

14 Ant-Plant Interactions: Their Seasonal Variation and Effects on Plant Fitness

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14.1 Importance of Interspecific Interactions

Interactions between species have the potential to influence many evolutionary processes including patterns of adaptation, genetic variation, community organization, and the stability of species (Bondini and Giavelli 1989; Rico-Gray 2001). Similar to species, interspecific interactions can evolve and multiply, forming links between species that affect their evolutionary trajectories through time (Thompson 1999). Organisms in nature are not isolated, and to survive and reproduce, have adapted combinations of their own genetic information and that of other species in the process of coevolution (Thompson 1999). Furthermore, the effect of interspecific interactions may encompass more than two species, e.g., via top-down and bottom-up forces in a community (Dyer and Letourneau 1999).

Interspecific interactions change in space and time and are based on cost/benefit systems, so a continuum from antagonism to mutualism should be expected (Thompson 1994; Bronstein 2001). A species may be antagonistic in one stage of its life cycle while mutualistic in another; whereas a population or species may be antagonistic in one portion of its distribution or habitat while another population of the same species may be mutualistic in another portion of its distribution (Puterbaugh 1998). Interspecific interactions can be defined on the basis of whether the net effect or outcome of the interaction is an increase or decrease in fitness, or no effect (neutral) for each interacting species; thus, basically two types of interactions can be considered: antagonistic and mutualistic (Rico-Gray 2001).

This chapter discusses the importance of nectar to ants, the effect of ants on plant fitness (either mediated by nectaries or Homoptera), plus seasonal variation and diversity of interactions in the tropical coastal regions of the Yucatan Peninsula and Veracruz, Mexico. Tropical coastal dunes are rich envi-

ronments for ant-plant interactions, yet diversity of interactions, seasonality and the effect of ants on plant fitness have rarely been studied.

14.2 Richness and Seasonal Variation of Ant-Plant Interactions

Interactions of species vary spatially and seasonally, and should be analyzed using a landscape approach (Bronstein 1995; Ortiz-Pulido and Rico-Gray 2000). Ant-plant interactions vary in their probability of occurrence along environmental gradients and under different disturbance regimes (Koptur 1992; Rico-Gray et al. 1998). The pattern of interactions in different ecological conditions (Cushman and Addicott 1991) and between habitats (Barton 1986), also exhibits significant temporal variation (Alonso 1998). The structure of ant communities and of ant-plant interactions has been studied in a variety of habitats, assessing that neither the spatial nor the temporal dimensions can be ignored (Herbers 1989). Ant assemblages are very dynamic and extrapolating superficially similar characteristics from one ant community to another may lead to erroneous inferences, precluding broad generalizations (Herbers 1989; Feener and Schupp 1998).

Ant-plant associations in tropical sand dunes are abundant (e.g., over 350 specific associations have been recorded in the coastal vegetation of central Veracruz, Mexico (Rico-Gray 1993; C. Díaz-Castelazo and V. Rico-Gray, unpubl. data) relative to temperate semiarid or humid mountain sites (Rico-Gray et al. 1998)). Studies at two coastal sites in Mexico [La Mancha in Veracruz (Rico-Gray 1993; Rico-Gray and Castro 1996; Rico-Gray et al. 1998;

Table 14.1. Results from the generalized linear models fitted to the number of ant-plant interactions, minimum temperature and precipitation per month data curves. (Modified from Rico-Gray et al. 1998)

Source	χ^2		df ^a	Explanation of variation (%)		Probability	
	LM ^b	SB		LM	SB	LM	SB
Temperature	9.713	12.33	1	32.38	17.98	<0.005	<0.001
Precipitation	0.0034	2.605	1	-	0	NS	NS
Interaction	13.91	0.328	1	46.38	0	<0.001	NS
Residual	6.3678	53.31	8				
Total	29.991	68.57	11	78.76	17.98		

^a Degrees of freedom

^b LM, La Mancha, Veracruz (sand dune scrub, tropical dry and deciduous forests, mangroves); SB, San Benito, Yucatan (sand dune scrub, mangroves)

Oliveira et al. 1999), and San Benito in Yucatan (Rico-Gray 1989; Rico-Gray and Thien 1989a, b; Rico-Gray et al. 1989, 1998)] have shown significant within-habitat seasonal variation, as well as considerable variation among habitats in the number, diversity, and seasonal distribution of ant-plant interactions. The observations suggest that inter-habitat variation of ant-plant interactions is the effect of variation in environmental parameters (Table 14.1), e.g., the richness of plants with nectaries in the vegetation (C. Díaz-Castelazo and V. Rico-Gray, unpubl. data) and the richness in habitat heterogeneity. Thus, the diversity of the vegetation determines the nature of the ant community to a certain extent, and the diversity of the vegetation is driven by the abiotic environment (Rico-Gray et al. 1998).

