FORAGING AND FOOD CHOICE IN PHYTOPHAGOUS INSECTS

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Contents

Summary

The majority of insects that feed on plants specialize on a limited range of plant species. This specificity stems very largely from the insects' responses to plant secondary compounds. At least for many insects that feed on a particular plant taxon, hosts are identified through a combination of aversive responses to the secondary chemicals of nonhosts (which act as deterrents), and positive responses to specific chemicals, sign stimuli, associated with the host. Insect species that feed on a wide range of plant species, however, are less sensitive to deterrents and so find a wide range of plants acceptable without specific sign stimuli. Compounds that are deterrent to one species may be positive sign stimuli for others. The response to any compound depends on its concentration, its concentration relative to other compounds in the plant, the evolutionary history of the insect species, and experience of the individual insect.
Plant secondary compounds have had a major influence on insect speciation, but a tight coevolutionary link between insect and plant evolution, associated with changes in secondary chemicals, is much less important than was once believed.

1. The Occurrence of Phytophagy

Over 500 000 insect species are known be phytophagous, feeding on growing green plants. The major groups are listed in Table 1. The most abundant and most commonly encountered are from three orders of insects:

- Lepidoptera: butterflies and moths
- Coleoptera: beetles
- Hemiptera: sucking bugs

Nearly all species of Lepidoptera (about 200 000 species) are phytophagous as larvae (commonly called caterpillars). In the Coleoptera about 140 000 species are phytophagous and most of these are in two superfamilies, the Chrysomeloidea that include well known agricultural pests like the Colorado potato beetle (*Leptinotarsa decemlineata*), and the Curculionidae, weevils. In the other major order of phytophagous insects (Hemiptera), all the Sternorrhyncha and Auchenorrhyncha (often grouped together as Homoptera; including aphids and plantfhoppers) are plant feeders, while amongst the Heteroptera most Pentatomomorpha (stink bugs) and some Cimicomorpha have this habit. Amongst the other orders, the Phasmatodea (leaf and stick insects) are exclusively phytophagous although the numbers of species are relatively small. In the Orthoptera, all Acridoidea (grasshoppers) and most Tettigonioidea (katydids) are plant feeding. Many Diptera (two-winged flies) are also phytophagous, although this is not true of the majority. The most important phytophagous families of flies are Cecidomyiidae (gall flies), Agromyzidae (leaf miners) and Tephritidae (fruit flies). Amongst the Hymenoptera, all Symphyta (sawflies and related insects) are plant feeders, while gall wasps occur in the Cynipoidea. In all instances the larvae are the major feeding stages and sometimes the adults do not feed at all or have a different feeding habit. In the Lepidoptera, for example, the adults of many species visit flowers to obtain nectar, which serves as a fuel for flight but usually contributes only minor amounts of amino acids. In other cases, however, notably in Coleoptera, Orthoptera, and Hemiptera, larvae and adults have the same food habits and adult feeding plays a major part in obtaining the reserves needed for egg production.

Amongst aquatic insects, phytophagy is common in Trichoptera (caddis) and also occurs in some Ephemeroptera (mayflies) and Plecoptera (stone flies). These are not considered in this article because very little is known of the roles of chemicals in their food selection.

Order	Main phytophagous taxa	Common name	Feeding stage	Species in taxon	Phytophagous species
Orthoptera					
	Tettigonioidea	bush crickets	larvae, adults	5,000	4,500
	Acridoidea	grasshoppers	larvae, adults	10,000	10,000
Phasmatodea		leaf, stick insects	larvae, adults	2,500	2,500
Hemiptera	Sternorrhyncha	aphids	larvae, adults	15,000	15,000
	Auchenorrhyncha	plant hoppers	larvae, adults	36,500	36,500
	Heteroptera	sucking bugs	larvae, adults	17,500	10,500
Thysanoptera					
	Terebrantia	thrips	larvae, adults	2,500	2,000

Coleoptera					
	Chrysomeloidea	leaf beetles	larvae, adults	70,000	70,000
	Curculionoidea	weevils	larvae, adults	57,000	57,000
Diptera					
	Cecidomyiidae	gall flies	larvae	4,000	4,000
	Agromyzidae	leaf miners	larvae	1,800	1,800
	Tephritidae	fruit flies	larvae	4,000	4,000
Lepidoptera		butterflies, moths	larvae	200,000	200,000
Hymenoptera					
	Symphyta	sawflies	larvae	5,000	5,000
	Cynipoidea	gall wasps	larvae	2,300	1,500

Table 1. The main groups of terrestrial phytophagous insects. Many other groups include some phytophagous species.

