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Feeding Strategies and the Guild Concept Among Vascular Feeding Insects and Microorganisms

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Introduction

Two large orders of insects—the Hemiptera and Homoptera—possess mouthparts that are highly modified for piercing tissues and extracting their fluid contents. Food sought by hemipterans may be the blood of vertebrates [e.g., Cimicidae (bed bugs)], the hemolymph of other invertebrates [e.g., Reduviidae (ambush bugs) and Gerridae (water striders)] or the cytoplasm and sap of plants [many Miridae (plant bugs) and Pentatomidae (stink bugs)] (76). The Homoptera are strictly plant feeders (23), the only exceptions being several species of aphids with predatory early instars (2).

Cobben (23) studied the morphology of the piercing-sucking mouthparts in relation to the evolutionary history of the two orders. Carter (17), Miles (74), Forbes (40), and Forbes and MacCarthy (41) have also reviewed this subject. Despite the great diversity of tissues from which food is derived, the piercing-sucking mouthparts of these orders have the same general structure. The needlelike stylet bundle that actually penetrates the tissue consists of two pairs of stylets. The inner pair or maxillary stylets interlock in such a way that two channels are formed between them. The smaller channel is used to inject saliva into the food; the larger one is the food canal through which liquid food is ingested. The inner, maxillary stylets are enclosed and supported by the outer pair of mandibular stylets. The latter are typically barbed on their ends, to anchor the stylet bundle in the prey tissue or, in some taxa, to rip and tear cells apart so their contents can be ingested.

Although the actual feeding sites of the insects in plant tissues are not
visible, it is straightforward to kill the insects while they are feeding, and subsequently to section the plant tissue to determine the location of the stylets. In addition, all Homoptera and some Hemiptera [Pentatomorpha (stinkbugs)] secrete a saliva that gels rapidly as their stylets penetrate the plant (74). The gelled saliva forms a sheath around the stylets and remains in place after the insect has finished feeding. This so-called stylet sheath is readily stained in plant sections, and provides, for most species, a second, unambiguous view of the actual tissue fed upon and the route through the plant taken to reach it. The exceptions are aphids and perhaps some mesophyll feeders that extend their stylets beyond the sheath during feeding (61, 75; D. Ullman, personal communication).

Studies of the stylets and stylet sheaths in plant tissues of Homoptera and phytophagous Hemiptera have shown that there are three distinct feeding sites of piercing–sucking insects. They are (1) the xylem and (2) phloem vascular tissues, and (3) the nonvascular tissues, including the mesophyll of leaves and the endosperm of seeds. Each presents unique problems in terms of tissue location and food quality and quantity, and requires adapted feeding modes. We now wish to review these three feeding modes and to discover why the tissue selected tends to be a conservative character in evolution, often characteristic of entire families or subfamilies. We shall also review exceptions to these rules: species that are tissue generalists, and specialists that have switched to feed on tissues that are atypical of their taxa. Finally, we shall discuss the pathogens that also inhabit these plant tissues. These microorganisms also range from generalists to specialists on xylem or phloem, though they can subdivide these tissues on a much finer spatial and temporal scale than can the insects. Therefore, insect and microorganism specialists on the same plant tissues are best considered as occupying different, only partially overlapping guilds.

**Xylem Feeders**

The xylem tissue carries nutrients and water in a continuous stream from the root to the aerial parts of the plant. Since xylem sap is easily collected in large quantities, as guttation liquids or as exudate from wounds (e.g., sugar maple sap) or cut stems, its chemistry is well known. Although it contains a wide variety of organic and inorganic nutrients, they occur in very low concentrations and in proportions unlike those in phloem or parenchyma (see 11, 19, 87, 88, 100, 102 for reviews).

For example, nitrogen is absorbed by the roots as nitrate or occasionally ammonia. It is partially or completely converted into amino acids and amides before being transported in the xylem. Typically only seven or eight amino acids are detectable in any sample, and the bulk of the nitrogen, up to 95%, may be bound in aspartic or glutamic acids and their amides.
Not only is this an unbalanced source of amino acids for insects (24), but it is also a very poor one. Xylem sap usually contains only 0.01–0.15% nitrogen (w/v), and may have as little as 0.0002% (w/v) (57). Amino acids may nevertheless constitute 98% of all the organic material in the xylem sap (133).

