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Nectar as fuel for plant protectors

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Introduction

Nectar is a sweet liquid produced by plants on various parts of the plant body. Most people are familiar with nectar in flowers, collected by bees to make honey, and utilized by a variety of floral visitors, some of whom serve as pollinators for the plant. Less familiar is extrafloral nectar, produced outside the flowers in extrafloral nectaries and usually not associated with pollination. Plants produce nectar in various ways (Elias 1983; Koptur 1992a), and whether they do it purposefully (secretion) or passively (excretion) has been the subject of debate between physiologists and evolutionary ecologists for many years (reviewed in Bentley 1977; see also Sabelis *et al.*, Chapter 4). Over evolutionary time, myriad selective forces have shaped not only the morphology and function of nectaries, but also the composition of the substances secreted and whether or not the structures secrete under different circumstances. Thompson's (1994) synthetic theory of the "co-evolutionary mosaic," in which different populations of a given species experience different interactions over space and time, helps to explain the variable findings researchers encounter in studying interactions between plants and predatory insects, especially those mediated by nectar (or other direct or indirect food rewards from plants). Carnivorous organisms, which can benefit plants as protectors, may rely on nectar as an energy source. If ants, wasps, other predators, and parasitoids are more likely to encounter their herbivore prey if they utilize a plant's nectar, mutualisms are thus promoted.

In this chapter I examine the many interactions promoted by nectar, with particular attention to its role in support of predatory insects on plants. Parallels will be drawn between systems involving nectar (primarily extrafloral, but also

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floral nectar) and those that involve insect analogs of extrafloral nectaries (honeydew-producing insects, alternative resources for predators), since the literatures are intertwined and discoveries in one area help answer questions in the other (see also Wäckers, Chapter 2). In all areas examined, I highlight an arbitrary selection – acknowledging a particular bias towards ants – out of many studies chosen for their relevance, but my review of the subjects covered here is by no means complete.

Floral and extrafloral nectaries

Floral nectar is one of the primary rewards for animals visiting flowers, and is produced in flowers in a variety of locations. Most commonly, floral nectaries are located between the reproductive and sterile whorls of a flower, outside the androecium (stamens) of the flower. In monocots, septal nectaries are the norm, located on the surface of the ovary where the carpels (its component parts) come together to create the septae (or divisions) of the ovary. Nectar may be secreted and left exposed to the environment and visitors, open to all who might come, or pouring out of flowers if it is not collected. Many plants are economical in their production of nectar, and limit access to the nectar to visitors that are the right size, shape, or behavior to effect pollination. In some flowers nectar is produced by one flower part and collects in another, e.g., in *Viola* spp. where the nectar is produced from the lower staminal filaments and collects in a spur formed by the petal bases.

Extrafloral nectaries are known from ferns and flowering plants (Bentley 1977; Elias 1983; Koptur 1992b) but not yet recorded in gymnosperms. Though scientists have long been interested in extrafloral nectaries, their occurrence in many floras has not been carefully studied, and important contributions to our knowledge of the distribution and basic biology of extrafloral nectaries are still being made (Galetto and Bernardello 1992; Fiala *et al.* 1994; Hunter 1994; Morellato and Oliveira 1994; Valenzuela-Gonzalez *et al.* 1994; Fiala and Linsenmair 1995; O'Brien 1995; Oliveira and Pie 1998; Zachariades and Midgley 1999; Dejean *et al.* 2000b; Junqueira *et al.* 2001; Bluthgen and Reifenrath 2003) and could certainly continue for many years. Extrafloral nectaries are simply nectaries located outside the flowers, and may more specifically be named with reference to their position (e.g., foliar nectaries, petiolar nectaries, bracteal nectaries; or simply "nectaries" in ferns, which do not have flowers!). The position of extrafloral nectaries and the timing of their functioning suggest vulnerabilities in a plant that may benefit from protection by organisms attracted to the nectar. For example, the inflorescence bracts and stem tips of

Caryocar (Oliveira 1997) attract ants that reduce herbivores that attack its young leaves and reproductive parts; the nectaries on unfurling fronds of *Polypodium plebeium* (Koptur *et al.* 1998) attract ants that deter herbivory during leaf expansion. Nectar-imbibing organisms visit the nectaries to fuel their own energetic and nutritional needs, and in doing so are placed in proximity to plant parts that are vulnerable to enemies.

Possessing floral nectar is not a prerequisite for producing extrafloral nectar; not only do ferns not have flowers, but many flowering plant species with no floral nectaries have prominent extrafloral nectaries. Sometimes the extrafloral nectaries function as do most floral nectaries, attracting visitors to the vicinity of the flowers to inadvertently pollinate them. *Acacia terminalis* has large reddish foliar nectaries that are visited by passerine birds in Australia that pollinate the flowers located on branches with leaves (Knox *et al.* 1985). Australian *Acacia* species lack floral nectaries and most are entomophilous, mostly pollinated by bees collecting pollen and extrafloral nectar (Kenrick *et al.* 1987; Thorp and Sugden 1990). *Marcgravia* and *Norantea* (Marcgraviaceae) inflorescences have large nectaries at the base of each pedicel, and their self-incompatible flowers are pollinated by bats (*Marcgravia*), hummingbirds, and passerine birds (*Norantea* spp.) foraging on the nectar (Sazima and Sazima 1980; Sazima *et al.* 1993; Pinheiro *et al.* 1995).

Some floral nectars may also have a protective function, attracting non-pollinating visitors that protect the plant against detrimental herbivory (Dominguez *et al.* 1989; Yano 1994; Altshuler 1999). In lowland tropical dry forests of coastal Veracruz and in the Zapotitlan Valley (Mexico), ants are more commonly associated with floral nectar and nectar on plant reproductive structures than they are with extrafloral nectar on vegetative plant parts (Rico-Gray 1993; Rico-Gray *et al.* 1998).

Floral and extrafloral nectar

Nectar is an aqueous solution of sugars, amino acids, and other components including lipids, vitamins, and other compounds (Baker and Baker 1973, 1983; Baker 1977). Nectar is consumed by a variety of organisms that interact with plants in a variety of ways, and there has been much research conducted to illuminate patterns of nectar use by visitors and the resultant effects on plants that produce the nectar.