2. Diet Breadth

About 75% of all terrestrial plant-feeding insect species feed on only a limited range of plant species; plants outside this range are rejected if they are encountered. Some species only feed on plants within a particular species or genus. They are said to be monophagous. Others feed on a wider variety but are still limited to plants within a particular family. These are oligophagous. Species that feed on plants from more than one family are called polyphagous. Examples of species exhibiting these different degrees of specificity are given in Table 2. Some polyphagous species occur in all the major orders of phytophagous insects but they usually comprise less than 25% of all the plant-feeding species. Grasshoppers, however, are an exception. In this group of insects more than 50% of species feed on plants from more than one family, and monophagy is very uncommon.

	Insects		Hostplants	
Species	Common name	Order	Common name	Genus/family
Monophagous				
Bootettix argentatus	creosote grasshopper	Orthoptera	creosote bush	*Larrea*
Nilaparvata lugens	brown planthopper	Hemiptera	rice	*Oryza*
Bombyx mori	silk moth	Lepidoptera	mulberry	*Morus*
Chrysolina quadrigemina		Coleoptera	St. John’s wort	*Hypericum*
Dacus oleae	olive fruit fly	Diptera	olive	*Olea*

Diprion hercyniae	spruce sawfly	Hymenoptera	spruce	*Picea*
Oligophagous				
Locusta migratoria	migratory locust	Orthoptera	grasses	Poaceae
Acyrthosiphon pisum	pea aphid	Hemiptera	legumes	Fabaceae
Pieris brassicae	cabbage butterfly	Lepidoptera	crucifers	Brassicaceae
Leptinotarsa decemlineata	Colorado potato beetle	Coleoptera	potato family	Solanaceae
Delia brassicae	cabbage root fly	Diptera	crucifers	Brassicaceae
Athalia glabricollis	sawfly	Hymenoptera	crucifers	Brassicaceae
Polyphagous				
Schistocerca gregaria	desert locust	Orthoptera	many	
Aphis fabae	black bean aphid	Hemiptera	many	
Spodoptera littoralis	cotton leaf worm	Lepidoptera	many	
Diabrotica virginifera	western corn rootworm	Coleoptera	many	
Ceratitis capitata	Mediterranean fruit fly	Diptera	many	
Tenthredo atra	sawfly	Hymenoptera	many	

Table 2. Examples of insect species with different diet breadths from the main orders of insects

The term "polyphagy" does not imply that the insect will eat any plant species. Even the most catholic of plant-feeding insects, like the desert locust (*Schistocerca gregaria*), rejects many species of plant. In one series of observations carried out in India this species was recorded as readily eating 160 plant species, eating a further 29 with great reluctance, and not eating 9 at all. These included the neem tree (*Azadirachta indica*), which is not eaten by the desert locust even when neighboring plants are completely defoliated. Extracts of the seeds of this tree have been widely used as an antifeedant in crop protection against a variety of pests. The species that were eaten were from 21 different families, but other representatives of the same families were amongst those less readily eaten.

Even among plants that are eaten, the amounts eaten in one meal are very variable. This is true not only for polyphagous species, but for many oligophagous species, too. Figure 1A shows the results of laboratory experiments in which the African migratory locust, an oligophagous species that feeds primarily on grasses, was offered a variety of plant species. None of over 100 broad leaved plants (dicotyledons) was eaten in large amounts, and this was true of most monocotyledons other than the grasses, but moderate amounts of a few species from both taxa were eaten to some extent. By contrast 75% of 20 grass species were eaten to repletion, and none was rejected without feeding. In a parallel experiment (Figure 1B), the desert locust, a polyphagous species, fed on most plants and some were eaten in large amounts. These included grasses, other monocotyledons, and dicotyledons.

