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Extrafloral Nectary-Mediated Interactions Between Insects and Plants

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I. NECTAR, NECTARIES, AND EXTRAFLORAL NECTARIES

A. DEFINITIONS

Nectaries are plant secretory structures of diverse morphology and anatomy. They can be located on virtually any part of the plant body (nectary locations are usually characteristic of the species or genus), but the most familiar nectaries are those located in flowers.

The nectar produced in floral nectaries serves as a reward for floral visitors and is the primary physiological cost paid by the plant in nectar-based pollination systems. The animals that imbibe and collect nectar inadvertently transfer pollen (thus benefitting the plant), but visit flowers for the purpose of meeting their energetic and nutritional needs.

The remainder of nectaries are located outside the flowers and are, therefore, termed *extrafloral* nectaries. The majority of extrafloral nectaries do not involve pollination, and their function is not as uniform as that of floral nectaries, as this review will examine. They are visited by a wide variety of animals for the energy and nutrition considerations mentioned above; however, the associated effects on the plants range from beneficial (patrolling of plant surfaces and disturbance of herbivores; enhanced predation and parasitism of plant feeders) to harmful (attraction of herbivorous insect adults who, in turn, oviposit on the plant; distraction of nectar-collecting pollinators from flowers), depending on the ecological context.

This paper will examine the importance of extrafloral nectaries in mediating interactions between insects and plants. First, I will consider the function and distribution of extrafloral nectaries in the plant kingdom. Second, I will examine the reciprocal effects of nectar on insects, and insects on nectar. Third, I will consider the myriad interactions between plants and insects based on extrafloral nectaries. I will then proceed to examine the complex interactions between insects visiting nectaries on plants with extrafloral nectaries and the resulting effects on the plants.

B. MORPHOLOGY AND ANATOMY

1. Locations on the Plant Body

Extrafloral nectaries may be found on virtually every vegetative and reproductive structure.[106] On leaves, nectaries occur on the petiole, the rachis (of compound leaves), the upper and lower surfaces of the blade, the leaf margin, and on stipules (outgrowths of the leaf base, common in Leguminosae and Rosaceae). Nectaries may occur on young stems, especially in the vicinity of nodes (e.g., *Polygonum* spp.[305]). In a few species, nectaries are located on the cotyledons (e.g., *Ricinus communis*[359]).

Extrafloral nectaries on inflorescences and on the external part of flowers, but not directly involved with pollination, are common. Nectaries may be on the outer surface of bracts or involucres (e.g., *Helianthella quinquenervis*[163]), on sepals (e.g., *Bixa orellana*[32]), or petals (e.g., *Paeonia* spp.[277,359]). Some plants have extrafloral nectaries that are produced outside the flowers but still function in attracting pollinators (see Section IIIA).

In some plants the floral nectaries continue to function after the corolla abscises. This phenomenon has given rise to the term *postfloral* nectaries (e.g., *Mentzelia nuda*;[185] *Thevetia ovata,* personal observation). Some plants have glands on the surface of developing fruit (e.g., *Crescentia* and other Bignoniaceae;[110] *Annona glabra,* personal. observation).

Other structures on the plant body may look like nectaries but produce other materials (e.g., hydathodes, oil glands, and resin glands). It is important to analyze secretions and to determine that nectar is being secreted rather than resins,[162] oil, or water.[209] The presence of sooty molds can indicate whether or not sugar secretions are present (Pemberton, personal communication), but even here, sugar may be from Homoptera rather than nectaries.

2. Structure, Complexity, and Types

The levels of complexity vary among extrafloral nectaries. The simplest nectaries are nonvascularized, without a well-defined internal structure. These may be externally formless, pit nectaries, or most commonly, scalelike nectaries.

All nectaries that are known to be vascularized have a well-defined external structure, ranging from sessile to raised to stalked glands (trough, saucerlike, to cupular in shape). Most nectaries are vascularized by both phloem[124] and xylem, the vascular strands terminating beneath the secretory cells.[101] Some nectaries are only fed by phloem; nectaries are distinguished from hydathodes by vascularization, at least in part, by phloem. The secretory cells are located below the epidermis (one to three layers thick), and have conspicuous nuclei and dense cytoplasm, numerous mitochondria, and abundant endoplasmic reticula, indicative of high metabolic activity.[100-102]

Extrafloral nectaries range in size and complexity from a simple pore (or single cell delivering its contents) to large, stalked, cup-shaped structures centimeters in diameter. Many botanists have sought to classify extrafloral nectaries in various groups of plants using a variety of criteria: developmental patterns, organographic relationships, and

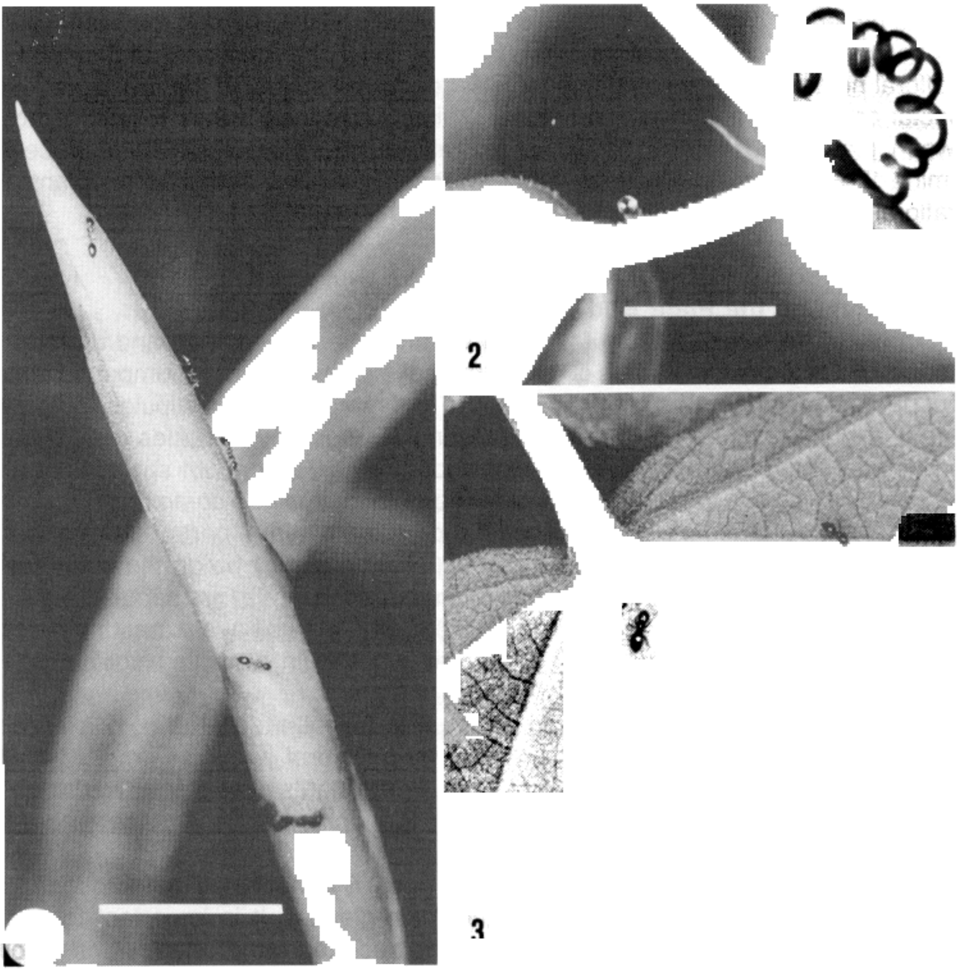

PLATE 1. Bar scales = 1 cm.
FIGURE 1. Ants visiting formless nectaries on young inflorescence of *Tillandsia balbisiana* (Bromeliac
FIGURE 2. Nectar droplet on elevated nectary of *Passiflora suberosa* (Passifloraceae).
FIGURE 3. Ants visiting pit nectaries on abaxial leaf surface of *Urena lobata* (Malvaceae).

phylogenetic distribution.[106] A variety of types of extrafloral nectaries are illustrated in Figures 1 to 7.

Zimmermann[359] categorized extrafloral nectaries according to their structure anc position into six basic groups (a to f below); Elias[106] added a seventh group (g below).

1. Formless nectaries — with no structural specialization, but may be colored in contrast to background (*Costus; Paeonia; Tillandsia,* Figure 1; *Myrsine,* Figure 4)
2. Flattened nectaries — glandular tissue closely pressed against underlying tissue, common on leaf surfaces (*Chrysobalanus,* Figure 5; *Dipterocarpus*)

   Pit nectaries — glandular tissue sunken in tissue of other organs, in depressions as large as or larger than the nectary (*Urena*, Figure 3; *Inga punctata)*

   Hollow nectaries — cavities in other organs with a narrow channel extending to the surface; the cavities are lined with secretory trichomes (*Conocarpus*)

   Scalelike nectaries — glandular trichomes modified for nectar production and secretion (*Mucuna, Bauhinia* stipules, *Plumeria*)

