

Factors affecting ant (Formicidae: Hymenoptera) visits to the extrafloral nectaries of *Croton bonplandianum* Baill

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Abstract. *Croton bonplandianum* invites a set of ant species to its extrafloral nectaries. The composition and frequency of these nectariferous ants on the plant were distinctly different from those on the ground. We have investigated the factors that govern visitation pattern of the ant species to the plant.

The available pattern of nectar, and the age-related increase in the nectar content influence the ant visitation. Availability of nectar in small dispersed units specifically encourages the visits of individual foragers and discourages the group foragers. Increase in the nectar content of the plant with aging, favours the host occupation by the nomadic ants, *Tapinoma melanocephalum* F. A few species such as *Pheidole woodmasoni* Forel could not harvest the nectar in the plant due to their inability to climb. Differences in the habitat preferences of ants affect their composition on the host plants.

Keywords. *Croton bonplandianum*; ant-plant mutualism; seed dispersal; nectar presentation.

1. Introduction

Flowering plants display mutualistic relations with ants for various advantages like protection against pests (Janzen 1966; Bentley 1977a; Schemske 1980) and dispersal of seeds (O'Dowd and Hay 1980; Ganeshaiyah and Umashanker 1988). For this purpose, plants attract ants by offering them shelter, protein bodies (Janzen 1966) and nectar (Bentley 1976, 1977a, b). However, the attraction of ants by plants may not be restricted to a few species (Schemske 1982); for instance, all the nectariferous ants may visit extrafloral nectaries. Such random or undirected visits may not be profitable to the plant, especially if the ant species differ in their ability to reciprocate rewards. Hence selection might favour the development of special plant features that regulate the ant species visiting the plant in order to maximise their benefits; besides, certain specific behavioural traits of ants may also contribute to such a specificity.

In this paper, we investigate these aspects in a mutualistic system between *Croton bonplandianum* Baill (hereafter *Croton*) and a set of nectariferous ants, where a weak mutualism exists for the dispersal of seeds (Ganeshaiyah and Umashanker 1988). More specifically, we attempt to answer two questions:

- (i) In a weak mutualistic association like the *Croton*—ant system, is there any specificity in the ant visits to the plant?
- (ii) What features of the host and the ants contribute to such a non-random ant visits? We, however, have not attempted to test the adaptive significance of the plant to such specificity in ant visitation.

2. System

Croton is a monoecious annual herb and bears extrafloral nectaries on the stalks of developing fruits. The plant produces fruits in different successions called stages, each stage lasting for about 20 days (Umashanker and Ganeshaiah 1984). The number of nectaries per plant increases with each stage because of increase in both number of fruits per inflorescence and number of inflorescences per plant (table 1). The growth of the plant almost ceases after IV or V stage by when the plant bears about 110 inflorescences. Since the total number of nectaries in each plant would be constant after IV stage, only IV and V stage plants were used except when specified. Croton attracts a set of nectariferous ants which aid in seed dispersal (Ganeshaiah and Umashanker 1988).

3. Materials and methods

The study was conducted in a 10 acre plot along the ravines adjoining the UAS campus (Hebbal, Bangalore). Croton has established itself here in huge colonies atleast for the past 7–8 years (Umashanker and Ganeshaiah 1984). Based on the distribution of plants, the study area was divided into dense (5–10 plants/m²) and sparse (less than 1 plant/m²) zones. A preliminary census in the study area indicated that ant activity was high between 0800 and 1000 h, and 1600 and 1800 h. Hence observations were recorded during these hours of the day for 3 months avoiding cloudy and rainy days.

3.1 *Ant census*

Five plants of IV and V stages were randomly selected in each zone during each visit to experiment-plot; the species and the number of ants on each of these plants were recorded. The census of nectariferous ants was done by counting the number of ants attracted to cotton swabs soaked with 0.5 ml sugar solution (20% sucrose + 1% glycerine) displayed randomly on the ground 2–3 m away from the croton plants for 20–30 min. Another set of 30 plants of all the 5 stages were randomly selected and their ant composition and nests, if any, under these plants were also recorded.

