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WILD HOSTS OF PENTATOMIDS: Ecological Significance and Role in Their Pest Status on Crops

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ABSTRACT

Phytophagous stink bugs (Heteroptera: Pentatomidae) are important pests of many crops, feeding mostly on seeds and immature fruits. During feeding they introduce their stylets to remove the cells' contents. The resulting damage includes drop and/or malformation of seeds and fruits. As stink bugs are generally polyphagous, they feed on cultivated and uncultivated plants; consequently, wild host plants play an important role in the increase in population levels of agricultural pest species. These plants are important food resources for development of nymphs and reproduction of adults. Because these bugs are multivoltine and feed in general on temporarily restricted food plants, host-switching from food plants of nymphs to those of adults is common and has varying effects on adult performance depending on the quality of the foods involved. Although polyphagous, local populations of many pentatomid species may show specific feeding habits, restricting their host range to fewer plant species. The knowledge of host plant sequences, including cultivated and uncultivated hosts, and the use of wild hosts as trap plants will improve management of pest species. Finally, future research should focus on determining which plants are preferably used by stink bugs, how they affect insect performance, at what rate populations increase on these plants, and how effective natural enemies are at this time.

PERSPECTIVES AND OVERVIEW

The Pentatomidae is one of the largest families within the Heteroptera, with over 4000 described species (151). Of the eight subfamilies (i.e. Asopinae,

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Cyrtocorinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae, and Serbaninae), the subfamily Pentatominae is the largest and consists entirely of plant feeders (153). Members of this family are characterized by being round or ovoid, with five-segmented antennae, two-segmented tarsi, and a short scutellum that is more or less triangular; they are called stink bugs because they produce a disagreeable odor by means of their scent glands (6).

Most phytophagous pentatomids are polyphagous, feeding on cultivated and uncultivated plants. They are major pests of economically important crops throughout the world, including legumes such as soybean (59, 85, 134, 163, 165); cereals such as rice and wheat (9, 12, 18, 27, 35, 43, 65, 91, 94, 109, 112, 146, 148, 149, 157, 168, 177); and tree crops such as citrus (49, 61–64), oil palms and coconut (25, 88, 107, 142, 143), cocoa (113, 115, 181), and coffee (42, 98, 99). Because of their feeding habits, wild hosts play an important role in the buildup of pentatomids that are agricultural pests (1, 3, 14, 26, 27, 60, 69, 71, 78, 81, 86, 102, 115, 120, 128, 130, 133, 136, 141, 150, 152, 166, 170, 172, 179). The importance of wild hosts in the buildup of populations on crops is magnified in tropical and subtropical regions where pentatomids are able to reproduce during most of the year because suitable food plants are also available year round.

To better understand pentatomid/crop-plant interactions it is necessary to review feeding processes, the nature of injury caused by the phytophagous species, the role of wild hosts in nymph and adult biology, the effect of nymph to adult host-switches on adult biology, polyphagy/host plant sequences, and specific feeding habits. All of the above factors are critical components of pentatomid nutritional ecology (129, 133, 137, 171, 172). Because of the extent and complexity of the subject covered in this review, discussion is based on information on the interactions of pentatomids pests of soybean and their wild hosts in the northern area of Paraná state (23°11′S latitude, 51°11′W longitude), Brazil. Observations in this system provide a case study comparable to other studies carried out in the southern United States (69, 71), Australia (170, 172), and Japan (81), among others.

FEEDING AND NATURE OF DAMAGE BY PHYTOPHAGOUS PENTATOMIDS

Phytophagous pentatomids feed on various structures of the host plant, and as a consequence, the nature of the injury they cause is also variable. Seeds and immature fruits are preferred feeding sites (153). Those feeding on seeds inject a watery saliva containing digestive enzymes and suck out the liquefied contents; this mode of feeding probably evolved from a rasping-sucking type

of feeding (40). Excess saliva solidifies around the stylet to form a stylet sheath (54, 101). These sheaths remain in the plant tissue after feeding and serve as a record of feeding activity (7, 8, 53, 175, 183).

The injury caused by pentatomids feeding on seeds has been described in detail for many crops. For example, on soybean, feeding punctures on seeds cause minute darkish spots, and chalky appearing air spaces are produced as the cells' contents are withdrawn (102). Later, dark discoloration may surround the punctures, and the inner membrane of the seed coat may be fused to the cotyledons (5, 19, 77, 102, 164). On rice seeds, stink bug feeding during the early stage of endosperm development (the milk stage) results in either empty glumes or severely atrophied kernels. Feeding during later stages (dough and hard stages) results in a chalky discoloration around the feeding site. Rice showing this damage is called pecky rice; it is structurally weakened and often breaks under mechanical stress during milling (e.g. 26, 27, 84, 95, 148, 162). On fruits such as pecan, damage during early season fruit development in the liquid endosperm stage (the water stage) causes black pit or black heart, and shucks adhere tightly to the fruit shells. After the water stage, feeding sites on kernels cause brown to dark spots, which become sunken and pithy (183 and references therein). On cocoa, injury by pentatomids results in premature ripening of the fruits; stylet penetration of the pod cortex results in malformed or atrophied beans, which are brown instead of pink, and which dry and lack the sugary mucilage that covers normally developed beans (39, 93, 116). Feeding on vegetative tissues may cause darkening of stems (as in soybean) or leaf wilt and eventually plant death (as in potato) (38, 127, 145). Finally, the transmission of microorganims during the feeding process magnifies the potential damage caused by pentatomids to their hosts [e.g. transmission of the yeast spot disease *Nematospora coryli* to soybean (see references in 134) and transmission of the flagellate protozoan *Phytomonas* spp. to palm trees (25, 89, 142, 143)].

