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Biomass Allocation in the Dioecious Tropical Palm *Chamaedorea tepejilote* and Its Life History Consequences

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Abstract The patterns of resource allocation are described for a dioecious tropical palm, *Chamaedorea tepejilote*. Resource allocation was measured by harvesting fifteen plants of *C. tepejilote*. The relative allocation of biomass in the stem increased with the size of the plant; that in the leaves decreased and that in the other structures remained roughly constant. Female plants showed a greater total reproductive effort, though male plants produced more inflorescences during the flowering season. Both male and female plants allocated more resources to prop root than to hypogeal roots. The annual productivity of reproductive and vegetative parts of *C. tepejilote* was estimated using allometric relationships for different plant structures and from demographic data obtained from the field. Annually, female plants allocated significantly more resources to leaves than male plants. Yearly productivity of inflorescences was higher for male plants, while female plants had greater total reproductive productivity (inflorescences and fruits). Correlation analysis showed an increase in reproductive effort with plant size, and an inverse relationship between fecundity and probability of survival, fecundity and residual reproductive value, and reproductive effort and life expectancy; these relationships suggested a cost in reproduction. Additionally, mature plants with different growth rates exhibited differences in fecundity: tall plants (>2.5 m height) that grew more than 40 cm in height in four years had lower values of fecundity in comparison to plants of slower growth. These data were discussed in the context of the implications in the life history of a dioecious tropical plant.

Key words: *Chamaedorea*, dioecious, palm, reproductive cost, resource allocation, tropical rain forest.

Sex-related differences in dioecious plant species are well documented. Male and female plants may differ substantially in life history traits (Barrett and Helenurm, 1981; Meagher and Antonovics, 1982), phenology (Bawa, 1980a, 1983; Bullock and Bawa, 1981; Bullock et al., 1983; Herrera, 1984), competitive ability (Putwain and Harper, 1972; Onyekwelu and Harper, 1979) and niche partitioning (Cox, 1981; Freeman et al., 1976). The sexual differences have been seen as a differential use of resources, suggesting a different reproductive cost for each sex (Putwain and Harper, 1972; Bawa, 1980b).

The objective of many studies on resource allocation has been to find the relation between the amount of resources devoted to reproductive parts and the amount devoted to vegetative parts, assuming these allocations are competitive and that they have different consequences for survivorship and future fecundity. The basic concepts of the cost of reproduction (Bell, 1980; Reznick, 1985) and reproductive effort (Schaffer, 1974; Charlesworth and Leon, 1976) have been used in order to describe theoretical models about life histories and their evolution.

There are many studies concerning the reproductive biology of temperate plants that make estimates of resource allocation, but relatively few studies have addressed this problem for perennial tropical plant species (Snell and Burch, 1975; Piñero et al., 1982; Clark and Clark, in press). Data comparing biomass and nutrient allocation of males and females are available for only one species under natural conditions (Bullock, 1984).

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As part of a long-term project on the population dynamics of *Chamaedorea tepejilote* Liebm., a dioecious palm in a tropical lowland rain forest of South East Mexico, we have studied the differences in growth pattern and reproductive behavior of male and female plants of this species (Oyama, 1987; unpublished). In this paper, we report measurements of resource allocation for female and male plants of *C. tepejilote* in a natural population. Additionally, following the models proposed by Pianka and Parker (1975), we relate the demographic parameters with the different size-classes of male and female plants of *C. tepejilote*, in order to assess the possible patterns of the reproductive cost.

Materials and Methods

1. *Study Site*

The site of study was the Estacion de Biologia Tropical "Los Tuxtlas", a field station of the Universidad Nacional Autonoma de Mexico. The station is located near Catemaco in the State of Veracruz (18°34′–18°36′N and 95°04′–95°09′W). The vegetation of the area is tropical rain forest with trees up to 35 m tall and understory vegetation dominated by palms, mainly *Astrocaryum mexicanum* and *C. tepejilote*. Mean yearly rainfall is 4700 mm and mean monthly temperature is 23.4°C. A more detailed account of the characteristics of the area is given in Lot-Helgueras (1976) and Ibarra-Manriquez and Sinaca-Colin (1987).