Sucrose and other sugars are often, but not always, detectable in xylem sap; reported concentrations vary from 0% (w/v) in broccoli (Brassica oleracea) (87), to 0.0005% (w/v) in the bean Vicia faba (57) and 0.5% (w/v) in the sugar beet (Beta vulgaris) (37). The various minerals absorbed by the roots, such as calcium, iron, phosphorus, potassium, and sulfur, are also carried upward in the xylem. Alkaloids and other secondary compounds may also be present (100).

There is little nutritional requirement for xylem-feeding insects to be host-specific. Since xylem cells are large, xylem feeders can have relatively large stylets, which can be used to probe rapidly for food. Xylem sap is chemically quite simple, with most organic constituents already in the form in which they can be absorbed across the gut wall. The sap does not vary greatly between plants, except when it carries secondary defensive chemicals. Therefore, xylem feeders should have little difficulty in locating and digesting their food, regardless of which plant species it is in. Of course, once a xylem cell is located, the insect can feed for hours or even days without moving.

Although xylem feeders need not be host-specific, there is good reason to expect them to be tissue-specific. After all, there are a number of barriers to feeding on xylem sap, in addition to the initial one of being able to insert mouthparts nondestructively into single xylem cells. The next barrier to xylem feeding derives from the fact that xylem sap is under tension, and must be pumped from the plants. As a result, xylem-feeding insects are characterized by an enlarged clypeal region that supports the large cibarial muscles required to suck xylem sap (84). Raven (100; see also 64) analyzed the energetics of this process in detail; he showed that the cibarial pump consumes a significant fraction of the energy that the insects derive from the xylem sap. Furthermore, this cost is greater at higher feeding sites on plants, due to increased xylem tension and decreased nutrient levels. This, Raven suggested, may explain why the nymphs of many Cercoptidae and all Cicadidae feed on xylem in the roots.

The extremely low nutrient concentrations in xylem sap present another obstacle to feeding. Although there is less nitrogen in xylem sap than in any other plant tissue except wood, carbohydrates, not nitrogen, are probably the limiting compounds for xylem sap feeders (66, 100). Xylem-feeding insects must pump and ingest extraordinary amounts of this fluid to obtain sufficient food energy. In addition, these insects have specialized guts called filter chambers that can extract nutrients from this dilute sap against the osmotic potential without simultaneously absorbing lethal amounts of water (19, 45 for reviews). This is a critical factor, since the
volume of sap ingested far exceeds the volume of the insects. Adult spittlebugs [Philaenus spumarius (L.)] excrete up to 2.1 g of processed xylem sap, 280 times their own fresh body weight, per day (57). The leafhopper Draeculacephala minerva Ball processes 2.5 g of fluid per day (58), while another leafhopper, Graphocephala atropunctata (Signoret) (= Hordnia circellata) ingests 100–1000 times its own fresh body weight per day (77, 79). These feeding rates are among the highest in the animal kingdom.

These two predictions—of host generality but tissue specificity—among xylem feeders are generally borne out in nature. The xylem feeders include most of the spittlebugs or froghoppers (Hemiptera: Cercopoidea) (12, 32, 48, 56, 57, 83, 123, 133), all cicadas (Hemiptera: Cicadidae) (19, 131), and all leafhoppers (Hemiptera: Cicadellidae) in the tribe Cicadellinae and probably those in the related tribes Evacanthinae and Mileewanae as well (15, 38, 58, 84, 116, 123). The spittlebugs, in particular, are famous for their catholic feeding habits. The meadow spittlebug P. spumarius = leucopthalimus was reported feeding on 91 species of plants in 29 families at one site in Ontario, including “all dicotyledonous herbs of sufficient size” except milkweed (Asclepias syriaca L.), as well as woody plants, a sedge, and even an equisetum (98). This same insect feeds on at least 165 host plants in Finland (49), although other spittlebugs are even more polyphagous at local sites (49).

Phloem Feeders

The phloem tissue provides an alternative, very different resource for piercing–sucking insects. Efficient use of this resource requires specialized morphological, physiological, and behavioral adaptations that differ sharply from those required for xylem feeding. The phloem feeders are the best known of the three guilds discussed here, and the nature of their food supply is critical to their ecology.