Looking for patterns in nectar composition and its utilization, Herbert and Irene Baker collected hundreds of nectars from many locations. Their extensive analyses revealed that the sucrose/hexose ratios of the nectar correspond to the main type of visitor utilizing floral nectar (Baker and Baker 1983, 1990), enabling prediction of probable pollinators by analysis of nectar sugars (an additional floral character to include in "pollination syndromes"). There is also a statistically significant tendency for amino acids to be correlated with pollinator types (Baker and Baker 1986). Some researchers have objected to these generalizations, concerned that the age and condition of flowers, as well as pollen contamination, may affect apparent nectar composition (Gottsberger *et al.* 1990). Secreted nectar certainly changes and the chemical composition of what has accumulated on the nectaries (and what therefore is used for chemical analysis) is not identical with what has been secreted by the glands. However, as correlations made from large sets of laboratory measurements and field observations, the findings of the Bakers are robust.

The Bakers also observed that nectars open to the air are hexose-dominated, whereas concealed nectars may be sucrose-dominated, and sucrose-dominated nectars open to the air for some time degrade to hexose-dominated nectars, presumably through the actions of microorganisms degrading sucrose to its hexose components (Baker and Baker 1983). They extended their sugar-ratio observations to fruit (Martinez del Rio *et al.* 1992) and studies on various birds found that those which prefer hexose-dominated foods lack sucrase, the enzyme needed to digest sucrose, in their intestinal tract (Martinez del Rio *et al.* 1988, 1989; Martinez del Rio and Stevens 1989; Martinez del Rio and Karasov 1990).

Many organisms can distinguish sugars by taste, and some show distinct preferences for sucrose or hexose sugars (Martinez del Rio 1990; Rusterholz and Erhardt 1997; Koptur and Truong 1998; Blüthgen and Fiedler 2003). In a quest to discover any potential ant-attracting compounds from natural nectar sources, the sugar preferences of a variety of pest ant species were investigated (Koptur and Truong 1998). Most pest ant species preferred fructose over the other sugars, when a preference was demonstrated (interpreted as shorter time to discovery of the bait and more total ants at the bait). Fire ants (*Solenopsis invicta*) can even distinguish between the diastereomers D- and L-glucose (Vandermeer *et al.* 1995). In all species there is potential for individual variation in taste, but only the dominant species can exercise their ability to discriminate (Blüthgen and Fiedler 2003).

Nectars range from dilute (10% sugar or less) to highly concentrated (70% sugar or more), and the viscosity of nectar corresponds to sugar concentration. Viscosity may affect the ability of visitors to drink nectars. If the nectar is concealed in a floral spur or tube, and must be obtained through a long proboscis, it must be dilute enough to travel up by capillary action; in contrast, nectars produced in sunny, dry environments may be viscous and collected in open mandibles, especially extrafloral nectars (Corbet *et al.* 1979; Willmer and Corbet 1981; Wäckers, Chapter 2). The greater the sugar content of nectar, the greater its energetic reward for the visitor that can harvest it. Many studies have shown floral visitor preferences for larger nectar quantities over smaller quantities, and for nectars with higher sugar concentrations (Ricks and Vinson 1970; Bennett and Breed 1985; Lanza 1988, 1991; Galetto and Bernadello 1992; Burd 1995). However, there is likely an optimal nectar concentration curve for most visitors due to slow intake of highly concentrated nectar (e.g., Roces *et al.* 1993).

In plants that possess both floral and extrafloral nectars, the sugar concentration and composition of the nectars can differ dramatically. *Inga* floral nectars are sucrose-dominated and much more dilute compared to extrafloral nectars, which are hexose-dominated and much more concentrated (Koptur 1994). *Inga* flowers are visited by a variety of flying animals, and pollinated primarily by hawkmoths (Sphingidae) and hummingbirds (Trochilidae) (Koptur 1983, 1984a); their extrafloral nectaries are visited by ants, flies, and wasps (Koptur 1984b, 1985). Cashew (*Anacardium occidentale*) is and romonoecious and has nectar in both hermaphrodite and male flowers, and extrafloral nectar on the panicle (Wunnachit *et al.* 1992). All three of the nectars have very high sugar concentrations (greater than 70%), and the panicle nectar had a significantly higher sugar content than the floral nectars. All of these cashew nectars were hexose-dominated, with similar sucrose/ hexose ratios.

The amino acid complements of the different nectars of the same plant species may also differ (Baker *et al.* 1978), though nectars cluster more in accordance with taxonomy than function (Koptur 1994). In many plants, the more concentrated extrafloral nectars tend to have greater amino acid contents (Blüthgen *et al.* 2004). However, extrafloral nectar of cashew had more amino acids than its floral nectar, but the overall amino acid content of floral nectar was about three times that of the extrafloral nectar (Wunnachit *et al.* 1992). Galetto and Bernardello (1992) analyzed extrafloral nectars of Argentinian Bromeliaceae and found them to have very high sugar concentrations and to be sucrose-dominated, with amino acids present in all species studied. Amino acids are important constituents of extrafloral nectars of pitcher plants (Dress *et al.* 1997). Amino acids have been shown to be important in the attraction of ants to extrafloral nectars and artificial nectar solutions (Lanza 1988, 1991; Wagner and Kay 2002), and Lanza *et al.* (1993) demonstrated that the amino acid content in *Passiflora* extrafloral nectar increases when plants are defoliated, and that it is preferred by ants over nectar from nondefoliated plants.

(Non-pollinating) visitors to nectar

Visitors to plant nectar encompass a wide array of animals, whose effects on the plant secreting the nectar range from positive to negative (Rico-Gray 2001). The effect of the plants on the visitors is usually positive (providing liquid nourishment), and plants may actually manipulate their visitors via nectar secretion patterns (see below). Many visitors to floral nectar pollinate the flowers they visit, a benefit to the plant and essential for maintaining genetic diversity via sexual reproduction. The extent to which genetic diversity is enhanced is related to the mobility of the visitor: crawling insects (such as ants or beetles) tend to move pollen within individual flowers and plants more than do flying insects such as butterflies, bees, and moths. Non-pollinating visitors fall into a number of categories: nectar robbers, herbivores, plant prey (for carnivorous plants), and plant protectors.

