Some of the highest levels of abundance of plants with extrafloral nectaries occur in desert plants such as this *Opuntia acanthocarpa* in the Anza Borrego Desert. Photograph by June Latting.

EXTRAFLORAL NECTARIES IN CALIFORNIA PLANTS

by Suzanne Koptur

EXTRAFLORAL nectaries are plant glands, located outside flowers, that secrete nectar, the basis for a variety of plant/animal interactions ranging from beneficial to detrimental. They range in complexity from fissures in the leaf epidermis to anatomically elaborate structures, and in size from a few micrometers to nearly three-quarters of an inch in diameter.

The location and position of extrafloral nectaries on plants are related to their ecological role. Extrafloral nectaries on leaves and stems can feed ant bodyguards that disturb, attack, remove, or repel herbivores. They also provide food for predatory wasps and parasitic wasps and flies that attack herbivore larvae and adults; the benefit to the plant may be a reduced loss of vegetative tissue to herbivores. Nectaries located on or near reproductive parts of the plant (in inflorescences, on bracts, and on flower buds) can support beneficial insects that protect the plant against herbivory on buds, flowers, and developing seeds.

Surveys of the California flora for presence and abundance of plants bearing extrafloral nectaries have revealed that some habitats have no native plants whatsoever with extrafloral nectaries. Kathy Keeler, from the University of Nebraska, surveyed for nectaries in perennial native grassland, riparian forest, deciduous forest, and chaparral in

northern California. The only native species with nectaries she found is *Helianthella californica* (Asteraceae), raising the question as to why this type of plant defense is not favored in these northern California habitats.

Desert communities of California, however, tell a different story. Robert Pemberton, from the USDA Agricultural Research Service, surveyed warm desert communities in the Colorado and Mojave deserts in Southern California and found some of the highest levels of abundance of plants with extrafloral nectaries recorded for the temperate zone. He sampled in several habitats, and found that desert wash had 23.9 to 27.7 percent cover of plants with extrafloral nectaries, creosote bush scrub had zero to 6.58 percent cover, and sand dunes had zero to 1.36 percent. He found eleven species with extrafloral nectaries: *Opuntia acanthocarpa*, *O. basilaris*, *O. bigelovii*, *O. echinocarpa*, and *Ferocactus acanthodes* (Cactaceae); *Chilopsis linearis* (Bignoniaceae); *Fouquieria splendens* (Fouquieriaceae); *Acacia greggii* and *Prosopis juliflora* (Fabaceae: Mimosoideae); *Prunus fasciculata* and *P. fremontii* (Rosaceae). He reasoned that this unlikely appearance of a water-based defense system (nectar is an aqueous solution of sugars and other solutes) in the desert may relate to the appearance of leaves and flowers only in periods of water availability. The defense is there only when these tissues are being produced. Protection of new growth and reproductive tissues may be more important in the desert since the opportunity for regrowth is restricted by limited water.

Despite Pemberton's findings, there are relatively few native California plant species with extrafloral nectaries. It may be that in the drier climates of California, plants more easily evolved chemical and mechanical defenses against herbivores (witness the numerous plants with aromatic and/or hairy foliage). Yet there are also some naturalized exotic plants that have extrafloral nectaries and benefit from visitors to these nectaries in Northern California.

Myrmica ruginodis ants on *Vicia sativa* in Heslington village, North Yorkshire, England. Photographs by the author unless otherwise noted.

Vetches and Ants

Common vetch (*Vicia sativa*, Fabaceae: Papilionoideae) was introduced to California from Europe as a forage crop for large mammal herbivores. It has escaped from cultivation to become naturalized in grassy fields and semi-disturbed habitats in Berkeley and the San Francisco Bay Area. These plants have stipular nectaries (on outgrowths of the leaf base), often purple in color, which are visited by bees, flies, small moths, and ants. Ants are by far the most abundant visitors to the nectaries, especially the introduced Argentine ants. Other species of ants visit vetch nectaries in areas of California where Argentine ants are not found.

Plants frequently escape their coevolved herbivores in a new habitat, but these vetches in California are not pest-free; their leaves are eaten by caterpillars of geometrid moths, alfalfa weevils, and black bean aphids. The paucity of these herbivores on plants with ants suggested that the presence of ants deters herbivores, and so a simple field experiment was performed in Tilden Regional Park, Alameda County, to test the ant-protection hypothesis. I did this research as a project for Herbert Baker's evolutionary ecology class.