Phloem sap is more difficult to acquire in pure form than is xylem sap. Its chemistry has been studied in detail for a few plants, particularly in relation to carbohydrates (124) and nitrogenous compounds (65, 87, 88, 137). Sucrose and other oligosaccharides, the photosynthate from the leaves, constitute 90% or more of the organic material in the phloem sap. These sugars are usually found in concentrations of 10–25% (w/v), roughly three orders of magnitude greater than their concentrations in the xylem sap. Nitrogen is available in the phloem in the form of amino acids and their amides, as in xylem sap. However, a greater variety of amino acids occur in the phloem, and the total amino acid concentration is slightly higher than that in the xylem, reaching 0.03–0.4% (w/v). Many other compounds, including organic acids and phosphates, sterols, vitamins, and even large amounts of ATP are also present. The phloem is more than
just a transport system for the plant’s energy molecules; recent work suggests that it is also a medium of active biosynthesis of particular compounds (102).

The harvesting of phloem sap presents a number of unique problems to insects, different from those facing xylem feeders. First, the sieve tube cells through which sap travels are tiny; if an insect is to tap this vascular stream without destroying it, the insect’s stylets must also be tiny. Such delicate stylets cannot be plunged randomly through plant tissue in search of the phloem. It is common for phloem feeders, especially smaller ones such as aphids and coccids, to insert the stylets between cells, where they follow an extracellular path to the food. This penetration is typically aided by enzymes contained in the saliva. It may take only a few minutes, but often requires several hours to reach the phloem. There is even one report of aphids requiring 3 days to penetrate to the phloem tissue of their woody host (92). The insects can withdraw their stylets rapidly when disturbed, but this can be expensive in terms of lost feeding time (92). Phloem feeding favors a sedentary habit (see 114 for discussion); it is fortunate that phloem is so rich in sugars, which, when excreted, can be used to “buy” the protection of ants (125).

A second problem for phloem-feeding insects is that of locating the small bundles of sieve tubes within the plants. Indeed, when phloem feeders are placed on unsuitable hosts, the insects often do not locate or ingest from the phloem, despite repeated probing (13, 70, 92 for review). In one case, the stylets were observed to pass within 3–5 μm of the phloem, without recognition (72). It is clear that in suitable host plants, the stylets move nonrandomly; there are frequent reports of the stylets turning directly toward the phloem while within the plant, or of being withdrawn and inserted repeatedly about a vascular bundle until a sieve tube is located (92). This nonrandom probing is probably mediated by both physical and chemical stimuli within the plants. The stylets of aphids (86, 127), leafhoppers (42), planthoppers (43), and psyllids and whiteflies (39) are innervated, apparently with proprioceptors that direct stylet movements within plants (9, 89, 127). In addition, aphids (71, 128), leafhoppers (4, 5), and psyllids (119) have precibarial sensilla that probably mediate chemical cues for tissue location (6). These features are not unique to phloem-feeding Homoptera; however, phloem feeders may be more dependent on internal plant cues to locate their food than are mesophyll and perhaps xylem feeders.

Unlike xylem feeders, phloem feeders need not actively ingest their food. Phloem sap rises in stems at rates of 1 m or more per hour, under pressures of 20–40 atm. When aphid stylets are cut off, phloem sap continues to flow out the cut stylet tip, at the same rate at which intact aphids excrete sap, and at rates comparable to the maximum observed for phloem sap within plants (77). Once the insects have inserted their stylets into the phloem, the sap is forced into their guts. The insects can regulate this
flow, using their precibarial valve (4, 5, 71, 119), but given their poorly
developed cibarial pumps, it is not clear that they ever need to augment
the flow (92, 100).

If insects required only carbohydrates in their diets (as is often assumed
in animal foraging theory), a phloem sap diet of 10–25% (w/v) sugar would
be superb. In fact, phloem-feeding insects consume far more sugar than
they use, and excrete as much as 95% of it as honeydew (77, 78). Feeding
rates vary from 0.57 mg/day for the leafhopper Orosius argentatus (Evans)
(27) to 1.6 mg/day for the aphid Myzus persicae (Sulz.) (28) and 48 mg/
day for the large willow aphid Tuberolachnus salignus (Gmelin) (77; see
37, 92 for reviews). These rates represent between 2 and 32 times the
fresh body weights of the insects per day, which are lower than those
recorded for xylem feeders, but are still high. There is little doubt that
phloem-feeding insects must maintain such high feeding rates, and waste
so much carbohydrate, in order to obtain sufficient amounts of essential
nitrogen (see reviews 66, 73, 120, 121, 132).