Nectar robbers

All sequestered nectar may be subjected to robbing by visitors who manage to collect the nectar without touching floral reproductive parts, apparently taking advantage of the plant. Note that "robbing" is used in a broad sense – sometimes a distinction is made between robbers and thieves, based on whether or not the flowers are physically damaged (see, e.g., Romeis *et al.*, Chapter 7 – thieves leave the flower undamaged), but here the actual mechanism of theft is left in the middle.

By definition, nectar robbers utilize nectar with no direct benefit to the plant (Maloof and Inouye 2000). Robbing is, however, not always detrimental to the plant; robbers may enhance pollination in some indirect ways, e.g., they may decrease self-pollination and increase genetic diversity by making pollinators move farther. Some nectar robbers decrease nectar volume and may cause legitimate pollinators to visit more flowers (Colwell *et al.* 1974). Flower mites, for example, live inside the flowers and can decrease nectar volume to such an extent that flowers are visited less by hummingbirds (Colwell 1995; Lara and Ornelas 2001); however, the flower mites can also act as secondary pollinators. In certain systems, nectar robbery may be an integral part of the mutualism between plants and their pollinators (Morris 1996): bumblebees rob nectar from mature flowers and buzz-pollinate earlier stage flowers on the same plants; the nectar they rob may entice them to legitimately pollinate other flowers. *Mertensia paniculata* stems with robbers excluded donate less pollen and set fewer fruit than those with robbing. Robbed flowers of *Anthyllis vulneraria* in Spain set more seed than unrobbed flowers, because the robbers' bodies effect pollination (Navarro 2000). Extrafloral nectar can be robbed as well, if visitors imbibe nectar with no benefit to the plant, as the Japanese white-eye bird (*Zosterops japonica*) taking extrafloral nectar of the tropical almond (*Terminalia catappa*) in the Bonin Islands (Pemberton 1993), or opportunistic ants that do not provide benefit to their host plant, such as *Cataulacus* on *Leonardoxa africana* (Gaume and McKey 1998). The function of calyx and bud nectaries of *Thunbergia grandiflora* in Malaysia was hypothesized to be for ant protection against nectar-robbing carpenter bees, but ants apparently protect the inflorescences against herbivores (Fiala *et al.* 1996).

Herbivores

Certain herbivores may be attracted to plants by nectar, or by other insects that are attracted to nectar. Among those that are attracted to plants by extrafloral nectar, and that are more likely to oviposit on the plant than if it did not have nectaries, are Lepidoptera with ant-tended caterpillars. *Saraca thaipingensis*, a legume tree with extrafloral nectaries of peninsular Malaysia, is host to 10 species of lycaenid butterflies, and females of some species oviposit exclusively on trees occupied by their specific host ants (Seufert and Fiedler 1996). Wagner and Kurina (1997) found that lycaenid butterflies lay substantially more eggs on *Acacia constricta* plants with ants than plants without ants, using ants as oviposition cues. Ant-tended butterfly caterpillars may even drink extrafloral nectar (DeVries and Baker 1989), adding “insult to herbivory”! Some ant-tended herbivores may also exhibit inducible defenses, secreting more honeydew to elicit ant protection when they are threatened (Agrawal and Fordyce 2000). Homoptera may also be attracted to plants that secrete nectar. The gregarious, polyphagous tettigometrid *Hilda patruelis* is frequently found on fig-bearing branches of *Ficus sur* in South Africa, where ants tend fig secretions as well as the homopterans (Compton and Robertson 1991).

Plant prey

A special case of nectar use exists in some carnivorous plants. Pitcher plants (Sarraceniaceae, Nepenthaceae, Cephalotaceae, Bromeliaceae) secrete extrafloral nectar on their pitcher leaves to lure insects that may fall into the pitchers to be digested as prey (Joel 1988). Ants are frequent visitors and sometimes become food for the pitcher plants, but probably not as often as various flying nectar-drinking insects.

Plant protectors

Plant-protecting predators and parasitoids are more likely to discover their prey/hosts after having been recruited to the plant by nectar. Ants are common on plant foliage foraging for food, and often affect the herbivores of the plants on which they forage (Oliveira *et al.* 2002). Fiala *et al.* (1996) found that ant-free inflorescences of *Thunbergia grandiflora* in Malaysia were attacked and destroyed by moths (Pyralidae) whereas buds were normally protected from these herbivores by the presence of ants. Ant–plant protection studies have contributed much to theory of mutualism and to our understanding of species interactions (Bronstein 1998). Many interactions between ants (and other protectors) and plants are facultative: the plant and the ant can survive without the other, but with diminished fitness. These facultative associations tend to rely solely on the plant providing extrafloral nectar (e.g., Torres-Hernandez *et al.* 2000) – see Box 3.1 for some examples of facultative ant–plant relationships in the legume family. In some cases the ants may build their nests on the surface of the plants bearing nectaries, as seen in *Clerodendrum fragrans* in Southeast Asia (Jolivet 1983) or *Inga sapindoides* in Panama (S. Koptur, personal observation). Ants may even hide the nectaries from competitors by constructing shelters of debris over the nectaries (Eskildsen *et al.* 2001), though this may alternatively be interpreted as protecting the nectar from rain.

Enhanced plant resources make plants bigger, and larger plants provide more resources for herbivores and potentially for mutualistic predators in bottom-up trophic cascades. Studies by Letourneau and Dyer yielded no evidence for bottom–up control of predators, but robust evidence for top–down indirect effects on host plant biomass by predators (Letourneau and Dyer 1998; Dyer and Letourneau 1999a, 1999b). A study of wood ants and birch herbivores came to similar conclusions: predation by ants on herbivores created the "green island" effects much more than their soil amelioration could explain (Karhu and Neuvonen 1998). Interestingly, wood ants are the sole ant that demonstrated some level of antiherbivore defense on bracken fern (Heads and Lawton 1985). *Acacia constricta* plants with ant nests below them were associated with greater fruit set than plants without ant nests; ant numbers were higher on these plants (which bear extrafloral nectaries), but ants did not appear to reduce damage from leaf herbivores; fruit set enhancement may be due to nutrient enhancement (Wagner 1997). It would be interesting to measure extrafloral nectar production in both sets of plants.