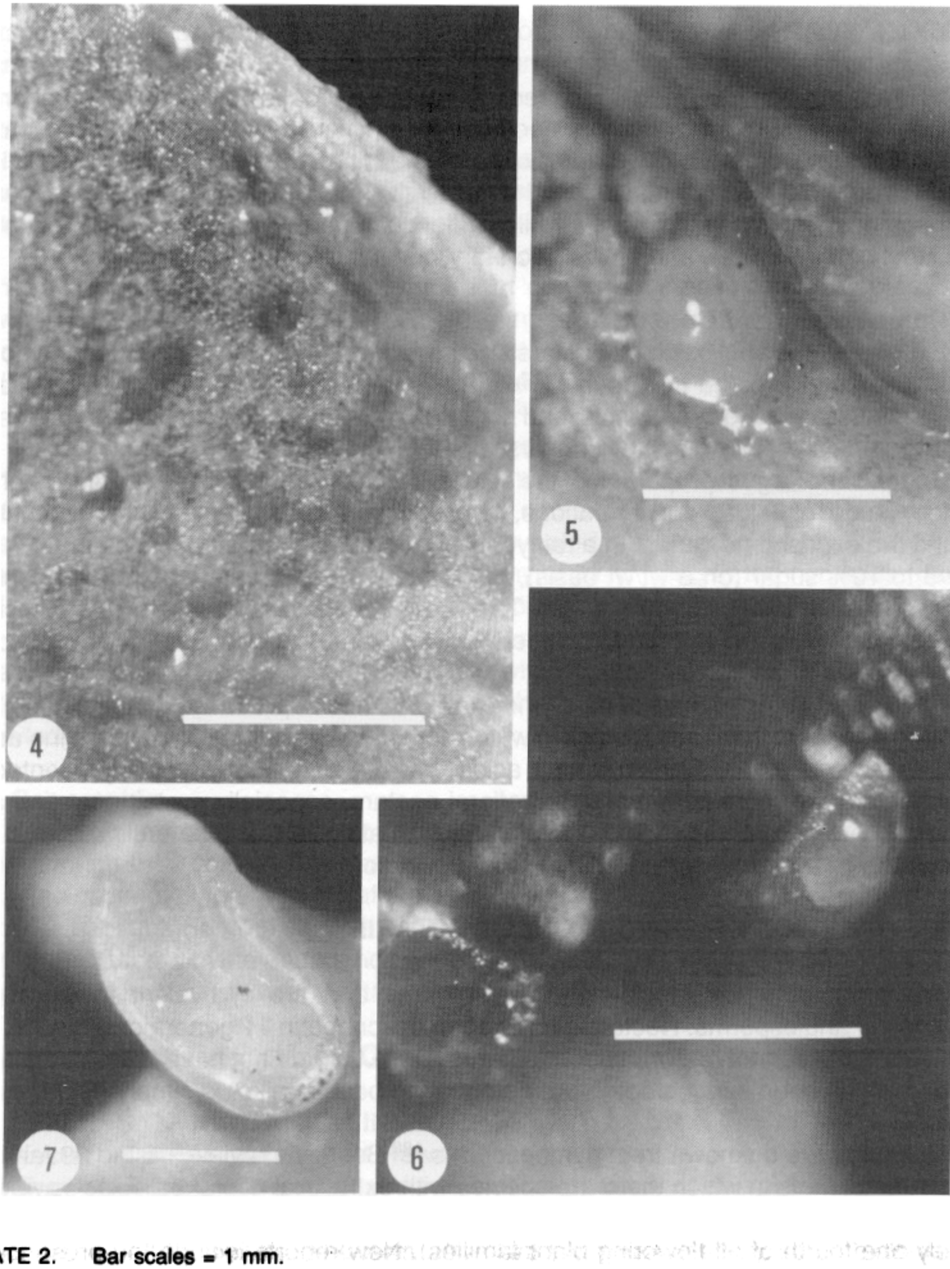

PLATE 2. Bar scales = 1 mm.
FIGURE 4. Formless nectaries of *Myrsine floridana* (Myrsinaceae) located on abaxial leaf surface at base of leaf on either side of midrib.
FIGURE 5. Flattened nectary on new red leaf of *Chrysobalanus icaco* (Chrysobalanaceae) located on abaxial leaf surface near leaf base.
FIGURE 6. Paired, elevated nectaries on stipels of young leaves of *Erythrina herbacea* (Fabaceae).
FIGURE 7. One of a pair of elevated, cupular nectaries on petiole of *Passiflora alata* (Passifloraceae).

6. Elevated nectaries — nectaries that have glandular tissue raised above ground tissue (except the scalelike, which are in their own category) (*Erythrina,* Figure 6; *Passiflora,* Figures 2 and 7)
7. Embedded nectaries — secretory tissue totally embedded in tissues of other organs (*Leonardoxa, Vigna* inflorescence nectaries)

C. EXTRAFLORAL NECTAR

1. Secretion

Nectar secretion has been described as a passive process by some researchers,[33] and some have purported to show nectaries to function as "sap valves," eliminating excess carbohydrates from growing points of the plant when they shift from sink to source status. An experimental test of the "sap-valve" hypothesis provided no evidence that nectaries function in this way,[17] while evidence for ecological functions is mounting (see Sections II and III), and active secretory mechanisms certainly exist.

2. Composition and Constitution

Extrafloral nectars, like floral nectars, are aqueous solutions of sugars, amino acids, lipids, and other organic compounds.[12,15] The other compounds include antioxidants and substances (alkaloids, phenols, and nonprotein amino acids) that may be deterrents or are potentially toxic to nectar drinkers.[15,115,140,141,169]

Sugar is the largest proportion of the solutes in nectars, and extrafloral nectars show a wide range of sugar concentrations, largely influenced by the microenvironment around the exposed nectaries. In a rainy, misty climate, the extrafloral nectar may have only 5 to 10% sugar (on a wt/wt basis), but in a sunny, dry climate extrafloral nectars are frequently in excess of 50% sugar. The sugar concentrations of extrafloral nectars show a much wider range than floral nectars of the same species, even when collected from nectaries protected by bags.[205]

Amino acid complements of floral and extrafloral nectar produced on the same plant usually differ,[11] but there are species in which both have the same essential amino acids (e.g., *Inga brenesii*[205]). Certain amino acids that are only sometimes represented in floral nectars are more common in extrafloral nectars, especially cysteine/cystine and lysine, asparagine, and tyrosine,[16] presumably relating to the different nutritional requirements of ant or wasp "guards", and of pollinators.

D. DISTRIBUTION OF EXTRAFLORAL NECTARIES

1. Taxonomic

While not common, nectaries occur in ferns and are equivalent to extrafloral nectaries of angiosperms. Nectaries have been described in 11 genera of ferns.[209] The term *extrafloral* cannot really be used for ferns, since they do not have flowers; the term *extrasoral* has been suggested,[209] but perhaps the best moniker is simply *nectaries* for ferns.

Nectaries are unknown from gymnosperms.[188] Bentley's review[33] listed 39 families of flowering plants in which there are species with extrafloral nectaries. Elias' review[106] shows extrafloral nectaries to occur in 68 angiosperm familes in 35 orders (approximately one fourth of all flowering plant families). New reports include the presence of extrafloral nectaries in the Myrsinaceae,[266] Bromeliaceae, and a variety of subtropical and tropical species that have only recently been discovered to have extrafloral rewards (by observing live plants in the lab or greenhouse, rather than plants in the field with formless, nonobvious nectaries with all reward removed [87,88,311] (personal observation). A list of 93 families and 332 genera in which extrafloral nectaries have been reported to occur is presented in Table 1.

Floral nectaries are not a prerequisite for extrafloral nectaries in a plant species; extrafloral nectaries occur both on plants with floral nectaries (*Passiflora, Inga, Vicia*) and on plants without them (*Acacia, Mimosa, Anadenanthera, Cassia*).

In addition to nectaries that are morphologically part of the plant, arthropod-induced galls can also produce nectar.[348] Pathogens can also induce secretions similar to extrafloral nectar: Percival[278] includes the ergot fungus (*Claviceps purpurea*) and the pycnidia of the rust *Puccinia poarum* in a summary of nectar sources.

2. Life Form

Extrafloral nectaries are found on representatives of all plant life forms: herbs, shrubs, trees, vines, lianas, and epiphytes. They are commonly active on developing parts (e.g., new leaves, flowers, and fruits).

Annual plants (with only one growing season prior to reproduction and death) tend to have extrafloral nectaries in positions that can directly enhance the protection of flowers and fruit (see Section III.F.3); an annual plant may thereby maximize seed production during the single reproductive event.[206] Examples of this are *Vicia sativa*[199] and *Cassia fasciculata.*[19,189] Perennial herbs also often have inflorescence-associated extrafloral nectaries: *Paeonia,*[277] *Costus* spp.,[307,308] and *Calathea ovandensis.*[157]

Vines use other plants for support and, therefore, contact vegetation at many points. Bentley[34] concluded that this life form was more likely than others to capitalize on protection by crawling ants visiting extrafloral nectaries (see Section III.F). Studies of *Passiflora*[320,321] and *Byttneria*[153] vines have revealed that a variety of potentially beneficial insects visit the extrafloral nectaries, many of them flying to the nectaries (parasitoid wasps and flies, see Section III.G), in addition to crawling ants.

A variety of epiphytic flowering plants[87] have extrafloral nectaries; some of these are inhabitants of ant gardens,[196] providing ants with nectar (see Sections III.C. and III.D). Some epiphytic ferns[209] have nectaries, though their ecological role has not yet, to my knowledge, been studied.

3. Geographic

Extrafloral nectaries can be found on plants in both the tropics and the temperate zone, though they are more common in tropical areas (Table 2). Within a geographic area, the cover of plants with extrafloral nectaries usually varies among[182,204,250,276] and within[277] habitats. Some biologists have sought to correlate extrafloral nectary-bearing plant abundance with the abundance or activity of ants at different sites,[31,179,204,207] and in general, have found fewer nectary-bearing individuals in areas with few or no ants.

II. RECIPROCAL EFFECTS

A. EFFECTS OF NECTAR ON INSECTS

1. Nectar as an Attractant and Reward

Since sugars provide a quick and easily utilized source of energy for many kinds of animals (invertebrate and vertebrate), nectar is an appealing and attractive commodity when presented by a plant. The term *attractant* has been used by some biologists to describe the function nectar serves initially for pollinators to flowers,[112] but since the nectar is usually discovered after the animals are attracted by some other means (visual displays, odors, or movement), the term *reward* is more appropriate.