PENTATOMIDS AS AGRICULTURAL PESTS

Most phytophagous pentatomid species of economic importance belong to the subfamilies Pentatominae, which contains most of the plant pests (6, 153), and Edessinae, which has some pest species in the genus *Edessa* (157). The economic importance of these insects varies greatly from species to species, and within species, depending on the plant being fed upon.

Pests of Leguminous Crops

Among the several pentatomid pests of legume crops, the southern green stink bug *Nezara viridula* is perhaps the most important. A species probably of

Ethiopian origin (68), it is now cosmopolitan (23, 51, 134, 163) and very polyphagous, feeding on plant species in more than 30 families, with preference for legumes and brassicas (e.g. 28, 29, 52, 58, 66, 144, 157, 163, 169, 173).

Piezodorus guildinii, a neotropical pentatomid, is a major pest of soybean and some other legumes such as common bean, pea, and alfalfa; it has been reported occasionally from coffee, cotton, guava, and sunflower (134 and references therein). Wild host plants include species of indigo legumes (*Indigofera* spp.) in the southern United States (135), Colombia (46), and Brazil (120). It also feeds on legumes of the genus *Sesbania* and *Crotalaria* (117, 119, 135). The related species *Piezodorus hybneri* also feeds on soybean in India and in several other countries in Asia (85, 159). In Japan, it is likely that the first nymphal generation from overwintered adults develops on noncrop hosts, with resulting adults migrating into soybean fields as the crop reaches podding stage (50).

Species of *Euschistus*, particularly *E. heros* in the neotropics (134) and, to some extent *E. servus* in the Nearctic (85), cause injury to soybean. The first species is somewhat polyphagous, feeding on legumes in addition to soybean, and on species of the Solanaceae, Brassicaceae, and Compositae (32, 90, 91). It also has been reported to feed on weeds associated with the soybean crop, such as the euphorb *Euphorbia heterophylla* (100) and the star bristle *Acanthospermum hispidum;* this last plant plays a role in the phenology of *E. heros* (130). The second species, *E. servus*, feeds on several uncultivated hosts; the main ones are sowthistle (*Sonchus oleraceous*), peppergrass (*Lepidium virginicum*), and vetch (*Vicia* spp.) in the southeastern United States (71).

The genus *Acrosternum* contains several pest species of legumes. In North America, *Acrosternum hilare* is a major pest of soybean (102, 165). Several cultivated and uncultivated host plants have been reported (71, 102, 152, 166, 180). Lima beans, peaches, and cotton have been listed among the cultivated plants; the latter two are preferred among nonlegumes (166, 180). Uncultivated preferred hosts include black-haw, *Viburnum prunifolium*, which is reported as very suitable to raise this species of pest (180), elderberry (*Sambucus canadensis*), black cherry (*Prunus serotina*), black locust (*Robinia pseudoacacia*), dogwood (*Cornus drummondi*), and honey locust (*Gleditsia triacanthos*) (69, 71, 102, 166). Other *Acrosternum* species that are pests of legumes include *A. armigera* on soybean in South America (16, 94), *A. marginatum* on soybean and common bean in North and South America (48, 134), and *A. acuta* on soybean and pigeon pea in Africa (59, 76, 165).

There are many other pentatomids that are pests of legumes. Examples include: the neotropical *Edessa meditabunda*, which feeds on soybean, pea, alfalfa, and many species of Solanaceae, including tomato and potato (94, 145,

157); *Dichelops (Neodichelops) furcatus* and *Dichelops (Neodichelops) melacanthus*, which feed on soybean, alfalfa, and common bean in South America (16, 37, 94, 138, 146); *Aspavia armigera*, a pest of cowpea and soybean in Africa (31, 159); and *Halyomorpha mista*, which feeds on several horticultural plants in Japan, including the legumes pea and kidney bean, but which also may feed on fruit trees (73).

Pests of Nonleguminous Crops

Among the major pentatomid pests of nonleguminous crops, the small rice stink bug, *Oebalus poecilus* (=*Solubea poecila*), is perhaps the most important pest of rice in South America (18, 43, 149, 168). Although it shows feeding preference for the Gramineae such as rice, barley, oat, corn, and wheat, it also is associated with soybean, cotton, and guava (94, 157); these last are only occasional hosts. It has been reported from 42 species of host plants in the state of Rio Grande do Sul, Brazil, and increasing numbers have been captured on sorghum in this state (1–3). *O. poecilus* can be reared successfully in the laboratory on the weed *Polygonum punctatum* (158). Another species, *Oebalus ypsilongriseus*, has a similar host range in South America (21, 32, 94, 140, 157).

