leaf lamina is unique, fan-shaped in seedlings, feather-shaped in other post-seedling stages and divided into many segments. It grows while closed, forming an arrow-like structure in the middle of the crown. This arrow in seedlings is formed by the folding (towards the top) of the fan-shaped leaf along a vertical axis parallel to the main axis of the plant body. The arrow in post-seedling stages is constituted by the folding (towards the top) of the lamina segments along the main axis (central rib) of the leaf, also vertical and parallel to the plant main axis. Therefore, the main
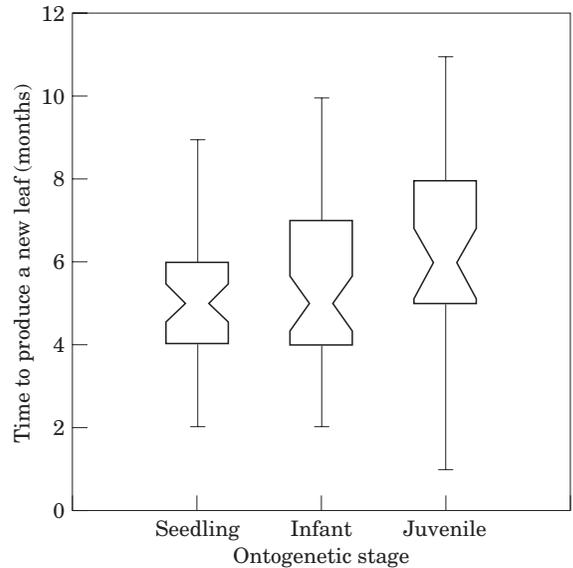
FIG. 1. Time (in months) to produce a new leaf for three ontogenetic stages of *Euterpe edulis*. Each box contains 50 % of all data. The notch in each box represents the 95 % confidence interval of the median, which is represented by the narrowest point of the box. Vertical lines (whiskers) represent the first and the fourth 25 % (quartiles) of the data.

dimension of growth in this phase is linear. After the arrow ceases to grow, the lamina segments begin to unfold from the top to the base of the arrow. After opening there is no further increase in the surface area of each segment nor in their numbers (Fig. 2). Lamina length in the closed (arrow) phase was directly related to its final area (Fig. 3).

The mean monthly growth rate of the leaf lamina (arrow length) did not change over sequential measurements for the seedling stage (Kruskal-Wallis test, $\chi^2 = 2.53$, $P = 0.77$). However, for the infant stage ($\chi^2 = 20.72$, $P < 0.01$) and the juvenile stage ($\chi^2 = 36.26$, $P < 0.001$) there were significant differences in growth rate between measurements. Infants showed a lamina growth rate that increased from the first to the fourth measurements (first 120 d), and then declined during the following three measurements (last 90 d). Lamina growth rates of the juvenile stage during periods 2 to 4 (30 to 120 d) were about 50 % greater than in other periods, all of which had about equal growth rates (Table 2). These

TABLE 1. *Mean number, length and width of leaf segments, mean total leaf surface area and mean number of leaves per plant for the three initial ontogenetic stages of* Euterpe edulis

	Leaf segments			Total leaf area (cm²)*	Number of leaves per plant
Stage	Number	Length (cm)	Width (cm)		
S	6·2 $\pm$ 0·8[a] (73)	8·02 $\pm$ 2·36[a] (146)	0·66 $\pm$ 0·17[a] (146)	23·1 $\pm$ 11·7[a] (73)	1·7 $\pm$ 0·5[a] (36)
I	7·7 $\pm$ 2·2[a] (87)	12·70 $\pm$ 5·03[b] (185)	0·86 $\pm$ 0·27[b] (185)	64·5 $\pm$ 65·9[a] (87)	3·0 $\pm$ 0·9[b] (30)
J	56·1 $\pm$ 23·6[b] (92)	28·74 $\pm$ 10·77[c] (276)	1·38 $\pm$ 0·60[c] (276)	1594·4 $\pm$ 1003·9[b] (92)	3·4 $\pm$ 1·1[b] (30)

* Analysis of variance was performed on square root transformations of the original data.

