

On the Function of Floral Nectar in *Croton suberosus* (Euphorbiaceae)

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## On the function of floral nectar in *Croton suberosus* (Euphorbiaceae)

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In this paper we propose that the role of floral nectar in *Croton suberosus* is the attraction of herbivore predators rather than reward for pollinators. The flowers of this monoecious plant species present several features associated with anemophily and wind is the prime pollen vector. Furthermore, in the field, levels of herbivore damage to the leaves are extremely low, even though laboratory tests indicate that the foliage is readily acceptable. Experimental herbivore addition to plants of *C. suberosus* shows that *Polistes instabilis* wasps act as defenders while they forage in search of floral nectar. In the deflowered plants treatment, the rate of activity of wasps on the plants was much lower than in intact controls.

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### Introduction

A great deal of study has been devoted to pollination systems in which floral nectar plays a preponderant role in maintaining visitation by animals which inadvertently pollinate the flowers (Heinrich and Raven 1972, Baker and Baker 1975). Present literature interprets floral nectar almost exclusively in these terms. In a second type of mutualistic interaction involving nectar, some plants produce rewards sought by animals which also actively repel or attack herbivores. Although more costly or complex rewards are common (protein or fat bodies, nest sites (Beattie 1985)), nectar is a major component in maintaining associations with predatory “defenders” in many plant species (e.g. Janzen 1966, 1973, Elias and Gelband 1975, Bentley 1976, Tilman 1978, Schemske 1980, Koptur 1985). In all instances known to date, the nectar taken by the defenders is produced in extrafloral nectaries, and ants are the only defenders involved.

Hespenheide (1985) proposed that where nectar is the only reward for defending insects, this fits the requirements of wasps better than those of ants. With respect to nectar production, we do not know of evi-

dence involving floral nectaries in defense by means of a flower visitor. Interestingly, the compositions of floral and extrafloral nectars tend to be different (Baker et al. 1978). Also, visitation of (pedestrian) predators to plant parts is reinforced by the situation of nectaries on or immediately adjacent to those parts (Keeler and Kaul 1984). We have observed a population of *Croton suberosus* HBK (Euphorbiaceae) in which extrafloral nectar is apparently lacking, but the nectariferous flowers are frequently visited by predatory wasps, especially *Polistes instabilis* (Vespidae). Also, damage to the foliage by herbivores is exceptionally low in this plant population. This lead us to ask: 1) if floral nectar attracts predators of potential herbivores, rather than or in addition to attracting pollinators, and 2) if the wasps play some role in defense against herbivores.

### Materials and methods

#### Study site and species

We studied a population of *C. suberosus* in the Chamela Biological Station of the National University of Mexico (U.N.A.M.). The station is located less than two km

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from the Pacific coast in the state of Jalisco, Mexico, at about 19°30' N and 105°03' W, at an elevation of about 100 m. The mean annual precipitation is 748 mm (1977–1984) and the rainy season lasts four months (July–October) (Bullock 1986). The vegetation is tropical deciduous forest, with semideciduous forest along the major seasonal watercourses (Rzedowski 1978, Lott et al. 1987).

The plant of study is a deciduous shrub about 1.5 m high. It is distributed on the lowlands of the states of Jalisco, Michoacán, Guerrero and Oaxaca, on the Pacific coast of Mexico (Martínez 1988). In the study site it usually grows in open (disturbed) areas and occasionally it grows into the edges of the forest. Most of the branches produce several inflorescences during a given reproductive season. The inflorescences are produced during the wet season, thus inflorescences are always present when leaves are also present.

*Croton suberosus* is monoecious, and flowers of both sexes produce nectar and are visited by diverse insects, including hymenopterans (bees and wasps), coleopterans, and lepidopterans and, with less frequency, hemipterans. However, there is evidence that wind plays the most important role in the pollination of this plant (Domínguez and Bullock, in press). Field experiments with mesh bags showed that fruit production did not differ significantly between bagged (visitors excluded) and control plants in which visitors had free access to the flowers (fruit set for bagged plants =  $0.41 \pm 0.26$ , control plants =  $0.49 \pm 0.26$ ; ANOVA  $P > 0.20$ ) (Domínguez 1985). Additionally it was shown, experimentally (by enclosing female flowers), that fruit production is not the result of apomixis (Domínguez 1985).