In the southern United States, *Oebalus pugnax* is a major pest of rice (27, 35, 65, 109, 112). This bug also feeds on several wild grasses, such as *Echinochloa crusgalli*, *Echinochloa colonum*, *Digitaria sanguinalis*, *Panicum dicotomiflorum*, *Phalaris minor*, *Paspalum urvillei*, and *Sporobolus poiretti*; the last two are preferred hosts (27, 110).

Other stink bug pests of Gramineae include the following: the neotropical species *Mormidea notulifera*, which feeds on rice, wheat, oat, but also on the legume lupine (91, 157); *Thyanta perditor*, which is a pest of wheat, rice, and sorghum (4, 11, 33), but may feed on soybean (123, 178); *Tibraca limbativentris*, the so-called big rice stink bug, which feeds on rice, wheat, and several wild grasses (94, 146); the grain bug *Chlorochroa sayi*, which is a pest of wheat, barley, and rye in the United States (12); and several species of *Aelia*, which are pests of cereals, particularly wheat, in the Middle East and in the Mediterranean basin (9, 177).

Other pentatomid pests of nonleguminous crops include the following: the tomato stink bug, *Arvelius albopunctatus*, which feeds mostly on cultivated (tomato and potato) and uncultivated Solanaceae, and on sunflower, pepper, eggplant, okra, and soybean in South America (41, 134, 146, 157); *Edessa rufomarginata*, a pest of a variety of plants, mostly Solanaceae, such as tobacco and potato in South America (103, 147, 157); *Dolycoris baccarum*, a pest of cereals, sunflower, and tobacco in the Paleartic Region and most Mediterranean countries (15, 86, 184); *Eurydema rugosum* and *Eurydema pulchrum* pests of brassicas in Asia, particularly in Japan (82, 104, 111); *Palomena angulosa*, a

pest of various crops in Japan such as potato and rapeseed, and also of alfalfa and beans (55, 56); *Bagrada cruciferarum*, a pest of oilseeds and vegetables in India, particularly of cauliflower (24, 174); and *Cuspicona simplex* associated with solanaceous plants and sometimes pest of potatoes and tomatoes in Australia (44, 45).

Pests of Trees

There are several pentatomid species that feed on trees of economic importance. Among them is *Biprorulus bibax*, which is an important pest of citrus in Australia; it feeds on all varieties of commercial citrus, although lemon, *Citrus limon*, and mandarin, *Citrus reticulata*, are preferred (49, 62, 64). The main wild host is desert lime, *Eremocitrus glauca*, on which the bug overwinters (61, 63).

The brown-winged green bug, *Plautia stali*, is a serious pest of fruit trees in Japan. It feeds on mulberry, peach, plum, persimmon, cherry, grape, and pomegranate. Studies have been conducted on its use of food plants and on the flying ability of adults (105, 106, 155, 156). Other pentatomid pests of trees include species of *Lincus*, such as *Lincus lobuliger*, an important pest of coconut in Brazil (107, 142, 143) and *Lincus* spp. that are pests of oil palms in Ecuador and coconut in French Guiana (25). The *Antestia* and *Antestiopsis* species complexes in Africa, which for the most part are restricted to the plants of the family Rubiaceae such as coffee, *Coffea arabica* and *Coffea canephora* (42, 98, 99). *Bathycoelia thalassina*, a major pest of cocoa, *Theobroma cacao*, in most of the cocoa growing countries in West Africa, also feeds on mangoes (*Mangifera indica*), kola (*Cola acuminata*), and *Citrus* spp. (113, 115, 181). The coconut spathe bug, *Axiagastus cambelli*, occurs in the Papua New Guinea region as a pest of coconut, *Coccus nucifera*, and also feeds on betel nut palm, *Areca* sp. (88). Some of the polyphagous species, such as *N. viridula*, *A. hilare*, and *Euschistus* spp., which prefer annual legume crops, may feed on perennial trees of economic importance as well (67, 180, 182).

ROLE OF WILD HOST PLANTS IN PENTATOMID BIOLOGY

Most of the published papers on the above-mentioned pentatomid species, and some other species as well, deal with various aspects of the insects' feeding on cultivated hosts; relatively little work has been done on the importance of wild hosts to buildup of populations before they disperse to cultivated hosts and vice versa. In most instances authors only present lists of wild hosts; they include little or nothing on the importance of these hosts in the biology of nymphs and adults.

Role in Nymphal Biology: Examples from Legume Feeding Pentatomids

The role of wild hosts to the nymphal biology of pentatomids is variable, but importance of the hosts is measured by their suitability for development and production of healthy adults (1, 14, 57, 69–71, 118–120, 123, 127, 128, 130, 132, 133, 137, 141, 155, 170, 171). The first challenge for nymphs is to find a suitable host because eggs may be laid far from their host plants (87) and young nymphs have a limited dispersal ability (122, 154).