Different superscripts in the same column show a significant difference between the values (Tukey test, $P < 0.05$). S, Seedling; I, infant; J, juvenile. *n* (in parentheses) is the number of segments, number of leaves or number of individuals according to the variable analysed.
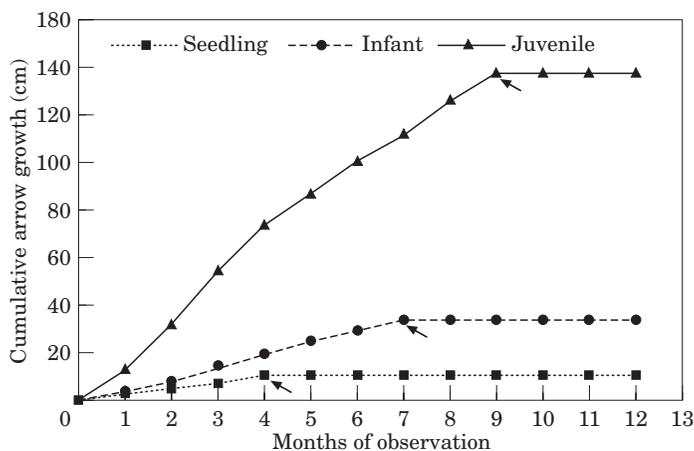
FIG. 2. Cumulative mean growth per measurement of closed leaf. The interval between each pair of consecutive measurements was 30 d. Arrows indicate leaf emergence (opening).
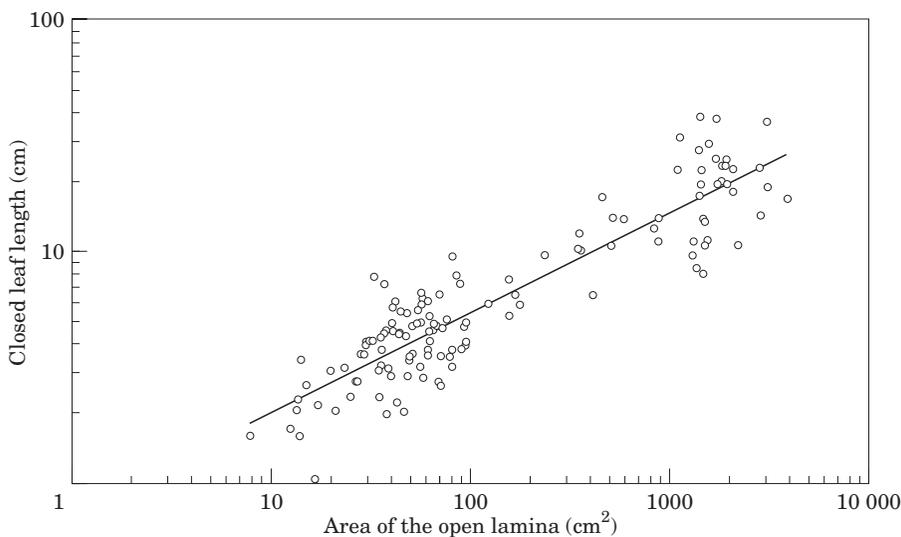
FIG. 3. Relationship between closed leaf length and open lamina area ($\log G = 0.432 \log A - 0.130$, $r^2 = 0.818$, $P < 0.001$, $n = 133$).

TABLE 2. *Mean monthly growth rate of closed leaves* ($cm \pm s.d.$) *sampled for three initial ontogenetic stages of* Euterpe edulis