The presence of extrafloral nectaries increases the number of predators (especially ants) on a plant, and ants on plants frequently reduce herbivory or enhance plant reproduction. Though ants are the main predator in most of the examples in this section, it is important to recognize that other arthropods, such as spiders (Ruhren and Handel 1999) and wasps (Cuatle and Rico-Gray 2003; see also Olson *et al.*, Chapter 5 and Eubanks and Styrsky, Chapter 6) that are attracted to extrafloral nectar also can act as effective defenders of plants.

Box 3.1 Extrafloral nectaries: examples of facultative mutualisms in the legume family (Fabaceae)

Many families of plants are characterized by extrafloral nectaries, but the Fabaceae has many diverse genera bearing extrafloral nectaries on various parts of the plant body. I discuss one example from each of the three subfamilies, but this is not entirely representative of this enormous family.

Vicia

Extrafloral nectaries have been shown to serve as a generalized defense, wherever the plants might live. In their native habitat the nectaries may have co-evolved with ants and other biotic protective agents over long periods of time, and their protective agents may repel new herbivorous species on the plant in question. However, there may be many specialized herbivores that have outsmarted the defense system. An example is the common vetch, *Vicia sativa*, a weed in natural areas of northern California (USA) that has a truly facultative mutualism with ants (in many locations, the non-native Argentine ant, *Iridomyrmex humilis*). Eliminating ants by excising the nectar-bearing stipules resulted in plants losing more leaf area to externally feeding herbivores than control plants with intact nectaries and attendant ants (Koptur 1979), which also decreased fruit and seed set in plants with nectaries and ants removed. When common vetch was studied in its native land (UK: Koptur and Lawton 1988), we found specialized herbivores (most important were caterpillars that silked leaves together and fed inside their shelters, and others that fed inside developing fruit) that actually benefited from the presence of ants.

Lysiloma

Some plants may be long-lived, but have relatively short-lived leaves that are quite palatable to herbivores and benefit from ant protection during their development. *Lysiloma bahamensis* is a native tree of pine rocklands and hardwood hammocks of south Florida (USA). *Lysiloma* is dry-season deciduous, with leaves lasting less than a year. Leaves have extrafloral nectaries that attract four species of ants (*Pheidole dentata*, *Pseudomyrmex elongata*, *Pseudomyrmex simplex*, and *Solenopsis geminata*) in Everglades National Park, and exclusion experiments during the period of leaf expansion showed that ants reduce leaf damage from herbivores (S. Koptur, unpublished data). Caterpillars were more numerous and herbivory was greater on trees in pinelands than trees on hammock edges (Rodriguez

Figure 3.1 *Pheidole megacephala* ant at *Cassia bahamensis* foliar nectaries in Miami.

1995), and though ant activity (as well as several other plant species with extrafloral nectaries) was greater in pinelands than in hammocks (Koptur 1992b), ants were more common on hammock *Lysiloma* trees than on pineland counterparts.

Cassia

Unlike the species of the Fabaceae described above, *Cassia* have no floral nectaries (their floral reward is categorized as "pollen only"), but most species have petiolar nectaries (Fig. 3.1). The morphology of these nectaries varies among the species: in some the nectaries are flat pads, in others nectaries are elongated into points. The genus *Cassia* (*sensu lato*, including *Senna* and *Chamaecrista*) has been studied in many locations, and is an important group of plants in the formulation of ant–plant interaction theory. Schimper (1903) excised *Cassia* nectaries to learn their function, and finding no change, concluded they did not have a physiological role. Boecklen (1984) found no support for the "protectionist hypothesis"; in his exclusion experiments with *Cassia fasiculata* (he used both nectary excision and tanglefoot banding at two sites) treatment plants produced as many fruit as control plants. Kelly (1986) used small fences ringed with tanglefoot to exclude ants from *Cassia fasiculata* and found that ant protection and plant fecundity varied geographically; Barton (1986) demonstrated striking spatial variation in ant–plant interactions of this species. Using clear nail polish to eliminate nectar in *Chamaecrista nictitans*, Ruhren and Handel (1999) found that spider predators chose plants with active extrafloral nectaries over those with nectaries blocked, spending most of their time on these plants and enhancing seed set of the plants despite the presence of a bruchid predator immune to spider defense. Large-scale ant-exclusion experiments conducted with both potted and naturally occurring *Senna occidentalis* in east Texas (USA) demonstrated that introduced fire ants greatly reduce foliar damage to plants by caterpillars and enhance fruit and seed set (Fleet and Young 2000). In southern Florida several species of *Cassia* (*sensu lato*) occur. All serve as host plants for sulfur butterflies (Pieridae) of the genus *Phoebis*. *Phoebis sennae*, the cloudless sulfur, is a native species; *P. philea*, the orange-barred sulfur, is naturalized in Florida, colonizing south Florida from Mexico in the 1920s (Glassberg 1999). Caterpillars of both species are much more common on *Cassia bahamensis* than on *C. ligustrina* (S. Koptur, unpublished data); nectar secretion patterns and perhaps nectar constitution of *C. ligustrina* may be more attractive to ants, and their presence may deter oviposition and deter young caterpillar presence on *C. ligustrina* (S. Koptur, personal observation). On most of the *Cassia* species, caterpillars feed on new growth, often eating flowers and sometimes preventing fruit development (their damage has a large impact on plant fitness). Plants in natural habitats appear to have greater reproductive success than plants in gardens and urban/suburban landscape settings where ants and other protective agents are often less abundant (S. Koptur, unpublished data).

Abiotic and biotic influences on nectar production

Nectar production is influenced by a number of factors, physical and biotic. Sunlight, soil moisture, and humidity are factors that can affect nectar secretion in plants. Sunlight promotes photosynthesis, which produces sugars, also involved in nectar production. Well-watered plants have adequate turgor and extra water available for nectar production. Many succulent plants of xeric habitats use their valuable water to make nectar, attracting both pollinators and protective agents. Relative humidity affects the concentration of nectar Corbet *et al.* 1979), with lower humidity promoting evaporation of water from nectar, leaving exposed nectars more concentrated than when conditions are humid.