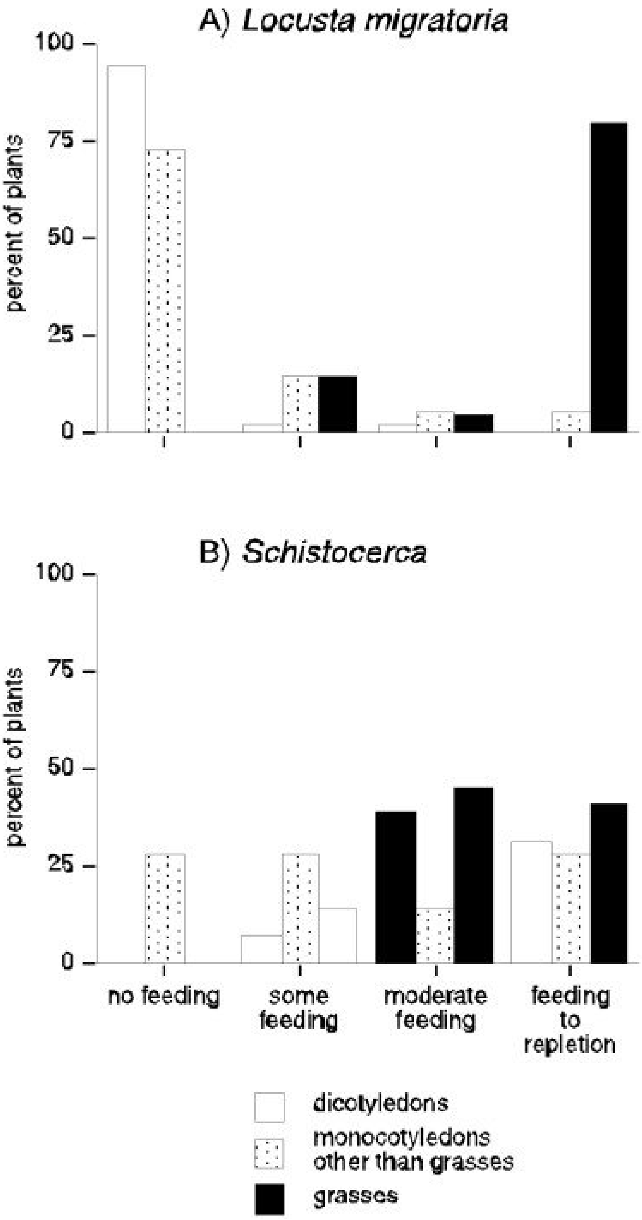

Figure 1. Acceptance of different plants by an oligophagous and polyphagous insect. A. *Locusta migratoria* rejects most broad-leaved plants (dicotyledons) and the majority of monocotyledonous plants other than grasses without feeding at all. All the grasses tested are eaten to some extent and the insect feeds to repletion on the majority. This species is oligophagous in grasses. B. *Schistocerca gregaria* eats nearly all the plants offered to it. Some plants from each of the categories are eaten in very large amounts. This species is polyphagous. Source: data from Bernays E.A. and Chapman R.F. (1978). Plant chemistry and acridoid feeding behavior. *Biochemical Aspects of Plant and Animal*

Coevolution (ed. J.B. Harborne), pp. 99–141. London: Academic Press.

Specificity relates to the part of plant that is eaten, in addition to the species of plant. Many caterpillars and grasshoppers are leaf eaters consuming all the tissues of a leaf, but others are more specific. The larvae of some species make tunnels within a leaf, eating the mesenchyme and vascular tissues, but leaving the epidermis. They are called leaf miners. Others, stem borers, make tunnels in the stems of plants, and yet others feed on the roots. The reproductive and fruiting parts of plants also provide food for some species. Table 3 gives examples of insects that, at least to some extent, specialize on different parts of the sorghum plant.