The high sugar content of phloem sap gives it a high osmotic potential;
ingested sap will tend to absorb water across the gut wall and could de-
hydrate the insects. This problem is magnified greatly by the large volumes
of food ingested. Not surprisingly, the digestive tracts of phloem-feeding
insects are specialized to handle both the large volumes and their high
osmolarities (45). Aphids convert as much as 40% of the sucrose into the
trisaccharide melezitose, before then excreting it. Owen (85) interpreted
this as a highly sophisticated form of mutualism, in which the aphids fed
nitrogen-fixing bacteria in the soil below, ultimately benefitting the plant
on which they or their progeny were feeding. An alternative hypothesis
with some experimental justification is that the aphids convert sucrose to
melezitose to reduce the osmotic pressure across their gut wall.

Phloem feeding is the predominant pattern throughout the suborder
Sternorrhyncha. This includes psyllids (34, 35, 53, 126, 136), whiteflies
(50, 52, 90, 107; see also 3 and 14, both cited in 122), most aphids (92 for
review), and many scale insects (10, 31, 44, 107). Phloem feeding is also
characteristic of certain groups in the other major suborder, the Auchen-
orrhyncha. These are the treehoppers (Membracidae) (60), the planthop-
pers (Fulgoroidea) (17, 38, 108), and most leafhoppers (8, 15, 29, 36, 38,
60, 97, 103, 111, 123). Phytophagous hemipterans do not typically feed in
the phloem, although they may ingest small amounts of phloem sap.

Unlike xylem feeders, phloem-feeding insects tend to have narrow host
ranges. For example, only one psyllid species in the world is known to
feed on plants of two families, while 76 of the 80 British species and 86
of the 110 Czechoslovakian species are restricted to feeding on plants of
a single genus (30, 54). Also, of the 445 European species of aphids that
lack an obligate alternation of hosts, 407 and 440, respectively, feed on
plants of a single genus and family (30). This extreme host specificity may
result from either of two factors discussed above. First, the internal plant
cues employed by the insects to locate and recognize the phloem apparently differ among plant species, preventing efficient foraging on more than a few, similar host species (13, 70, 82, 115). Also, the insects may be under strong selection to synchronize their life histories with that of particular host plants in order to exploit brief peaks of nitrogen availability in the phloem of those plants (73, 93, 94, 113).

Mesophyll Feeders

Insects that feed on the mesophyll tissues of leaves require a different set of adaptations than do vascular feeders. There is no difficulty in locating the tissue, since, apart from the veins, it consists essentially of the whole leaf. Nor is the tissue inaccessible; even first-instar nymphs of the leafhopper *Euterpex melissae* Curtis have stylets longer than the average thickness of their host plant’s leaves (91). In comparison with xylem or phloem sap, the quality of the food ingested is very high. The cytoplasm, with its content of nucleoplasm and organelles, is richly endowed with a balanced mixture of proteins, carbohydrates, lipids, nucleic acids, vitamins, and minerals. The challenge for mesophyll feeders is to obtain enough of this rich food. This problem has been overcome in different ways by homopteran and hemipteran mesophyll feeders.

Many homopteran mesophyll feeders ingest the contents of only one cell at a time. Pollard (91) has provided an excellent review of the morphological and behavioral adaptations that allow *E. melissae* to obtain sufficient food with this strategy. Not surprisingly, these adaptations allow for the rapid location and ingestion of the contents of individual cells. These leafhoppers have relatively large stylet bundles that are plunged rapidly into the leaf. The stylets do not insinuate themselves slowly between cells using digestive enzymes, as with many phloem feeders, but simply pierce intervening cells on their way to the food. The maxillary stylets first puncture and then rapidly empty the cell; a third-instar nymph can empty a typical palisade cell (5 x 10^-6 mm^2) in about 10 sec. Chloroplasts are larger than the food canal, 5.1 by 3.4 μm versus 3.6 by 2.0 μm, and are apparently disrupted before being ingested. Once a cell has been emptied, the stylets can be rotated and maneuvered to penetrate successively a large number of nearby cells, without being removed from the tissue. Air rushes into the emptied cells, leaving a characteristic clear spot or stippling of the leaf. Individual adults of *E. melissae* feed for about 7 min before removing their stylets and moving to another site on the leaf.