The sprawling, climbing habit of *Vicia* did not allow straightforward exclusion of ants with tanglefoot resin; but the position of the nectaries on stipules made it pos-

sible to remove nectaries by excising the stipules as the leaves developed. On control plants, an area of tissue equivalent to the size of a stipule was removed from the lowest leaflets of each leaf. Plants that had their stipules (and nectaries) removed, and therefore had fewer ants on them, suffered significantly greater damage to their leaves and set substantially fewer fruit and seeds. There was no damage to seeds from herbivores, but loss in leaf area translated into less fruit set. I concluded that the weedy Argentine ants protect the foliage of the weedy common vetch in a non-coevolved, facultative mutualism.

Vetches in the Wild

I had always been curious about how the nectaries affected interactions among these vetches, herbivores, and ants in their native habitats, and I had the opportunity to study this during a NATO postdoctoral fellowship year in England, where I worked in the lab of John H. Lawton at the University of York. After a few years studying tropical trees for my doctoral research at Berkeley, I was looking forward to working on annual plants of short stature, and looked on the vetches as a great system in which to test some ideas that had grown out of my work on the relative benefit to plants with extrafloral nectaries from different guilds of visitors to the nectaries.

When a plant is in its native habitat, not only are the coevolved pollinators present, but all its herbivores and protective agents as well, with a long history of interaction.

The position of the short-pedicelled vetch flowers in the axils of leaves puts them in close proximity to the stipular nectaries, so the attraction of ants to nectaries could result in protection of flowers and/or developing fruit as well as leaves. In its native habitat in Britain, more guilds of herbivores feed on the common vetch, including insects whose larvae feed inside developing pods such as moths in the genus *Cydia* (Torticidae).

In north Yorkshire, the only ants we found visiting vetch nectaries were *Myrmica ruginodis*. Parasitic wasps also visited nectaries, including two species also reared from the pod-feeding larvae of *Cydia* spp., *Scambus planatus*, and *Campoplex punctulatus*. A much wider variety of herbivores were external feeders on leaves and stems, including moths (caterpillars of the tortricids, *Cnephasia* spp., and an unidentified Noctuidae); weevils (*Sitona lineatus*, *Phyllobius* spp., *Apion gyllenhali*, *Ceutorhynchus assimilis*); a cantharid beetle, *Cantharus livida*; and the aphid *Megoura viciae*.

The ants were only partially successful at removing the surface-feeding weevils and caterpillars from the vetches, and so plants suffered greater levels of damage than did the same vetch species in California (though less than twenty percent damage on average). Far more devastating, however, were the internally feeding *Cydia* caterpillars.

Common vetch, *Vicia sativa*, with the Argentine ant, *Iridiomyrmex humilis*, visiting its stipular nectaries in the San Francisco Bay Area of California (UC Botanical Garden).

The female *Cydia* moths oviposit on the sepals or the ovary of the vetch flowers, perhaps at night while the ants are in their nest. The caterpillar hatches, enters the pod, feeds on developing seeds, and grows inside the pod, exiting by boring a hole in the pod wall and dropping to the ground to pupate in the leaf litter. Once the caterpillar is inside the pod, it is impervious to ants; and more important, in protecting the vetches, the ants inadvertently protect the caterpillars from their own natural enemies. When ants are on plants, they use the nectar that the parasitoid wasps might use, and even repel the parasitoids. These wasps lay their own eggs on or in the caterpillars, resulting in the death of the host caterpillar and providing biological control of the herbivore.

We surveyed plants at six sites that varied in the abundance of ants. Damage and presence of externally feeding herbivores were assessed on marked plants over the growing season. We sampled pods from unmarked plants at each site and reared larvae found for identification and estimates of parasitism (as demonstrated by the *Cydia lunulana* larva parasitized by *Scambus planatus*. The sites with the greatest ant activity had lower rates of parasitism of *Cydia* larvae and greater damage to seeds; this is counter to the expectation that ants protect plants against herbivores.