Plant part	Insect species	Common name	Order
seed head			
	Heliothis armigera	earworm	Lepidoptera
	Contarinia sorghicola	Sorghum midge	Diptera
	Dysdercus superstitiosus	cotton stainer	Hemiptera
	Calocoris angustatus	earhead bug	Hemiptera
stem	*Chilo partellus*	Sorghum stem borer	Lepidoptera
	Busseola fusca	maize stem borer	Lepidoptera
	Sesamia cretica		Lepidoptera
	Atherigona soccata	Sorghum shoot fly	Diptera
leaves	*Mythimna separata*	Oriental armyworm	Lepidoptera
		various grasshoppers	Orthoptera
phloem	*Peregrinus maidis*	shoot bug	Hemiptera
	Rhopalosiphum maidis	maize aphid	Hemiptera
	Schizaphis graminum	green bug	Hemiptera
roots	*Phyllophaga crinita*	white grub	Coleoptera
	Tetraneura bdomalis	root aphid	Hemiptera

Table 3. Examples of insect species that feed on different parts of a *Sorghum* plant

3. Foraging Strategies

This article is concerned with the role of plant secondary compounds in the foraging behavior of phytophagous insects; how do insects locate and recognize their hostplants? Because winged adult insects are so much more mobile than their larvae, they have the primary role in dispersion and host finding, and since the adults commonly lay their eggs on appropriate hostplants for their larvae, the larvae usually are not required to locate their host. Even in these cases, however, larvae do retain the ability to distinguish between host and non-hostplants.

Locating a hostplant from a distance may be achieved either by oriented movements towards it, or as a result of nondirected movements. The only information an animal can obtain about a plant from a distance is its appearance and its smell. Plants are, however, highly variable in shape and color, and so for most insects appearance is unlikely to provide a specific recognition cue. Plant odors, on the other hand, are often specific and serve as recognition cues for many insect species.

Plant odors always comprise a complex of many different volatile compounds, some of which are end products of fatty acid metabolism and so are common to the odors of many plant species, while others are secondary compounds, which are often relatively specific to particular plants. Although the odor is probably produced continuously by a plant, it does not form a continuous stream or plume as it is blown away by the wind. Turbulence and small changes in wind strength and direction result in the formation of small pockets of air containing odor, separated from each other by regions of "clean" air, air without the odor. As a result, there is no stable concentration gradient along which an insect might find its way to the source. Instead, the odor provides an insect with an alerting stimulus, alerting it to the fact that there is a hostplant somewhere nearby. The direction of the host is given by the wind. Moving upwind will bring the insect closer to the source of odor, and the perception of its hostplant odor causes an insect to orient into wind. Such orientation is called positive anemotaxis, and insects use two different strategies to accomplish the upwind movement. The cabbage root fly, *Delia radicum*, turns to face into the wind before it takes off. It then flies in a straight line for about 50 cm before landing and reorienting. This process is repeated until it reaches the hostplant. Insects that are already in flight, however, turn into the wind and then proceed upwind in a series of zigzagging movements across the wind, analogous to a yacht tacking into the wind. This behavior perhaps enables the insect to make more frequent contact with pockets of air carrying the odor. This is necessary for it to continue its generally upwind displacement; if it does not receive this information it flies off in a different direction tending to be displaced downwind. Plant odors and the insects making oriented movements towards plants are considered briefly in Section 6.

There are few well-documented examples of insects locating their hostplants by nondirected (often called "random") movements. This may indicate that it is an unusual occurrence, but probably is a reflection of the difficulty of studying this phenomenon. It might be expected that such a strategy would be found in polyphagous species, and the best-known examples are two polyphagous aphids, *Aphis fabae*, the black bean aphid, and *Myzus persicae*, the green peach aphid. The process is not strictly random because the insects favor landing on certain colors. The insects are, for most of the time, carried downwind, only making directed movements towards a landing site when the wind speed is very low. After landing, the insects assess the plant with respect to its suitability as a host species and also its nutritional suitability. If the plant is appropriate, the insect remains; if it is not, the insect takes off and resumes the search.

By whatever means the insect arrives on a plant, it then determines that this is the appropriate host species. Odor may be involved in this, although there is almost no information of the possible importance of plant odor near the plant surface. In every instance that has been investigated in any detail, however, the insect has been shown to use its sense of taste. "Taste" for the insect involves receptors on the feet, and perhaps

other parts of the body, as well as those associated with the mouthparts, and is more appropriately called “contact chemoreception”. At this stage, nonvolatile plant secondary compounds are nearly always involved. Sections 4 and 5 deal with this aspect of foraging.
For many insects a single plant provides food and shelter for the whole developmental period. This is true, for example, of apterous (wingless) aphids, and the larvae of most Lepidoptera and phytophagous Coleoptera. Other insects are much more mobile, however, and in these cases experience of one food may affect what the insect eats next. This important aspect of foraging is considered in Section 4.4.