2. *Methods*

The data of this paper originate from two sources: i) demographic data obtained from the monitoring of 810 individuals of *C. tepejilote* in three 600 m^2 permanent observation plots at Los Tuxtlas. On these plots the survivorship, growth and reproductive behavior of each plant were followed during four years (1981–85) (Oyama, 1987; unpublished), ii) biomass allocation measured from 15 plants harvested completely in 1984, taking care not to damage delicate structures such as roots. Six female, six male and three juvenile plants were chosen including adult plants of about the same size for both sexes, and covering the range of height for this species (three plants 1.50 to 2.50 m, and three more than 2.50 m of each sex). The plants were separated into roots (hypogeal and prop), stem, leaves and reproductive structures. These materials were dried at 80°C and each structure was measured for the analysis by correlations of allometric relationships between the size of the plant parts and their dry weight, for later estimation of annual allocation patterns. Demographic data were used to estimate the annual productivity in biomass.

The parameters used for the estimations of reproductive costs were obtained as follows. Reproductive effort of females was estimated relating the annual productivity in reproductive structures (inflorescences and fruits) with the annual productivity in vegetative parts. The expectation of life and the residual reproductive value (Vx^*) were estimated following Pianka (1978). The fecundity as the number of fruits, the probability of survival of an individual plant and differences in growth rates were obtained recording the average of four years of observations in a previous study (Oyama, 1987; unpublished).

Results

1. *Resource Allocation*

Figure 1 shows the differences of biomass (dry weight) allocation for the harvested individuals of *C. tepejilote*. As the plants increase in height, biomass allocated to reproductive structures and stem increases, while leaf biomass decreases. The general pattern was very similar for both sexes, except that female plants had a greater allocation to reproduction (on average 2.3 times more).

The correlations for dry weight and linear or area measurements for different structures of the plant are presented in Table 1. Highly significant relationships were obtained in all cases. Estimates of the annual dry weight allocation for inflorescences, stem, leaves and roots were possible with these correlations (Table 2). The fruit biomass production was estimated as the product of mean dry weight of each fruit and the mean number of fruits produced annually. Females produced more biomass in leaves than males ($t=6.81$; $P<0.001$), although males produced significantly more leaves per year (males=2.3, females=2.02; $F=20.14$, $P<0.001$-Oyama, 1987; unpublished). In contrast, males produced more biomass in inflorescences than females ($t=3.24$; $P<0.05$). However, if we consider all the reproductive biomass (inflorescences and fruits for females), the difference between the sexes changes with a greater allocation by females (Table 2).

2. *Reproductive Effort*

The mean reproductive effort, defined as the percentage of biomass in reproductive parts relative

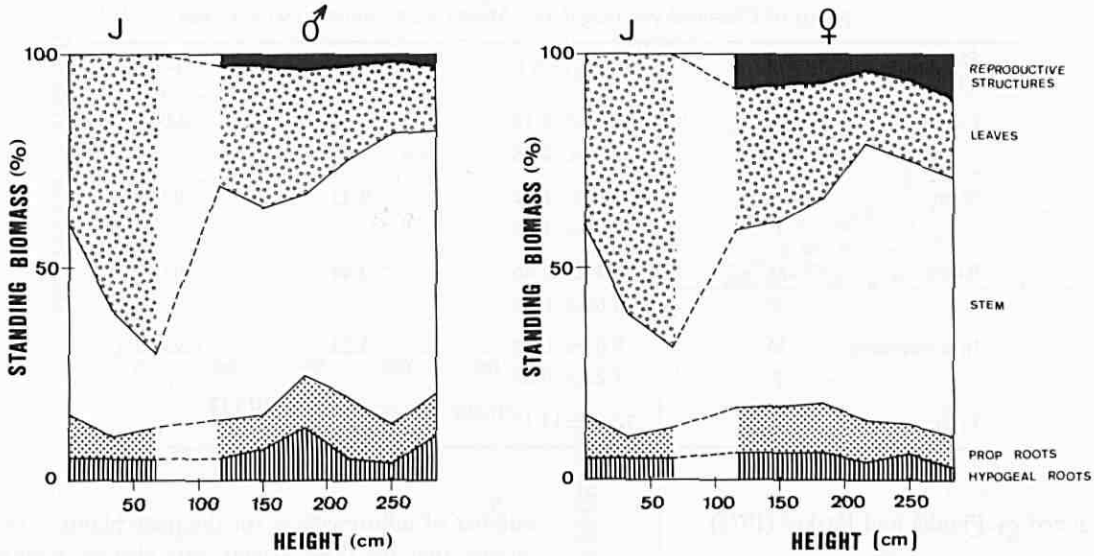

Fig. 1. Allocation patterns of standing biomass (dry weight) for juvenile (J), male and female plants of *Chamaedorea tepejilote*.

to the total annual productivity was 34 %, considering all adults. Reproductive effort increased with height of the plants up to 3.0 m, after which there was a decrease in the tallest plants (Fig. 2). The values ranged from 7% to 49%.