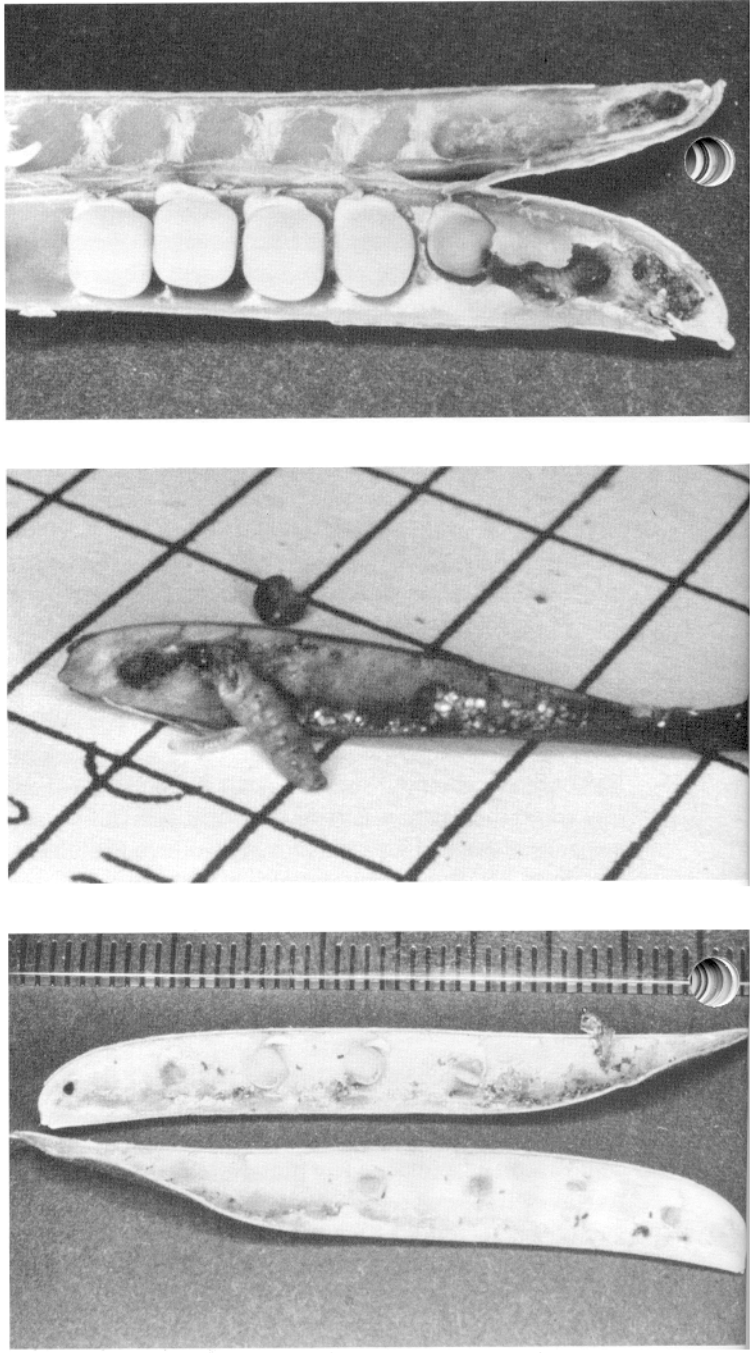
It is common for a *Cydia* larva that is not parasitized to damage every seed in a pod. Although a partially or slightly damaged seed may germinate and be able to produce a new plant, these new plants will not grow enough to reproduce. Damage inflicted in summer by the caterpillars prevents the seeds from overwintering, as the damaged seed coat allows the seeds to imbibe water from the autumn rains and germinate to produce plants that will

freeze and die in the cold Yorkshire winter months to follow.

In native environments specialist herbivores evolve that can short-circuit plant defenses, including ants at extrafloral nectaries. In the indigenous vetch system *Cydia* moths apparently exploit ant protection: when in pods on plants with ants, they are protected from their parasitoids. Where these herbivores are abundant ant protection can be a problem: vetches in areas of high ant activity and high *Cydia* abundance are damaged heavily and set much less viable seed than their counterparts in areas with either low ant activity and few *Cydia* or low ant activity and abundant *Cydia* where the conniving caterpillars are kept in check by their parasitoids.

Generalized Defense

Extrafloral nectaries offer a good generalized defense system especially well-suited to an exotic plant species that escapes its coevolved herbivores in a new environment and faces herbivore pressure only from generalist feeders. I would like to offer a friendly amendment to Baker's Law, in which the tendencies of successful weedy species are described, to include extrafloral nectaries as a likely defense strategy for plant species that are good colonizers. Perhaps some current student of California flora might be interested in seeing how common extrafloral nectaries are on introduced species in California. And I hope the search will continue for new examples of extrafloral nectaries in the native flora, as well as investigations into their ecological roles in California plants.



Opened green pod (top) with second instar *Cydia lunulana* larva consuming seeds. Fourth instar *Cydia* larva (middle) with larva of the ectoparasitoid (attaches to the outside of, rather than inside of, host) *Scambus planatus*. Mature pod (bottom) that has hosted a *Cydia* larva that has exited to pupate; every seed has been damaged, and will not make it through the winter.

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