In the Homoptera, mesophyll feeding is characteristic of but not restricted to the leafhopper subfamily Typhlocybinae (15, 29, 46, 47, 55, 91, 97, 103, 106, 107, 111, 123). This is an advanced subfamily of leafhoppers on morphological grounds, suggesting that mesophyll feeding is not the
ancestral pattern (but see 100). Mesophyll feeding is also characteristic of some scale insects (Coccoidea) (16, 31, 105, 107) and of many root-feeding aphids of the family Adelgidae (92). These Homoptera are all small, perhaps representing one constraint of feeding on mesophyll cells one at a time. Mesophyll feeders have narrow to moderate host ranges (20, 21, 67, 110). Of all the Homoptera, these insects are most likely to contact and ingest plant secondary compounds, a circumstance that may play a major role in restricting host ranges.

The phytophagous Hemiptera have a different solution to the problem of obtaining adequate amounts of nutrients from mesophyll. Mirid (plant-) bugs, Tingid (lace-) bugs, and Pentatomorpha (stinkbugs and allies) all have what Cobben (23) calls a "predatory" feeding habit. These Hemiptera use their barbed stylets to slash back and forth, lacerating large numbers of cells at a time. The contents of these cells are then flushed out with saliva and ingested. This is a far less discriminating feeding mode, but it permits higher rates of food intake and is compatible with the body sizes in excess of those of homopteran mesophyll feeders. The large stylets that slice through plant tissue so easily are also capable of piercing and feeding in animal tissues. In fact, of all the herbivorous insects with piercing-sucking mouthparts, only these large mesophyll-feeding hemipterans are commonly facultative predators of other insects.

Overlap Between Feeding Modes

Because the types of feeding we have discussed here are so different, the insect strategists that utilize them can be considered to be members of three distinct feeding guilds. For example, mesophyll feeders may lack the behavioral, morphological, and physiological adaptations for gentle tapping of vascular tissue or for ingesting and processing large amounts of nutritionally poor food. Not surprisingly, when five species of mesophyll-feeding leafhoppers were confined to the stems, petioles, or leaf midveins of their host plants, they fed for only a few hours, and usually died within a day (106). Of course, mesophyll feeders might ingest the contents of vascular cells if their stylets encountered them by chance. This is more likely to occur among the mesophyll-feeding hemipterans, whose stylets slice into large areas of tissue at each feeding, than among the leafhoppers that usually feed on single cells in the "islets" between minor veins (91). Even in that case, however, such incidental feeding (or perhaps destruction of) occasional vascular cells leaves the vascular system essentially intact.

Similarly, many vascular feeders do not feed to any significant degree in mesophyll tissues. For one thing, they are unlikely to be able to ingest mesophyll sap as rapidly as can mesophyll specialists. In addition, they frequently lack the nutritional capability to utilize mesophyll cell sap food
completely if it were ingested. For example, xylem and phloem feeders have only a few enzymes for hydrolyzing sugars in their saliva; they lack the esterases, proteinases, amylases, phosphatases, and phosphorylases that mesophyll feeders possess (74, 103). These indications are supported by experimental results. Phloem-feeding leafhoppers died more rapidly when fed an artificial diet of starch, gluten, and oil emulsion than when fed on simple sugars and tryptophane (103). When confined to mesophyll, the potato leafhopper [Empoasca fabae (Harris)] died almost as fast as if no food were offered; it normally feeds on phloem sap (106). In a more detailed study with yet another phloem-feeding leafhopper [Circulifer tenellus (Baker)], Bennet (8) showed that when caged on mesophyll, the insects died slightly faster than when fed on pure water, and not quite as fast as when starved completely. Survival on the phloem tissue was quite high. No such experiments have been performed with xylem feeders, but they would likely show the same result.

There is often little overlap between the vascular and nonvascular feeding Homoptera and phytophagous Hemiptera. In addition, the vascular feeders themselves consist of two groups with little in common. Phloem feeders passively ingest a nutritionally rich sap at the rate of 2–32 times their body weight per day. Xylem feeders, with the assistance of powerful muscles, suck from 100 to 1000 times their body weight per day of a nutritionally dilute sap. The guts and gut endosymbionts of the insects differ, and are adapted for their special foods (45). As a result, artificial diets for the two kinds of insects are vastly different (116). In addition, they face opposite water balance problems from the ingestion of such large amounts of fluid. Phloem feeders must have special adaptations to avoid dehydration, while xylem feeders must avoid absorbing too much water.