The discovery of the presence of nectar is a compelling force for animals to seek out and use more of the nectar. Agronomists have found that crop cultivars without nectaries will receive better pollination if interplanted with cultivars with nectaries.[44] Ecologists have found that crop plants without nectaries can benefit from beneficial insects attracted and supported by nectar-producing weeds growing around the fields.[5] In addition, ants will recruit to new nectar sources, e.g., artifical nectaries on beans.[31]

Many extrafloral nectaries are colored, providing a visual cue for animals to locate the nectar (*Vicia*, *Pteridium*, *Costus*, *Cassia*, *Lysiloma*). In many, the presence of

Table 1
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
PTERIDOPHYTA all families combined	
Angiopteris (1)	45
Cyathea (1)	45, 310
Drynaria (1)	45, 83, 131
Hemitelia (Cnemidaria) (1)	45, 310
Holostachyum (1)	358
Merinthosorus (1)	358
Platycerium (1)	233
Photinopteris (1)	233
Polybotrya (1)	209
Polypodium (1)	209
Pteridium (1)	149, 150, 151, 213, 230, 215, 217, 271, 288, 336
ACANTHACEAE (Asteridae: Scrophulariales)	
Aphelandra (7)	92, 102
AGAVACEAE (Liliidae: Liliales)	
Sansevieria (5)	16, 335
Yucca (8)	178
ANACARDIACEAE (Rosaceae: Sapindales)	
Family	106
Holigavna (1)	359
ANCISTROCLADACEAE (Dilleniidae: Theales)	
Ancistrocladus (1)	245
ANNONACEAE (Magnoliidae: Magnoliales)	
Annona (8)	personal observation
APOCYNACEAE (Asteridae: Gentianales)	
Plumeria (2)	248
Thevetia (9)	personal observation
ARACEAE (Arecidae: Arales)	
Philodendron (2)	87, 88
Spathodea	293
ASCLEPIADACEAE (Asteridae: Gentianales)	
Calotropis (1,2)	9, 136
Ceropegia (1)	310
Dregea (= *Wattakaka*)(1,2)	9, 136
ASTERACEAE (Asteridae: Asterales)	
Centaurea (1)	178, 359
Helichrysum (1,7)	261
Helianthella (7)	163
Helianthus (1,7)	178, 277
BALSAMINACEAE (Rosidae: Geraniales)	
Impatiens (1,2,4)	16, 109, 277, 323

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
BIGNONIACEAE (Asteridae: Scrophulariales)	
Family	97
Adenocalymma (8)	110
Amphilophium (8)	110
Amphitecna (8)	110
Anemopaegma (6,8)	16, 110
Arrabidaea (1,8)	110, 266
Bignonia (1,6)	160, 310, 331
Campsis (1,5,6,8)	107, 108, 328
Catalpa (1,5,8)	277, 310, 326
Chilopsis (1,6,7)	276
Crescentia (8)	110
Cybistax (1)	266
Distictella (8)	110
Haplophragma (8)	110
Incarvillea (8)	110
Jacaranda (1,8)	250
Kigelia (3)	82, 331
Melloa (8)	110
Memora (8)	110
Newbouldia (1)	310
Pachyptera (7,8)	110
Spathodea (1,8)	110, 310
Tabebuia (1)	268
Tanaecium (8)	110
BIXACEAE (Dilleniidae: Violales)	
Bixa (4,6)	32
BOMBACACEAE (Dilleniidae: Malvales)	
Family	337
Eriotheca (2)	266
Ochroma (1)	259, 260
BROMELIACEAE	
Tillandsia (5)	Keeler, pers. comm.
BURSERACEAE (Rosidae: Sapindales)	
Protium	250
CACTACEAE (Caryophyllidae: Caryophyllales)	
Ancistrocactus (4)	239
Epiphyllum (8)	87, 88
Ferocactus (4, areolar)	42, 277, 304
Opuntia (4, areolar)	276, 279, 359
CAPPARIDACEAE (Dilleniidae: Capparales)	
Family	106
Capparis (1)	359
Cleome (6)	16
CAPRIFOLIACEAE (Asteridae: Dipsacales)	
Sambucus (1,4)	81, 113, 128
Viburnum (1,2,3)	277

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
CARYOCARACEAE (Dilleniidae: Theales)	
Caryocar (6)	263, 266
CARYOPHYLLACEAE (Caryophyllidae: Caryophyllales)	
Silene	80 (suspect — Pemberton)
CEPHALOTACEAE (Rosidae: Rosales)	
Cephalotus (1)	172, 173
CHRYSOBALANACEAE (Rosidae: Rosales)	
Chrysobalanus (1)	340
Hirtella (1)	268, 310
Licania (1)	266
Parinari (1)	310
COMBRETACEAE (Rosidae: Myrtales)	
Conocarpus (2)	190
Laguncularia (2)	340, pers. obs.
Terminalia (2)	10, 266, 268, 359
CONVOLVULACEAE (Asteridae: Polemoniales)	
Cuscuta (1,2,4)	306
Ipomoea (2,6)	23, 177, 181, 188, 329
Pharbitis (*Ipomoea*) (2)	277
COSTACEAE (Commelinidae: Zingiberales)	
Costus (7)	307, 308
CRASSULACEAE (Rosidae: Rosales)	
Adromischus (7)	16
CUCURBITACEAE (Dilleniidae: Violales)	
Family	262
Cayaponia (2)	310
Cucurbita (1)	158, 159, 277
Lagenaria (2)	277, 359
Luffa (1,6)	277, 359
Momordica (1,5)	106, 277, 359
Siolmatra (2)	310
Trichosanthes (1)	277
DICHAPETALACEAE (Rosidae: Celastrales)	
Family	106
Dichapetalum (1)	106, 359
DIONCOPHYLLACEAE (Dilleniidae: Violales)	
Family	245
Dioncophyllum	324
Triophyphyllum (1)	245, 310
DIOSCOREACEAE (Liliidae: Liliales)	
Dioscorea (2)	36, 73, 138, 269, 270, 277, 346, 310

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
DIPTEROCARPACEAE (Dilleniidae: Theales)	
Anisoptera (1)	310
Dipterocarpus (1)	129
Dryobalanops (1)	129
Hopea (1)	129, 310
Monotes (1)	310
Parashorea (1)	310
Shorea (1)	129, 310
Upuna (1)	310
Vateria (1)	310
Vatica (1)	129
EBENACEAE (Dilleniidae: Ebenales)	
Diospyros (1)	10, 70, 268, 277, 359
Euclea (1)	70
Maba (1)	70
Royena (1)	70
ERICACEAE (Dilleniidae: Ericales)	
Vaccinium (1)	277
EUPHORBIACEAE (Rosidae: Euphorbiales)	
Acalypha	310
Alchornea (2)	25, 250
Aleurites (1,2)	28, 29, 310
Aparisthmium	250
Bertya	310
Caperonia	310
Cephalocroton	310
Claoxylon	310
Conceveiba	250
Cnidoscolus (1,2)	Pemberton, pers. comm.
Croton (1,2)	38, 93, 96, 250, 310
Crotonogyne (1)	310
Excoecaria	310
Hevea	79, 123, 272, 310
Hieronyma (1)	268
Hippomane (1)	pers. obs.
Homolanthus (1,2)	352
Hura (1)	106, 359
Jatropha (1,3)	310
Macaranga (1,2)	310, 352
Mallotus (1,2)	26, 277
Manihot (1)	Pemberton, pers. comm.
Mareya	310
Micrandra	310
Pedilanthus (1)	86
Poinsettia (5)	345
Richeria (2)	268
Ricinodendron	310
Ricinus (2,5)	17, 139, 176, 277, 310, 359
Sapium (1,2)	277, 310
Sebastiana (3)	310
Tragia	310

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
FAGACEAE (Hamamelidae: Fagales)	
Quercus alba (1)	Robert J. Marquis, pers. comm.
FLACOURTIACEAE (Dilleniidae: Violales)	
Idesia (2)	277, 359
FOUQUIERIACEAE	
Fouqueria splendens (6)	276
GESNERIACEAE (Asteridae: Scrophulariaceae)	
Codonanthe (1,4,6,8)	87, 88, 195, 357
GOODENIACEAE	
Scaevola (1)	Pemberton, pers. comm.
HUMIRIACEAE (Rosidae: Linales)	
Family	106
Vantanea (1)	359
HYDRANGEACEAE (Rosidae: Rosales)	
Family (rare)	106, doubtful—Pemberton
ICACINACEAE (Rosidae: Celastrales)	
Emmotum	250
IRIDACEAE (Liliidae: Liliales)	
Iris (6)	277
LEGUMINOSAE	
Acacia (1)	48, 49, 52, 57, 167, 236, 237, 238
Affonsea (1)	359
Albizzia (1)	213, 277, 310
Anadenanthera (1)	266, 268
Bauhinia (1,3)	16, 266
Brownea (7)	62, 241
Caesalpinia (1)	10, 277, 310
Calliandra (1)	359
Calpocalyx	241, 310
Canavalia (2,5)	10, 359
Cassia (1,2,5)	19, 43, 189, 213, 241, 266
Copaifera	310
Crotalaria (3,10)	10, 16, 241, 359
Cylicodiscus	310
Delonix (2)	241, 359
Desmanthus (1)	178
Dichrostachys (2)	310
Dipteryx	250
Dolichos (3,5)	277, 359
Entada (3,4)	10, 220, 310
Enterolobium (1)	266, 268, 310
Erythrina (3,6)	220, 316, H. Hernandez, pers. comm.