Upon hatching, pentatomid nymphs remain atop the egg shells, usually without feeding (92, 96). This behavior seems to allow the nymphs to acquire symbionts by tapping shells of hatched eggs with their mouth parts (10).

Feeding activity begins during the second stadium. Although most pentatomids are polyphagous, nymphal developmental time and survivorship on wild hosts are variable; also, nymphs usually take a longer time to develop and will have greater mortality rates on these hosts compared to cultivated crops such as soybean, *Glycine max* (Table 1). However, there are examples where wild hosts apparently are more suitable than soybean, which allows faster nymphal development and/or lower mortality: for example, stadia of *A. hilare* on black cherry (*Prunus serotina*), redbud (*Cercis canadensis*), elderberry (*Sambucus canadensis*), coffee senna (*Cassia occidentalis*), and honey locust (*Gleditsia triacanthos*); *E. servus* on peppergrass (*Lepidium virginicum*), coffee senna, and wild lettuce (*Lactuca canadensis*); *N. viridula* on coffe senna, hemp sesbania (*Sesbania emerus*), and bag-pod sesbania (*Sesbania vesicaria*) (in this last case, immature seeds were artificially exposed); and *P. guildinii* on *Sesbania aculeata* and indigo (*Indigofera endecaphylla* and *Indigofera truxillensis*) (see Table 1).

In northern Paraná, nymphs of *N. viridula* feed and may complete their life cycle on several wild hosts: dakota mustard (*Brassica kaber*), lanceleaf crotalaria (*Crotalaria lanceolata*), showy crotalaria (*Crotalaria spectabilis)*, beggarweeds (*Desmodium tortuosum* and *Desmodium canum*), wild soybean (*Glycine wightii*), hairy indigo (*Indigofera hirsuta*), other indigo species (*I. truxillensis* and *Indigofera suffruticosa*), siberian motherwort (*Leonurus sibiricus*), radish (*Raphanus raphanistrum*), and castor bean (*Ricinus communis*). In this last case, only late instars were eventually found (128, 132, 133; AR Panizzi, unpublished observations). Nymphs will feed on these hosts throughout the year, even during the less favorable "winter" season (June–August); late instars may be found on wild hosts, showing a somewhat arrested development (AR Panizzi, unpublished observations).

Besides identifying the wild hosts that allow nymphal development, it is essential to monitor the insects (nymphs and adults) on these hosts to determine the host impact on the buildup of populations (e.g. 69, 71, 120, 130, 170,

Table 1 Development time and mortality of various pentatomid nymphs feeding on different wild hosts and on soybean *Glycine max*

Nymph species/host species[a]	Total development time (days)[b]	Total mortality (%)	References
Acrosternum hilare			
Albizia julibrissim	34.5	48.0	(69)
Campsis radicans	38.6	34.0	(69)
Cassia occidentalis	29.9	0.0	(69)
Cercis canadensis	24.1	2.0	(69)
Cornus florida	—	100.0	(69)
Gleditsia triacanthos	33.6	4.0	(69)
Ligustrum sinemse	48.8	40.0	(69)
Photinia serrulata	39.1	30.0	(69)
Prunus serotina	23.0	0.0	(69)
Sambucus canadensis	24.4	2.0	(69)
Glycine max	29.5	12.0	(69)
Euschistus heros			
Euphorbia heterophylla	20.8–21.3	21.5	(141)
Glycine max	23.1–23.9	28.6	(141)
	23.9	16.5	(176)
E. servus			
Cassia occidentalis	29.5	6.0	(69)
Erigeron canadensis	46.3	94.0	(69)
Lactuca canadensis	32.4	2.0	(69)
Lepidium virginicum	24.0	0.0	(69)
Ligustrum sinense	—	100.0	(69)
Raphanus raphanistrum	32.1	10.0	(69)
Rubus sp.	25.5	12.0	(69)
Glycine max	25.4	8.0	(69)
Loxa deducta			
Leucaena leucocephala	56.0-56.6	82.6	(131)
Glycine max	35.8	68.8	(131)
Nezara viridula			
Albizia julibrissim	—	100.0	(137)
Brassica kaber	26.1–27.5	25.0	(128)
Cassia fasciculata	29.4	42.0	(69)
Cassia fasciculata	—	100.0	(137)
C. occidentalis	26.7	0.0	(69)
Crotalaria lanceolata	27.2–33.9	85.0	(137)
C. spectabilis	37.3	26.0	(69)

(*Continued*)

