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Ecological Aspects of the Interaction between *Chamaedorea tepejilote*, a Dioecious Palm and *Calyptocephala marginipennis*, a Herbivorous Beetle, in a Mexican Rain Forest

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ABSTRACT

Chamaedorea tepejilote Liebm. ex Mart., an abundant dioecious palm in the lowland rain forest of Los Tuxtlas (Southeast Mexico), typically bears evidence of leaf damage by *Calyptocephala marginipennis* Bohem. (Chrysomelidae). The beetles markedly prefer this palm in comparison to other plants on this site, including other sympatric species in the same genus. Additionally, beetles showed some marginal preference for the foliage of female plants under experimental and field conditions. Sex-related phytochemical attributes of the palm, such as secondary compounds and nutritional characteristics of the foliage, did not differ markedly between sexes and did not seem to be the proximal causes of the inter-sexual differences in herbivory. Thus, the hypothesis that differences in resource allocation to defense and nutritional quality, resulting from sex-related differential allocation to reproduction, is not supported by this study. This investigation suggests that plant-herbivore interactions in palms may be as complex as those of other flowering plants.

Studies on the interactions between herbivores and plants in tropical communities have been increasing markedly in recent years (Coley 1983, Dirzo 1984, Janzen and Waterman 1984, Marquis 1984, among others). Also, much empirical evidence has been obtained which can be used for the development of theories of plant-herbivore interactions (see Crawley 1983, Rosenthal and Janzen 1979, Strong et al. 1984). In this expanding field, some work-

ers have made studies regarding intraspecific differences in herbivory in the context of polymorphic plant systems in temperate zones (e.g., Jones 1966, Cates 1975, Dirzo and Harper 1982a). Dioecy constitutes one of the most common polymorphic systems, particularly in some Neotropical communities (Croat 1979, Bawa and Opler 1975, Bawa 1980, Flores and Schemske 1984, Bawa et al. 1985). Suggestion in the literature of sex-based differences in herbivory include male inflorescences suffering higher levels of predation than female inflorescences (Fryxell and Lukefahr 1967, Bawa and Opler 1978) and cases in which herbivores preferentially feed either on leaves of female (Danell et al. 1985, Lovett Doust and Lovett Doust 1985) or male (Agren 1987) plants. However, folivory is extremely poorly known for dioecious tropical plants, particularly palms.

In the lowland rain forest of Los Tuxtlas, Southeast Mexico, *Chamaedorea tepejilote*, a dioecious understory palm, normally bears extremely variable levels of leaf damage and we explored the possibility that this variation might be explained, to some degree at least, by inter-sexual differences. The plants on this site are normally eaten by *Calyptocephala marginipennis*, a chrysomelid beetle which appears to be largely monophagous. We measured the selectivity of this insect for the leaves of each sex in the field and laboratory. Also, we attempted to correlate the effect of

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herbivory with differences in contents of secondary compounds and nutritional characteristics of the sexes.

Materials and Methods

Study Species. The palm genus *Chamaedorea* includes approximately one hundred species distributed through Neotropical forests from Brazil and Bolivia to Guatemala and the Central part of Mexico (Standley and Steyermark 1958, Uhl and Dransfield 1987). All the species in the genus are dioecious (H. Quero, pers. comm.). In Los Tuxtlas, Mexico, *C. tepejilote* is a common palm that forms dense patches in the forest understory where slight natural disturbances have occurred. The tallest individuals reach up to 5.0 m in height. Plants of both sexes bear from 3 to 5 leaves. The plants flower from October through December. Both sexes have yellow green flowers; male flowers tend to be slightly smaller (1.5 to 2.5 mm) than females (2.5 to 3.5 mm). Single female plants can bear from 5 to 400 fruits (Oyama 1984). Mortality of adult plants is due mostly to branches or other debris falling from the canopy. Tree falls frequently break apical meristems and kill the palms (Oyama 1987, 1990).

Eight species of *Calypsocephala* have been reported in Neotropical forests from Mexico to Brazil, paralleling the geographic distribution of the *Chamaedorea* species. The beetles are small (ca. 6 mm long) with pale brown elitrae and a dark line at the margin. This insect feeds on leaves of *C. tepejilote* making specific longitudinal ruptures along the leaf veins, which are easily recognized in the field.

Study Site. This study was conducted in a 600 m² permanent plot in a lowland rain forest in the Gulf of Mexico (95°14'–95°09'W, 18°34'–18°36'N), in the biological reserve Estación de Biología Tropical Los Tuxtlas at 150–650 m altitude.