Seasonal variation of ant-plant interactions is illustrated using research conducted at La Mancha, Veracruz, Mexico (Fig. 14.1). The number of ant associations with extrafloral nectaries (efns) and nectaries located in the reproductive structures (floral or circum-floral) of plants exhibited seasonal changes throughout the year (Rico-Gray 1993; Rico-Gray et al. 1998; Oliveira et al. 1999). Ant/efn associations increased significantly during the wet season (Spearman, $r=0.58$, $P<0.001$), and were constant throughout the year in comparison with other plant resources. Most plant species in tropical dry forests produce a flush of new leaves at the onset of the rainy season (Bullock and

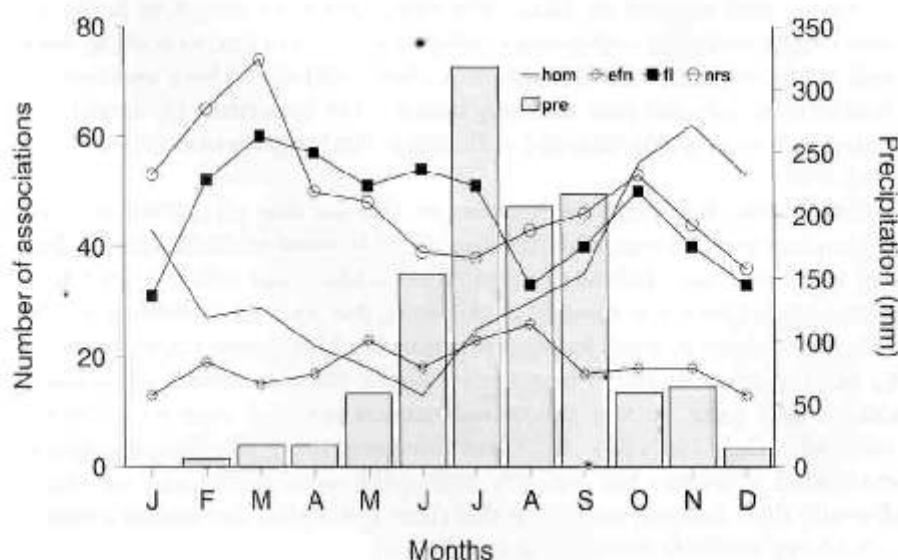


Fig. 14.1. Number of ant-plant associations registered per month per food resource for the tropical the coastal vegetation at La Mancha, Veracruz, Mexico. *hom* Homopteran honeydew; *efn* nectar from extrafloral nectaries; *fl* floral nectar; *nrs* nectar from reproductive structures; *pre* monthly precipitation. (Modified from Rico-Gray 1993)

Solís-Magallanes 1990). Extrafloral nectaries are associated with leaves and many studies have shown that secretion of extrafloral nectar is greatest during periods of rapid vegetative growth, e.g., the expansion of new leaves. Ant presence is highly correlated with peaks of nectar flow, and an increase of ant/efn associations would therefore be expected as new leaves appear. Ant associations with reproductive structures (Spearman, $r=-0.59$, $P<0.001$) and flowers (Spearman, $r=-0.76$, $P<0.001$) peaked during the dry season, and decreased during the wet season.

There are two main flowering peaks in the dry tropical lowlands of Middle America, one in mid-dry season and one at the start or during the wet season (Bullock and Solís-Magallanes 1990; Castillo and Carabias 1982). These major periods of flowering are supplemented by erratic flowering of many species year-around, presenting ants with year-round sources of liquids and energy. Ant associations with honeydew-producing Homoptera increased significantly after the start of the rainy season (Spearman, $r=0.70$, $P<0.001$) and decreased abruptly once the dry season began. During the warm-humid months plants produce new soft vegetative tissues, creating ideal feeding conditions for Homoptera (Cuautele et al. 1999). Interestingly, there was a significant negative association (Spearman, $r=-0.66$, $P<0.001$) between the number of ant visits to flowers and to Homoptera. Ant/Homoptera associations decrease sharply during the dry season, while ant-flower associations peak at this time. This complementary pattern may reflect the use of alternative resources with similar nutritional value, as 62.5% of the ant species using floral nectar also foraged for honeydew. Ants have been shown to prefer and select sugar solutions containing a complex mixture of amino acids to sugar-only solutions (Lanza 1988; Smith et al. 1990; Völkl et al. 1999), and they also discriminate between poor and rich homopteran honeydew, preferring honeydew rich in trisaccharides and with higher total sugar concentration (Völkl et al. 1999).

Finally, the simultaneous increase in the number of ant/efn and ant/Homoptera associations, and the decrease in the number of ant/circum-floral and ant/flower associations during the wet season, may reflect a decrease in nectar production. It is more likely, however, that ants are switching to alternative food sources (efns, honeydew-producing Homoptera). Ants could also be feeding on a variety of insect prey during the wet season, when insects exhibit their peak activity in lowland tropical seasonal vegetation (Smythe 1982; Rico-Gray 1989; Rico-Gray and Sternberg 1991). In summary, because more food resources are available during the wet season, ants are able to diversify their foraging activity at that time. During the dry season ants concentrate on available limited resources.