3.2 *Effect of splitting the nectar quantity*

The nectaries in Croton are sparsely distributed. To test if this split pattern of nectar availability in the plant differentially attracts group and individual foragers, cotton swabs soaked with 0.5 ml of sucrose solution were displayed either entirely as a single unit or in 10 split units at a distance of 1 m around the nests of two ant species, viz. *Monomorium indicum* (individual forager) and *Pheidole woodmasoni* (group forager). Five nests of each species were chosen and each was provided with one of the two patterns of nectar availability at a time, in a random sequence. The experiment was repeated for 10 days assigning the two treatments randomly to the nests everyday. The number of ants visiting each unit of cotton swab in 15 min was recorded.

Table 1. Age, height, number of inflorescences and nectaries per inflorescence of different stages of *C. bonplandianum*.

Stage	Age (days)	Plant height (cm)	Inflorescence		Nectaries per inflorescence
			Mean	Range	
I	20-25	16.4 ± 0.8	1.00	—	2.3 ± 0.06
II	35-40	25.5 ± 0.8	3.52	3-6	4.0 ± 0.11
III	50-60	33.7 ± 0.2	15.32	10-22	6.4 ± 0.18
IV	65-75	38.6 ± 0.6	52.20	40-85	7.5 ± 0.36
V	75 and above	44.3 ± 2.9	113.00	90-260	8.5 ± 0.32

3.3 Effect of elevation of nectar

Nectar in the plant is available at a height of 16-45 cm above the ground. To test, the effect of such elevated nectar presentation, cotton swabs saturated with 0.5 ml of sucrose solution were displayed at the tip of a 30 cm twig inclined in angles of 0°, 30°, 60° and 90° against the ground level at a distance of 1 m from the nest. The number of ants visiting the cotton swabs in 15 min were recorded.

3.4 Statistical analysis

The data on ants per plant and frequency of plants with ants were analysed for regularity, commonness or abundance of ants following the Poisson technique suggested by Williams (1964). The ant diversity was compared by using Shannon-Weaver index.

4. Results

4.1 Ant composition and their differential visits

The diversity of ants in the dense zone was higher than that of the sparse zone, and the composition of ant species also differed between dense and sparse zones (table 2). There were no qualitative differences between the composition of the species of ants on the ground and that on the plant; almost all the ant species recovered on the ground were also recovered from the plant, except *Pheidole woodmasoni* which was never recovered from the plants in the sparse zones, though, they were found abundantly on the ground (table 2).

If ant visitation to the plant is directed merely by the presence of nectar, then all the ants recovered from the ground should be represented in corresponding frequencies on the plant also. However, the frequencies of ants on the plants differed from those on the ground in both the zones (figure 1). Figure 2 shows the ratios of percentage of each ant species on the plant and on the ground. These ratios reflect the number of ants of a species found on plant for every ant of the same species found on the ground. Accordingly all the species showing a ratio of more than one can be considered as attracted by the plant and those showing less than one as distracted. Figure 2A shows that 5 species of ants exhibited a ratio of more than 1.5

Table 2. Species of ants found and their diversity on the plant and ground of sparse and dense zones.

Name	Abbreviations used	Dense zone		Sparse zone	
		Plant	Ground	Plant	Ground
<i>Meranoplus bicolor</i> * (Guerin)	MB	+	+	+	+
<i>Polyrhachis exercita</i> (Walker)	POL	+	+	-	-
<i>Camponotus sericeus</i> (Fabricius)	CS	+	+	+	+
<i>Tapinoma melanocephalum</i> * (Fabricius)	TAP	+	+	+	+
<i>Crematogaster</i> sp.	CRMT	+	+	+	+
<i>Solenopsis geminata</i> (Fabricius)	SOL	+	+	+	-
<i>Camponotus compressus</i> (Fabricius)	CC	+	+	+	+
<i>Camponotus rufoglaucus</i> (Jerdon)	CR	+	+	-	-
<i>Pheidole woodmasoni</i> * Forel	PHI	+	+	-	+
<i>Monomorium indicum</i> * Forel	MI	-	-	+	+
Diversity index		0.7449	0.6998	0.3127	0.5052

*These ants carry seeds.