3. *Reproductive Costs*

Several expressions for reproductive cost were evaluated for the females. First, a relationship between the probability of survival of an individual plant and its fecundity ("the survival cost", Bell, 1980) yielded a significant decay ($r=-0.77$), as fecundity increased (Fig. 3a). Similarly, the life expectancy as related to reproductive effort showed a significant inverse relationship ($r=-0.71$) (Fig. 3b). Finally, we calculated the residual reproductive value (Vx^*), defined as the reproductive value in future years of an individual (Fisher, 1958; Williams, 1966; Pianka and Parker, 1975) as a function of present fecundity (Fig. 3c). A significant negative relation ($r=-0.86$) between the residual reproductive value and fecundity was found, as

Table 1. Allometric relationships between linear (LM) and area (AM) measurements and dry weights (DW) of different structures of male and female plants of *Chamaedorea tepejilote*. N=sample size. Males and females were analyzed separately only in variable 1.

Variable	Sex	Model	r	N	F	P
1. Inflorescence (LM) vs Inflorescence (DW)	Male	$y=-1.43+0.16x$	0.62	37	22.7	<0.001
	Female	$y=-1.0+0.13x$	0.81	33	57.6	<0.001
2. Stem (LM) vs Stem (DW)		$y=-63.71+2.08x$	0.90	14	57.2	<0.001
3. Leaves (AM) vs Leaves(DW)		$y=-1.65+0.004x$	0.92	27	128.2	<0.001
4. Stem (LM) vs Roots (DW)		$y=-32.0+0.57x$	0.75	12	13.2	<0.01

Table 2. Annual productivity of different structures of male (M) and female (F) plants of *Chamaedorea tepejilote*. Means were compared with a *t*-test.

Structure of the plant	Sex	Mean(g)±S.E.	t	P
Leaves	M	46.48± 2.19	6.81	<0.001
	F	70.64± 2.78		
Stem	M	15.43± 1.62	0.45	>0.05
	F	16.29± 1.02		
Roots	M	4.44± 0.46	0.44	>0.05
	F	4.68± 0.29		
Inflorescences	M	8.05± 0.83	3.24	<0.05
	F	4.23± 0.83		
Fruits	F	72.64±14.17		

predicted by Pianka and Parker (1975).

4. *Relationship between Growth and Reproduction*

The cost associated with reproduction may also be seen in terms of a trade-off between current vegetative growth and fecundity. In Fig. 4 we present three groups of plants (for males and females) separated according to their net increments in stem elongation in four years: slow growers (1–20 cm in 4 years); moderate growers (21–40 cm) and fast growers (>41 cm). There were positive regressions between the two first groups of plants: a) slow growers: males $r=0.43$, $P<0.05$; females $r=0.59$, $P<0.01$; b) moderate growers: males $r=0.60$, $P<0.001$; females $r=0.47$, $P<0.05$. It is evident, also, that there were sex-related differences: in general, for a given height, there was a greater number of inflorescences for the male plants. This implies that for these growth rate groups, females need to attain a greater height to produce a given number of inflorescences. Secondly, for the fast growers of both sexes (Fig. 4c), there is a decline in the production of inflorescences with height, particularly after plants have attained 2.5 m in height, suggesting an inverse relationship between growth and reproduction (males $r=0.50$, $P<0.05$; females $r=0.59$, $P<0.05$).

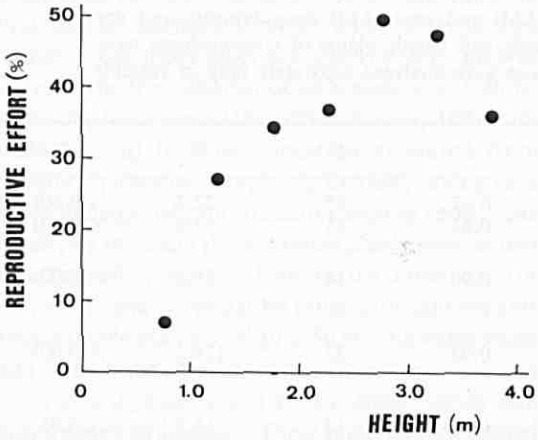

Fig. 2. Relationship between the reproductive effort and the height of female plants of *Chamaedorea tepejilote*.