Table 1 *Continued*

Nymph species/host species[a]	Total development time (days)[b]	Total mortality (%)	References
Croton glandulosus	43.5	80.0	(69)
Datura stramonium plants[c]	38.7	59.5	(170)
Desmodium canum	—	100.0	(132)
D. tortuosum	22.0–23.5	65.0	(137)
D. tortuosum	24.0–26.3	86.7	(132)
Glycine wightii	25.0–27.5	93.3	(132)
Ebelmoschus esculentus	33.5	10.0	(69)
Indigofera hirsuta	—	100.0	(137)
Lepidium virginicum	—	100.0	(69)
Leonurus sibiricus	30.4–31.9	25.0	(128)
Ligustrum sinemse	28.8	2.0	(69)
Macroptilium lathyroides plants[c]	33.5	61.7	(170)
Melilotus indica plants[c]	47.6	63.7	(170)
Physalis virginiana plants[c]	47.5	65.0	(170)
Prunus serotina	29.3	78.0	(69)
Raphanus raphanistrum	35.4–39.3	56.2	(133)
Raphanus raphanistrum	27.5	2.0	(69)
Rapistrum rugosum plants[c]	44.1	65.2	(170)
Ricinus communis	42.3–42.6	60.2	(128)
Ricinus communis plants[c]	50.2	86.5	(170)
Sesbania aculeata	—	100.0	(132)
S. emerus	20.3–20.8	10.0	(137)
S. vesicaria seeds (immature)	20.5–22.2	40.0	(137)
S. vesicaria pods	—	100.0	(137)
Trifolium repens plants[c]	64.0	98.4	(170)
Glycine max	26.2–26.3	60.0	(121)
	25.2–27.8	28.9	(132)
	25.9–26.0	15.0	(133)
	23.0	2.0	(69)
	22.9–23.2	22.5	(137)
Glycine max plants[c]	32.8	25.5	(170)
Piezodorus guildinii			
Indigofera endecaphylla	21.9–22.0	12.5	(120)
I. hirsuta	24.9–25.9	58.3	(120)
I. suffruticosa	28.5–30.3	84.2	(120)
I. truxillensis	22.0–22.3	26.7	(120)
Sesbania aculeata	22.2–22.6	25.0	(119)
Glycine max	20.2–21.2	52.5	(119)
	19.7	—	(139)

[a]Unless otherwise indicated, all hosts are fruit.
[b]From second stadium to adult.
[c] Fruiting plants.

172). Usually, pentatomid nymphs require fruits or seeds to complete their development (references in 161); young nymphs may have different feeding habits than older nymphs or adults (54, 55).

Role of Wild Hosts in Adult Biology

Upon reaching the adult stage, bugs may disperse to other host plants (see next section on the effect of nymph to adult host-switch) or remain on the same host. The suitability of hosts to adults may be evaluated by recording certain life history parameters (e.g. longevity and fecundity; Table 2). In general, stink bugs will perform better on cultivated hosts than on wild hosts, but, as do nymphs, adults may perform better on a certain wild host than on a cultivated one (see adults of *N. viridula* on *S. emerus* and adults of *P. guildinii* on *Indigofera* spp. and *S. aculeata* compared to soybean; Table 2). Therefore, knowing the effect of the various wild host plants on nymph/adult performance will help in the management of selected certain favorable hosts to mitigate their role in the buildup of pest populations (see section on management of wild hosts to control pest species).

Food plants of adults and nymphs may differ, and it is important to know if the wild host is used only as a food source or for reproduction. For example, in Japan, *N. viridula* adults will feed and even mate on certain plants, but will oviposit on other plant species, despite the polyphagous feeding habits of this stink bug (81). Similarly, in northern Paraná, castor bean (*R. communis*) is used by *N. viridula* as a temporary host, as a source of water and/or nutrients and for basking behavior of adults and late instar nymphs, but not for reproduction (AR Panizzi, unpublished observations). The weed star bristle (*A. hispidum*) is used as a temporary food source by adults of *N. viridula* and *E. heros*; they will feed on stems of this plant (atypical behavior, for they are usually seedfeeders) but will not reproduce on it (in fact, this plant is suspected to be toxic because it drastically reduces the longevity of these bugs, particularly that of *N. viridula*; Table 2). In Florida, the bag-pod sesbania (*S. vesicaria*) is eventually used as food by *N. viridula* adults, which will mate but not oviposit on this plant. A possible explanation for this case is that early nymphs are unable to reach the seeds inside the pods because of a large air space between the pod walls and the seeds. Feeding tests have demonstrated that all nymphs on the pods will perish, but only 10% of the nymphs that have access to exposed seeds will die (AR Panizzi & F Slansky Jr, unpublished data).

When food plants become scarce and abiotic factors (e.g. temperature, photoperiod) become unfavorable, adult stink bugs will show different overwintering strategies. In more temperate zones, adults will overwinter in deciduous woods, in above-ground habitats, underneath dead leaves, and elsewhere (e.g. 1, 3, 69, 70, 109, 126). However, in more tropical regions, some species will

Table 2 Longevity and fecundity of various pentatomid adults feeding on different wild hosts and on soybean *Glycine max*