Number of measurement	Seedling		Infant		Juvenile	
	Mean $\pm$ s.d.	n	Mean $\pm$ s.d.	n	Mean $\pm$ s.d.	n
1	2.3 ± 1.0	12	3.4 ± 2.1	83	13.2 ± 8.8	46
2	2.5 ± 1.4	21	4.1 ± 2.8	83	18.7 ± 10.6	56
3	2.2 ± 1.7	9	5.8 ± 5.4	61	22.7 ± 15.8	46
4	3.4 ± 2.7	5	5.9 ± 4.2	39	18.9 ± 11.2	35
5	—	—	5.8 ± 3.3	18	13.5 ± 8.2	23
6	—	—	4.3 ± 2.8	6	13.7 ± 11.1	19
7	—	—	4.2 ± 3.1	4	10.9 ± 3.9	14
8	—	—	—	—	14.3 ± 9.2	9
9	—	—	—	—	11.4 ± 9.4	5

The mean interval between two consecutive measurements was 30 d; the date of the first measurement varied from leaf to leaf.

differences show that the investment in growth was greater at the beginning of the leaf growth in the more developed stages.

Mean leaf lamina growth rates (arrow lengths) differed between ontogenetic stages when measurements were pooled (Kruskal-Wallis test, $\chi^2 = 321.42$, $P < 0.001$), and also for each measurement ($\chi^2 = 67.47$, 97.85, 65.02, 42.05 between seedling, infant and juvenile stages, and 14.46 and 9.99 between infant and juvenile stages, respectively, from the first to sixth measurements; all $P < 0.001$). The differences in growth rates show that the investment in growth was different for each ontogenetic stage.

Petiole growth

Once opened, the leaf lamina did not change its area (Fig. 2) except by loss to herbivory, and only the petiole grew
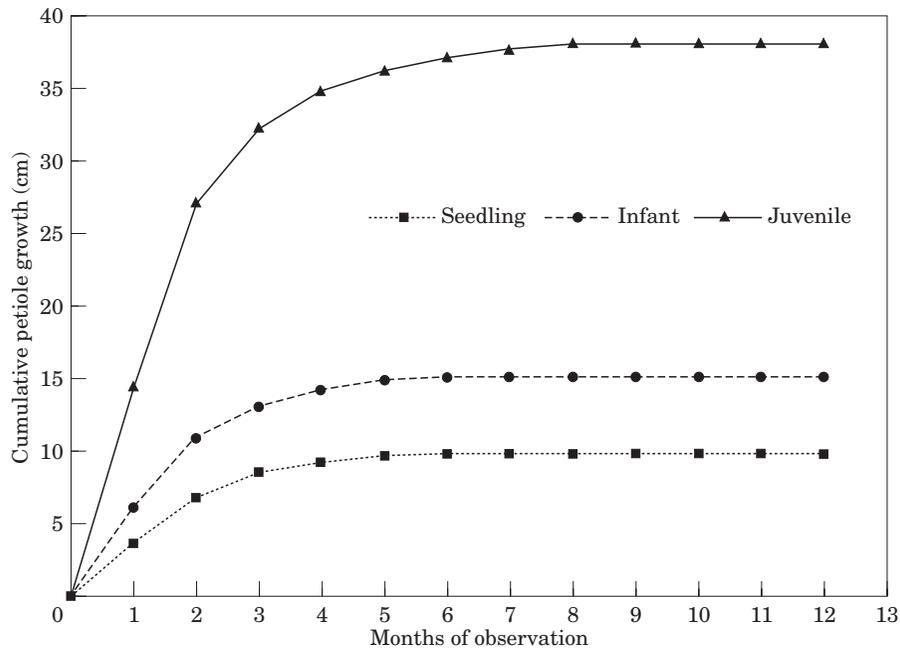
FIG. 4. Cumulative mean growth per measurement of petiole in 30 d periods after leaf opening.