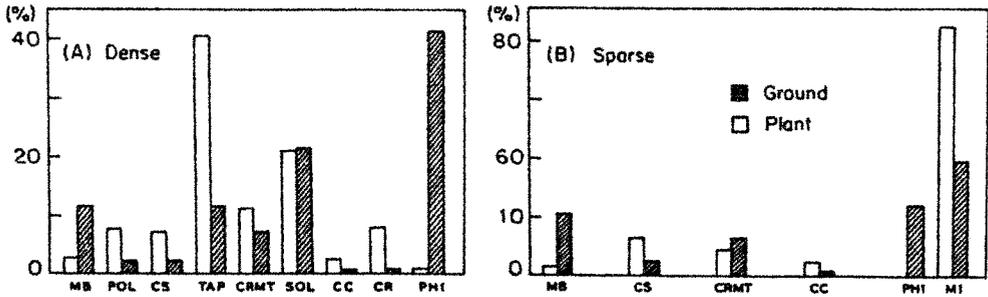


Figure 1. Frequency of different species of ants found on ground and plant in (A) dense and (B) sparse zones (letters of alphabet refer to species, vide table 2).

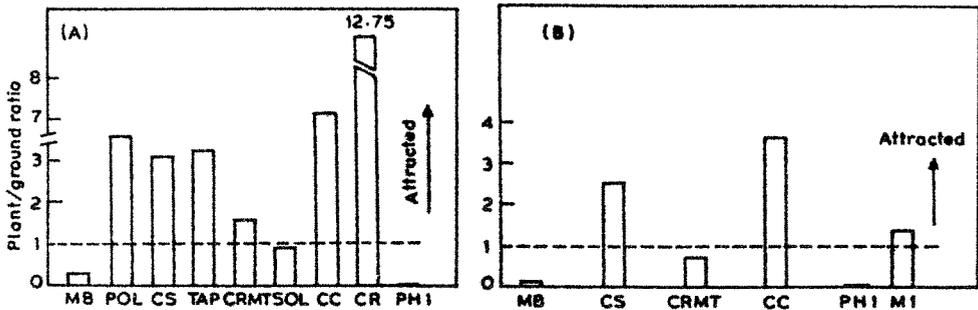


Figure 2. Ratio of frequency of ants on plant to that on ground of different species of ants in (A) dense and (B) sparse zones (letters of alphabet refer to species, vide table 2).

and two species less than 0.5 in dense zone. Similar differences were also observed in sparse zone. *Camponotus sericeus* and *C. compressus* have shown increased attraction to the plants in both the zones, while *Meranoplus bicolor* and

P. woodmasoni exhibited decreased attraction to the plant. These results indicate that the ant species differ in their visitation to the plant, or the plant exhibits differential attraction of the ant species.

Figure 3A provides a relative classification of ant species as regular or irregular and abundant or rarely available on plants. The ants differed considerably in these features. For instance, *Tapinoma melanocephalum* occurred irregularly, but in abundant numbers in the dense zones while *Camponotus sericeus* was common and regular. In sparse zone *M. indicum* occurred regularly and abundantly while *P. woodmasoni* was rare (figure 3B).

4.2 Plant factors influencing ant visits

Table 3 summarises the foregoing results for 4 selected ant species. Some species are attracted by the plant, while some are distracted. They also differed in their visit patterns. These differences can either be due to the plant features and/or due to the innate behavioural features of the ants. We tested the involvement of these factors using a few representative ant species (table 3). Though, it would be difficult to list all the plant features that affect the ant visit, we tested the involvement of (i) pattern of nectar availability on the plant, and (ii) the age of the plant in relation to the nectar quantity.

4.2a Availability of nectar: The individual and group foragers differ in their response to the resource quality of the foraging area (Davidson 1977). Utilising the

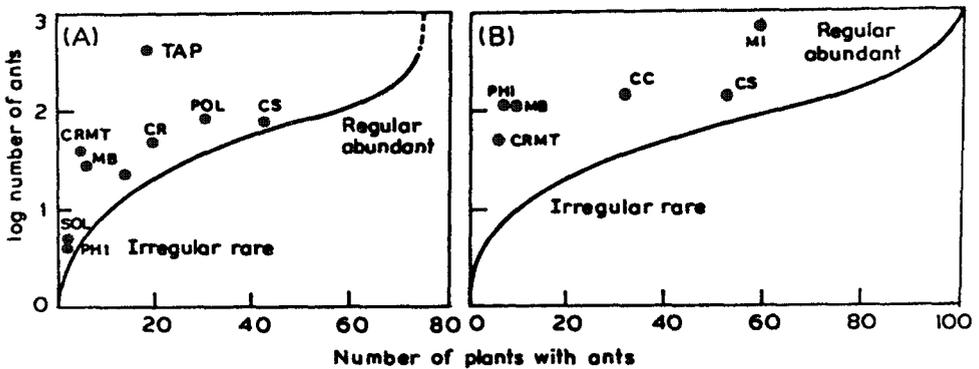


Figure 3. Classification of ant species as rare or abundant, and regular or irregular in (A) dense and (B) sparse zones (letters of alphabets refer to species, vide table 2).