#### Damage by folivores

Damage by folivores was estimated by sampling 20 individuals, selecting at random five branches from each of 20 shrubs. Five leaves were taken from each branch. The percentage of leaf area removed was evaluated assigning each leaf to one of the following categories: 0, no damage; 1, 1–5% of lamina area removed; 2, 6–12%; 3, 13–25%; 4, 26–50%; 5, 51–100%. An index of damage was calculated for each plant, as  $ID = \sum n_i (i)/N$ , where  $n_i$  is the number of leaves in category  $i$ , and  $N$  is the number of leaves sampled (25).

#### Acceptability tests

The low levels of herbivore damage to leaves of *C. suberosus* in the field might be due to unpalatability to herbivores. This possibility was explored indirectly by means of acceptability tests with two insect herbivores: adults of *Chtaenopodia tamaulipensis* (Orthoptera: Acrididae) and larvae of *Hipercombe* sp. (Lepidoptera: Arctiidae). These two herbivores had been observed eating foliage of *C. suberosus* in the field (R. Martínez, pers. comm.), as well as the foliage of many other plants

of different families at this site (our obs.), so they may be considered generalists.

The animals were starved for five hours before the experiments. Each herbivore ( $n=5$  *Chtaenopodia* and 20 *Hipercombe*) was placed alone next to a leaf of *C. suberosus* of known area, in a plastic box covered with mosquito netting. After 12 h, the remaining leaf area was measured to calculate the percentage consumed. Area measurements were made with a LI-COR 3000 portable area meter.

#### Activity pattern of flower visitors

The diurnal pattern of insect visits was obtained from censuses made every 30 min between 0700 and 1800 hours, during three days, on 16 plants. Each plant was observed at 30 min intervals, counting visitors present and those arriving during a period of one minute. The number of visitors was counted on each plant, with separate tallies for Lepidoptera, Coleoptera, Hemiptera and Hymenoptera. All the visitors were then collected, and later identified to the level of family or lower taxa.

To test the role of flowers in attraction of wasps, an additional 12 plants were censused for five days. On six of these all the inflorescences were experimentally removed. Censuses were made as described above, except that foliage visitors were also included. The attraction and defense argument would be falsified if wasp visits were as frequent to plants without as with flowers, such visits being a routine part of foraging and not attracted by nectar.

#### Nectar production curves

The nectar production curves were derived from sampling all flowers (18 male, 16 female) on five inflorescences that were isolated in veil cloth bags. Nectar was collected with 3  $\mu$ l micropipettes at intervals of two hours from 0700 until 1800 hours when nectar production had ceased.

#### Experimental introduction of herbivores

To test if some insect visitors to *C. suberosus* can afford protection from herbivores, larvae of *Hipercombe* sp. were introduced. The larvae were individually placed on a leaf, and tethered by a cotton thread (approximately 25 cm long) to the petiole. The treatment groups consisted of 1) branches from which the inflorescences had been removed, and 2) branches with intact inflorescences. The treatments were distributed in pairs, on nearby branches of the same plant, such that the difference between treatments could be due only to the presence or absence of the inflorescence. A total of 31 paired repetitions were made, using a total of 16 plants, on 13–14 September 1986. In each case, it was noted if the larva was attacked. Observations were made

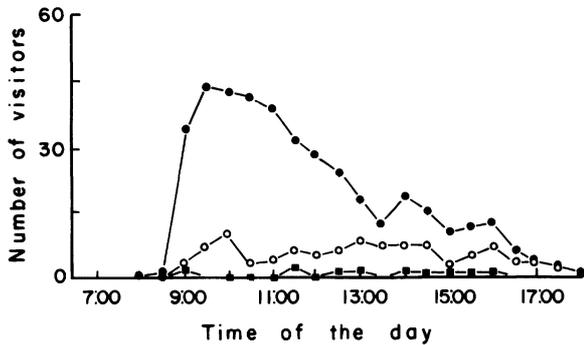


Fig. 1. The diurnal course of insect visitors to the flowers of *Croton suberosus*. The visitors have been grouped into three major guilds: phytophagous insects (●), predators (○) and potential pollinators (■).

throughout the activity period of the visitors (0800–1830 hours).