TABLE 3. *Mean monthly growth rate of petioles* (cm ± s.d.) *sampled for three initial ontogenetic stage of* Euterpe edulis

Number of measurement	Seedling		Infant		Juvenile	
	Mean ± s.d.	n	Mean ± s.d.	n	Mean ± s.d.	n
1	3·7 ± 2·3	31	6·1 ± 4·6	48	14·4 ± 8·7	48
2	3·1 ± 1·8	39	4·9 ± 2·8	58	12·7 ± 7·4	55
3	1·8 ± 1·7	36	2·1 ± 1·8	51	5·2 ± 4·6	46
4	0·7 ± 0·8	36	1·2 ± 1·4	43	2·5 ± 4·7	40
5	0·4 ± 0·7	36	0·6 ± 0·9	40	1·4 ± 2·9	36
6	0·2 ± 0·4	35	0·2 ± 0·3	38	0·8 ± 1·9	35
7	0·1 ± 0·2	34	0·0 ± 0·1	34	0·7 ± 1·6	31
8	0·1 ± 0·2	30	0·1 ± 0·3	31	0·4 ± 0·9	30
9	0·0 ± 0·2	30	0·0 ± 0·0	25	0·0 ± 0·0	25
10	0·0 ± 0·0	27	0·0 ± 0·0	20	0·0 ± 0·0	22
11	0·0 ± 0·0	23	0·0 ± 0·0	15	0·0 ± 0·0	19
12	0·0 ± 0·0	11	0·0 ± 0·0	9	0·0 ± 0·0	15

The mean interval between two consecutive measurements was 30 d; the date of the first measurement varied from leaf to leaf.

(Fig. 4). There were significant differences in mean growth rate of petioles over the measurement periods within each stage: seedling (Kruskal-Wallis test, $\chi^2 = 262.26$, $P < 0.001$), infant ($\chi^2 = 301.94$, $P < 0.001$) and juvenile ($\chi^2 = 274.72$, $P < 0.001$).

Mean petiole growth rates were different between onto-genetic stages only during the first three measurements ($\chi^2 = 48.19$, 69.14 and 11.56, respectively; all $P < 0.005$). Petiole growth decreased for all stages as the leaf aged (Fig. 4, Table 3). The rather drastic decreases in petiole growth rate from the second to fifth measurements (30 to 150 d) probably indicate that the interval of time between measurements of petiole growth should have been smaller.

Seedlings took 2 to 9 months to complete petiole growth, while infants and juveniles took 2 to 8 months (Table 3). The final petiole length was positively related to leaf area (Fig. 5), thus the greater the lamina surface the longer the petiole.

Leaf mortality

Only the leaves not damaged by herbivores were con-sidered here, i.e. whose cause of mortality was not herbivory. Very few of the 212 leaves produced during the second period of study (December 1992 to December 1993) had died by the end of the study. Six of the 74 new leaves of seedlings died, respectively 83, 110, 211, 237, 318 and 346 d after appearing. Five of the 76 new leaves of infants died, with respective ages of 106, 216, 236, 297 and 311 d. Only two of the 62 new leaves produced by juveniles died, after 61 and 314 d. The death of three leaves which appeared in seedlings numbered in the first period was recorded in the second study period after 236, 309 and 396 d. Six leaves produced by infants in the first study period survived 160, 290, 307, 437, 449 and 449 d. No death of any new leaves produced by juveniles in the first study period was observed. Many other leaves born in the first period of study were still alive by the end of the second period of study. This means that the leaf lifespan could be greater than 28 months in any stage. We noted also that the more developed the ontogenetic stage the greater the leaf lifespan, although this could not be quantified.