14.3 Importance of Nectar to Ants in Tropical Seasonal Environments

Ants frequently visit flowers (Fig. 14.2) and other reproductive parts (e.g., buds, inflorescence spikes, fruits) (Fig. 14.3) of plants in a variety of environments (Rico-Gray and Thien 1989a; Puterbaugh 1998), especially in the lowland dry tropics. Ants are typically considered to be robbers of floral nectar that decrease plant fitness (e.g., McDade and Kinsman 1980; Norment 1988). Some evolutionary trends in floral morphology associated with a decrease in the range of effective pollinators, have also been thought to increase plant adaptedness by excluding non-pollinating nectarivores, such as ants (e.g., Herrera et al. 1984). Nevertheless, a high number (up to 40%) of plant species in tropical coastal habitats possess flowers visited by ants foraging for nectar (Rico-Gray 1980, 1989, 1993; García-Franco and Rico-Gray 1997; Rico-Gray et

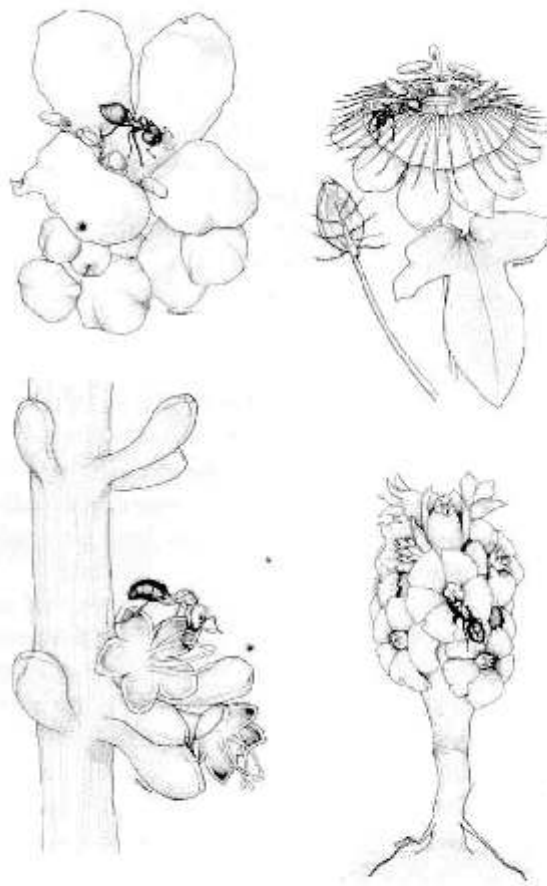


Fig. 14.2. Ants foraging for floral nectar, clockwise from top left: *Crematogaster brevispinosa* and *Avicennia germinans*, *Camponotus* sp. and *Passiflora foetida*, *Camponotus sereiceiventris* and *Bdallophyton bambusorum*, and *Camponotus planatus* and *Coccoloba uvifera*.



Fig. 14.3. Examples of ants foraging for circum-floral nectar, clockwise from top. *Pseudomyrmex* sp. foraging on the calyx and petals of *Iresine celosia*, *Pseudomyrmex* sp. foraging on the calyx and floral peduncle of *Canavalia rosea*, and *Ectatomma tuberculatum* foraging on the fruit of *Myrmecophyla christinae*

al. 1998; Oliveira et al. 1999), which suggests ants play an important role in nectar consumption in these coastal habitats. If ants were merely robbing nectar, there should be a considerable decrease in fitness of many individual plants. Alternatively, a yet undiscovered mutualistic interaction may be occurring, besides possible pollination. Here we analyze the importance of nectar to ants in tropical coastal seasonal habitats.

Plants are defended against herbivory in many ways, e.g., by covering themselves with tough, spiny or inedible surfaces, sclerophylly, suffusing their tissues with chemical deterrents, toxins or digestibility-reducing compounds or by employing the services of animals like ants to ward off herbivores (Koptur 1991, 1992). There is a strong relationship between some of these characteristics and low plant nitrogen concentrations (Mattson 1980). Moreover, nitrogen deficiencies are usually accompanied by increased tissue toughness, reducing the digestibility of the plant material by increasing indigestible bulk and hydrogen bonding with carbohydrates and proteins (Chauvin and

Gueguen 1978; Mattson 1980; Coley 1983). Several of these attributes are common in plants living in dry environments and function as adaptations to cope with low moisture (Mattson 1980), making plants less palatable to herbivores, and reducing food sources during the dry season (Smythe 1982) resulting in few food alternatives for insects that prey on herbivores. Plant organs with high turnover rates (flowers, fruits, seeds) invariably contain higher nitrogen concentrations than more quiescent tissues (Mattson 1980; Koptur 1984). Thus, plant reproductive structures and associated nectar may be the most 'attractive' plant parts available as food during the dry season. When the wet season begins, the increasing moisture triggers prolific new vegetative growth that is both nitrogen-rich and succulent; consequently, there is an abundance of herbivores and other insects that prey on them, and diets may change with the availability of new food resources (Mattson 1980; Smythe 1982; Rico-Gray and Sternberg 1991).