Adult species/host species[a]	Longevity (days)	Fecundity (eggs/female)	References
Euschistus heros			
Acanthospermum hispidum plants[b]	41.8–62.2	0	(130)
Euphorbia heterophylla	—	61.7	(141)
Glycine max	—	98.8	(141)
	71.8–119.9	287.2	(176)
Loxa deducta			
Leucaena leucocephala	18.5–33.9	65.6	(131)
Glycine max	15.6–20.0	27.0	(131)
Nezara viridula			
Acanthospermum hispidum plants[b]	6.1–7.8	0	(130)
Brassica kaber	33.7–40.1	107.4	(128)
Crotalaria lanceolata	32.1–35.3	29.0	(137)
Datura stramonium plants[b]	—	30.8[c]	(170)
Desmodium tortuosum	29.4–41.8	61.0	(137)
Leonurus sibiricus	55.6–62.0	91.7	(128)
Macroptilium lathyroides plants[b]	—	0[c]	(170)
Physalis virginiana plants[b]	—	56.8[c]	(170)
Raphanus raphanistrum	30.0–54.5	68.8	(133)
Rapistrum rugosum plants[b]	—	94.3[c]	(170)
Ricinus communis	16.1–24.9	0	(128)
Ricinus communis plants[b]	—	95.0[c]	(170)
Sesbania emerus	—	273.9	(137)
S. vesicaria	20.0–20.3	40.0	(137)
Trifolium repens plants[b]	—	0[c]	(170)
Glycine max	36.5–39.4	110.0	(137)
Glycine max	47.0–65.0	203.7	(133)
Glycine max	42.2–47.9	99.3	(121)
Glycine max plants[b]	—	124.8[c]	(170)
Piezodorus guildinii			
Crotalaria lanceolata	—	58.2	(136)
Indigofera endecaphylla	83.4–111.7	315.5	(120)
I. hirsuta	—	204.8	(136)
I. hirsuta	38.3–42.5	115.2	(120)
I. suffruticosa	15.9–25.6	196.7	(120)
I. truxillensis	52.3–67.9	507.7	(120)
Sesbania aculeata	—	205.1	(119)
Glycine max	51.2–88.1	28.0	(137)
Glycine max plants[b]	34.0–41.2	31.1	(139)

[a] Unless otherwise indicated, all hosts are fruit.
[b] Fruiting plants.
[c] Nymphs/female.

breed continuously [e.g. *N. viridula* in northen Paraná (34)] while others will enter a state of oligopause [e.g. *E. heros* (126)]; *E. heros* is known to accumulate lipids to survive the nonfeeding period (125).

Effect of Nymph to Adult Host-Switching in Adult Performance

Many species of pentatomids often disperse from their nymphal hosts to feed on other plant species during their preoviposition period. Although nymph to adult host-switching seems to be a common event in the biology of pentatomid bugs, not many studies have been published on how host plants of nymphs affect adult performance (i.e. the relative reproductive contribution to the next generation), except for *N. viridula* (75, 118, 129, 133, 137, 170, 171) and, to a lesser extent, for *P. guildinii* (119, 136) and *E. heros* (141).

Nymph to adult host-switching may have a positive or negative effect, or no effect at all on adult performance, depending on the quality of the foods involved. For example, *P. guildinii* adults feeding on pods of the highly suitable foods sesbania (*S. aculeata*) and hairy indigo (*I. hirsuta*) performed better when they fed on the same plant as nymphs than compared to adults that fed as nymphs on a moderately good nymphal food [soybean (*G. max*) or common bean (*P. vulgaris*) pods] (119, 136). Similarly, the extremely polyphagous *N. viridula* performed better when adults and nymphs fed on pods of the highly suitable hemp sesbania (*S. emerus*) than compared to adults that fed as nymphs on pods of the common bean, *P. vulgaris* (137). The neotropical brown stink bug, *E. heros*, had increased mortality rates when nymph-to-adult food changed from fruits of the euphorb *Euphorbia heterophylla* to fruits of soybean, and the percentage of females ovipositing was greater when adults fed on fruits of the euphorb only compared to those that switched from soybean to euphorb and vice versa (141).

Results of several studies indicate that adequate nymphal food can alleviate partially the deleterious effects of poor adult food, and an adequate adult food will mitigate the impact of an unsuitable nymphal food (117, 119, 129, 133, 136, 137, 141, 171). However, it is unclear which of these foods and insect developmental stage combinations has the greatest effect on insect fitness. At least for insect fecundity, the latter case seems to be better because fecundity seems to be more dependent on the quality of food taken by adults (74). Also, a suitable adult food rich in lipids will increase not only reproductive performance but resistance to starvation. For example, *N. viridula* previously fed sesame will survive >40 days without food, compared to 10 days when previously fed soybean, because of greater lipid storage when fed sesame (124); this may not be true for nymphs (AR Panizzi & CC Niva, unpublished data). These results indicate that food quality on nymph and nymph-to-adult food switching are both important in the nutritional ecology of pentatomid

nymphs and adults and deserve further study, particularly when involving wild hosts.

POLYPHAGY AND HOST PLANT SEQUENCE

Pentatomids use a variety of host plants within and between generations. Both nymphs and adults move among same or different plant species (e.g. 17, 26, 27, 30, 47, 69, 71, 102, 114, 122, 150, 154, 155, 166, 179), which may be colonized in sequence.