There is direct evidence that phloem and xylem feeders often do not overlap in diet. Examination of stylet sheaths in plant tissues frequently shows little contact with phloem tissue by xylem feeders (see references above), and vice versa, with exceptions noted below. In addition, there are dozens of plant diseases whose agents are confined to the phloem, and several in xylem, that are vectored by homopterans. Potential vectors of these diseases have been carefully screened. In general, diseases restricted to the phloem tissue cannot be transmitted by insects that normally feed in the xylem, and xylem-restricted diseases cannot be vectored by insects that characteristically feed in the phloem (95, 116). This is not simply the result of vector specificity of the disease agents. For example, Pierce’s disease of grapes is transmitted by 23 species of leafhoppers and three species of spittlebugs, all of which feed in the xylem, where the causal bacterium occurs. Similarly, the California aster yellows disease, which is confined to the phloem, is transmitted by 24 species of leafhoppers that feed in the phloem, but none that feed in the xylem (116). Thus, evidence provided by feeding tracks and vector specificities is strong that phloem and xylem feeders often have fastidious diets.
Many families and subfamilies of Homoptera feed characteristically in only xylem, phloem, or mesophyll. For this reason, we conclude that the morphological and chemical differences between these tissues are sufficiently great that (1) insect species adapted to feed efficiently in one cannot do so in the others, and (2) evolutionary shifts from one feeding speciality to another are rare. However, there are exceptions to both rules. First, some insect species can feed in different tissue types, either at different stages of development or concurrently. The sugarcane froghopper [Aeneolamia varia saccharina (Distant)] is a sequential specialist: nymphs feed on xylem, while adults specialize on the border parenchyma cells (48). Other species are true generalists in that they feed alternatively in various tissues: these include certain aphids (33, 69, 70), leafhoppers (29, 80, 115), and psyllids (119). [These examples are to be distinguished from cases of insects feeding in a variety of tissues in unsuitable or resistant hosts, while suffering reduced survival and or fecundity (13, 70, 82).] Obviously there are no absolute barriers to feeding on several kinds of plant sap, though such generalists may be less efficient feeders on any one kind of sap than are, say, xylem or phloem specialists.

In addition, one can readily find examples of evolutionary shifts in diet among tissue specialists. For example, Empoasca fabae (Harris), the potato leafhopper (106), and E. flavescens Fabr. (15) feed in phloem, although at least eight other species in the genus and virtually all other Typhlocybinae feed in mesophyll (see section on mesophyll feeders). Also, Pseudococcidae feed on either phloem or mesophyll (or both) (16, 31, 44, 107), indicating that some species have shifted their diet (and perhaps that others are in transition). Finally, biotype A of the greenbug [Schizaphis graminum (Rondani)] is a phloem specialist, while biotype B, which supplanted it as a major pest of some wheat varieties, feeds in the mesophyll (104).

Janzén (59) pointed out that all insect species feeding on a plant species interact with one another through their effects on the plant. This is true, provided the insects are actually feeding on the same individual plants, and the damage from their feeding is sufficiently intense. However, it does not invalidate the assignment of the insects into different feeding guilds. With some exceptions, the Homoptera and phytophagous Hemiptera can be divided into groups feeding on three distinct tissues: xylem, phloem, and mesophyll. The two vascular feeders remove water and photosynthesize, respectively, while only the mesophyll feeders directly reduce the amount of photosynthetic tissue in the plant. If the insects of any group do affect their host plant significantly, then these effects will have the greatest consequences for other members of their group. This alone justifies the separation of the species on the plants into guilds. Even when feeding damage to the plants is minimal and interactions between members of a guild are unimportant, it is still a useful classification. It combines species sharing a wide range of morphological, physiological, and behavioral adaptations to the utilization of similar food, much as the classification
of vertebrate herbivores into ruminants and nonruminants; these species might be expected to share other aspects of their ecologies as well.

Vascular Prokaryotes: Guild Members?

Certain plant pathogens pose intriguing problems for development of a unified guild concept, and deserve comment in a chapter with significance for disease transmission. The feeding strategies utilized by mesophyll-, phloem-, and xylem-feeding homopterans have entirely different consequences for transmission of plant disease. Mesophyll feeders are not known to transmit plant disease, presumably because their target cells are destroyed by the feeding process. Homopterans that feed in phloem and xylem, on the other hand, transmit an array of plant pathogens, including many organisms that induce diseases of serious economic importance (116). These pathogens utilize the same general resources as the insects that feed in vascular tissue: should they be elected to guild membership?