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
LEGUMINOSAE (continued)	
Gagnebina (1)	359
Gilbertiodendron (1)	310
Glottidium (1)	241
Glycyrrhiza (1)	178
Glycine (1)	241, 35
Hardenbergia (3)	213
Hippocrepis (3)	241
Humboldtia (1,3)	
Hymenaea (1)	
Inga (1)	201, 202, 250, 310
Lablab (3)	241, 359
Leucaena (2)	241
Leonardoxa (1)	105, 240
Lotus (3)	241, 285
Lysiloma (1)	359
Macrolobium (1)	310
Mimosa (1)	250, 310, 359
Mucuna (3)	220
Newtonia	310
Parkia (1)	310
Pellegriniodendron (1)	310
Pentaclethra (1,4)	16, 30, 241
Phaseolus (3,5)	277, 359
Physostigma (5)	241, 359
Piptadenia (1)	310, 359
Pithecellobium (1)	85, 104, 250, 310
Plathymenia (1,4)	266, 268, 359
Prosopis (1,2)	276
Robinia (3)	277
Senna (1,2)	241, 359
Serianthes (1)	359
Sesbania (1)	241
Stryphnodendron (1)	266, 268, 359
Vicia (3,6)	117, 199, 208, 211
Vigna (3,5)	210, 273
Xylia (1)	359
LILIACEAE (Liliidae: Liliales)	
Hemerocallis (6)	277
LINACEAE (Rosidae: Linales)	
Linum	106 doubtful
.OASACEAE (Dilleniidae: Violales)	
Mentzelia (9)	184
LOBELIACEAE	
Centropogon (6)	B. Stein, pers. comm.
LOGANIACEAE (Asteridae: Gentianales)	
Family (rare)	106
LYTHRACEAE (Rosidae: Myrtales)	
Lafoensia (1)	266

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
MALPIGHIACEAE (Rosidae: Polygalales)	
Acridocarpus (1)	310
Aspicarpa (1)	310
Gaudichaudia (1)	310
Heteropteris (1)	266, 359
Stigmaphyllon (3)	16, 359
MALVACEAE (Dilleniidae: Malvales)	
Family	166
Alyogyne (1)	313
Cienfuegosia (1)	310
Decaschistia (1)	310
Dicellostyles (1)	310
Gossypium (1,7)	1, 2, 161, 251, 310, 344
Hibiscus (1,6)	10, 277, 310
Julostylis (1)	310
Kydia (1)	310
Thespesia (1)	310
Urena (1)	310
MARANTACEAE (Commelinidae: Zingiberales)	
Calathea (7)	157, 309
Ischnosiphon (7)	16
MARCGRAVIACEAE (Dilleniidae: Theales)	
Marcgravia (5)	290
Norantea (1,5)	268
MELASTOMATACEAE (Rosidae: Myrtales)	
Family (rare)	106
MELIACEAE (Rosidae: Sapindales)	
Carapa (1)	222, 287
Cipadessa (1)	221
Swietenia (1)	222
MORACEAE (Hamamelidae: Urticales)	
Ficus (8)	69, 250
MUSACEAE (Commelinidae: Zingiberales)	
Family (occasional)	106
MYRSINACEAE (Dilleniidae: Primulales)	
Myrsine (1)	Pemberton, pers. comm.
Rapanea (1)	266
NEPENTHACEAE (Dilleniidae: Sarraceniales)	
Nepenthes (1)	172, 173, 359
OCHNACEAE (Dilleniidae: Theales)	
Ouratea (1,3)	266
OLEACEAE (Asteridae: Scrophulariaceae)	
Ligustrum (1)	277
Osmanthus (1)	248, 277
Syringa (2)	277

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
ONAGRACEAE (Rosidae: Myrtales)	
Oenothera (1,5,8)	178
ORCHIDACEAE (Liliidae: Orchidales)	
Family	170
Ansellia (4,5)	20
Arundina (6,8)	187
Aspasia (5,6)	119
Brassavola (4,5,6)	119
Catasetum (4,5,6)	119
Caularthron (4,5,6,8)	119
Dimerandra (4,5)	119
Encyclia (4,5)	119
Epidendrum (4,5)	20, 119
Eulophiella (8)	16
Gongora (4,5)	119
Notylia (5,6)	119
Oncidium (4,5)	119
Scaphyglottis (5)	119
Schomburgkia (5,6,8)	298, 299, 300
Spathoglotis (6,8)	165
Trigonidium (4,5)	119
Vanilla (5)	119
PAEONIACEAE (Dilleniidae: Dilleniales)	
Paeonia (6)	277, 359
PASSIFLORACEAE (Dilleniidae: Violales)	
Adenia (1)	310, 359
Crossostema (1)	310, 359
Deidamia (1)	310, 359
Hollrungia (1)	310, 359
Passiflora (1,2,7)	100, 242, 310, 319, 320, 321, 359
Smeathmannia (1)	310
PEDALIACEAE (Asteridae: Scrophulariales)	
Ceratotheca (10)	249
Sesamum (10)	249, 277
Rogeria (10)	249
Sesamothamnus (10)	249
PLUMBAGINACEAE (Caryophyllidae: Plumbaginales)	
Family	106
POACEAE (Commelinidae: Cyperales)	
Andropogon (1)	41, 50, 51
Eragrostis (1,4)	277, 359
POLYGALACEAE (Rosidae: Polygalales)	
Family	106
POLYGONACEAE (Caryophyllidae: Polygonales)	
Polygonum (2)	178, 277, 305
Reynoutria (2)	277

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
PROTEACEAE (Rosidae: Proteales)	
Adenanthos (1)	213
Leucadendron (1)	213
Leucospermum (1)	213
PUNICACEAE (Rosidae: Myrtales)	
Punica (1)	277
RHAMNACEAE (Rosidae: Rhamnaceae)	
Family	106
Colubrina (1)	340
RHIZOPHORACEAE	
Rhizophora (1)	Pemberton, pers. comm.
ROSACEAE (Rosidae: Rosales)	
Crataegus (1)	310
Cydonia (1)	310
Prunus (1,6,7)	98, 198, 274, 277, 291, 310, 339
Pyrus (1)	310
Rosa (2,3,5)	178, 277
Sorbus (1)	310
RUBIACEAE (Asteridae: Rubiales)	
Alibertia	250
Amaioua	250
Faramea	250
Hamelia (9)	33
Morinda (9)	Pemberton & Koptur, pers. obs.
Myrmecodia (9)	88
Sickingia (8)	J. Stout, pers. comm.
Tocoyena (6)	266, 268
RUTACEAE (Rosidae: Sapindales)	
Zanthoxylum (1)	277
SALICACEAE (Dilleniidae: Salicales)	
Populus (1,2)	76, 77, 277, 343
Salix (1,2)	178
SAPINDACEAE (Rosidae: Sapindales)	
Family (rare)	106
SARRACENIACEAE (Dilleniidae: Sarraceniales)	
Darlingtonia (1)	172, 173
Drosera (1)	137, 342
Heliamphora (1)	172, 173
Sarracenia (1)	172, 173
SCROPHULARICEAE (Asteridae: Scrophulariales)	
Melampyrum (1)	310
Paulownia (1,6)	277, 359

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Family (order): Genus (position of nectaries)	Ref.
SIMAROUBACEAE (Rosidae: Sapindales)	
Ailanthus (1)	46, 67, 178, 277
Simarouba	250
SMILACACEAE (Liliidae: Liliales)	
Smilax (1)	10
SOLANACEAE (Asteridae: Solanales)	
Markea (6,8)	87,88
Solanum (1,2,4)	6, 178
STERCULIACEAE (Dilleniidae: Malvales)	
Ayenia (1)	74
Byttneria (1)	8, 153
STYLIDIACEAE (Asteridae: Campanulales)	
Stylidium (1)	212
TILIACEAE (Dilleniidae: Malvales)	
Grewia (1)	277
Triumfetta (1)	pers. obs.
TURNERACEAE (Dilleniidae: Violales)	
Turnera (2)	11
URTICACEAE (Hamamelidae: Urticales)	
Pilea (1)	27
VERBENACEAE (Asteridae: Lamiales)	
Aegiphila (1)	266
Amasonia (1)	235, 246
Avicennia (2)	114, 297
Baillonia (1)	235, 246
Callicarpa (1)	235, 277
Casselia (1)	235, 246
Citharexylum (1)	235, 246
Clerodendron (1)	10, 235, 246, 277
Dipyrena (1)	235
Duranta (1)	235
Faradaya (1)	10, 235
Lampaya (1)	235
Monochilus (1)	235
Raphithamnus (1)	235
Stachytarpheta (1)	235
Vitex (1)	250
VITACEAE (Rosidae: Rhamnales)	
Cissus (3)	16
VOCHYSIACEAE (Rosidae: Polygalales)	
Callisthene (4)	268
Qualea (4,5)	265

Table 1 (continued)
TAXONOMIC DISTRIBUTION OF PLANTS WITH EXTRAFLORAL NECTARIES

Note: Families are listed alphabetically, with order designated afterward. Genera in which nectaries have been reported in at least one species are listed; however, not all species in these genera necessarily have extrafloral nectaries. References for each species are not exhaustive, but only examples. The position of nectaries, if known, is indicated by numbers: 1 = on leaf; 2 = on petiole; 3 = on stipules and/or stipels; 4 = on stems; 5 = on pedicels, peduncles, or stems of inflorescence; 6 = on petals or sepals; 7 = on bracts; 8 = on fruit, capsule, or pod; 9 = on ovary (postfloral); 10 = aborted flowers or bud scars.

glistening droplets of nectar may provide a visual stimulus. While many flowers have odors that serve to attract pollinators, floral and extrafloral nectars themselves do not have obvious odors. Olfaction is probably not involved in the detection of locations of extrafloral nectaries.

2. Insect Nutrition

The same chemicals required for growth of a protozoan or cells of a vertebrate are also required by the cells of an insect.[144] Phytophagous insects require the following components in their diets: water, carbohydrates, proteins and amino acids, lipids, water-soluble vitamins, minerals, water, nucleic acids, purines, and pyrimidines.[125] In addition, sterols and certain fatty acids are required by most species.[144] Many insect predators (members of the Neuroptera, Heteroptera, Coleoptera, Lepidoptera, and Hymenoptera) eat both insects and noninsect foods.[143] Predators and parasitoids have the same qualitative nutritional requirements for larval growth and development as phytophagous insects,[143] but quantitatively predators require a much higher ratio of protein to carbohydrate in their diet (1:1 in species studied) than plant feeders.