## Results

### Folivory

The average index of leaf damage among all the individuals sampled was  $0.458 \pm 0.05$  (s.d.). The average index did not exceed 1.5 for any individual (range 0–1.3). According to the established scale, this maximal value corresponds to ca. 5% of leaf area consumed. This value was close to that of 3.4% encountered in a longer-term study of *C. suberosus*, but contrasted with a value of 16% for the sympatric *C. pseudoniveus* (R. Martínez, pers. comm.). Also, the average of 0.458 was significantly less ( $t=27.8$ ,  $P<0.001$ ) than the average obtained in a study of 15 tree species at Chamela (Filip et al. 1989).

### Acceptability

In contrast to the low levels of damage found in the field, a large percentage of the leaf area was consumed in the bioassays. The individual *Chtaenopodia* consumed an average of 70.0% ( $\pm 28.4$ ) and the *Hipercombe* larvae consumed 57.9% ( $\pm 15.2\%$ ) of the leaf area offered.

### Activity patterns

The visitors could be grouped into three guilds: predators, including various genera of wasps (which were also nectarivorous) and an hemipteran; phytophages, with various species of Coleoptera, Hemiptera, and potential pollinators (i.e., insects which indistinctly visited flowers of both sexes), consisting of only one species of bee. The wasps foraged mainly for nectar on the flowers, while the beetles fed on pollen and ate flower parts, particularly of the male flowers (tepals and anthers).

The diurnal course of insect visits to *C. suberosus*

flowers (Fig. 1, see also Appendix) clearly showed that predators and phytophagous insects were the most important visitors. The potential pollinators represented only 2% of the total number of visits. The phytophages were active principally from 0830 to 1300 hours, and had a peak at 0930 hours. The predators as a guild did not show a marked peak but were present in roughly constant numbers all day (0830–1700 hours).

Comparing activity patterns between plants with and without inflorescences (Fig. 2), both wasps and beetles visited shrubs with flowers more frequently. The visitation rate to inflorescences was high from 1030 until 1700 hours for both wasps and beetles, but on plants without inflorescences, the only visitors registered were two wasps and seven beetles.

### Nectar production

Male and female flowers showed similar curves of nectar production (Fig. 3), starting between 0800 and 0830 hours, and later remaining constant until about 1600 hours in male flowers and 1400 hours in females. Nectar production ceased completely before 1800 hours.

Although the maximum rate of nectar production in female flowers was almost twice that in males, the latter were the principal source of attraction because they are, on average, four times more abundant than female flowers (Domínguez and Bullock, in press). The abundance of *Polistes instabilis* was correlated with the nectar production rate ( $r=0.70$ ,  $P<0.05$ ).

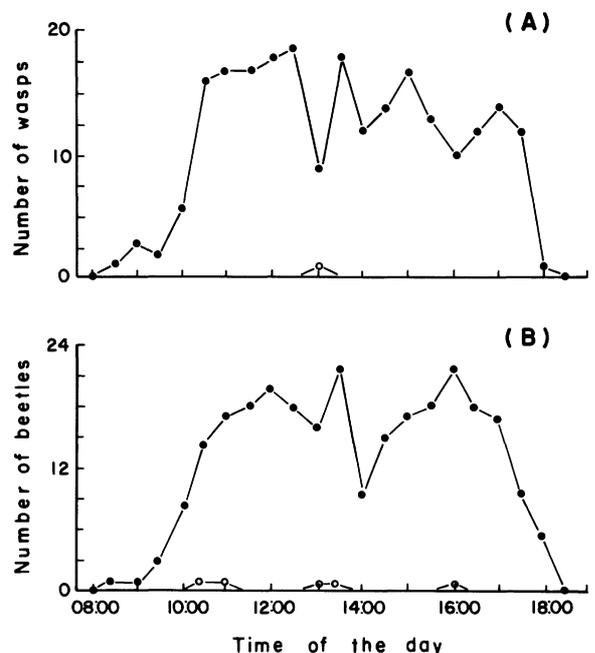


Fig. 2. The activity patterns of wasps (A) and beetles (B) to *Croton suberosus* plants with intact inflorescences (●) and with inflorescences removed (○).