Some defensive food supplements are affected by nutrient availability. Field experiments demonstrated that food body production by *Macaranga triloba* is limited by soil nutrient supply at the plant's natural growing site (Heil *et al.* 2001a, 2002). In myrmecophytic *Cecropia* species (Folgarait and Davidson 1995), glycogen-rich Müllerian bodies increased with greater carbon and nitrogen levels in greenhouse studies, whereas lipid- and amino acid-rich pearl bodies increased under conditions of high nutrient levels and low light (which contribute to an excess of nitrogen); carbon-based defenses (tannins and phenolics) reached higher concentrations in lower nutrient conditions. *Cecropia* do not produce nectar, but predictions for plants that do, suggest that nectar (carbon-based) should not be affected by nutrient limitation as food bodies might be. Studies are needed examining the effects of nutrient enhancement on nectar production in plants with extrafloral nectaries.

Removal of nectar has been shown to increase total nectar output in flowers of some plants (Cruden and Hermann 1983; Koptur 1983; Gill 1988; Pyke 1991), providing the plants with a way to respond to increased visitation by producing more nectar. Some plants with extrafloral nectaries produce more nectar when extrafloral nectar is removed, as demonstrated in careful studies with *Macaranga tanarius*. In this species, when nectar was removed at 3-hour intervals, nectaries produced on average 2.5 times more nectar than if it was collected only once a day (Heil *et al.* 2000). Some plants will maintain constant levels in active nectaries when nectar is not removed (*Inga densiflora*, *I. punctata*, *Vicia sativa*), while others will secrete continuously whether nectar is removed or not (*Polypodium plebeium*, *Turnera ulmifolia*, *C. ligustrina*). Careful quantification and field observations of these differences may reveal differing strategies in attracting protective agents, and in avoiding colonization by fungi.

Extrafloral nectar production may be an inducible anti-herbivore defense in some plants (Koptur 1989). Both artificial defoliation and insect herbivory have been shown to increase nectar secretion in a number of plants with extrafloral nectaries (Stephenson 1982; Koptur 1989; Stevens 1990; Wäckers and Wunderlin 1999; Heil *et al.* 2000; Wäckers *et al.* 2001). Moderate artificial damage to leaves of *V. sativa* increased extrafloral nectar volume secreted for 2 days following the damage (Koptur 1989). Leaf damage to *V. faba* caused a dramatic increase in the number of extrafloral nectaries on stipules (Mondor and Addicott 2003), interpreted as an adaptive plastic response. Agrawal and Rutter (1998) postulated that physical damage to leaves or other plant parts may trigger plant signals such as plant sap release or green leaf volatiles that attract ant defenders. Ants are recruited to a number of cues associated with herbivory (leaf damage, caterpillar presence, plant sap, and hexanal) in *Cecropia* (Agrawal 1998). Kawano *et al.* (1999) found that volatile substances (that serve as a generalized parasitoid attractant) were emitted after leaf damage on extrafloral nectary-bearing *Fallopia* spp. (Polygonaceae). Brouat *et al.* (2000) demonstrated that leaf volatiles influence ant patrolling by attracting ants to the younger leaves where their protection is needed. Induced defenses may be favored over constitutive defenses in plants for many reasons (Karban and Baldwin 1997; Agrawal and Karban 1999), including economy, reduced host-finding by specialists, reduced susceptibility to pathogens, increased variability in food quality for herbivores, increased herbivore movement and dispersion of herbivory, and reduced pollinator deterrence. Heil *et al.* (2001b) showed that extrafloral nectar production is elicited by jasmonic acid, as an induced defensive response to herbivory and artificial damage in *Macaranga tanarius*.

Hypotheses on the function of extrafloral nectar production

Why have extrafloral nectaries arisen in such a wide variety of plants? Apparently they impart some selective advantage to plants that possess them. The historical development of the “protectionist” and “exploitationist” views of extrafloral nectar production are reviewed by Bentley (1977). For the sake of completeness, I discuss these competing hypotheses here, prior to discussing two other alternatives that have received recent attention.

Hypothesis 1 – exploitation of plant physiological waste products

Nectar secretion has been envisioned a passive process, the nectaries functioning as “sap valves,” excreting excess carbohydrates from growing points of the plant when they shift from photosynthetic sink to source (reviewed by Bentley 1977). The concept of extrafloral nectar as secretion of excess carbohydrates to achieve a more balanced carbohydrate/nutrient level has not been supported by experimental evidence (Baker *et al.* 1978).

Hypothesis 2 – to attract protective agents

The plant protection hypothesis has been repeatedly supported in investigations conducted to decide between this and the preceding hypothesis (Janzen 1966, 1967; many studies reviewed in Bentley 1977; Buckley 1982; Jolivet 1986; Koptur 1992a; and many newer examples discussed in this chapter), notwithstanding that interactions vary spatially and temporally, and several studies have found no evidence of protection.

Hypothesis 3 – to prevent flower plundering

Kerner (1878) proposed that the role of extrafloral nectaries is to distract ants from flowers. Plants potentially lose energy invested in floral rewards if these rewards were taken by non-pollinating visitors like ants, so if ants could be occupied outside of flowers, the floral rewards could be "better spent" on worthy pollinators. Though some floral nectars appear to be repellent to ants (Feinsinger and Swarm 1978; Guerrant and Fiedler 1981; Prys-Jones and Willmer 1992), many are readily eaten when accessible (Frankie *et al.* 1981; Koptur and Truong 1998; Rico-Gray *et al.* 1998). Due to their ubiquity and abundance it is not surprising that ants are known to pollinate certain species (Hickman 1974; Peakall *et al.* 1991; Gomez and Zamora 1992, 2000; Gomez *et al.* 1996; Bosch *et al.* 1997; Puterbaugh 1998; Schuerch *et al.* 2000) despite apparent drawbacks, such as limited pollen movement and antibiotic substances on ant-bodies which negatively affect pollen germination and pollen tube growth (Beattie *et al.* 1984; Wagner 2000). Though ants assist seed set in east African acacias by protective patrolling during flowering and fruit development, they are repelled from flowers by a volatile chemical signal during the time they might interfere with pollination (Willmer and Stone 1997). Recent experimental work shows such floral repellents to be widespread among plants, to be effective against most ants, and to potentially prevent ants from parasitizing plant–pollinator mutualisms (Ghazoul 2001).