The assemblage of xylem-inhabiting prokaryotes is diverse, and includes extreme cases of generalist and specialist organisms (1). At one end of the spectrum, fungal or bacterial vascular wilt pathogens gain access to tracheal elements through wounds, including those made by insects. The fungi (e.g., Corynebacterium, Fusarium, Verticillium) or bacteria (e.g., Xanthomonas, Pseudomonas, Erwinia), after entering the xylem, produce pectinases and cellulases that degrade the tracheal walls. Materials released by this process then are transported in the vessels, and eventually obstruct the vessel pores and block the transpiration stream, leading to wilt of the plant. When the organisms break through the walls they are also able to multiply in parenchymal tissue. Thus, these generalists truly overlap vascular and parenchymal tissue in their feeding strategies.

More interesting and germane to a discussion of the guilds of xylem specialists are those organisms that do not destroy the xylem tissue once they have entered it. These are the bacteria that cause such diseases as ratoon stunt of sugarcane (109) or Pierce’s disease of grapevines (51). Although these pathogens attract attention as a result of the extensive damage that they cause on crops, their natural maintenance cycles are not well understood. In the case of Pierce’s disease, the fastidious causative bacterium is evidently widely distributed in a variety of plant hosts (51), and is transmitted by a wide variety of cicadelline leafhoppers, which are commonly regarded to be xylem feeders (96, 118). These pathogens, unlike the generalist Gram-negative bacterial pathogens, do not multiply in conventional media, and specialized media are required for their cultivation (25, 26).

In general, the specialized media that have been successful for xylem pathogens contain much lower concentrations of nutrients than media used for cultivation of phloem pathogens. Failure of more complex media seem
to be ascribable to oversupplies of nutrients, rather than failure to supply critical, limiting substances. Thus, the principal adaptive basis for utilization of xylem appears to involve interconversion of scarce nutrients from one form to another, or to utilize nutrients present in critically limiting quantities.

The array of pathogens inhabiting the phloem is also diverse. Among phloem-inhabiting prokaryotes (102) may be included spiroplasmas (helical, wall-less motile prokaryotes) (129) and a loosely defined group of non-cultivable "yellows" agents (68) that are recognized and differentiated on the basis of specific symptomatology. Also included is a taxon of small fastidious bacteria, all of which have so far escaped efforts at cultivation (63, 135). The fact that yellows agents and fastidious phloem-limited bacteria resist cultivation, whereas spiroplasmas can be cultivated in a variety of media, emphasizes the nutritionally diverse abilities of different taxa that apparently utilize the same habitat (namely phloem). With phloem pathogens, it has been more difficult to discern nutritional overloads. Rather, the common approach to cultivation has been to supply as many nutrients as possible (130). Chemically defined media have been designed for several spiroplasmas of insect habitats (18). Components that have proved to be essential for spiroplasmas include amino acids, carbohydrates, sterols, vitamins, and nucleic acid precursors; it is likely that all these substances normally occur in sieve elements inhabited by the spiroplasmas.

Discovery of a diverse assortment of spiroplasma species in association with insects (22) makes it possible to assess the habitats of these microorganisms in relation to their nutritional specialization. The 25-odd cultivable spiroplasma species now under study exhibit a bewildering array of nutritional capabilities. For example, although pathways for arginine catabolism are often present, some species lack this pathway. Similarly, the degree of dependence on glucose or other fermentative pathways differs profoundly among isolates and between species. Chang and Chen (18) felt that the different requirements they observed were related to habitats of the organisms. If there is a single unifying factor in the ecology of known spiroplasmas, it is that all are closely linked to restricted host-defined habitats. Since the biochemistry of each host differs, in some cases profoundly, the genomes of the organisms have become modified for the realities of the habitat to which they have become adapted. Recent studies, in fact, suggest that there is a distinct correlation between the "clonality" of microbial clusters and the homogeneity of the habitat in which the organisms live (101). For example, Mycoplasma pneumoniae, a pathogen that is closely associated with mucosa of the human respiratory tract, occurs as a tight cluster of homogeneous strains (101). In contrast, Acholeplasma species of the granularum cluster, which tend to be isolated from a variety of habitats, are not so tightly clustered. Spiroplasma species that have proved difficult or impossible to cultivate always seem to be in
special habitats. For example, the sex-ratio spiroplasmas of *Drosophila*
that are vertically transmitted through the egg and selectively eliminate
male progeny steadfastly resisted cultivation (134). Thus, in a single genus
of microorganisms, there appears to exist a range of nutritional adaptations
that range from generalist to mutualist. This is not to say that other im-
portant features of life history strategies are unimportant to these micro-
organisms. The requirement to find a means for dispersal to new habitats
remains equally imperative. In this regard, the homopteran strategists that
share the vascular tissues with the spiroplasmal and mycoplasmal path-
ogens of course play a central role.