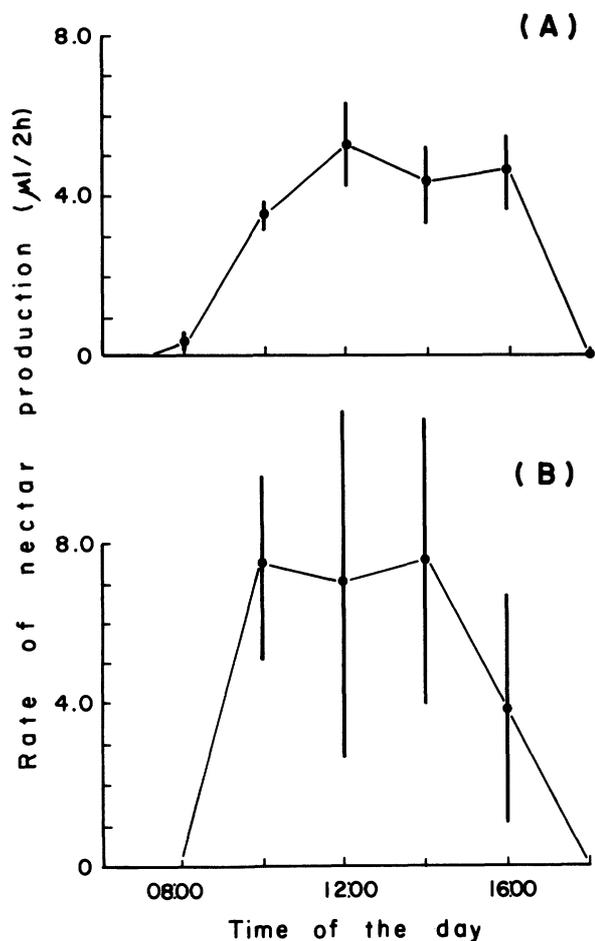


Fig. 3. Nectar production rates for male (A) and female (B) flowers of *Croton suberosus*. The values are means  $\pm$  sd.

#### Experimental addition of folivores

Of all the insect visitors to *C. suberosus*, only *Polistes instabilis* actively attacked the introduced folivores. Larvae associated with inflorescences were attacked significantly more often than larvae on deflowered branches ( $\chi^2=5.23$ ,  $0.025 > P > 0.01$ ) (Tab. 1). It is important to note that in all cases the larvae were attacked *after* the wasps had taken the floral nectar. Wasps were observed to fly toward the larvae (presumably after these were located from a given distance); larvae were then killed and partly eaten in situ. The remainders of a killed larva were macerated and prepared as a ball of dead tissue which was then transported to the wasp's nest.

#### Discussion

Several lines of evidence suggest that nectar production in the flowers of *C. suberosus* is not essential to pollination. Field experiments with mesh enclosure bags showed that fruit production did not differ significantly

from control plants in which insects had free access to the flowers (Domínguez and Bullock, in press). The flowers present several features associated with (though not exclusive to) anemophily. The tepals are green and unexpanded. The female flowers present branched, long styles, are located below the male flowers, and are few in number compared with the males. Also, the stamens are highly exerted on male flowers. Furthermore, nectar is an unpredictable resource for visitors, because production by female flowers is extremely variable (Fig. 3). There is no particular morphological fit between anthers, stigmas and visitors. Beetles are common visitors but their activity is largely destructive to the flowers and to pollen, and their apparent mobility is low. Likewise, most flower visitors concentrate their activities on male flowers; the infrequent visits to female flowers are done generally by destructive insects.

We observed eight species of wasps foraging for nectar on *C. suberosus*, but only *Polistes instabilis* also defended the plant from the experimentally introduced *Hipercombe* sp. larvae. Several of the other wasp visitors are presumably habitual predators of caterpillars of *Hipercombe* or of other species. Hesperheide (1985) suggested that defense by parasitic wasps rather than by ants occurs in *Byttneria aculeata*. Like *C. suberosus*, *B. aculeata* produces only nectar for visitors, while many myrmecophilous plants produce more varied (and costly) rewards. We suppose that predatory insects are more advantageous to the plant than parasitic insects since the latter leave the folivores active for some time. Wasps in general might have disadvantages as "bodyguards" compared with ants in being less numerous and less sedentary. However, predatory wasps may perceive prey from much greater distances and can remove larger prey than ants or parasitic wasps.

Other insects that might provide protection to *C. suberosus* are the predatory hemipterans (Reduviidae).