An innovative approach to testing Kerner's hypothesis was taken by Wagner and Kay (2002). These researchers conducted experiments with artificial plants bearing different arrays of nectars of different qualities to simulate floral nectar and extrafloral nectar. They found that fewer ants (of both species tested) visited floral nectaries when extrafloral nectar sources were present, evidence that extrafloral nectaries might indeed distract ants from flowers. They found that workers of one ant species preferred sugar solutions with amino acids over sugar alone, as has been demonstrated for other species (Lanza 1988, 1991; Bluthgen and Fiedler 2003), corroborating the idea that extrafloral nectars' relatively high concentrations of amino acids have evolved under selection pressure from ants.

Hypothesis 4 – to lure ants away from tending honeydew-producing insects

Becerra and Venable (1989) published a thought-provoking idea that extrafloral nectar production is selected to distract ants from homopterans, reducing recruitment of ant-tended insects and concomitant damage to plants. Many researchers responded with observations and experiments from their own systems (e.g. Del-Claro and Oliveira 1993), mostly refuting their hypothesis.

Fiala (1990) reported that more ants visit homopterans than extrafloral nectaries on six species of *Macaranga*. She reasoned that nectar secretion may be less constant than honeydew, and this may be why ants prefer scale insects. Bluthgen *et al.* (2000) observed that honeydew collection from Homoptera in the Amazonian rainforest canopy was usually monopolized by a single species of dominant ant, whereas extrafloral nectaries, in contrast, attracted a wider array of ants, with more co-occurrence of ant species on plants with nectaries. Dejean *et al.* (2000b) came to similar conclusions for the ant mosaic in a Cameroonian rainforest: dominant ants prefer Homoptera, the rest depend on extrafloral nectaries. In South Africa, *Anoplolepis steingroeveri* ants prefer homopterans to extrafloral nectar of *Mimetes fimbriifolius* (Proteaceae), and two species of *Crematogaster* commonly tended scale insects and nested in Proteaceae plants with extrafloral nectaries (Zachariades and Midgley 1999). Ants in Mexico have been observed to switch between extrafloral nectar and honeydew, preferring extrafloral nectar in the driest conditions (Moya-Raygoza and Larsen 2001). Also, Rico-Gray (1993) reported that two-thirds of ant species in lowland dry forest of Veracruz (Mexico) foraging for floral nectar switched to homopteran honeydew, with an alternating pattern through the year. However, another recent study (Engel *et al.* 2001) found that ants visited the more concentrated extrafloral nectar even in the presence of the higher quality (containing melezitose) honeydew from aphids. See Box 3.2 for additional examples of the relative attractiveness of extrafloral nectar and honeydew to ants.

All hypotheses considered

These four hypotheses are not mutually exclusive, and they all have received some support. Undoubtedly they all provide valid explanations in specific cases. However, the most generally applicable seems to be the second. Extrafloral nectaries have most likely been selected because of the selective advantage imparted to individuals that possess them, and predatory insects visiting the nectaries and providing the plants with some protection is the most likely evolutionary scenario. There are certainly examples of plants with both nectaries and ant-tended Homoptera, but in most cases the ants prefer the honeydew to extrafloral nectar (see also Box 3.2). And ants do like floral nectar, when they can get it, though they may often prefer extrafloral nectar due to its higher concentrations of sugars and amino acids. So extrafloral nectaries may serve myriad functions, but may primarily have evolved to promote protection of plant parts vulnerable to herbivores.

Box 3.2 Ants, extrafloral nectar, and honeydew

According to some authors, phloem sap can be extracted in two main forms: extrafloral nectar and honeydew (Blüthgen *et al.* 2000; Blüthgen and Fiedler 2002). (We will allow them to overlook floral nectar and plant sap exuded through fissures in the plant body.) Extrafloral nectaries attract a wider array of ants than honeydew, with more co-occurrence of

Figure 3.2 *Paratrechina longicornis* ants and coccid scale on cultivated *Annona* sp. In Miami.

ant species utilizing it than honeydew sources (which are more often monopolized by dominant ant species). Extrafloral nectaries are perhaps more important for general ant nourishment. High-performance liquid chromatography (HPLC) analyses of honeydew and nectar reveal that honeydew sources have a higher number and higher concentrations of amino acids than most nectar sources (Blüthgen *et al.* 2004; Wäckers, Chapter 2). Ants tending Homoptera often protect their Homoptera from enemies (Del-Claro and Oliveira 1999, 2000) and may protect plants hosting the Homoptera in ways similar to ants visiting extrafloral nectaries (Messina 1981; and others, see below) (Fig. 3.2). However, the majority of honeydew-producing herbivores are not tended by ants (Bristow 1991; Sakata and Hashimoto 2000), and ants do not always benefit honeydew-producing herbivores.

Homopterans may appear at first to be insect analogs of extrafloral nectaries (Dansa and Rocha 1992; Koptur 1992a), and interactions between ants and Homoptera are considered mutualistic (Way 1963; Bach 1991; Del-Claro and Olivera 1999, 2000), but unlike the secretion of extrafloral nectar, the plant has no control over how much sap the honeydew-producing insects ingest (Becerra and Venable 1989). Some amount of control may be effected by the tending ants, and indeed the resident ants of many myrmecophytes tend honeydew-producing insects in or on the plant body. In turn, Homoptera may attract ants by honeydew flicking: *Guayaquila xiphias* treehoppers flick honeydew to attract ground-dwelling ants to tend the treehoppers on their host plants (Del-Claro and Oliveira 1996; Oliveira *et al.* 2002). Lepidoptera and Homoptera may interact in unusual ways:

a Neotropical riodinid butterfly, *Alesa amesis*, was discovered to be entomophagous (previously unknown in New World Lepidoptera). It oviposits preferentially on a variety of host plants upon which one ant species tends Homoptera (DeVries and Penz 2000), not for their honeydew, but for the caterpillars to eat the homopteran nymphs.