Herbivory

Thirty three per cent of the 112 leaves (112 individuals, first period of study) showed some degree of damage by
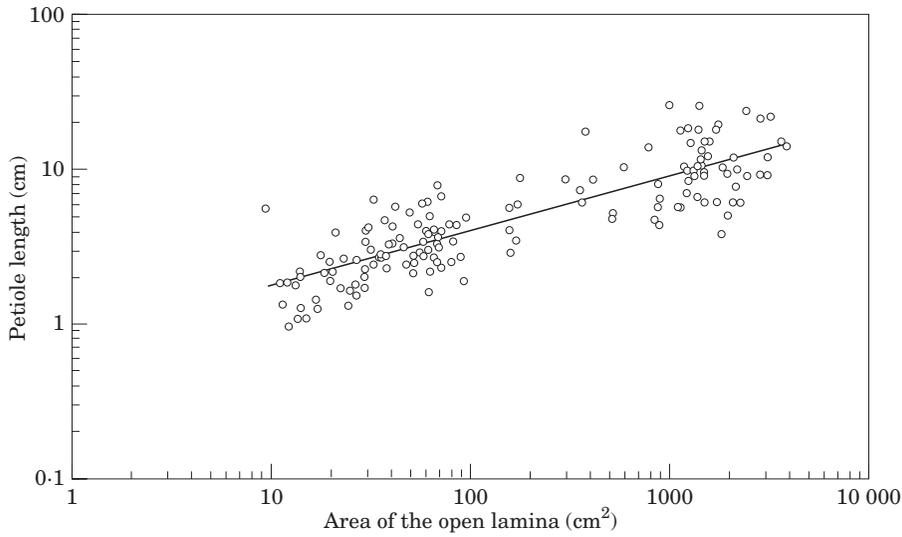
Fɪɢ. 5. Relationship between petiole length and lamina area ($\log G = 0{\cdot}352 \log A - 0{\cdot}106$, $r^2 = 0{\cdot}707$, $P < 0{\cdot}001$, $n = 151$).

Tᴀʙʟᴇ 4. *Percentage of leaves with marks of herbivory by different agents in three initial ontogenetic stages of* Euterpe edulis

Ontogenetic stage	Herbivores					Total	n
	Suckers	Chewers	Damping-off	Miners	Multiple attack*		
Seedling	8·2	2·0	10·2	—	2·0	22·4	49
Infant	7·1	9·5	7·1	7·1	14·3	38·1	42
Juvenile	19·0	4·8	—	—	9·5	33·3	21
Total	9·8	5·4	7·1	2·7	8·0	33·0	131

* More than one herbivore.
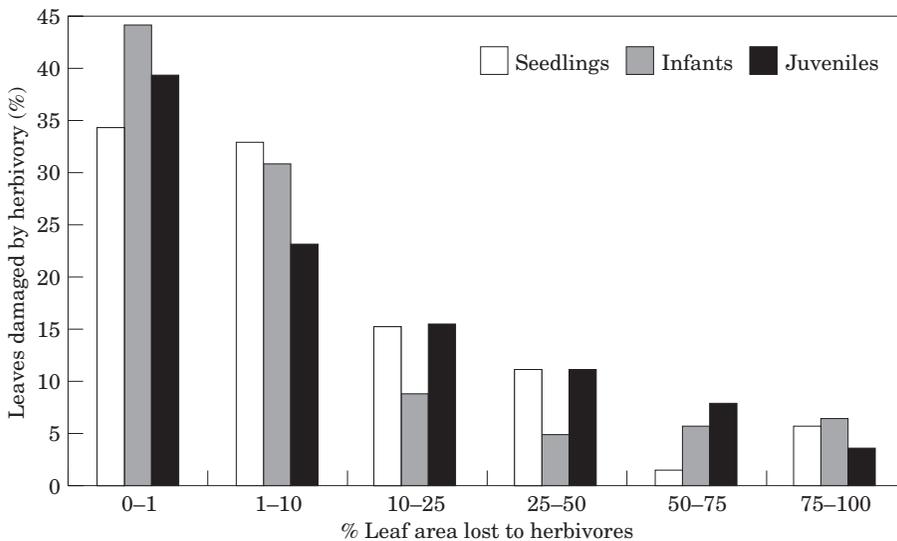
Fɪɢ. 6. Relative frequency (%) of leaves damaged by herbivores in many classes of leaf area lost (%) in three initial ontogenetic stages of *Euterpe edulis*.

herbivory (Table 4). Suckers were the most frequent agents, followed by necrosis-inductors causing damping-off, chewers and miners. The proportion of plants attacked by

herbivores varied among stages: infants suffered the greatest attack, followed by juveniles and seedlings. Herbivore agents varied among stages: seedlings were mostly attacked

TABLE 5. *Leaf mortality factors* (%) *in three initial stages of* Euterpe edulis

Ontogenetic stage	Leaf mortality factors			
	Suckers	Unknown	Total	*n*
Seedling	12·2	14·3	26·5	49
Infant	7·1	7·1	14·3	42
Juvenile	0·0	0·0	0·0	21
Total	8·9	8·9	17·8	112

by necrosis-inductors and suckers; infants by many agents; and juveniles by suckers.