*Polistes instabilis* regularly visits *C. suberosus* to take nectar, principally from male flowers. The correlation between nectar production and number of wasps, as well as the absence of wasps when inflorescences were removed, suggest that *Polistes instabilis* is attracted to the plant by the inflorescences in search of floral nectar. The same response was found in beetles, but their feeding was destructive. Pollen is a prime object of beetle

Tab. 1. Results of the experiments of introduction of *Hipercombe* sp. larvae on leaves of *Croton suberosus*. (For results of the statistical analysis see text)

	Number of larvae	
	attacked	not attacked
Inflorescence present	20	11
Inflorescence removed	10	21

foraging (Crowson 1981), but the plant cannot cease producing pollen. On the other hand, for a wind-pollinated plant the production of floral nectar represents an energetic cost without apparent advantage and should be eliminated by natural selection. In fact, anemophilous species typically do not produce floral nectar (Whitehead 1973). An interesting interspecific comparison is that at Chamela *C. pseudoniveus*, a species pollinated by wind, does not have floral nectar (C. A. Domínguez, pers. obs.).

Although several Euphorbiaceae bear extrafloral nectaries attractive to animals (e.g. those of *Omphalea* spp. visited by ants (R. Dirzo, pers. obs.) and the wasp-visited extrafloral nectaries of the congeneric species *C. billbergianus* (Hespenheide 1979)), *C. suberosus* does not present them.

The reason why the production of floral nectar is maintained in *C. suberosus* may be its role in the attraction of insect predators, but alternative explanations exist: 1) the cost of nectar production may be of such a nature or magnitude that it does not affect fitness; 2) floral nectar may be only an anachronistic character that has not yet been eliminated as a relict of a previous adaptive system (see Janzen and Martin 1982); 3) floral nectar may be a reward for insects with a role, as pollinators, secondary or complementary to anemophily with respect to quantity of pollinations, but particularly important for xenogamy and for the maximum distance of pollen movement.

The consumption of foliage of *C. suberosus* in experimental conditions suggests that unpalatability is not the reason why plants are not damaged in the field. In comparable studies of acceptability with generalist orthopterans, it is rare to obtain such high consumption values, except for highly acceptable plants such as lettuce (*Lactuca sativa*) (Jiménez 1988). The two insect species used in our study are generalist folivores, so it is unlikely that they have any specialized detoxification mechanisms (Strong et al. 1984). Longer-term experiments on herbivory could give more definitive evidence, and it would be interesting to compare damage between robust adults, shaded adults and juvenile plants, since these groups of plants show marked differences in inflorescence production.

On the basis of the available data, the interaction between *Polistes instabilis* and *Croton suberosus* can hardly be interpreted as a result of coevolution (see Janzen 1980, Dirzo 1983). Moreover, Keeler (1981) argues that similar sorts of protection involving extrafloral nectaries should be mostly facultative rather than coevolved. A plausible explanation is that of opportunistic mutualism, whereby nectar production that served other functions in the past, now serves as a reward for animals that secondarily provide defense. This does not deny that floral nectar might still maintain a role in attracting pollinators, although our data suggest that if this is so, it certainly must occur at a very minor level. Even in animal-pollinated plants, the at-

traction of wasps to floral nectar is very common (e.g. Heithaus 1979) and may often result in increased foraging for prey on those plants.

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#### Appendix. Insect visitors to the flowers of *Croton suberosus*

Visitors	Resource sought	
Hymenoptera		
Wasps		
	<i>Ammophila</i> sp.	nectar and pollen
	<i>Eumenes</i> sp.	nectar and pollen
	Eumenidae 1	nectar and pollen
	Eumenidae 2	nectar and pollen
	<i>Montezumia mexicana</i>	nectar and pollen
	<i>Pachymenes</i> sp.	nectar and pollen
	<i>Polistes instabilis</i>	nectar and pollen
	<i>Polistes major</i>	nectar and pollen
Bees	<i>Heriades</i> sp.	nectar and pollen
Ants	<i>Zacryptocerus</i> sp.	nectar and pollen
Coleoptera		
	Cantharidae	pollen
	Cerambycidae	pollen
	<i>Stenobatyle eburata</i>	pollen
	<i>Stenophenos rubidus</i>	pollen
Hemiptera		
	Coreidae	sap
	Reduviidae	prey
	Scutelleridae	sap
Lepidoptera		
	<i>Euptoieta hegesia hoffmanni</i>	nectar
	Lycaenidae	nectar

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