Methods. We recorded herbivory on

the leaves of male and female plants in the field using two methods: a) an instantaneous measurement based on broad categories of damage, and b) estimates of leaf area loss during a 3-month period. For the first method, leaf damage was scored on an A to D scale ($A \leq 25\%$; $B > 25 \leq 50\%$; $C > 50 \leq 75\%$; $D > 75\%$) in all the leaves of 48 male and 45 female plants. The leaves of each plant were separated into four age categories (I–IV). Contingency analyses (after a heterogeneity test for the leaves of different age) were carried out to assess the distribution of categories of damage of the leaves of both sexes. b) For the second method, leaf damage was also scored with a grid of 893 points on a transparent plastic sheet (10 cm × 5 cm). This grid was placed on the adaxial surface of the pinnae in a way that we could count the number of visible points coinciding with ruptures of the lamina (as a product of herbivore damage). We took care to check all types of damage and differentiated them from the specific damage produced by *C. marginipennis*; this was, by far, the most abundant type of damage (see Oyama 1984). We then calculated an index of leaf area removed as the quotient of the number of points registered (ruptured) to the total number of points of the grid (i.e., 893). Following this second method, we recorded the cumulative damage on the leaves by marking a permanent area of observation (of equal size to the grid) on the last two (youngest) leaves produced by the plant. We recorded the damage monthly for three consecutive months. For this analysis, we chose randomly 15 individuals of each sex in three categories of height (0 to 2.0 m; 2.0 to 3.5 m; > 3.5 m). Two-way analyses of variance were done in function of sex and height (age) of the plants, after arcsin transformation of the data.

In a second line of investigation, intact pinnae of male and female plants of the same size and age were bagged together and exposed to 6 beetles previously starved

Table 1. Contingency analysis for the number of leaves of different age of male (M) and female (F) plants of *Chamaedorea tepejilote* in each category of damage. Values in parentheses below each pair of values are the absolute deviations from those expected if beetles damaged leaves regardless of sex; the sign of the deviation is shown in parentheses after each value. Chi-square analyses are shown for leaf age, the pooled data of leaves and the heterogeneity among them.

Leaf age	Sex	Category of beetle damage				Total	χ^2	df	P
		A	B	C	D				
I	M	905	7	6	6	924	6.96	3	n.s.
	F	1,045	15	1	6	1,067			
II	M	827	46	13	11	897	1.29	3	n.s.
	F	929	60	11	14	1,014			
III	M	711 (+)	72 (-)	22 (+)	19 (-)	824	26.88	3	<0.001
	F	690 (-)	147 (+)	21 (-)	34 (+)	892			
IV	M	(38)	(33)	(1)	(6)				
	F	470 (+)	122 (-)	40 (-)	28 (-)	660	36.76	3	<0.001
Pooled	M	314 (-)	153 (+)	43 (+)	56 (+)	566			
	F	(48)	(26)	(5)	(17)				
Total							71.89	12	
Heterogeneity	M	2,913 (-)	247 (-)	81 (+)	64 (-)	3,305	31.07	3	<0.001
	F	2,978 (+)	375 (+)	76 (-)	110 (+)	3,700			
							40.82	12	<0.001

for 24 hours. The experiments were carried out in a laboratory arranged for this purpose. We recorded the leaf area consumed for each type (sex) of plant 12 and 24 hours after. Each experiment consisted of six replicates. Statistical analyses (t-tests) were done to compare the mean leaf area eaten of male and female plants. All the statistical analyses were done following Zar (1974).

A third line of study consisted of a phytochemical screening of secondary compounds (alkaloids, tannins, flavonoids, saponins and cyanogenic compounds) and nutritional characteristics (protein, fiber, sugar, minerals and fat contents) as possible factors affecting the intensity of herbivory. Young and mature leaves of each sex were collected, dried and analyzed in the laboratory (see Dominguez (1979) for a description of techniques for analyses of secondary compounds, and Flores (1977) for a description of techniques for assessing nutritional characteristics).