The percentage of leaf area lost to herbivory did not vary significantly among stages ($\chi^2 = 10\cdot46$, d.f. = 8, $P = 0\cdot23$) (Fig. 6). In all three stages, most leaves lost relatively little area (up to 10% of the total area).

Mortality was 17·0% of the total number of leaves in the population of the first period of study (Table 5). Twenty-five per cent of these leaves had already suffered damage by herbivore agents. Necrosis-inductors caused damping-off by inducing necrosis in the petiole, although the leaf surface remained intact, and were responsible for the death of 8·0% of the leaf population. The greatest number of leaves showing damping-off was observed in October and November 1991. The most frequent agents of damping-off in the region are species of Cercopidae (Homoptera) and Curculionidae (Coleoptera), which have nocturnal activity and could not be observed. A proportion (8·9%) of the marked leaves died by unknown factors.

Leaves of seedlings suffered the greatest mortality rate, first from unknown causes, and second from necrosis-inductors (Table 5). Leaves of infants were killed equally by both unknown causes and damping-off. Leaves of juveniles died only due to senescence. Although no external mortality factor was observed in the juveniles studied, branches falling from trees caused the death of leaves of other *Euterpe edulis* plants in the neighbourhood.

DISCUSSION

The observed maximum leaf lifespan classifies *Euterpe edulis* as having long-lived leaves (Chabot and Hicks, 1982; Lowman, 1992).

The leaf production rate was not dependent on ontogenetic stage; instead it was fairly constant among the stages, thus indicating the existence of a plastochronic rhythm of macroscopical production of new leaves (Dale, 1982). However, the leaf area was directly dependent on the plant ontogenetic stage. Therefore, the hypothesis that the greater the photosynthetic surface (raw material) per plant the greater the production of new leaves (Piñero, Martinez-Ramos and Sarukhán, 1984) did not hold for *E. edulis*. This palm grows continuously in a manner classified as 'free growth' by Meyer and Montgomery (1987). In plants with free growth it is likely that leaf assimilates are translocated and used in the growth of new leaves. Thus the contribution to further carbon assimilation, and so the value of leaves to the plant, is greater while they are young (Harper, 1989*b*).

In this case, early senescence of leaves is expected. For *E. edulis* leaves the situation could be different. Although it could not be quantified, the leaf lifespan in this palm seemed greater the more developed the ontogenetic stage. The number of leaves per plant and the total leaf area per plant were greater in the more developed ontogenetic stages. As leaf growth rate was directly related to leaf area, we suggest that the exported leaf assimilates are invested not in the production of new leaves, where the rate was constant, but in increasing the leaf growth rate. Therefore, the attainment of a larger photosynthetic area per plant would be done through: (*a*) avoiding losses of an entire leaf by herbivory; (*b*) opening larger leaves by means of faster leaf growth; and (*c*) accumulating leaves through greater leaf longevity.

Height growth of the stem is slow in palms (Tomlinson, 1961) and occurs by continuous leaf production from a single terminal meristem (Van Valen, 1975; De Steven, 1989), which is protected by the imbricated leaf sheaths (Holttum, 1955). As the palm is unbranched, the growth of the petiole is the only way for the photosynthesizing surface to rise above the forest floor, reaching greater quantities, and more suitable qualities, of light.

Expansion is the most vulnerable period in the lifetime of a leaf (Aide, 1993), but the initial investment in leaf construction by *E. edulis* is made with maximum protection because the leaf grows while closed. After the leaf has been constructed and opened, the investment changes to locate the leaf in the aerial environment by means of petiole growth. Petiole growth in long-petiolate leaves of unbranched palms can simulate branch growth in a much less expensive way (Givnish, 1984). The consequence of this growth may be the domination of space and the positioning of photosynthesizing tissue so that the net photosynthetic gain may be greater. Exploitation of patches of light in higher strata of the canopy is critical to continued plant growth and survival (Campbell, Grime and Mackey, 1992) and thus influences the development of arborescent palms (Kahn, 1986).