Discussion

It is generally assumed that female plants allocate greater amounts of resources to reproduction due to requirements of fruit and seed development. The comparison of resource allocation to reproductive parts in dioecious species must be carried out throughout the reproductive season because during blooming, males can produce significantly more inflorescences (in number and dry weight) than females; later, only the females provide energy for the development and maintenance of the fruits. This difference was found in *C. tepejilote* and it seems to occur in other species such as *Cirsium arvense* (Lloyd and Myall, 1976), *Silene dioica* (Gross and Soule, 1981) and *Aralia nudicaulis* (Barrett and Helenurm, 1981).

We found, also, that female plants of *C. tepejilote* allocate more resources to leaves than males. This "extra-foliage" appears to provide the requirements of energy necessary for the maintenance of the fruits. This also occurred in other species. For example, in *Chamaelirium luteum* female plants produce more leaves than males, providing sufficient

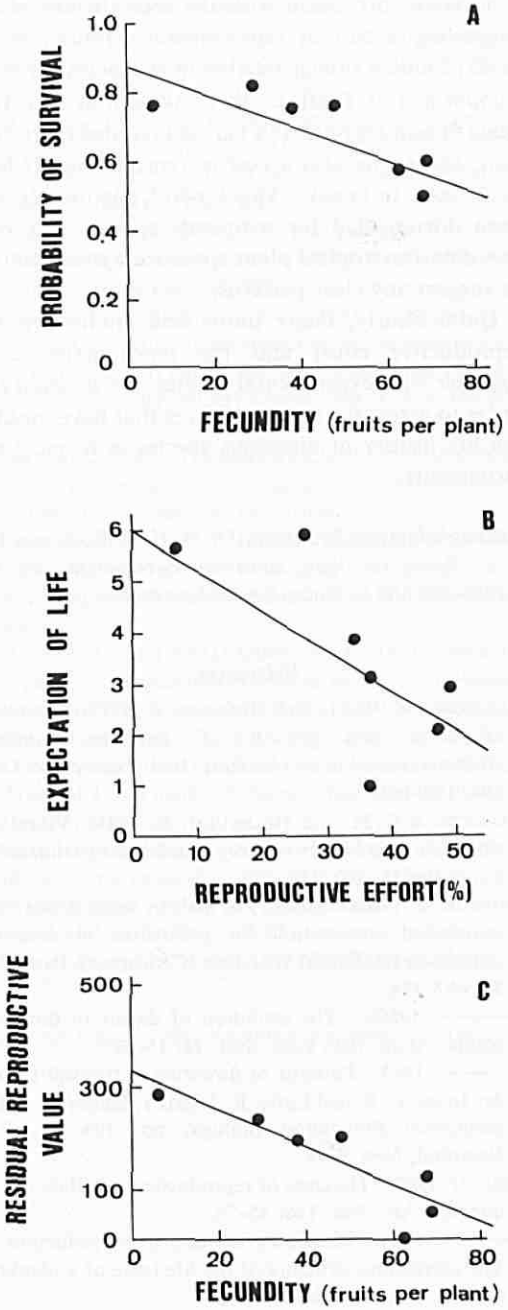

Fig. 3. Relationships between (a) fecundity and probability of survival, (b) reproductive effort and expectation of life and (c) fecundity and residual reproductive value for female plants of *Chamaedorea tepejilote*.