Table 3. Consistency of visits and abundance of 4 selected species of ants on *C. bonplandianum*.

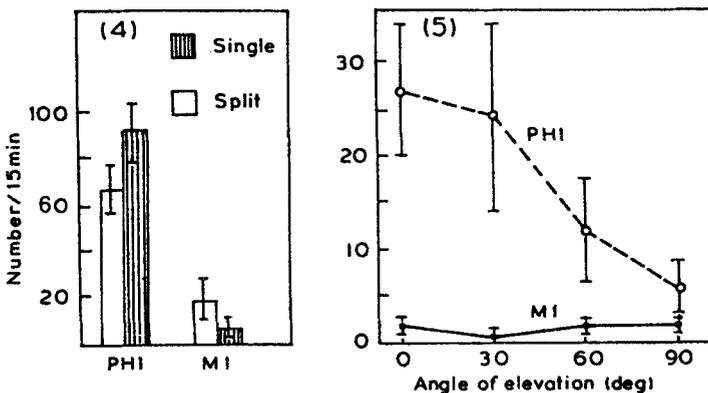
Species	Area	Visitation features		
		Consistency	Abundance	Attraction
<i>Tapinoma melanocephalum</i>	Dense	Irregular	Abundant	Attracted
<i>Monomorium indicum</i>	Sparse	Regular	Abundant	Feebly attracted
<i>Camponotus sericeus</i>	Dense and sparse	Regular	Common	Attracted
<i>Pheidole woodmasoni</i>	Dense and sparse	Irregular	Rare	Distracted

feed back information of the scouts, group foragers tend to visit the resource spots which pay high dividends to the cost expended in harvesting. Hence, they can be expected to preferentially harvest the rich resource spots. The nectar in *Croton* is presented at 15–45 cm above the ground in split units of 5–1000 small nectaries at the bases of fruits. Each nectary produces 12–40 μg of glucose/h. We hypothesized that such a split pattern of nectar availability might cause differential attraction of group and individual foragers. Figure 4 shows that the total number of *P. woodmasoni* decreased considerably from 92 (in a single unit nectar presentation) to 63 (when the same quantity of nectar was in split units). On the other hand, *M. indicum* showed increased visits from 4.5 in a single unit presentation to 18.63 when presented in split units. Thus the split availability of nectar elicits differential response among the ants.

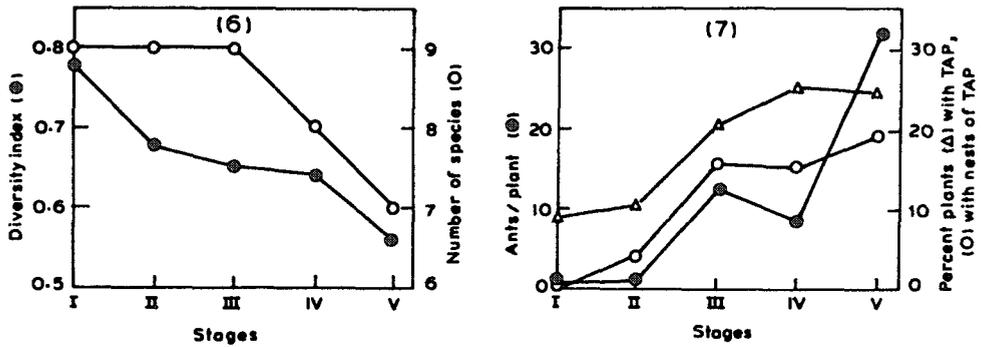
Figure 5 shows the differential ability of the ants to harvest the nectar at varied slopes. *M. indicum* did not differ in harvesting the nectar when available at different levels of inclination, while *P. woodmasoni* preferred to harvest the nectar available at lower inclinations and avoided the nectar with steep inclinations. The dispersed pattern of nectar availability in small units on the vertically oriented racemes of *Croton*, selectively eliminated *P. woodmasoni* from harvesting it, while *M. indicum* remained unaffected.