Results

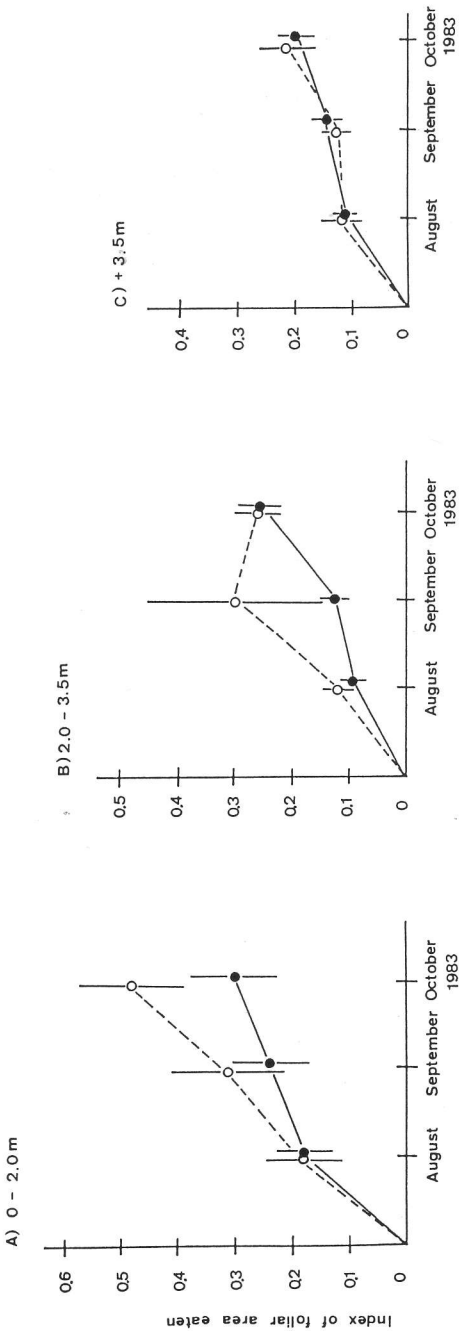
In the survey of leaf damage scored on a visual scale, the heterogeneity test between leaves of different age was significant ($\chi^2 = 40.82$; $P < 0.001$) and the results of each leaf age were examined independently (Table 1). The heterogeneity appears to be due to the fact that leaves in categories I and II did not show sex-related differences while categories III and IV were the only cases where sexes differ in the levels of damage. Moreover, the leaves of the youngest category were mostly undamaged (905/924 for female and 1,045/1,067 for male plants) and damage gradually increases with leaf age. Thus, sex-related differences could only be detected when damage was high in general. For leaves of age categories III and IV, clearly females were over-represented in the heaviest category of damage (D) and in category B, while males were under-represented in these categories. Males, in

contrast, were over-represented in the lightest category of damage (A) and females under-represented (Table 1).

The time-course of damage for male and female plants of the three categories of size (Fig. 1) showed that leaves with herbivory were high in the young (smallest) plants and decreased with plant age. An inter-sexual difference was only apparent in the smallest plants after 3 months. The statistical analysis revealed that the effect of plant sex was not significant ($F = 1.41$; $P > 0.05$) while plant size significantly affected the level of damage ($F = 5.01$; $P < 0.05$). The interaction size \times sex was also not statistically significant ($F = 0.82$; $P > 0.05$).

The feeding trials carried out under controlled conditions showed a significant preference for female tissue when recordings were made 12 hours after ($t = 3.017$; $P < 0.01$, Table 2). However, the intensity of the preference decreased when the beetles were maintained within the bagged plants for 24 hours ($t = 2.367$; $P > 0.05$), suggesting that the proximal factors determining the relative acceptability reduce their influence with time. There was not any preference for male plants.

The chemical screening of secondary metabolites showed the presence of flavonoids and tannins in the young and mature leaves of plants of all three size categories of both sexes (Table 3a). Alkaloids, saponins and cyanogenic compounds were not detected in any plant size of either sex. The nutritional analysis showed some qualitative differences in fiber, fat, minerals and sugar contents between sexes.



1. Time-course of the cumulative leaf damage between male (●) and female (○) plants of *Chamaedorea tepejilote*, by *Calyptrocephala marginipennis*. Values are means of ± 1 S.D. the index of leaf damage. A to C represent individuals of different height. (The index, when multiplied by 100, gives an estimate of the percent leaf area damaged per plant; details about the index, see text.)



2. Leaf of *Chamaedorea tepejilote* showing heavy damage by the beetle *Calyptocephala marginipennis*.

The values of the first three were slightly greater in the leaves of male plants and the latter was greater in female plants (Table 3b). Unfortunately, these chemical data are not amenable to statistical analyses, but the differences appear to be only marginal.

Table 2. Comparison of feeding preferences of *Calyptocephala marginipennis* for the leaves of male (M) and female (F) plants of *Chamaedorea tepejilote*. n represents the number of assays and the values are means \pm 1 S.D.