Cushman (1991) postulated that host plants could mediate (ant-tended) herbivore–ant interactions via differences in plant host quality and effects on tended-herbivore fitness. Indeed, some ants switch their roles as mutualists and predators, tending insects for honeydew but also eating the same insects at certain times. In some circumstances, plants may benefit from ants tending Homoptera if ants deter herbivory by other insects (Messina 1981; Compton and Robertson 1988, 1991; Dansa and Rocha 1992; Rashbrook *et al.* 1992; Figueiredo 1997; Moog *et al.* 1998).

Some aphids may attract ants, while others may repel ants (Sakata and Hashimoto 2000); ants preferred tending *A phiscraccivora* to extrafloral nectaries of *Vicia faba* and avoided tending *Megoura crassicauda* in microcosm experiments in Japan. Ants tending *A. craccivora* were more likely to consume *Megoura*. Offenberg (2000) maintains that the evolution of extrafloral nectaries and the evolution of ant–aphid associations may be correlated, and that aphid species (in two families) associated with ants tend to utilize host plants with extrafloral nectaries, and that aphids on host plants with extrafloral nectaries are more likely to evolve associations with ants.

Ant–plant mutualism

Obligate relationships between ants and plants are found in many myrmecophytes, i.e., plants with inhabitant ants, nesting in special structures or hollow stems (Janzen 1966, 1967; Jolivet 1986, 1998). Ants may even induce domatia formation in some species (Blüthgen and Wesenberg 2001). Many myrmecophytes provide food for their ants via nectar and/or food bodies. *Acacia cornigera* supplies its resident *Azteca* ants not only with extrafloral nectar, but also with lipid-rich Beltian bodies produced on the tips of leaflets (Janzen 1966, 1967). Interestingly, myrmecophytic *Acacia* species in Africa apparently produce only extrafloral nectar, while those in central America produce both nectar and food bodies. In the genus *Leonardoxa* there is a match between nectary size (and number) in plants and tending of homopterans by associated ants (McKey 1991); nectar and homopteran secretions are alternative food for ants. Thus on many myrmecophytes nectaries are lacking and ants may tend honeydew-producing insects on the plants.

The presence of ants can also directly influence the production of food rewards produced by the plant, as demonstrated experimentally for food body production in *Macaranga triloba* (Heil *et al.* 1997). The production of food bodies inside the stems of *Piper coenocladum* takes place in response to occupation of their hollow stems by ants (Risch and Rickson 1981; Letourneau 1983). *Cecropia* feed the ants that nest in their hollow stems via Müllerian bodies produced on specialized areas of the leaf bases (Janzen 1969; Schupp 1986). Some plants provide only pearl bodies, produced on the surface of the leaves, e.g., *Ochroma* and other species (O'Dowd 1982) and *Maieta guianensis* (Vasconcelos 1991).

In their study of Panamanian forest plants, Schupp and Feener (1991) found that plants with ant rewards (extrafloral nectaries and/or food bodies) are overrepresented in secondary habitats. Ants are much more abundant on *Caryocar brasiliense* shrubs than on nearby plants without extrafloral nectaries, and are much more likely to attack termite baits and presumably insect herbivores on *Caryocar* plants (Oliveira 1997). Though this protection did not translate into greater fruit set on ant-tended individuals of *Caryocar*, another cerrado plant (*Qualea multiflora*) experienced less damage to buds and flowers when ants were not excluded from plants, and plants with ants had greater fruit set (Del-Claro *et al.* 1996). Ant visitors to the extrafloral nectaries of *Opuntia stricta* substantially reduced herbivore damage and increased fruit set by 50% on ant-tended branches over ant-excluded branches (Oliveira *et al.* 1999). Exclusion experiments on *Stryphnodendron microstachyum* saplings showed that ants visiting extrafloral nectaries benefit plants, not by killing herbivores but by bothering them, so that they damage plants less, and ant-visited saplings grew taller than ant-excluded individuals (De la Fuente and Marquis 1999). Some myrmecophytes benefit from the presence of ants not only in reduced folivory, but may hold their leaves longer and gain higher stature due to ant occupation (Fonseca 1994).

In most ants, only workers collect the nectar, sometimes transferring it to other workers to eat or to feed the rest of the colony. Some ant species show behavioral specialization, with some workers serving as prey-hunters, and others as nectar-collectors (Passera *et al.* 1994). Such task partitioning (Ratnieks and Anderson 1999) may make for more efficient patrolling and plant protection, where dedicated foragers may be more likely to protect the resources important to their colony.

Many plants with extrafloral nectaries have been shown to benefit from associations with more than one species of ant, though ant species often differ in their protective ability (Schemske 1982; Koptur 1984a; Mody and Linsenmair 2004). In Cameroon, some ants (arboreal-nesters with diurnal activity) visiting the extrafloral nectaries of the pioneer tree *Alchornea cordifolia* provided substantial protection against the variegated locust, *Zonocerus variegatus*, while other species (ground-nesting, nocturnally active arboreal foragers) did not, except during outbreaks of the locust (Dejean *et al.* 2000a). Daily turnover of ant species has been documented in a number of systems, such as *Ouratea hexasperma* in Brazilian cerrado (Oliveira *et al.* 1995) and *Opuntia stricta* (Oliveira *et al.* 1999). Sympatric species with extrafloral nectaries may host different ant assemblages that vary between day and night (Hossaert-McKey *et al.* 2000). Labeyrie *et al.* (2001) found that *Passiflora glandulosa* benefits from visits from two sympatric ant species in French Guiana, one of which is active diurnally, the other nocturnally. Sympatric *Passiflora* species studied in successional neotropical forests of Costa Rica were not associated with particular ant species, or vice versa (Apple and Feener 2001).

Even plants with demonstrated mechanical defenses may benefit from ants visiting extrafloral nectaries in some circumstances: spinescent *Acacia drepanolobium* are protected from (young) giraffe herbivory by ants visiting extrafloral nectaries on shoot tips, acting aggressively against the vertebrates (Madden and Young 1992). Other impressive examples of a mechanically defended plant that benefits from ants are seen in species of *Opuntia* (Pickett and Clark 1979; Oliveira *et al.* 1999).

