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Relationships between insect pests and weeds: an evolutionary perspective

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Weeds are an important plant resource for insects, although feeding by insects on weeds can have both positive and negative effects on crop productivity. Weeds also indirectly affect crops via their influence on beneficial insects, and by harboring plant and insect diseases. Weeds may affect the ability of dispersing insects to locate crop plants. The host relationship between insects and plants is highly variable, ranging from very specialized to generalized feeding behaviors. Despite the myriad interactions of weeds and insects, many aspects of the relationship are predictable. Most insects, including crop pests, are specialists, and preadapted to feed only on some plants, often within a single plant family. Even polyphagous insects often have a distinct preference hierarchy, feeding more widely only when preferred hosts are unavailable. Use of plants by insects is a dynamic interaction, with characteristics of the insect (e.g., mandible structure) and the plant (e.g., allelochemicals) affecting feeding behavior. Thus, weeds that are closely related to crops are particularly important in harboring insects that attack those crops. Crop production practices should seek to sever the taxonomic association between the crop and the weeds found within the crop, and nearby, by eliminating weeds related to the crop. This will make it less likely that insects will move easily from weed to crop plants, that damaging population densities of insects will develop in the field, and that insect vectors that harbor plant diseases will be harbored in the field. Particularly important integrated pest management practices include crop rotation, reduced use of chemical herbicides, and management of weeds in noncultivated areas.

Key words: Allelochemicals, crop management, insect feeding behavior, insect mandible structure, preadaptation to hosts, plant disease transmission, weed hosts, weed management.

The earliest insects were not plant feeders, but insect diversity expanded greatly as angiosperms became diverse and abundant in the Cretaceous period (about 100 million years ago) (Zherikhin 2002). Plants were, and remain, an abundant resource for the insect groups that have overcome the various evolutionary barriers (both physical impediments such as a tough epidermis, and biochemical challenges such as toxins) presented by plants. It often is surprising for non-entomologists to learn that most insects have not adopted green plants as a food resource; only about one-third of the orders of insects and about 45% of insect species feed on living plants (Strong et al. 1984). The fact that there is so much green vegetation is sometimes taken as evidence that plants are normally well protected from insect herbivory. However, plants often are less adequate nutritionally than are more protein-rich food sources such as dead animals or even microbe-infested plant material, so in addition to the aforementioned physical and biochemical hurdles, insects must deal with low nutrient content if they adopt plants as a food substrate.

Nevertheless, many insects have evolved a strong association with plants. These usually are herbivores (though some display beneficial relationships with plants, principally by serving as pollinators). From the perspective of crop production, insects can be quite destructive, particularly in crop monocultures, where they damage many crops throughout the world. The importance and nature of crop-feeding (including forest-feeding) insects are well documented, and it is generally acknowledged that our horticultural practices (e.g., inadvertent removal of plant defenses during the crop breeding process, monocultural practices, and other ill-advised cropping decisions) have exacerbated insect-related problems in crops (Herzog and Funderburk 1986; Smith and McSorley 2000). Less well understood is the relationship of insects to weeds. An important relationship between weeds and insects clearly exists—after all, crops were bred from natural flora. Indeed, the review by Norris and Kogan (2000) comprehensively summarizes the agricultural literature on insect-weed relationships. No attempt will be made to repeat this recent review; instead, I will discuss an aspect not previously covered in detail: the evolutionary aspects of insect-weed relationships, and suggest how knowledge of this relationship can impinge on strategies and tactics of integrated pest management.