There are several reports on sequences of host plants used by different species of pentatomids (e.g. 1, 3, 27, 69, 71, 81, 102, 115, 150, 152, 155, 160, 163, 166, 170, 172, 182). Some examples are given here on colonization of wild and cultivated plants by some pentatomids common in northern Paraná (Figure 1). *N. viridula* concentrates on soybean plants during the summer, which are very abundant at this time, but the pest is also found to a lesser extent on common bean, *P. vulgaris*; two to three generations are completed on these crops. During fall, adults move to wild hosts; these include star bristle (*A. hispidum*) and castor bean (*R. communis*), upon which the species feeds but does not reproduce, and wild legumes, such as *D. tortuosum* and *Crotalaria* spp., upon which it feeds, reproduces, and completes a fourth generation. During late fall and early winter, it completes a fifth generation on radish (*R. raphanistrum*) and mustards (*Brassica* spp.). During winter, *N. viridula* may feed, but will not reproduce, on wheat, *Triticum aestivum*. During spring, a sixth generation is completed on siberian motherwort *L. sibiricus*.

A second species, the less polyphagous *P. guildinii*, also completes two to three generations on soybean and common bean during summer. A fourth generation is completed during fall on indigo legumes, *Indigofera* spp. The bugs remain on these plants during the winter but do not reproduce [this species is less adapted to lower temperatures than is *N. viridula* (13)]. A fifth generation is completed on indigo in the spring (Figure 1).

A third species, *E. heros*, also will produce two to three generations on soybean and common bean during spring. During this time, it may feed but will not reproduce on the euphorb *E. heterophylla*. As soybean is harvested by the end of summer, adults eventually will feed on star bristle, *A. hispidum*, moving later to shelters underneath leaf litter where they remain until the next summer (Figure 1). This bug is known to accumulate lipids and to not feed during overwintering (125, 126). *E. heros*, despite completing fewer generations than the former two species, is the most abundant species during the summer. Perhaps this is because its hiding beneath dead leaves allows it to escape detection by parasites and predators during most of the year, resulting in greater survivorship; this should be investigated further. It is known, however, that *E. heros*

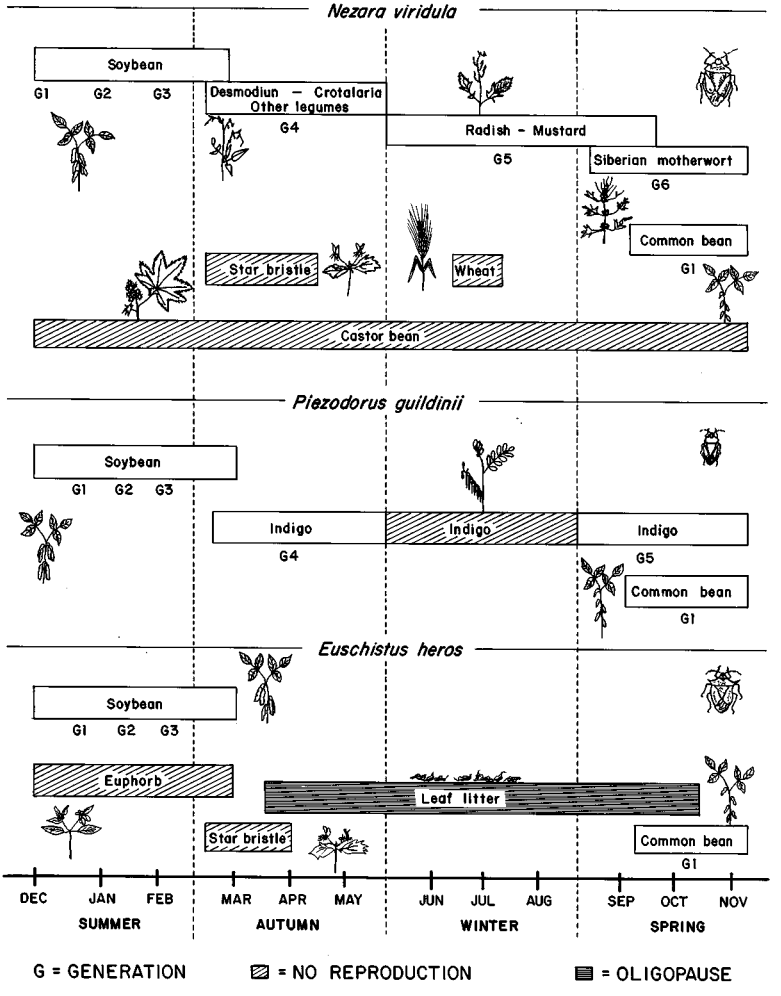

Figure 1 Wild and cultivated plant species of the host-plant sequences used by successive generations of three different species of pentatomids in northern Paraná state, Brazil (blank boxes indicate occurrence of reproduction). This figure is based on published information generated from 1985 to 1995 (117, 119, 120, 126, 128, 130, 132, 133, 141) and on unpublished observations by AR Panizzi.

is less susceptible to pathogens (DR Sosa-Gomez, personal communication), has a greater resistance to starvation (125), and better resists handling and poor rearing conditions in the laboratory (AR Panizzi, personal observations).