Many plant species in the tropical dry seasonal vegetation along the Gulf of México (central portion of the state of Veracruz) and the Caribbean (Yucatan Peninsula) flower during the dry season. Flowering is not simultaneous, but there is always at least one species in flower from December through June (Rico-Gray 1989, 1993; Rico-Gray et al. 1998). Throughout the dry season ants forage for the nectar produced on the buds, flowers, and fruits of many species (Rico-Gray 1980, 1989, 1993; Rico-Gray et al. 1998), representing at least a third of the flora. The floral and circum-floral nectar produced by these structures is probably the major liquid-energy source for ants during the dry season, since there are few alternative food sources, such as insects or new vegetative growth (e.g., soft plant tissues are sometimes chewed by ants to extract the sap). Owing to food shortage during the dry season in tropical seasonal habitats, ants will rely on the nectar produced by flowers and other reproductive structures. Thus, nectar may play an important role not only in insect nutrition but in water balance as well. And, since plant reproductive organs are thus particularly vulnerable in the dry season, there should be high selection for defense by ants.

14.4 Effect of Ants on Plant Fitness

Insect herbivores may consume nearly all types of plant tissue, and the damage may occur at any stage of a plant's life cycle. However, since herbivore damage includes both vegetative and reproductive tissue, the impact of herbivory on plant fitness may vary with the type of tissue being consumed (Marquis 1992). Numerous plant traits are hypothesized to have evolved as a response to selection exerted by herbivores, including structural, chemical, physiological, and life history traits (Marquis 1992). One of such defense strategies involves mutualistic associations with ants, and many plant species

produce domatia and/or food rewards to attract ants which in turn provide the plant with some protection against herbivores (Del Claro et al. 1996; De la Fuente and Marquis 1999).

Extrafloral nectaries are nectar-secreting organs found on virtually all above-ground plant parts not directly involved in pollination (Elias 1983; Koptur 1992) (Fig. 14.4). Plants bearing efn's are distributed worldwide, and available evidence suggests that these glands are more common in tropical than in temperate environments (Coley and Aide 1991). Although efn's attract a variety of nectar feeders (Koptur 1992; Pemberton and Lee 1996; Cuautele et al. 1999), ants are by far the most frequent visitors to efn-bearing plants both in temperate and tropical habitats (Oliveira and Brandão 1991). Many field

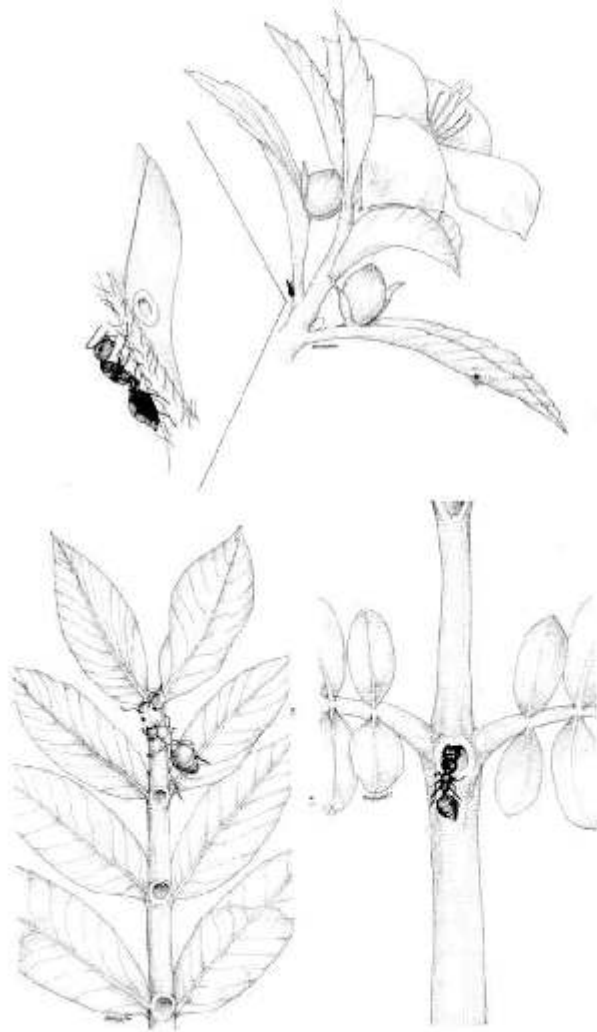


Fig. 14.4. Ants foraging for extrafloral nectar, clockwise from top. *Crematogaster brevispinosa* foraging for the nectar produced by nectaries located at the base of the leaf petioles of *Turrona ulmifolia* and a nectary located on the rachis of the foliole of a Leguminosae, and *Camponotus abdominalis* foraging for nectar produced by the foliar nectaries of *Inga vera*

experiments have demonstrated that ants visiting efn may increase plant fitness by deterring leaf herbivores (e.g., Koptur et al. 1998), bud or flower herbivores (e.g., Rico-Gray and Thien 1989a; Oliveira et al. 1999), and seed predators (e.g., Inouye and Taylor 1979; Keeler 1981). Some plants, however, receive no apparent benefit from ant visitation (O'Dowd and Catchpole 1983).