Insects from 10 orders have been documented taking nectar or visiting nectaries (Table 3). The most commonly noted insect visitors to extrafloral nectaries are Hymenoptera, followed by Diptera and Lepidoptera. Nectars and honeydew are foods for many entomophagous insects[142] and are important supplements to encourage the control of plant pests by beneficial insects. Some insects may eat only plant or animal tissue as larvae, but nectar as adults; and others get nutrition from other sources, in addition to nectar (pollen, fruit, animal tissue, secretions, blood) throughout their lives. The extent to which an insect depends upon nectar in its diet is related in part to the nutritional value of the nectar. For example, floral nectars used by long-lived adult Sphingidae (Lepidoptera), which feed on only nectar, have lipids that may replenish the fat body and prolong the life of the moth.[205] Certain Lepidoptera (*Heliconius*) enrich their diet of nectar by soaking pollen grains in nectar, increasing the amino acid concentration of the solutions they imbibe.[132]

Nectar use increases the longevity of many beneficial insects. The longevity of the parasitoid *Campoletis sonorensis* was reduced, and its host was parasitized less on nectarless than nectar-producing cotton.[229] *Geocoris* spp. (big-eyed bugs) survived longer when caged on nectar-bearing *Polygonum* as opposed to nectarless plants.[64] When prey was scarce, the longevity of *Geocoris pallens* fluctuated according to the availability of extrafloral nectar on cotton.[90] Predatory mites may take plant exudates[94] but rely primarily on pollen and phytophagous mites for their nutrition.

Nectar provides an important source of nutrients for adult Lepidoptera. The size of the fat body in adult Lepidoptera is related to larval size and larval nutrition, and larval nutrition may generally determine the reserves available for oogenesis.[66] Nonetheless, the longevity of many adult Lepidoptera is positively influenced by nectar consumption, thereby prolonging reproductive life; water and nutrients assimilated by adult females

Table 2
COVER OF PLANTS WITH EXTRAFLORAL NECTARIES IN DIFFERENT LOCATIONS – TEMPERATE TO TROPICAL

% Mean cover	Location	Vegetation types	Ref.
0%	N. California, USA	Native grassland 0% Riparian forest 0% Deciduous forest 0% Chapparal 0%	180
0 – 14.2%	Nebraska, USA	Deciduous forest 1.8% Riparian forest 1.3% Tallgrass prairie 0% Sandhills prairie 8.3–14.2%	182
0 – 27.8%	S. California, USA	Desert bush scrub 0.1–6.6% Desert wash 23.9–27.8% Sand dunes 0–1.4% Yucca-agave 3.7%	276
7.5 – 55%	Korea	Deciduous forest 7.5%, 23%, 55%	277
2 – 34%	Everglades Florida, USA	Sawgrass prairie 2% Rockledge pinelands 34% Hardwood hammock 23%	204
0 – 28%	Jamaica	Forested second growth (0 m) 28% Same, at 1310 m 0%	179
7.6 – 20.3%	SE Brazil	Cerrado (woody spp. only)	266
21.6–31.2%	SW Brazil	Cerrado (woody spp.)	266, 268
17.6–53.3%	Amazonian Brazil	Terra firme forest 19.1% Successional forest 42.6% Buritirana 29.7% Shrub canga 50%	250
10–80%	Costa Rica	Tropical dryforest hillside 40–80% Tropical riparian forest 10–40%	31
0–22%	Costa Rica	Lowland rain forest (0 m) 1–8% Lower montane cloud forest (1500 m) 3–22% high montane oak forest (3000 m) 0–3%	207

support metabolism for egg maturation.[66] For example, sugars in the adult diet enhance female longevity and the number of egg clusters in *Euphydras editha*.[103] DeVries and Baker[93] found that the ant-tended caterpillars of the myrmecophilous riodinid butterfly *Thisbe* that drank extrafloral nectar grew substantially larger than their counterparts that did not drink nectar. Presumably these larvae gave rise to larger adult females that could lay more eggs.

Table 3
ARTHROPOD NECTAR DRINKERS

	Family (or superfamily)	Ref.
ARANEAE		
	Oxyopidae	
	Salticidae	153
DIPTERA		
	Agromyzidae	153
	Aulacigastridae	153
	Blepharoceridae	99
	Cecidomyiidae	92, 153
	Ceratopogonidae	99, 153
	Chironomidae	153
	Chloropidae	153
	Clusiidae	153
	Culicidae	99
	Dolichopodidae	153, 177
	Drosophilidae	153, 254
	Lauxaniidae	153
	Milichiidae	153
	Muscidae	177
	Otitidae	177
	Platystomatidae	177
	Psychodidae	99
	Richardiidae	153
	Sarcophagidae	177, 286
	Sciaridae	153
	Sciomyzidae	177
	Sepsidae	153, 177
	Simuliidae	99
	Somatiidae	153
	Stratiomyidae	177
	Syrphidae	63
	Tabanidae	99, 177, 349
	Tachinidae	177, 218, 315, 341
ORTHOPTERA		
	Blattidae	153
HEMIPTERA/HOMOPTERA		
	Cicadellidae	92, 153
	Fulgoroidea	153
	Membracidae	92
HEMIPTERA/HETEROPTERA		
	Anthocoridae	1, 63, 356
	Lygaeidae	1, 64, 177, 356
	Miridae	1,153
	Nabidae	
	Pentatomidae	1, 177
	Reduviidae	153
NEUROPTERA		
	Chrysopidae	1, 63, 177, 333
	Hemerobiidae	63
	Mantispidae	177

Table 3 (continued)
ARTHROPOD NECTAR DRINKERS

	Family (or superfamily)	Ref.
COLEOPTERA		
	Brentidae	177
	Buprestidae	153
	Cantharidae	153, 177
	Carabidae	153
	Cerambycidae	177
	Chrysomelidae	153, 177
	Coccinellidae	1, 63, 153, 276
	Curculionidae	153, 208
	Dermestidae	254
	Elateridae	177
	Lampyridae	177
	Malachiidae	254
	Melyridae	1
	Nitidulidae	153
	Ostomatidae	177
	Scarabidae	338
	Tenebrionidae	177
DERMAPTERA		
	Earwigs	63
HYMENOPTERA		
	Apidae	89, 92, 121, 148, 177, 338
	Braconidae	1, 153, 202, 254
	Chalcididae	63, 153, 177, 254
	Cynipidae	153
	Diapriidae	63
	Encyrtidae	153
	Eulophidae	153
	Eumenidae	96, 254
	Eurytomidae	153
	Formicidae	
	Dolichoderinae	177, 199
	Formicinae	163, 177, 201
	Myrmecinae	163, 177, 201, 208
	Ponerinae	30, 177
	Pseudomyrmecinae	167, 177
	Halictidae	338
	Ichneumonidae	1, 65, 153, 208, 229
	Megachilidae	96
	Meliponidae	177
	Proctotrupoidea	153
	Pteromalidae	153
	Scelionidae	153
	Sphecidae	153, 177
	Thynninae	338
	Vespidae sensu lato	96, 177
LEPIDOPTERA		
	Lycaenidae	93, 96
	Morphidae	G. E. Martinez, pers. comm.
	Noctuidae	1, 2
	Pyralidae	1
	Riodinidae	93, 177
	Tortricidae	1

Most of the compounds dissolved or suspended in nectar are of nutritive value to insects. The most important of these components are sugars, amino acids, and lipids. Lipids in nectars may be metabolized by nectar-drinking insects, providing energy,[133] and in some cases they may be incorporated into the fat body, providing reserves that may prolong adult life. However, most extrafloral nectars do not contain much, if any, lipids. Some of the other organic constituents of nectar have been found to be of nutritional significance to certain herbivores when the compounds are contained in foliage (e.g., phenols[37]), but these compounds are present in relatively low concentrations in nectar. The water of the nectar can be of great value to insect visitors, especially in xeric habitats.[304]

a. Sugars

Carbohydrates provide energy and organic carbon for all nectar imbibers. When insects drink both nectar and blood, the blood is directed to the midgut, and the nectar sugars are directed to the crop.[47] Sugar solutions stimulate the chemoreceptors of many insects[91] and stimulate further feeding behavior.[55,247] In one study using stable isotope analysis, Fisher et al.[118] found that the carbon contribution of extrafloral nectar to ant diets ranged from 11 to 48%, differing with the ant species and season.

The three most common sugars in extrafloral nectar are the monosaccharides glucose and fructose, and the disaccharide sucrose;[15] other sugars found in nectars are arabinose, galactose, maltose, mannose, melezitose, melibiose, raffinose, and ribose (also cellobiose and stachyose in orchids).[15] Sucrose is the primary translocate in the phloem sap of plants, and the occurrence of other sugars in nectars indicates that nectar secretion is an active selective process, not just passive diffusion. Freshly secreted floral nectar of a plant species has a characteristic sugar composition and correlates with the primary pollinator type.[12,15] Freshly secreted extrafloral nectar may also be characteristic of a species, but since the nectar is immediately exposed to the drying and contaminating effects of the environment (microbes may hydrolyze sucrose to the component hexoses), the ratio of sucrose to hexose sugars is much more variable within a species. In plants with sucrose-dominated floral nectars, extrafloral nectars generally have much lower sucrose/hexose ratios. The sucrose/hexose ratio is, in general, lower for nectars more exposed to the environment, perhaps due to microbial degradation of sucrose: extrafloral nectars are generally not sucrose dominated, but have equal or greater amounts of the hexose sugars.