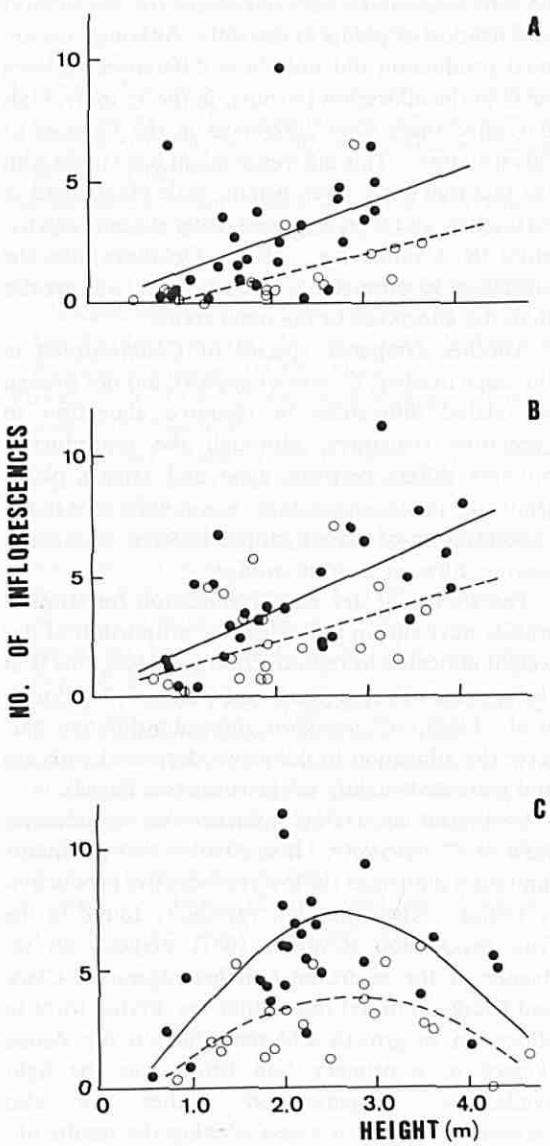

Fig. 4. Relationships between height and fecundity (no. of inflorescences) of three groups of plants of males (●—●) and females (○---○) of *C. tepejilote* with different growth rate: a) Slow growers: 0–20 cm in four years; b) moderate growers: 21–40 cm in 4 years; c) fast growers: >41 cm in four years.

photosynthetic surface for catching the necessary resources for reproduction (Meagher and Antonovics, 1982). This evidence suggests that for female plants to reproduce, enough resources need be accumulated to provide the necessary energy for the maintenance of the fruits. This could be achieved from an accumulation of resources based on more photosynthetic area.

Another difference between the sexes is the allocation of resources to roots. Male plants have a little more biomass in prop roots than females. This type

of root seems to be very important for the support and fixation of plants in the soil. Although the annual production did not show differences between sexes in the allocation to roots, in the 15 individuals harvested there were differences in the biomass of this structure. This difference might have to do with the fact that for a given height, male plants tend to be thinner, and therefore need better support and fixation (K. Oyama, pers. obs.). On the whole, the allocation to prop roots, in both sexes, was greater than the allocation to the main roots.

Another sympatric species of *Chamaedorea* in the same locality, *C. ernesti-augusti*, did not present sex-related differences in resource allocation to vegetative structures, although the reproductive biomass differs between male and female plants (Bullock, 1984). Also, there was a difference in the concentration of carbohydrates between sexes, suggesting different sites of storage.

The studies of dry weight allocation for tropical studies have shown that when the proportion of dry weight allocated to reproduction increases, this is at the expense of roots (Snell and Burch, 1975; Piñero et al., 1982). *C. tepejilote* showed a different pattern: the allocation to the leaves decreased with age and increased slightly to the roots (see Fig. 1).

Ecological constraints influence the reproductive yield of *C. tepejilote*. It is possible that pollinator limitation influences the low reproductive productivity found. Also, the high variability found in the fruit production (Oyama, 1987) suggests an influence of the environmental heterogenity. Clark and Clark (in press) found that the driving force in allocation to growth and reproduction for *Zamia skinerii* in a primary rain forest was the light availability. Experimental studies are also necessary in order to assess whether the results obtained in the field reflect plastic responses to environmental heterogeneity or constitute genetically determined responses. Several authors have found that field patterns of resource allocation disappear under controlled conditions (Abrahamson and Hershey, 1977; Hickman, 1977; Holler and Abrahamson, 1977).

Theoretically, the studies of allocation of resources assume a "trade-off" between reproductive and growth activities—the reproductive cost hypothesis (Bell, 1984). The analysis of survival cost (Bell, 1980) in *C. tepejilote* showed a significant negative relationship between the survival probabilities and fecundity. Also, the residual reproductive value and the expectation of life showed a negative correlation with the reproductive effort suggesting a cost of reproduction. Piñero et al. (1982) found a similar relation in *Astrocaryum mexicanum* at Los Tuxtlas. In *Z. skinerii* at least two years of non-reproductive period preceded reproduction, suggesting also a cost in reproduction (Clark and Clark, in press). This kind of relationship has been documented for temperate species, but very few data for tropical plant species are available yet to suggest any clear patterns.

Quite clearly, many more field studies on the reproductive effort and the reproductive cost, together with experimental studies, are necessary in order to assess the selective forces that have molded the life history of dioecious species in tropical environments.

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