Ant/plant mutualisms mediated by efn are facultative and non-specialized, as indicated by the wide variety of associated ant visitors (Bronstein 1998). In fact, ant-derived benefits to efn-bearing plants can vary with factors such as time (Tilman 1978), habitat type (Barton 1986), aggressiveness of ant visitors (Oliveira et al. 1987; Rico-Gray and Thien 1989a), as well as the capacity of herbivores to circumvent ant predation (Heads and Lawton 1985; Koptur 1984; Freitas and Oliveira 1996). Research on plant defense by ants in tropical sand dunes is scarce and mainly restricted to four systems [*Myrmecophyla* (*Schomburgkia tibicinis*) *christinae*, *Paullinia fuscescens*, *Opuntia stricta*, and *Turnera ulmifolia*], which, however, represent a wide range of mutualistic interactions between ants and plants.

14.4.1 *Myrmecophyla* (*Schomburgkia tibicinis*) *christinae* (Orchidaceae)

Myrmecophyla christinae is a large epiphyte inhabiting the sand dune scrub in the state of Yucatan, Mexico (Fig. 14.5). Its large, hollow pseudo-bulbs, each with an opening at the base, are inhabited by ants. At least 13 ant species live in the hollow pseudo-bulbs, in old inflorescence spikes or in the soil directly beneath the plants. Only five ant species are common foragers on the inflorescence of the orchid (*Camponotus abdominalis*, *C. planatus*, *C. rectangularis*, *Crematogaster brevispinosa* and *Ectatomma tuberculatum*). Several ant species may occupy the same plant, but strong territoriality separates the species; two species never occur or nest in the same pseudo-bulb. Only one ant species will dominate all the inflorescence spikes of a given orchid plant, and its workers will forage day and night, throughout the reproductive season of the orchid (December–June) for nectar produced at the tip of the developing inflorescence spikes, the apex of the floral buds, the base of the floral pedicels and on the fruits. The main herbivore is *Stethobaris* sp. (Coleoptera: Curculionidae). This snout beetle (size ca. 2.5 mm) is present in relatively large numbers during early inflorescence development, decreasing through flowering. They are very active and bore holes at the tip of the growing inflorescence spike, on the buds and flowers. The beetle's most damaging effect is on the inflorescence spike. Beetle attack prior to bud differentiation kills the spike; if attack is during bud differentiation, it decreases flower number. Attack to the fruits is not as important, because beetle numbers decrease towards the end of April. The rare presence of larger beetles (size ca. 30 mm) may cause severe damage to a few fruits.

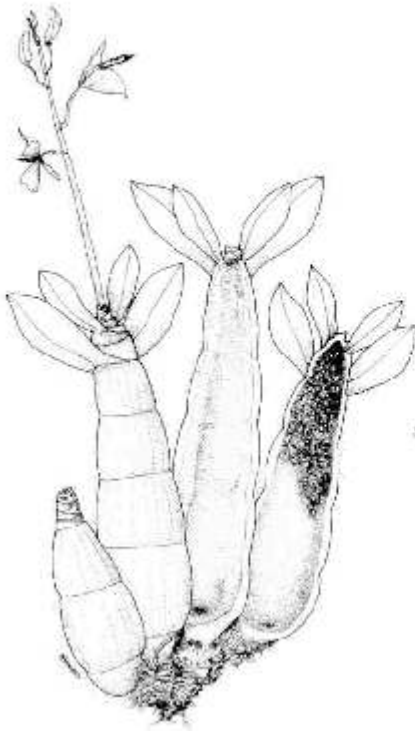


Fig. 14.5. A typical individual *Myrmecophylla* (*Schomburgkia tibicinis*) *christinae*. From left to right: external view of pseudo-bulb, pseudo-bulb with inflorescence, inside of pseudo-bulb without organic matter, inside of pseudo-bulb with organic matter (the last two show at the bottom the entrance hole for ants)

An ant exclusion experiment showed that orchids associated with the smallest ant species (*C. brevispinosa*) exhibited the highest number of dead spikes and produced the least number of fruits (Table 14.2). The possible protection offered by this ant species is negated because it herds the common citrus mealybug (*Planococcus citri*, Homoptera: Pseudococcidae) and by its small size relative to *Stethobaris* sp. (Rico-Gray and Thien 1989b). On the other hand, orchids associated with the largest ant species (*C. abdominalis*, *E. tuberculatum*) yielded significantly less dead inflorescence spikes, and produced significantly more flowers and fruits than control plants (Rico-Gray and Thien 1989a; Table 14.2). Furthermore, *C. brevispinosa* and the three *Camponotus* species pack some pseudo-bulbs with organic debris (dead ants and other insects, plant material, seeds) which are decomposed by bacteria and fungi, absorbed by the orchid, and utilized for growth and reproduction (Rico Gray et al. 1989). It is clear that in this ant/plant interaction, some ant species are antagonistic in one stage of the life cycle of the orchid while mutualistic in another.