4.2b *Age of the plant and nectar quality*: Diversity index of ants decreased from 0.7769 in the first stage to 0.5647 in the last stage (figure 6). These differences can be explained by the behavioural features associated with the ants and changes in nectar quantity with the stage.

Since the height of the plant increases with age *P. woodmasoni* which tends to avoid harvesting the nectar from steep slopes reduced its visits to the aged plants. On the contrary, the percentage of plants from which *T. melanocephalum* was recovered increased with the stage of the plant (figure 7). Besides, the percentage of the plants under which *T. melanocephalum* nests were recovered also increased with the plant stage. Along with this, there was also an increase in the number of *T. melanocephalum*. Being a nomadic ant, *T. melanocephalum*, shifts its nests very frequently to the sites where resource supply is stable (Ali 1981).



Figures 4 and 5. 4. Effect of split and single unit presentation of nectar on *Pheidole* (PHI) and *Monomorium* (MI). 5. Effect of elevation of nectar sources at different gradients on *Pheidole* (PHI) and *Monomorium* (MI).



Figures 6 and 7. 6. Shannon-Weaver diversity index and number of ant species recovered on plants of different growth stages. 7. Frequency of *Tapinoma* (TAP) on plants of different stages of growth and percentage of plants occupied by its colonies.

As the plant ages, the number of nectaries increases (table 1). Simultaneously, because of asynchrony in fruit set between the stages, the nectaries of the different stages overlap in their function, thus providing a continuous nectar supply. The aged plants, thus, constitute the most guaranteed sites of nectar supply encouraging *T. melanocephalum* to occupy them. These ants restrict their foraging area to the foliage of the plant under which they nest. Hence they were recovered only from a small proportion (0.25) of the plants in abundant numbers as the whole colony feeds on the same plant. This explains their abundant, though irregular visit pattern.

5. Discussion

The results indicate that *C. bonplandianum* exhibits differential attraction of ant species. This could be explained by the differences in the behavioural responses of ants to patterns of availability and amount of nectar in a plant. Involvement of the plant characters in regulating ant visits to higher plants is well known (Heads and Lawton 1984; Lawton and Heads 1984; Schemske 1982). For example, the height of inflorescence in *Costus* sp. determines the relative composition of arboreal and terrestrial ant species (Schemske 1982). The tendency of *M. indicum* to be arboreal than *P. woodmasoni* was found to affect their composition on *Croton* plants.

Since *C. bonplandianum* offers nectar in split units, visits of individual foragers were favoured against group foragers. Such differential response of group and individual foragers of ants to varied food densities has been reported by Davidson (1977). A comparison of composition of individual, intermediate, and group foragers on the ground with that on the plant indicated that plant attracted a greater proportion of individual foragers compared to group foragers (table 4). Such preferential attraction of individual foragers could be beneficial to the plant in dispersing the seeds because these ants are more likely to encounter the seeds on ground due to their tendency to move randomly (Davidson 1977). Ganeshaiyah and Umashanker (1988) have observed that individual foragers like *M. indicum* are involved in greater seed dispersal than group foragers. However, they did not test for any correspondence between the frequency of an ant species on plant with its seed

Table 4. Frequency of ants of different types of foraging on *C. bonplandianum* and ground.

Type of foraging	Ground (%)	Plant (%)
Individual	5.27	24.72
Intermediate	11.51	2.48
Group	83.20	62.85

dispersing ability; some ants like *Camponotus* spp. which do not disperse seeds were more regular than seed dispersing ants like *P. woodmasoni*. In other words, the ant-Croton relationship for seed dispersal seems to be a weak mutualism (Koptur 1984). This is evident from that the major seed dispersing ants like *M. indicum* are zone specific and are not always associated with Croton. The habitat differences in ant composition on plants as observed in the present study appears to be a common feature for all facultative ant-plant mutualistic relations (Bentley 1976).

In conclusion, the ant assemblage on *C. bonplandianum* appears to be affected by (i) the habitat and plant density, (ii) stage of the plant and the consequent increase in amount of nectar, and (iii) the pattern of nectar availability, though we cannot negotiate any stronger evidence, towards the evolution of specialised traits in this relationship.

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