The survivorship of polyphagous phytophagous pentatomids depends on the successive occurrence of host plants and presence of favorable hibernacula (83). Moreover, different overwintering habitats have a variable impact on winter survival of pentatomids (e.g. 69, 70, 79, 80).

LOCAL POPULATIONS OF PENTATOMIDS AND SPECIFIC FEEDING HABITS

Although considered generally polyphagous, phytophagous pentatomids may show feeding preferences for certain plant taxa. For example, generalist feeders such as *N. viridula* prefer legumes and brassicas (163), *P. guildinii* feeds mostly on legumes (134), *E. meditabunda* prefers legumes and solanaceous plants (94, 145, 157), etc. In spite of these and other trends, local populations may show different preferences and actually act monophagous or oligophagous rather than polyphagous, depending on host availability and time of exposure to restricted hosts (36). For instance, *N. viridula* adults from northern Paraná state do not do well on castor bean (*R. communis*), but adults from Queensland reproduce reasonably well on this host (Table 1), as do populations from Egypt, Florida, and Chile (28, 72; R Ripa, personal communication). This pentatomid has been reported to feed on corn in the southern United States (108) but has never been noted feeding on this plant in northern Paraná, despite their synchronized occurrence in this area (AR Panizzi, unpublished observations).

N. viridula individuals from India prefer pods of green bean, *P. vulgaris*, and individuals from the United States prefer pods of soybean, *G. max* (22). *N. viridula* nymphs from South Carolina survive (>50%) on *C. fasciculata* (69), but those from Florida do not (137). Local populations of *E. heros* are associated with the euphorb *E. heterophylla*, but in most cases it will not feed on this plant, even though the plant is suitable as food to nymphs and adults under laboratory conditions (141). These reports, and others, suggest that local populations of polyphagous pentatomids can develop specialized feeding habits, but how often and to what extent this occurs is poorly understood.

MANAGEMENT OF WILD HOSTS TO CONTROL PEST SPECIES

Knowledge of which wild host plants are used by pentatomids, how suitable they are for nymphal development and adult reproduction, what sequence of

hosts are used by sequential generations, and when dispersal occurs from these hosts to crop plants and vice versa is of great importance in designing strategies to manage pest species.

Despite the considerable number of studies on pentatomid/host interactions (e.g. 1, 3, 14, 20, 26, 27, 47, 69, 71, 81, 86, 97, 102, 114, 115, 120, 150, 152, 166, 170, 172, 182), few authors have suggested host manipulation as a control strategy of pentatomids. Examples include: recommendation of mowing to reduce breeding of *E. servus* on weed hosts to reduce damage to peach (182); elimination of wild hosts to decrease populations of the cocoa bug *B. thalassina* (115); elimination of weeds in rice production areas to reduce the populations of *Oebalus ornatus*, *Mormidea pictiventris*, and *Mormidea maculata* (20); use of the globe thistle *Echinops viscosus* (Compositae) as a trap plant to aggregate and control the berry bug *D. baccarum*, a pest of cereals, tobacco, and sunflower (86); and use of indigo legumes, *Indigofera* spp., as trap plants to control overwintering populations of *P. guildinii* before colonization of soybean fields (120).

Possible reasons to explain why manipulation of wild hosts is not more widely implemented as a control strategy of pentatomids include the following: (*a*) the polyphagous feeding habits of pentatomids, which require manipulation of multiple host species, make it difficult to monitor the trends of pest populations; (*b*) there is limited knowledge of pentatomids/wild host plants interactions; and (*c*) there is a lack of interest by growers who prefer more conventional control methods, such as use of insecticides, to control pest species directly on crops.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Many species of phytophagous pentatomids are important economic pests. Despite the amount of information regarding pest species, their damage potential to economically important plants, and control measures used, pests' impact on the production of crops remains at undesirable levels. Perhaps the most important reason to explain this is the lack of holistic studies on insect life history, stressing their interactions with wild host plants. The role of uncultivated plants in the biology of crop pests and beneficial insects (167) is, in general, poorly understood.

Most species of pentatomids spend only a third of their lifetimes feeding on spring/summer crops. The rest of the time they spend feeding and breeding on wild hosts or occupying overwintering sites (e.g. underneath dead leaves) provided by these hosts. During these latter periods and before colonization of crops, few studies have stressed the insects' biology. Questions concerning which plants are used by stink bugs, how beneficial they are to nymph and

adult performance, what hosts are preferred, what host sequence is used, at what rate populations increase in subsequent generations, what the impact of natural enemies is during this time, and others still need to be answered. In the control area, information on the time of invasion of crop fields by stink bugs should help to increase the efficacy of insecticide use. Furthermore, the use of wild hosts as trap plants to concentrate populations in small areas where they can then be eliminated, and reduction of wild hosts in production areas should mitigate the infestation potential of these pests.

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