Table 14.2. Results from the ant exclusion experiment. (Modified from Rico-Gray and Thien 1989a, b)

Parameter/treatment	CTL ^a	CB	CP	CR	CA	ET
No. of inflorescences used	62	62	62	62	62	62
No. of dead inflorescences	25	40	16	12	0 ^b	9 ^b
Dead inflorescences (%)	40.3	64.5	25.3	19.3	0	15.4
No. of flowers produced	441	198	642 ^b	547 ^b	824 ^b	742 ^b
No. of fruits produced	9	2 ^b	8	21	32 ^b	33 ^b
Ant size (mm)	-	2.5	3.5	5.0	8.0	10.5

^a CTL, control; CB, *Crematogaster brevispinosa*; CP, *Camponotus planatus*; CR, *C. rectangularis*; CA, *C. abdominalis*; ET, *E. tuberculatum*

^b Significantly different from control (χ^2 Yates corrected, $P < 0.01$)

14.4.2 *Paullinia fuscescens* (Sapindaceae)

Paullinia fuscescens is a deciduous, nectarless, woody vine, often found in association with the shrub *Randia laetevirens*, whose foliage is renewed with the onset of rains in June. They inhabit the sand dune scrub at La Mancha, Veracruz, Mexico. The interaction between *P. fuscescens*, the ant *Camponotus planatus* (Hymenoptera: Formicidae), and an unidentified aphid species (Homoptera: Aphididae) occurs during bud and flower development. Inflorescence growth usually starts in September; flowers are present during October (a few flowers may be present as late as March). Fruiting begins in October, and seeds are present until February or March.

In 1990, we examined 4312 inflorescences. Flower production averaged 134.6 flowers per inflorescence (range 88 to 344); fruit production ranged from 0 to 42 fruits per inflorescence. *C. planatus*, a generalist ant using a wide range of food resources (Rico-Gray, 1993), is present in the area throughout the year. *C. planatus* foraged for nectar produced by extrafloral nectaries of neighboring and sometimes intertwined individuals of *Passiflora* sp. (Passifloraceae). When the latter stops flowering in late September, their efns ceased to produce nectar, and the ants forage on the honeydew of aphids feeding on the inflorescences of *P. fuscescens*. Aphids feed at the beginning of the most stressful time of the year (dry season and winter) on plant tissues (young inflorescences) that are rich in energy and nutrients.

A three-year ant-aphid exclusion experiment showed that the outcome of this interaction varied between years (Table 14.3; Rico-Gray and Castro 1996). The ant-aphid association significantly reduced average seed production per inflorescence in the first two years, whereas it had no effect in the third year. These results assess that full benefits to plants harboring ant-tended Homoptera are rarely demonstrated. The effect of treatment (with or without

Table 14.3. Mean number of seeds (\pm SE) per inflorescence and percent of inflorescences with seeds in a plot with ants and aphids (control) and a plot with ants excluded (experimental) in 1990, 1991, and 1993 (n =number of inflorescences per treatment). (Rico-Gray and Castro 1996)

Response (RM-ANOVA)	Treatment	1990 ($n=344$)	1991 ($n=344$)	1993 ($n=344$)
No. seeds per inflorescence	Control	4.79aA ^a (± 0.34)	2.99aB (± 0.21)	2.98aB (± 0.18)
	Experimental	12.01bA(± 0.52)	3.08aB (± 0.26)	5.55bC (± 0.31)
Inflorescences (%) with seeds	Control	69.8 %aA	58.9 %aB	71.2 %aA
	Experimental	93.1 %bA	60.5 %aB	78.2 %bC

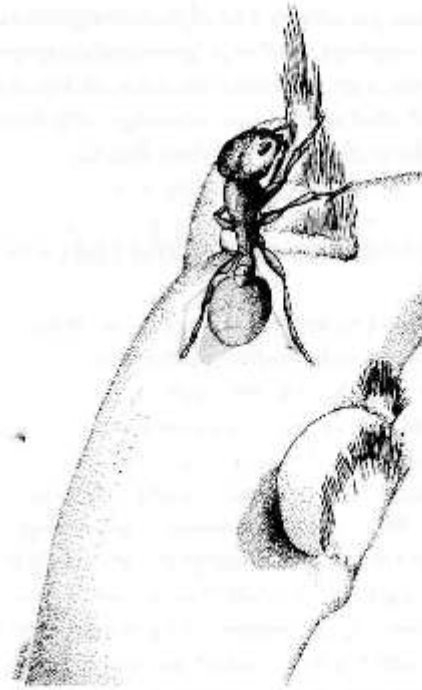
^a Treatment means or percentages within a year followed by the same lowercase letter are not significantly different ($P > 0.05$). Year means or percentages within a treatment followed by the same uppercase letter are not significantly different ($P > 0.05$)

ants and aphids) on percentage of flowers producing seeds changed across years ($G=48.92$, $df=2$, $P < 0.0001$). Furthermore, between-year variation in precipitation and temperature had an equal effect on the study plots (control, experimental), so within-year variation per plot was attributed to the effect of the ant-aphid association. Because of the importance of the conditional nature of interactions (Cushman and Addicott 1991; Bronstein 2001), the results suggest that (1) the presence of two potentially mutualistic species is not enough to generate mutualism; (2) habitat fragmentation, patch size and distribution, and location in space are vital to the outcome of an interaction; and (3) it is difficult to classify interactions as antagonistic or mutualistic, because geographically or seasonally, interactions can shift in their outcome.