Non-protective predators and counter-adapted herbivores

Although ants and other predators feed at extrafloral nectaries of South African Proteaceae, they do not reduce herbivory (Zachariades and Midgley 1999). Similar conclusions have been drawn from other southern hemisphere systems (O'Dowd and Catchpole 1983; Rashbrook *et al.* 1992) and elsewhere in the world (Barton 1986; Boecklen 1984; Tempel 1983; Heads and Lawton 1984; Lawton and Heads 1985).

A variety of herbivores are immune to ant predation, protected by their behavior or feeding mode (Heads and Lawton 1985; Eubanks *et al.* 1997). *Eunica bechina* caterpillars can find refuge from predatory ants on *Caryocar* in the Brazilian cerrado by climbing to the end of stick-like frass chains they build at leaf margins (Oliveira *et al.* 2002); *Smyrna blomfildia* caterpillars exhibit similar behavior on *Urera* plants (Machado and Freitas 2001). See Sabelis *et al.* (Chapter 4) for additional examples of what can be viewed as cheaters and thieves in the food-for-protection mutualism.

Biological control using extrafloral nectar

Biological control can be promoted by co-planting crop species with species possessing extrafloral nectaries (see Wilkinson and Landis, Chapter 10 and Gurr *et al.*, Chapter 11). Both floral and extrafloral nectar resources can be important in supporting insect parasitoids in agroecosystems (Stapel *et al.*

1997; Baggen *et al.* 1999; Olson *et al.*, Chapter 5; Heimpel and Jervis, Chapter 9). Stettmer (1993) suggests that extrafloral nectar of the cornflower *Centaurea cyanus* is an important food source for many beneficial insects and may be used to stabilize their population densities in agriculture when growing as a weed in crop borders. Floral nectar is generally a much shorter-lived potential resource for beneficial insects than extrafloral nectar. Ants can be effective biological control agents in neotropical agroecosystems: after experimentally reducing ants numbers with insecticides, pest pressure increased in maize monocultures and maize–bean bicultures (Perfecto and Sediles 1992).

The nectaries of *Theobroma cacao* can support *Pachycondyla* ants (predators of a variety of phytophagous insects) for biological control in cacao plantations (Valenzuela-Gonzalez *et al.* 1994), where there is a large arboreal ant community (Majer *et al.* 1994). Cashew has leaves covered with extrafloral nectaries, and inflorescences develop lying on the surface of leaves; the inflorescences also have nectaries on floral bracts (Rickson and Rickson 1998). Cashew crops may benefit from protection by ants and other predators if plantings are made with appropriate considerations for encouraging ants in countries where ants are normally regarded as undesirable in agroecosystems (Rickson and Rickson 1998). Even homopterans (extrafloral nectary analogs) have been suggested as a way to attract ants onto plants to protect them from gypsy moth attack (Weseloh 1995).

Co-adaptation and co-speciation

Some myrmecophytes produce extrafloral nectar (e.g., swollen-thorn *Acacia* spp.), but in many genera the ant-attracting trait of extrafloral nectar production is lost in favor of food bodies or hosting honeydew-producing insects. Food rewards offered by *Macaranga* in Malaysia affect ant colony size (Itino *et al.* 2001a), particularly in species where ants tending Homoptera regulate their own biomass by regulating the biomass of their honeydew-producers; in *Macaranga* species where ants feed on food bodies produced by the plants, ant colony size is larger. The authors postulate that energy transfer directly to ant from plant may be more efficient than transfer through another trophic level. In the paleotropical genus *Macaranga*, only the glands of non-myrmecophytic species function as nectaries; liquids secreted by glands of myrmecophytic species do not contain sugar (Fiala and Maschwitz 1991). Young plants of *Macaranga hosei* secrete extrafloral nectar until they are colonized by their mutualist ant partner. McKey (1988) described the same phenomenon for *Barteria*, where young plants have extrafloral nectaries, but larger plants, which have developed their domatia, lack extrafloral nectaries.

Some myrmecophytes provide compelling examples of co-accomodation (*Leonardoxa* spp.: McKey 1991) and co-speciation (*Macaranga* spp.: Itino *et al.*

2001b). *Leonardoxa africana* T3 feeds its resident ants via both extrafloral nectaries and Homoptera (Gaume and McKey 1998), and *Aphomomyrmex afer* eat small herbivore larvae, and disturb the feeding of larger larvae, protecting the plants against their microlepidopteran herbivores. Even small ants are very important in protecting plants against smaller chewing, and especially sucking, insect herbivores (Gaume *et al.* 1997); *L.africana* leaves with *Petalomyrmex* ants excluded did not expand as much as ant-tended leaves, likely due to damage from sucking insects. *Leonardoxa africana* plants benefit more from larger ant colonies (Rocha and Bergallo 1992; Gaume *et al.* 1998), and colonies are bigger when resident ants tend pseudococcids rather than coccids (pseudococcids are less expensive for the plant to support).

Myrmecophytic African ant acacias have large nectaries and hold their leaves longer than non-myrmecophytic congeners, and one species supports at least nine ant species, with widely varying relationships with the host plants (Young *et al.* 1997). All of these mutually exclusive resident ants collect nectar, some tend scale insects inside the plants, some eat the nectaries, and one species eats the axillary shoots rendering the host tree sterile but inciting more terminal shoots with healthier leaves and more extrafloral nectar.

Future directions

Interactions between plants and their protective agents fueled by nectar have repeatedly been suggested to have great potential for biological control. Ants especially may have drawbacks and present health hazards to agricultural workers, so ant protection is not always a simple solution, especially in areas where fire ants are abundant. This direct form of plant protection is not the only interaction that could benefit crops, however, and using nectar to encourage other predators and parasitoids of crop herbivores should certainly be pursued (see, e.g., Van Rijn and Sabelis, Chapter 8 and Heimpel and Jervis, Chapter 9).

We need to know much more about the ways that plants control the insect visitors to their nectar. Much recent work has examined how herbivory and other damage to plants can elicit greater production of nectar, and the mechanisms that may underlie this evolutionarily advantageous plant response. Inducible nectar production appears to be a widespread phenomenon, but many more systems warrant investigation. We have not yet adequately investigated all the environmental influences (such as nutrients, water, and sunlight) on nectar secretion (amounts and composition). More work is also needed in determining what makes some plants more attractive than others to various ants, and other nectar collectors.

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