Petiole growth can be a cheaper way of growing, and can simulate growth in stem height. Investment in stem growth would expend a great amount of energy without any certainty about the sufficiency of growth conditions—the plant would risk its energy stock in a process whose energetic income is uncertain (Bloom, Chapin and Mooney, 1985). Petiole growth may be less risky than stem growth. Once the photosynthesizing tissue reaches a certain position in space, net photosynthesis could act as a way of 'evaluating' how favourable environmental conditions are for growth. If conditions are favourable the plant could then invest some of its energy stock in stem growth. If conditions were not favourable the plant would not lose so much because the long lifespan of the leaf could compensate for the costs of its production and maintenance (Givnish, 1984). However, favourable conditions could be present only for a short time. Therefore, the stem growth response should not be immediate and the leaf should yield a critical net photosynthetic gain over a critical time, in a model analogous to the seed germination of pioneer species related to light quality and temperature (Vázquez-Yanes and

Orozco-Segovia, 1987). The positive relationships between petiole growth and leaf area and between leaf area and ontogenetic stage suggest that the more developed the stage of the plant the quicker the petiole could place its lamina in an upper position.

Leaves contain much of the plant's total nutrient stock and act as storage organs (Chabot and Hicks, 1982. Leaf aging and senescence are currently interpreted as part of a programmed reallocation of resources within the plant (Leopold, 1978; Thomas and Stoddard, 1980). These processes involve a complex series of coordinated processes that result in substantial removal of nutrients from the leaf (Chabot and Hicks, 1982). Leaf area loss is an important selective pressure since it decreases photosynthetic capacity (Nascimento and Hay, 1989). When nutrient removal is broken by a sudden mortality factor such as herbivory by petiole necrosis-inductor suckers, the nutrient balance is severely affected by the loss of an entire leaf. Thus the petiole necrosis-inductors among all the other herbivores may be more likely to affect individual plant survival and may be one of the causes of the high mortality rate found by Bovi, Godoy and Saes (1987b) for *E. edulis* seedlings.

Survival of the plant in response to herbivory or loss of leaf area seems to be dependent on the ontogenetic stage, as shown for other tropical palm species (McNaughton, 1979; Mendoza, Piñero and Sarukhán, 1987; Oyama and Mendoza, 1990). *Euterpe edulis* seedling and infant survival was severely affected by defoliation. This seems to be due to the kind of damage (caused by natural herbivores) and not to the relative leaf area consumed by herbivores, since the percentage of leaf area lost to herbivores did not differ statistically among stages.

The greatest herbivory rate occurred in the infant stage. In this developmental stage plant nutrition becomes independent of the reserves of the maternal plant stored in the seed (Gatsuk *et al.*, 1980) and the plant reaches a critical size for growth and survival. Therefore, the attainment of a minimum surface of photosynthetic area may be presumed necessary for successful growth of the plant in the future. This critical photosynthetic area would be attained in the infant stage, implying recruitment to the juvenile stage (Carvalho, 1995).

Mortality was inversely proportional to the stage of the plant, being higher in younger plants. A similar pattern has been observed in another palm species (Oyama, 1990). Because streams in the swampy area sometimes increase the volume of water (Silva, 1992) and seedlings have fragile roots, they are more likely to be uprooted and washed away than plants in other stages. An unknown but important mortality factor caused the disappearance of 8·9 % of the studied plants. Leaf herbivores (peccaries, tapirs, deers and agoutis) that could potentially eat seedlings are absent from the study site (Chiarello and Galetti, 1994). Nevertheless, small rodents (*Rattus* sp., for example) are potential seed and seedling predators, and have been observed in the study site (M. L. A. Bovi, pers. comm.). Further studies on growth and the role of herbivory for the survival of palms in all ontogenetic stages are important for modelling plantations and for management of both natural and commercial populations.

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