14.4.3 *Opuntia stricta* (Cactaceae)

Opuntia stricta is a succulent cactus that commonly occurs along the coastal dunes of the Gulf of Mexico and the Caribbean. Its flowers can be pollinated by bees and birds, and the fruits are consumed by several birds, rodents, and other mammals (Oliveira et al. 1999 and references therein). *O. stricta*'s efn's are located in the areoles of the developing tissue of emerging cladodes and flower buds. Ants actively visit the efn's on a round-the-clock basis (Fig. 14.6). The main herbivores of *O. stricta* in the sand dune scrub at La Mancha, Veracruz are (Oliveira et al. 1999): (1) *Narnia* sp. (Hemiptera: Coreidae), whose adults mate on the plant and egg batches (8–14) are laid on the spines, and nymphs and adults suck plant juice from cladodes and produce typical white rings around punctures; (2) *Hesperolabops* sp. (Hemiptera: Miridae): egg batches were not seen, and nymphs and adults suck plant juice from cladodes

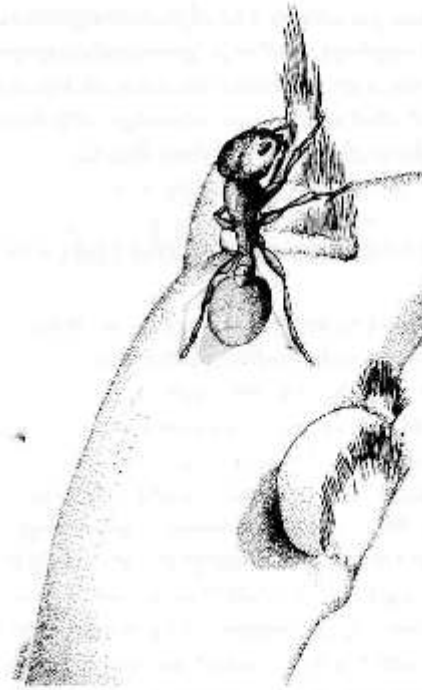
Fig. 14.6. *Opuntia stricta* with *Crematogaster brevispinosa* ant foraging nectar at an areole



and punctures are detectable by white dots; (3) Mining insects (Diptera): mining/feeding activity by developing larvae leave easily detectable tunnels within infested cladodes; and (4) a bud-destroying moth (Lepidoptera: Pyralidae, Phycitinae), which lays eggs on floral buds and developing cladodes, and larval burrowing/feeding activity within the plant organs leaves characteristic external marks.

The associated ant assemblage was formed by nine species distributed in four subfamilies, however, the dominant ant visitor changed markedly from day (*Camponotus plunatus*) to night (*C. abdominalis*). Cladodes of control (ants present) and treated (ants excluded) plants of *Opuntia* were equally infested by sucking bugs (*Narnia* sp., *Hesperolabops* sp.: Hemiptera) (RM-ANOVA, $F_{1,36}=0.067$, $P=0.797$), and mining Diptera, both before ($\chi^2=1.279$, $df=2$, $P=0.734$) and after ($\chi^2=0.973$, $df=2$, $P=0.807$) ant treatment. Damage to buds by a pyralid moth (Pyralidae: Lepidoptera), however, was significantly higher on treatment than on control plants ($X \pm SD$, 0.84 ± 1.92 vs 0.10 ± 0.3 , respectively; Mann-Whitney *U*-test, $U=893.0$, $P<0.0001$, $N=19$). Ant visitation to *Opuntia*'s cfn translated into a 50% increase in the plant's reproductive output, as expressed by the number of fruits produced ($X \pm 1$ SD) by experimental control (3.62 ± 1.80) and treatment (2.40 ± 0.34) branches (paired *t*-test, $t=2.564$, $df=18$, $P=0.0195$). Moreover, fruit production by ant-visited branches