The preferences of extrafloral nectar drinkers for various sugars has been investigated in several species: fire ants,[295] argentine ants,[199] various ants,[140] and *Paraponera* ants.[30] Ants prefer higher concentrations of sugars over lower concentrations, and they perfer sucrose and glucose over fructose. *Heliothis* moths are most responsive to sucrose followed by fructose and glucose, but do not respond to ribose, rhamnose, and raffinose.[292] Honeybees prefer sucrose to fructose, and fructose to glucose.[347] Bees can utilize most sugars, but certain ones are not nutritionally beneficial (e.g., rhamnose, lactose, melibiose), and mannose is poisonous to honeybees.[148]

b. Amino acids

Amino acids in nectar provide the building blocks for proteins that may be valuable to insects that subsist primarily or exclusively on a nectar diet. All insects that have been studied require the same 10 amino acids (found also to be necessary for the rat): arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine; and the same amino acids are required by adult insects for egg production.[144] However, disproportionately abnormal amounts of a single amino acid can inhibit growth.[275] Studies on honeybees have revealed 10 amino acids to be required by adult honey bees; early in life, these amino acids are obtained from pollen, and later they may be supplied by nectar.[148]

The significance of amino acids in the diet of nectar drinkers has been experimentally investigated[350] with *Colias* butterflies; they preferentially visit flowers that produce nectars rich in amino acids. The availability of amino acids extends butterfly production of maximum-sized eggs in later clutches,[253] while in lepidopteran species whose adults do not eat nitrogen-rich foods, age-dependent decreases in egg size reflect the depletion of nitrogen stores.[66]

The concentration of amino acids in nectar undoubtedly affects the taste of nectar.[16] Amino acids are detectable by the chemosensors of insects such as flies.[317] Flesh flies prefer sucrose solutions containing amino acids at concentrations comparable to those in floral nectar over plain sucrose;[286] they avoid sucrose solutions with histidine and lysine, but prefer glycine, at abnormally high concentrations. Similarly, fire ants prefer certain amino acids over others.[295] When given a choice between nectar solutions containing only sugar and nectar solutions containing sugars and amino acids, some insects have shown a preference for those containing both sugars and amino acids[164,214] (Koptur unpublished data).

Herbert and Irene Baker have observed that there seem to be two types of extrafloral nectars: those with high concentrations of amino acids and those with low concentrations. They suggested that this may correspond with the dietary habits of the ants that have coevolved with these plants: ants that are exclusively nectar drinkers would benefit from nectar rich in amino acids, whereas ants that eat insects and other animals would get their amino acids elsewhere and use nectar only as a source of liquid and ready energy. Hagen[142] postulated that the presence of some, but not all, the essential amino acids in some nectars may have evolved to ensure the presence of certain kinds of insects, but to prevent them from being totally dependent on nectar. When ants are not supplied all the amino acids they require for their broods, they become more aggressive in their patrolling and prey seeking.

3. Oviposition

A variety of Lepidoptera have been found to increase oviposition in proximity to nectar. Butterflies that oviposit on flowers may be stimulated to lay eggs when nectar is present[66] and may therefore lay more eggs in the vicinity of nectar sources.[252] Females of lycaenids and riodinids preferentially oviposit in the vicinity of ants,[10] whose presence may be regulated by nectar secretion. *Heliothis* moths that feed at cotton extrafloral nectaries are likely to oviposit on the plants.[232] Caterpillars of this species drink extrafloral nectar and may chew into cotton squares after nectar is consumed.[24] Cotton genotypes lacking nectaries are resistant to major lepidopterous pests.[231,232,354]

Insect predators often find their prey by first finding the suitable prey habitat and secondly the prey.[143] If adult parasitoids with entomophagous larvae are attracted to feed on extrafloral nectar, they may be more likely to discover suitable hosts for their offspring in the herbivore eggs and larvae feeding on the host plants[202,206] (see Section III.G).

4. Location

Ant nests are not located at random: while competition may be the overriding force in determining spatial dispersion of ant nests,[227] the location of food resources (e.g., nectar) may also be important determinants.[30,228,280,281,318] It is not unusual to find ant nests at the base of plants bearing extrafloral nectaries (e.g., *Chrysobalanus icaco* in south Florida) or plants that support Homoptera tended by ants (e.g., *Carex intumescens* in northern Michigan).

Bentley[31] demonstrated that by adding nectar droplets to bean plants, a protective ant force was recruited. A number of experiments have demonstrated that blocking or removing plant nectaries effectively decreases ant numbers on those plants.[43,149,199,336]

The presence of ants on plants with nectaries also influences the establishment of myrmecophytic epiphytes in which ants nest (e.g., *Solenopteris* ferns[134]). Davidson and Epstein[88] found that the principal plant inhabitants of ant gardens are over-represented on trees with extrafloral nectaries or dependable homopteran nectary analogs.

5. Population Biology

In order for beneficial insects that regulate problem pest insects to be established or recruited to an area, it may be necessary to have nectar resources to attract them and to support them through low pest times. Crops bordered by weeds or in weedy fields can fare better than well-manicured plantings because predators and parasitoids are more abundant.[4] Polycultures have more beneficial insects than monocultures,[224-226] due, in part, to the greater diversity of nectar rewards for these insects. Populations of 15 entomophagous arthropods were substantially larger in cotton with extrafloral nectaries compared with nectarless cotton cultivars.[1] However, removing nectaries of cotton has greatly reduced populations of certain homopteran[312] and lepidopteran[1,146,232] pests that are also attracted by extrafloral nectar.

6. Insect Behavior

The discovery of nectar resources by ants prompts a variety of responses: feeding, collecting, recruitment, and territoriality. Some ants are solitary foragers, and when they encounter nectaries will drink until replete; encounters with other insects during that time may result in some territorial aggressiveness (e.g., *Paraponera* on *Pentaclethra*[30]) but not necessarily. Worker ants treat extrafloral nectaries in the same way that they treat honeydew-producing insects; the more aggressive species defend the active nectaries, in many cases extending their territory over the entire plant.[156] In group foraging species, when one worker discovers nectar, it will drink until replete and then return to the nest and/or mark a scent trail to the resource, recruiting more individuals to take advantage of the nectar. Discovery of and recruitment to baits has been used to indicate ant activity and abundance at different sites.[31,179,202,204,208]

Resources of adequate quantities (determined by ant species and temperament) justify defending against interlopers, and this is the basis for ant defense of plants. While other insects alighting on plants may have no interest at all in nectar, the ants will remove them from the plant surface to protect their nectar resources. Many ant species may also utilize other insects on plants as food; the nectar serves to attract the ants to the foliage, where they wander around and discover insect prey. Ant-tended insects may not always benefit from ant care;[78] when times are tough, ants may eat their aphids rather than simply tend them for their honeydew (B. Edinger, personal communication).

Certain folivorous caterpillars exhibit the unusual behavior of positioning themselves on a plant not only to feed on leaves, but with their head in the extrafloral nectary.[93] Tiny *Apion* weevils feeding on foliage of *Vicia sativa* frequently drink nectar[208] and are camouflaged against the nectary, which is dark colored in contrast to the leaf.

B. EFFECTS OF INSECTS ON NECTAR

1. Nectar Quantity

There are two strategies in plants using floral nectar as a reward for pollinators: nectar is produced one time, and when removed, it is gone; or nectar is replenished as it is used, for the duration of the functional life of the flower. Animal visitors to flowers of the second strategy, therefore, have an effect on nectar quantity: the more the flowers are visited, the more nectar they produce.[75,200] Extrafloral nectars usually function for a much longer time than floral nectaries, e.g., over the period of expansion and maturation of new foliage (3 to 4 weeks) vs. 1 to 3 d of average flower duration. Most plants with extrafloral nectaries produce nectar in the absence of insects (e.g., in insect-free greenhouse conditions), and some accumulate large viscous quantities at the nectaries, obviously not dependent on insect removal or stimulation for continued secretion (e.g., *Turnera*). Other plants secrete small quantities of nectar to fill the nectaries, and replenish these small amounts when the nectar is removed (e.g., *Inga*).

Homoptera may decrease the amounts of extrafloral nectar produced, since a substantial amount of translocate is being diverted through these insects.[95] Ant-tended Homoptera are insect analogs of extrafloral nectaries, over which the host plant has no control, unlike real extrafloral nectaries.[206]

Herbivorous insects may increase the volume of extrafloral nectar secretion by their foliage-feeding activity. Sphinx caterpillars feeding on *Catalpa* resulted in greater nectar secretion on damaged leaves than on leaves without caterpillars.[326] Moderate levels of simulated damage to leaves of *Vicia* resulted in increased nectar production in stipular nectaries the day following the damage.[203] Experimental herbivory on leaves of *Campsis radicans* caused an increase in extrafloral nectar production on adjacent flower buds.[328] This propensity may constitute an inducible defense for certain plants that can respond to damage from herbivores by attracting more biotic protection (see Sections III.F and III.G).

2. Nectar Quality

Certain pollinators can introduce agents into floral nectar that alters the composition of the nectar, making it more suitable for a different guild of pollinator. Insect visitors to flowers may add amino acids by direct contact, salivation, damaging tissue causing cell leakage, and dislodging pollen into the nectar.[353] Hawkmoths that take the sucrose-rich nectar of *Inga vera* in the early evening may introduce fungi and bacteria into the flowers, which hydrolyze the sucrose into its hexose components, making the flowers more suitable for the bat visitors that come later.[15] Insects carry spores of yeasts and bacteria; *Drosophila* are primary vectors of yeasts, while muscoids, dolichopodids, and other insects frequently carry molds.[325] Bumblebees disperse spores of *Ustilago* fungus, the causal agent of anther smut disease, while gathering nectar and pollen from *Viscaria*.[171]

Extrafloral nectaries are, in general, more open and exposed than floral nectar, and they are more subject to the effects of the surrounding microclimate; in low humidity, nectars can be very highly concentrated. Perhaps because they are open to the introduction of spores and microbes from the air, which cause the hydrolysis of sucrose, extrafloral nectars tend to be hexose dominated when sampled. When extrafloral nectar is allowed to accumulate for days unsampled by visitors and open to the evaporative effects of the environment, nectar can become quite highly concentrated and viscous, and may even become so sticky that certain insects scrape it from the nectaries (personal observation).