Once transmission has occurred, the pathogens enter the phloem stream
of the plant and induce systemic infection. There is no evidence that the
phloem tissue of fresh plants chosen by the insects has a significant micro-
bial flora. Rather, the current picture of plant vascular tissue is one of
a tissue that is, despite the lack of an immune system with specific
memory, normally as aseptic as the vascular tissue of animals. Presumably,
the tissue is accessible only to organisms that can be introduced by the
specific feeding of phloem-specialist insects.

 inoculation of vascular plants is not a rare event in nature; widely sep-
ated, occasional transmission events would probably escape notice. In
fact, epidemics such as that associated with the destruction of tall coconut
in Jamaica and south Florida by the lethal yellowing mollicute have force-
fully called such transmission to attention (117). In certain instances of
disease transmission, multiple infections have been noted (112). For ex-
ample, the infection of phloem tissue by the aster yellows pathogen and
oat blue dwarf virus (7) has been demonstrated, and in California, si-
multaneous infection of hosts by *Spiroplasma citri* and a noncultivable
virescence agent, or by *S. citri* and the mycoplasmalike organisms (MLO)
causing either pear decline (99) or Western X-disease of stone fruits (62),
led to serious confusion concerning disease etiology before the dual nature
of the infections was realized. In the neotropics, it is common to find corn
plants that may be simultaneously infected by the corn stunt spiroplasma,
the maize bushy stunt MLO, and the maize rayado fino virus (81). In each
of these cases, the organisms may not only coinfect their plant hosts, but
are transmitted by the same leafhopper species [*Dalbulus maidis* (DeLong
and Wolcott)] and in some cases by the same individual insect.

The coexistence of different pathogens in phloem presents no conceptual
problem to competition theory. The phloem tissue evolves, in the life of
a single cell, from an actively living cell fully capable of supporting viral
multiplication, to a probably lifeless element, which then serves as a con-
duct for photosynthate transport. One can hypothesize that a single phloem
cell could, in its lifetime, support first a nondestructive virus, then a fas-
tidious mollicute, and, finally, a more nutritionally general spiroplasma
that utilizes the photosynthate of the plant rather than living protoplasm.

It is unlikely that insect parasites feeding on phloem tissue could sub-
divide its resources as finely as the plant pathogens. Thus, although insects, viruses, and prokaryotic microorganisms utilize the same plant tissue, we argue that the grain of exploitation, both spatial and temporal, is sufficiently different that insects and microorganisms cannot be thought of as members of the same guild; instead, the microorganisms themselves might be subdivided into guilds that depend on the stage in the life of individual phloem elements. Thus, viruses, spiroplasmas, and mycoplasmalike organisms may well comprise guilds of their own. Indeed, experiments in which competitive challenges have been deliberately induced (96) tend to support the concept that organisms of similar taxa may in fact be subject to general laws governing competition between organisms.

Summary

We reviewed the literature on Homoptera feeding to make the following points: (1) Homoptera typically feed either on phloem or xylem sap, or on the cytoplasm of mesophyll and other cells, though there are exceptions that feed more generally. (2) Each of these three feeding modes requires special morphological, physiological and behavioral adaptations, which may preclude feeding on other plant, let alone animal, tissues. (3) As a result, the food eaten by these insects is a conservative character in evolution, and often characterizes entire subfamilies or families. (4) Other features of the biology of the Homoptera, such as patterns of host specificity and their role as vectors of plant pathogens, may also be understood in light of their feeding strategies. For reasons 1–4, it is useful to categorize Homoptera, where possible, into three distinct feeding guilds. (5) Plant pathogens such as bacteria, fungi, viruses, and spiroplasmas that inhabit the vascular tissues also tend to be tissue specialists, though they can subdivide these tissues on a much finer spatial and temporal scale. As a result, the pathogens and the Homoptera that vector them are best considered members of different, only partially overlapping guilds.

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