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The associated ant assemblage was formed by nine species distributed in four subfamilies, however, the dominant ant visitor changed markedly from day (*Camponotus plunatus*) to night (*C. abdominalis*). Cladodes of control (ants present) and treated (ants excluded) plants of *Opuntia* were equally infested by sucking bugs (*Narnia* sp., *Hesperolabops* sp.: Hemiptera) (RM-ANOVA, $F_{1,36}=0.067$, $P=0.797$), and mining Diptera, both before ($\chi^2=1.279$, $df=2$, $P=0.734$) and after ($\chi^2=0.973$, $df=2$, $P=0.807$) ant treatment. Damage to buds by a pyralid moth (Pyralidae: Lepidoptera), however, was significantly higher on treatment than on control plants ($X \pm SD$, 0.84 ± 1.92 vs 0.10 ± 0.3 , respectively; Mann-Whitney *U*-test, $U=893.0$, $P<0.0001$, $N=19$). Ant visitation to *Opuntia*'s cns translated into a 50% increase in the plant's reproductive output, as expressed by the number of fruits produced ($X \pm 1$ SD) by experimental control (3.62 ± 1.80) and treatment (2.40 ± 0.34) branches (paired *t*-test, $t=2.564$, $df=18$, $P=0.0195$). Moreover, fruit production by ant-visited branches

those without ants (Kruskal-Wallis, $H=22.158$, $df=4$, $P<0.001$; Student-Newman-Keuls, $P<0.05$), and (2) the percent of leaf tissue removed by caterpillars of *Euptoieta hegesia* was significantly lower in plants with ants than in plants with ants excluded (Kruskal-Wallis $H=37.272$, $df=1$, $P<0.001$). Similar to results obtained for *Myrmecophyla christinae* (see above), ant presence is not synonymous with plant protection, and the level of protection by ants will depend on the size of the worker ants in a guild of ant visitors. Moreover, wasps visited efns when ants were excluded, exerting a higher level of protection than that offered by the smaller ant species.

Recent work has demonstrated that individuals of *T. ulmifolia* present less herbivorous damage and more unripe fruits when either ants (*Camponotus abdominalis*, *C. planatus*) or wasps (*Polybia occidentalis*, *Polistes instabilis*) were present, relative to plants in which both of these insects were excluded (M. Cuautle and V. Rico-Gray, unpubl. data). However, when both ants and wasps were present there was no increase in fruit production or decrease in herbivorous damage, relative to plants with either ants or wasps; apparently a competitive ant-wasp interaction does not allow for both these insects to simultaneously participate in plant protection (i.e., the protection exerted by ants and wasps is not additive) (M. Cuautle and V. Rico-Gray, unpubl. data). Finally, the differential effect of wasps and the dispersal by ants of *T. ulmifolia* elaiosome-bearing seeds are currently being studied in detail (M. Cuautle and V. Rico-Gray, unpubl. data).

14.5 Conclusion

Interspecific interactions are one of the most important processes influencing patterns of adaptation, variation of species, and community organization and stability. Ant-plant interactions vary in their probability of occurrence along environmental gradients and under different disturbance regimes, their outcome varies in different ecological conditions or between habitats, and they exhibit significant temporal variation. The structure of ant communities and of ant-plant interactions has been studied in a variety of habitats, assessing that neither the spatial nor the temporal dimensions can be ignored. Ant assemblages are very dynamic and extrapolating results from one ant community to another can lead to erroneous inferences, precluding broad generalizations.

Ant-plant associations in tropical sand dunes are abundant, relative to temperate semiarid or humid mountain sites. Studies at two coastal sites in Mexico, La Mancha in Veracruz and San Benito in Yucatan, show significant within-habitat seasonal variation, as well as considerable variation among habitats in the number, diversity and seasonal distribution of ant-plant interactions. They suggest that inter-habitat variation of ant-plant interactions is

the effect of variation in environmental parameters, richness of plants with nectaries in the vegetation, and richness in habitat heterogeneity.

Many components in the tropical seasonal vegetation along the Gulf of Mexico (state of Veracruz) and the Caribbean (Yucatan Peninsula) flower during the dry season. Flowering is not simultaneous, but there is at least one species in flower from December through June. Throughout the dry season ants forage for nectar produced by buds, flowers, and fruits of many species. The floral and circum-floral nectar produced by these structures is probably the major liquid-energy source for ants during the dry season, since there are not many alternative food sources, such as insects or new vegetative growth. Owing to food shortage during the dry season in these habitats, ants rely on the nectar produced by the reproductive structures as their main liquid-energy source. As plant reproductive organs are thus particularly vulnerable in the dry season, there should be high selection for defense by ants.

Research on plant defense by ants in tropical sand dunes is scarce and mainly restricted to four systems [*Myrmecophyla christinae* (Orchidaceae), *Paullinia fuscescens* (Sapindaceae), *Opuntia stricta* (Cactaceae) and *Turnera ulmifolia* (Turneraceae)], which, however, represent a wide range of mutualistic interactions between ants and plants. They demonstrate that: (1) ant presence is not synonymous to defense, protection from herbivores being related to ant size; (2) the outcome of the interactions varies between seasons; (3) ant-Homoptera associations can be more harmful than beneficial to the associated plant; (4) wasps may play a significant role in plant defense; and (5) these interactions are more complex than solely defense, for example, the feeding of plants by ants (*M. christinae*) or seed dispersal by ants (*T. ulmifolia*).

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