Careful nectar analyses have revealed that certain plants may alter the composition of their extrafloral nectar in response to herbivore damage. The amino acids of *Impatiens sultani* nectar change in their relative concentrations subsequent to artificial defoliation,[323] perhaps to make the nectar more attractive to insect protectors of the plant.

3. Insect-Induced Secretory Structures

Certain internally feeding, gall-forming insects occupy plant parts that subsequently develop nectaries. Cynipid gall wasps attacking oaks occupy round galls covered with glands,[348] and the ants visiting these glands protect the wasp larvae from their parasitoids.

Feeding lesions due to insects or other animals may weep plant sap, which, if well supplied by phloem, is a nectarlike substance. Sapsucker holes in tree trunks are visited by hummingbirds (which normally visit flowers) and a variety of insects. Wasps visit wounds on the stems of *Baccharis* to collect the nectarlike sap.[254]

III. INTERACTIONS BETWEEN INSECTS AND PLANTS

A. POLLINATION

1. Extrafloral Nectar as Pollinator Reward

Although extrafloral nectaries are defined as usually not being involved with pollination, there are some exceptions. In some plant genera, the nectaries are outside of the individual flowers, but are a part of the inflorescence, and visitors to these nectaries contact floral organs, carry pollen, and pollinate flowers. The best-known example of this is *Poinsettia* (Euphorbiaceae), the showy blossoms of which are made up of brightly colored bracts subtending a small inflorescence of unisexual flowers, including some large nectaries.[345] *Norantea* (Marcgraviaceae) is an epiphytic shrub with a pendant inflorescence, the individual flowers of which have long pedicels; at the base of each pedicel is a large, cup-shaped nectary.[268] The birds, bats, or other mammals that visit these nectaries must touch the flowers as they poke through to the nectaries.

Foliar nectaries serve to attract visitors that inadvertently contact the floral parts of some plant species. Floral nectaries have not been found in Australian *Acacia* species.[39] Bernhardt[40] concludes that *Acacia* are generally entomophilous, with an emphasis on bees associated with pollen reward and secondarily on extrafloral nectar. The Australian *Acacia terminalis*[191,192,197] has large, flattened foliar nectaries that are reddish in color and are visited by passerine birds that pick up pollen in their feathers and inadvertently pollinate flowers in the process. Bees and flies serve as active transporters of pollen in *A. terminalis* when they move to flowers after feeding at extrafloral nectaries.[191] Thorp and Sugden[338] observed passive vectoring of pollen by honeybees on *Acacia longifolia* while insects were foraging for extrafloral nectar on the phyllodes; the proximity of inflorescences to nectaries results in insects of that size (including native, presumably coevolved, Hymenoptera) brushing the blossoms as they feed at the nectaries. Birds were suggested as possible pollinators of Australian *Acacia pycnantha,*[122] because the nectaries function during flowering, and only on phyllodes among the inflorescences.

2. Pollinator Distraction

Extrafloral nectaries may serve to distract pollinators from flowers of a plant, a drawback as far as pollination is concerned. Darwin[84] noted that "humblebees" were more interested in the extrafloral nectaries of *Vicia sativa* than the flowers, and collected the nectar assiduously during the sunny morning hours, when it flowed most freely. Honeybees collect extrafloral nectar from the outer petal bases of *Iris pallasii* in Korea (Pemberton, personal commmunication) rather than enter the flowers (though they may not be good pollinators of this species).

3. Diversion of Flower Plunderers

The role of extrafloral nectaries as objects of diversion for animals that might visit flowers but not serve as pollinators was suggested by Kerner.[193] Niewenhuis[258] considered their role as deterrents to flower robbing, but found that the frequency of robbing in Buitenzorg Garden depended more on weather and the proximity of other plants in flower than on the protection of flowers by ants. The antibiotic compounds on the body surface of ants renders them ineffective pollen transporters for most plant species.[21] That ants like to visit flowers has been debated[14,115,140,169] and well documented,[141] and nectaries outside of flowers might indeed interrupt the progress of these usually nonpollinating insects to the flowers. But their presence at the extrafloral nectaries and vicinity can have a variety of benefits to the plants, as will be discussed below.

B. PLANT FEEDING BY ANTS — MYRMECOPHYTES WITH EXTRAFLORAL NECTARIES

Myrmecophytes can be defined as plants that live regularly and often exclusively in association with ants;[88] these are plants that house ants and exist symbiotically with their resident ant fauna. Many authors have restricted the use of the term ant plant to only true myrmecophytes, vs. any plant interacting with ants.[240] Most myrmecophytes offer not only shelter for their ants, but also some sort of nutritional supplement. Most common is the presentation of food bodies for the resident ants to harvest (Mullerian bodies on *Cecropia;*[296] food bodies on *Macaranga;*[116] and food bodies produced inside hollow nodes of *Piper coenocladum.*[223,301] Some myrmecophytes have extrafloral nectaries in addition to food bodies (*Acacia cornigera*[167]); others have only extrafloral nectar as a nutritional bonus for their resident ants (*Leonardoxa africana;*[240] *Platycerium* spp;[88,209] *Schomburgkia tibicinis*[300]).

C. ANT GARDENS — EXTRAFLORAL NECTARIES AND MYRMECOCHORY

The taxonomically diverse angiosperm flora characteristic of nest sites of arboreal ants has been dubbed "ant garden", due to the fact that the seeds of these plants are ant dispersed and carried to these nests, and the seeds are discarded (thereby planted) on the outside of the nest. All flowering plants that are ant garden epiphytes are ant dispersed, and the majority offer a visible food reward for the ants (aril, sticky pulp, or gelatinous matrix), though not in all ant-garden species is the attractiveness of seeds based wholly on nutritional concerns.[87] Epiphyte seeds with no obvious food substances are preferred by ants over some seeds with nutritional rewards;[88] these seeds, however, contain chemical attractants that may serve fungicidal purposes in controlling pathogens of ant nests.[314] Roughly 60% of ant-garden epiphyte species summarized by Davidson[87] have extrafloral nectaries (e.g., *Codonanthe, Epiphyllum, Markea, Myrmecodia*, and *Philodendron*), making them especially nice plants for the ants to have around as a food source close to home.[88,195,196]

D. HERBIVORE ATTRACTION — A DRAWBACK OF NECTARIES

Extrafloral nectar may serve as an attractant for insects that will feed on foliage after drinking nectar, including adult Lepidoptera and Coleoptera, which in turn may oviposit on the plant providing the nectar. This problem has been reported in cultivated cotton, where, under conventional cultivation conditions, nectariless varieties have less pest damage and greater yield than varieties with nectaries.[1,2] Adult *Apion* weevils, which feed on the foliage of *Vicia sativa* in England,[208] can be seen drinking nectar from the stipular nectaries. Riodinid and lycaenid butterflies usually use plant species with extrafloral nectaries as hosts, perhaps because they provide an enemy-free space[10] for their myrmecophilous larvae (tending ants ward off parasitoids[284]); the larvae can add "insult to herbivory" by drinking extrafloral nectar as well as consuming foliage.[93]

E. ANT GUARDS AND PLANT PROTECTION

Evidence for ants visiting extrafloral nectaries of plants and providing protection for the plants against their herbivores is ever increasing (many references contained in Bentley,[33] Buckley,[56] and Jolivet[174]), but it is not universally reported.[43,149,261] Ants can most easily be effective against herbivores that are on the surface of plants, and can provide a generalized defense against most insect herbivores that an introduced plant may encounter in a new habitat. The historical development of the "protectionist" and "exploitationist" views of the significance of extrafloral nectar production are reviewed by Bentley.[33] In her review, substantial evidence is cited for the "protectionist" hypothesis; as research continues in this field, there are additional demonstrations of ant protection, some negative evidence, and some more complex situations.

1. Obligate vs. Facultative Mutualisms

Janzen's pioneering experimental work[167] demonstrated that *Acacia cornigera* could not survive herbivore predation when their resident ant protectors, *Pseudomyrmex ferruginea*, were removed. These plants are myrmecophytes, housing the ants in the swollen stipular thorns, and providing nourishment for the ants via Beltian bodies and extrafloral nectar. A number of myrmecophytic ant-plant associations do not involve nectar and appear to be more facultative than the ant acacias: *Cecropia*,[296] *Piper coenocladum*,[301] and *Macaranga*.[116]

Most plants with extrafloral nectaries do not have resident ants, and their mutualistic relationship with ants is facultative. In these facultative associations, a plant's fitness increases when the plant is associated with ants, but plants can survive without ants. The nonspecialized nature of ants visiting extrafloral nectaries is demonstrated by Schemske's quantification of ant species assemblages on *Costus*: high ant species richness and similarity in the nectar composition of *Costus* spp. indicate generalized mutualisms with limited coevolution between the plants and ants.[308]