4. Plant Secondary Compounds: The Determinants of Diet Breadth

All insects, in general, have similar dietary requirements and there are few examples of insect species feeding on particular plant taxa because the species has specific dietary requirements. Even where this is true, nutrients may not provide the basis of selectivity. This is not to deny that some plants, or plant parts, are more favorable because they have higher quantities of particular nutrients, and insects may choose to eat them. Adult females of the Senegalese grasshopper *Oedaleus senegalensis* feed preferentially on the milky heads of sorghum, while during the nymphal stages they feed as readily on leaves. It is very likely that the developing grains provide a better source of protein that is used by the insect for synthesizing yolk. However, hostplant specificity appears usually to have evolved for some ecological reason other than nutrition, and the question addressed here is how insects choose the appropriate plants on which to feed. For many insects, this foraging behavior involves parental behavior in addition to the behavior of the individual insect, because many adult insects lay their eggs only on species of hostplant that are appropriate for larval development. This is true, for example, in many Hemiptera and most Lepidoptera. Hence a consideration of foraging by phytophagous insects must include a consideration of hostplant selection by ovipositing females.

In every case that has been studied in any detail, plant secondary compounds play a significant, and usually dominant, role in hostplant selection, and it is this role that is considered here. All phytophagous insects that have been investigated respond behaviorally to at least some plant secondary compounds. These responses may be either positive or negative with respect to the source of the compound and whether or not it is volatile. The odors of volatile chemicals can be detected at some distance from the source, while nonvolatile compounds require the insect to make contact with and taste them. Dethier and his colleagues called volatile chemicals *attractants* if they caused the insect to orient to and move towards the source of odor, or *repellents* if they caused the insect to move away. Compounds that had an effect when contacted were called *phagostimulants* if they stimulated feeding (or *oviposition stimulants* if they induced egg laying), or *deterrents* if they inhibited feeding or oviposition. Unfortunately, these useful distinctions are not always appreciated, yet they are important to gain a proper understanding of an insect’s behavior and what may be governing it. For example, insects may collect on a plant because it is acceptable once they have arrived, but they have not necessarily been “attracted” to it from a distance. The distinction is important because the latter indicates a positive response to the plant’s odor, while the former does not necessarily involve odor at all.

The behavioral responses of insects to these chemicals are determined by a number of factors: the concentration of the compound; its concentration relative to other compounds, both nutrients and other secondary chemicals; the genetic (evolved) background of the insect species; and the physiological state and recent experience of the individual insect.

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Biographical Sketch

R. F. Chapman was educated at London University. In 1951 he received a B.Sc. from Queen Mary College, in 1953 a Ph.D. from Birkbeck College, and in 1965 a D.Sc. He has held the following positions: 1954–1957 Scientific Officer, International Red Locust Control Service, Northern Rhodesia (now Zambia); 1957–1959 Research Scientist, Biological Research Institute, University of Ghana; 1959–1970 Lecturer/Reader/Professor, Department of Zoology, Birkbeck College, University of London; 1970–1983 Assistant Director, Anti-Locust Research Centre (subsequently, Centre for Overseas Pest Research), London (now Natural Resources Institute, University of Greenwich); 1983–1989 Visiting Lecturer, Department of Entomology, University of California, Berkeley; and from 1989 to the present Professor, Division of Neurobiology, and Joint Professor of Entomology, University of Arizona. He was visiting professor from 1975–1983 at the University of Hull, and in 1985 at the University of Queensland.

Two recent books are *The Insects: Structure and Function* (1988) and in 1994 (with E.A.Bernays), *Hostplant Selection by Phytophagous Insects*. He edited *Biology of Grasshoppers* (with A. Joern) and *Regulatory Mechanisms in Insect Feeding* (with G. de Boer). He has written scientific papers on various aspects of insect feeding, especially grasshoppers, insect sensory systems and insect/plant relations. He is Honorary Fellow of the Royal Entomological Society, Fellow of the Institute of Biology, and Fellow of the Entomological Society of America.