Sex	Leaf area removed (mm ²)	
	After 12 h (n = 24)	After 24 h (n = 24)
M	4.08 \pm 2.58	6.27 \pm 3.73
F	7.03 \pm 3.30	9.40 \pm 5.24
t	3.02	2.37
P	<0.05	n.s.

Discussion

The recognizable damage of *C. marginipennis* on the foliage of *C. tepejilote* in the field is an indication of the preference of the herbivore for this particular plant. Moreover, preliminary laboratory studies (Oyama 1984) strongly suggest that of the five sympatric species of *Chamaedorea* in Los Tuxtlas, *C. tepejilote* is, by far, the most acceptable food for *C. marginipennis*. On the other hand, these observations and laboratory results are not only indicative of the marked degree of preference on the part of the herbivore, but also suggest a tendency for exclusivity of this herbivore damage being experienced by the plant. The mature leaves of *C. tepejilote* accumulate the beetles' damage for several months and when combined with the fall of branches or other debris from the canopy constitute a major cause

Table 3. Chemical attributes of leaves of male (M) and female (F) plants of *Chamaedorea tepejilote*

a. Secondary compounds*						
Sex	Leaf age	Alkaloids	Saponins	Tannins	Flavonoids	Cyanogenic capacity
M	Young	—	—	+	++	—
	Mature	—	—	+	++	—
F	Young	—	—	+	++	—
	Mature	—	—	+	++	—

b. Nutritional components (%)						
Sex	Proteins	Fats	Fibers	Carbohydrates	Minerals	Total
M	20.56	3.77	31.11	32.42	12.14	100
F	20.55	3.53	27.41	37.70	10.81	100

* — = absent; + = present; ++ a more intense response.

of leaf death (Oyama 1987). Experiments of artificial defoliation showed detrimental effects on the growth and reproduction behavior of this plant (Oyama 1987, Oyama and Mendoza, 1990).

Another issue of this paper relates to the suggestive results for a marginal female tissue preference. Though in the laboratory there was consistently an initial preference for female tissue and in no case was male tissue preferably taken, the field data are not as conclusive although a similar tendency was observed for leaves of intermediate to old age. The elucidation of the role of other components of the natural history of the system (such as the role of beetles' own predators and parasitoids) is still obscure, but the results of this study (particularly those of the laboratory) warrant further study in more detail and of longer duration.

The screening of chemical components did not reveal any significant differences between sexes in the secondary metabolites and nutritional characteristics and thus did not give any hint as to what could be the proximate cause behind the marginal differential damage suffered by female plants.

A testable explanation for the differential herbivory can be proposed on the

basis of differences in resource allocation between male and female plants, in a similar way to that some authors have suggested for other polymorphic systems (Cates 1975; Dirzo and Harper 1982a, b). In these studies, there is an indication that one of the morphs, the one preferred by herbivores, displays also a greater competitive ability, growth potential, or reproduction, presumably as a result of lower investment of resources in defenses; the "defended" morph, instead, has fewer resources allocated to reproduction, growth or competitive ability. In *C. tepejilote*, female plants produce a substantially more costly reproductive structure (Oyama 1987, Oyama and Dirzo 1988): large, heavy inflorescences which then become heavy infructescences that remain attached to the plant for one year; male plants, in contrast, produce long, thin and ephemeral inflorescences which represent a much lower proportion of the biomass of the plant. These differences are, in principle, compatible with an interpretation on the grounds of differential resource allocation, which might lead to greater susceptibility to herbivory by female plants.

The documented studies of folivory on dioecious plants show contrasting results.

Lovett Doust and Lovett Doust (1985) found that female plants of *Rumex acetosella* suffer heavier damage than male plants and they hypothesized that female plants, with a lower leaf area, are in some way more capable of withstanding environmental buffeting than male plants. In contrast, Agren (1987) found that male leaves of *Rubus chamaemorus* were more damaged than female leaves. Different physiological responses of each sex in dioecious species have been documented (Crawford and Balfour 1983, Fox and Harrison 1981, Zimmerman and Lechowicz 1982) but they appear to be due to local conditions rather than a general pattern (Willson 1983).

The present paper provides some basic aspects of the natural history of the interaction between *C. tepejilote* and *C. marginipennis*; it exposes the complexity of the system and suggests that some species (populations) of palms may be engaged in as complex and exciting interactions with herbivores as those commonly reported for other flowering plants.

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