2. Protection of Vegetative Structures

Ants attracted to nectaries encounter and remove herbivores from the plant surface, providing protection for foliage in a variety of systems. Bentley[31] created artificial extrafloral nectaries on bean plants, attracting significantly more ants and resulting in significantly less damage than on control bean plants without nectar. The exclusion of ants from entire trees of *Acacia saligna* in Australia resulted in significantly greater numbers of herbivorous insects than on control trees; trees with ants excluded apparently gained less height and lost crown canopy area compared with controls.[236] Similar results, plus increased seed set, were found in *Acacia decurrens*[53] in the absence of membracids (see Section IV.A.). Foliar nectaries of *Prunus serotina* in Michigan attract *Formica obscuripes* ants, which control early instars of tent caterpillars.[339] Areolar nectaries of *Opuntia acanthocarpa* attract *Crematogaster opuntiae* ants, which defend the plants against cactus-feeding insects.[279] Argentine ants, *Iridiomyrmex humilis*, visiting stipular nectaries of weedy *Vicia sativa* in California reduced leaf damage, resulting in an increase in fruit and seed set.[199] Foliar and sepal nectaries of *Ipomoea leptophylla* are visited by ants, which decrease damage to flowers and seeds from grasshoppers and beetles.[181] Five species of ants visit the foliar nectaries of *Catalpa speciosa*, limiting herbivory by sphingid caterpillars and increasing fruit set.[326] A temperate passion vine, *Passiflora incarnata*, experienced greater herbivory and set less fruit when extrafloral nectaries were experimentally removed.[242] The survival and mortality of *Heliconius* caterpillars on neotropical *Passiflora* spp. are significantly influenced by ants visiting the foliar nectaries.[320,321] Saplings of neotropical *Inga* species are protected from foliage-feeding herbivores by a variety of ants in the lowlands of Costa Rica.[201] Nectaries on bracken fern, *Pteridium aquilinum*, attract ants that repel nonadapted herbivores from the plant surface in Yorkshire, England.[217] The foliar nectaries of *Cassia fasiculata* support protective ants that reduce damage[189] and increase plant fecundity.[19] Ant foraging is promoted on Brazilian *Qualea grandiflora* by nectaries on the stems, resulting in greater attack rates of live insect baits on foliage.[265] *Macaranga aleuritoides* saplings have foliar nectaries supporting 13 species of ants that limit damage from insect herbivores in Papua New Guinea.[352]

3. Protection of Reproductive Structures

Nectaries on or near plant reproductive structures can provide ant protection of developing flowers, ovules, and seeds. Nectaries on inflorescences of *Schomburgkia tibicinis* (Orchidaceae) attract ants that disturb the activities of curculionid beetles that bore holes at the tip of the growing inflorescence spike, which can kill the spike or decrease flower number (depending on the timing of the attack); ants can thus decrease the number of dead spikes and increase the number of mature fruit.[299] A similar interaction has been hypothesized for the orchid *Spathoglotis plicata*, but has not yet tested.[165] The sepal nectaries of *Bixa orellana* support ants that protect the developing seeds.[32] Ants visiting the nectaries on inflorescence bracts of *Aphelandra deppeana* enhance seed capsule formation.[92] *Campsis radicans* has five extrafloral nectary systems,[107] potentially providing not only protection for foliage but developing flowers and fruit as well.[328] Suppression of the boll weevil by the imported fire ant was observed in cotton (a crop with extrafloral nectaries) in Texas.[327] The phyllary nectaries of *Helianthella quinquenervis* attract five species of ants in the Rocky Mountains of Colorado that protect the inflorescences from predispersal seed predators.[163] Neotropical *Costus woodsonii* have nectaries on the bracts of the inflorescences that attract *Ectatomma* and other ants, which vary in their ability to protect the inflorescences from Diptera that oviposit in developing ovules.[307,308] Floral nectaries of *Mentzelia nuda* function after the corolla abscises ("postfloral nectaries"), attracting ants that protect the developing fruits from herbivores.[185] Neotropical *Calathea ovandensis* have nectaries on bracts of the inflorescence, a variety of ants that visit the nectaries, and many inflorescence herbivores that are controlled by the ants and specialized (ant-tended) herbivores that are not.[157]

4. Negative Findings — No Ant Protection Evident

Some studies have demonstrated no apparent benefit to plants from insects visiting their extrafloral nectaries. *Helichrysum* spp. (Asteraceae) in Australia have extrafloral nectaries on the bracts of the inflorescence, but ants visiting the nectaries had no significant effect on herbivore damage to developing seeds or parasitism of seed predators by parasitoids.[261] These authors found seasonal differences in seed damage and herbivore parasitization, not correlated with ant abundance, and therefore cautioned against generalization of the protection hypothesis to all plants with extrafloral nectaries.

Ant-exclusion experiments performed on bracken, *Pteridium aquilinum*, at three sites in New Jersey showed no significant differences in damage between fronds with ants and those without.[336] Substantial damage was inflicted on both groups by a variety of herbivores equally. Similar results were obtained in Australia (D. O'Dowd, personal communication) and England,[149,217] though the interpretation was that the ants kept any new species of herbivores from colonizing bracken (a taxon-level defense system); the contemporary herbivores were all specialized and adapted to survive with ants.[150] Only the large, aggressive wood ant, *Formica lugubris*, was found to have an effect on contemporary herbivores of bracken in the North York Moors, England.[151]

Three species of euphorbiaceous saplings in Papua New Guinea with foliar nectaries were subjected to ant-exclusion experiments; two showed no difference in the damage sustained between ant-access and ant-excluded branches.[352] These species had as many ants as did *Macaranga aleuritoides*, for which ant defense was demonstrated; but unlike *M. aleuritoides*, did not have lepidopteran larvae, the most damaging of the associated insects, as their dominant herbivores.

Overall, the proportion of studies that have examined the effects and found benefit for plants from ants visiting extrafloral nectaries are in the majority, representing a significant effect in general, since specialized herbivores are not necessarily important at all times. It is important, however, to not assume a wholly beneficial function until the particulars of a given system are examined.

5. Complex Situations — Temporal and Spatial Variation

a. *Temporal Variation*

In cool temperate habitats, nectaries are visited by ants during daylight hours only (e.g., British *Vicia sativa*)[208] whereas in more clement temperate and many tropical localities, nectaries secrete nectar and ants are actively visiting them around the clock[60,201] (Pemberton, personal communication). In Britain, this ant-less window permits oviposition by *Cydia* moths, whose larvae feed inside pods of *V. sativa* protected from ants and from their enemies by ants.

Many plant species have nectaries active only on young, rapidly developing tissues, allowing ant protection at a time when the tissues are especially vulnerable to herbivores.[241] For example, extrafloral nectaries of black cherry are most active during the first few weeks after budbreak, attracting large numbers of *Formica obscuripes,* which attack young instars of the tent caterpillar that are present during that same peak of nectar secretion.[339]

b. *Spatial Variation*

A plant species encounters a variety of interactive situations throughout its distribution. Various studies have shown relatively small-scale spatial variation in the effects of ants on plants, depending on factors such as the proximity to the ant nest,[163] the intensity of herbivory,[19] ant activity,[189,320,321] and the behavior of different ant species.[157,175,201,308] The particular combination of ants, other protective agents, and herbivores will determine how effective a plant's defenses are and how much damage the plants will sustain.[208]

The distance of plants from ant nests results in significant variation in the magnitude of the beneficial effects of ants.[163,177,339] In a study of the neotropical herb, *Calathea ovandensis*, ants were not equally distributed over sites, and spatial heterogeneity in seed production reflected differences in ant communities among sites.[157] Barton[19] found that where the abundance of both ants and potential herbivores was high, ants visiting extrafloral nectaries strongly increased the reproductive success of *Cassia fasciculata* in Florida; the strength of the protective effect varied widely among local populations, influenced by the density of both ants and herbivores. In Yorkshire, England, ant abundance varies widely between local sites where *V. sativa* occurs, as does the density of herbivores. Where surface-feeding herbivores predominate, ants benefit the plants; but where internal feeders are abundant, the ants deter parasitoids of these herbivores and the vetches suffer, rather than benefit from ant protection.[208]

c. *Specialized Herbivores*

In native environments, specialist herbivores evolve that can short circuit plant defenses, including ants at extrafloral nectaries. There are many cases of specialized herbivores using the plants despite the ants;[10,150,157,201,307] these specialized herbivores are most likely to occur in a plant's native habitat.

On ant acacias, caterpillars have been observed to drop down on a thread when disturbed by ants, and to climb back up later (K. Keeler and W. Haber, personal communication). Rolling leaves into protective shelters is common among caterpillars, and two of the three most common caterpillars eating the nectary-bearing *Inga* in lowland Costa Rica are "leaf sealers" (Hesperiidae and Gelechiidae), whose shelters probably provide them with some degree of protection from ants.[201]

Many lycaenid butterflies, whose larvae have nectar glands and are tended by ants, have host plants that have extrafloral nectaries. Atsatt[10] hypothesizes that this is because they find "enemy free space" in the midst of ants and nectaries (see Section IV.A).

Although the extrafloral nectaries on bracts of *Calathea ovandensis* attract ants that deter dipteran seed predators, a specialized herbivore, *Eurybia elvina*, is tended by ants and can feed unmolested on the inflorescences.[157] Path analysis was employed[309] to estimate the direct and indirect effects of various insect-plant interactions on flower and fruit production in *Calathea ovandensis.* Ant guards had a direct positive effect on flower number, and a resulting positive indirect effect on fruit set. Ant guards have a positive direct effect on the specialized, ant-tended herbivore, *Eurybia*, although damage from *Eurybia* is greater in the absence of ants than when ants are present.[157] *Eurybia* had a negative direct effect on flower and fruit numbers.

On bracken, externally feeding sawfly larvae regurgitate toxic juices from the host plant when disturbed by ants, and the ants are repelled by the emissions. Other herbivores feed internally and are protected from the ants.[150,217]

In a facultative mutualism between alien *V. sativa* and non-native ants, ant visitation to extrafloral nectaries reduced damage from folivores and increased seed set for plants attended by ants.[199] In those California plant populations, no herbivores attacked flowers and fruits, and overall herbivore pressure was low; the only herbivores seen fed externally on leaves and flowers. In the native habitat, more guilds of herbivores feed on *V. sativa*, including insects whose larvae feed and develop inside developing pods. *Cydia* moths apparently exploit ant protection: when in pods on plants with ants, they are protected from their natural enemies. Where these herbivores are abundant, ant protection can be a problem: vetches in areas of high ant activity and high *Cydia* abundance get damaged heavily, and set much less viable seed than their counterparts in areas either with low ant activity and low *Cydia* abundance, or with low ant and high *Cydia* abundance.[208]

6. Ant Behavior — Aggressive vs. Passive Ants

Bentley[33] observed that many ants species common on extrafloral nectaries are notoriously aggressive and suggested that this is very important in their protective function on plants, involving ownership behavior around nest sites and food resources, predatory behavior, and the pheromone-mediated attack response. Indeed, in many