Weeds Are a Food Resource for Insects

Weeds are a primary resource for many phytophagous insects. From the perspective of crop protection, this has both positive and negative aspects. In a positive sense, insect feeding on weeds makes water, soil nutrients, and sunlight more available to crop plants, thereby reducing weed competition with crops. Many insects feed exclusively, or nearly
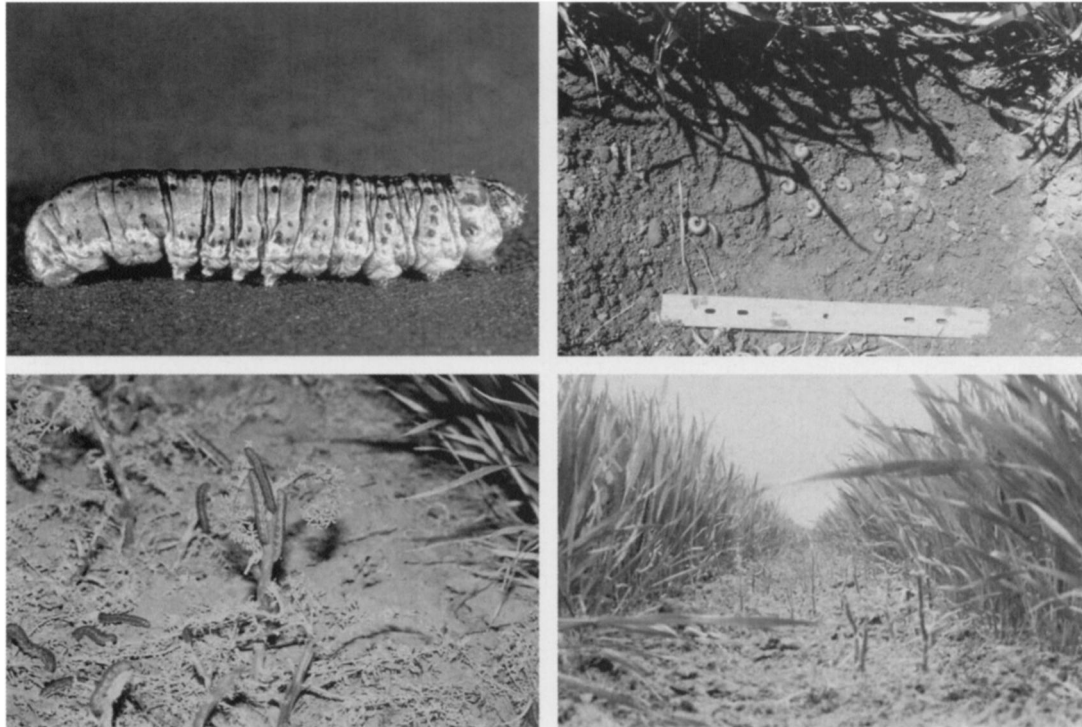
FIGURE 1. The army cutworm-weed-wheat relationship exemplifies some of the complexities in integrated management of crop pests. The cutworm larva (upper left) is nocturnal and not usually observed unless an effort is made to sample them, so farmers are often unaware of infestations early in the larval cycle. By digging away the upper soil (upper right) during the day, large numbers of cutworms may sometimes be found. Examination of the field at night (bottom left) reveals the cutworms climbing upon, and feeding on, a preferred weed host, tansy mustard. Examination of the wheat field during the daylight hours (bottom right) shows only the basal portion of the stems of tansy mustard between rows of wheat. Up to this point in time, there is no damage to the wheat. As the weeds are consumed by the insects, or if the farmer applies an herbicide to kill the weeds, the insects are forced to feed on the wheat.

so, on weeds. For example, the sesiid moth *Carmenta haematica* (Ureta) attacks only snakeweeds, *Guteirrezia* and *Grindelia* spp., in the family Asteraceae (Cordo et al. 1995). Other insects prefer weeds, but may damage crops readily in the absence of attractive weeds. For example, the Colorado potato beetle (*Leptinotarsa decemlineata* Say) prefers to oviposit on hairy nightshade (*Solanum sarrachoides* Sendtner) rather than on potato (*Solanum tuberosum* L.), and eggs are less abundant on potato in the presence of nightshade (Horton and Capinera 1990). This preference for weeds also has been exploited effectively through the introduction of selective herbivores for the biological suppression of adventive (invader) weeds, sometimes with spectacular success (Goeden and Andres 1999; Myers and Bazely 2003). This process, which strives to reunite a natural predator (in this special case, an herbivorous insect) with its prey (in this case, a weedy plant), is called classical biological control, or introduction biological control.

There are negative aspects associated with insect feeding on weeds, too, if the insect is not restricted in its feeding habits to the weed. When insects have a wide host range (oligophagous to polyphagous) they sometime move from weeds to crop plants, causing crop damage. Commonly, this follows weed destruction due to tillage or herbicides, but it also may be a more natural process, following weed senescence or consumption of the weed by the insects. Thus, a common recommendation in many crop production systems is to keep weed populations at a low level, not only within the crop field, but also in adjacent areas such as irrigation ditches and fence rows, as these sites are a common source

of insect inoculum for the crop field (Capinera 2001; Metcalf and Metcalf 1993).

The example of the army cutworm, *Euxoa auxiliaris* (Grote), will serve to demonstrate some of the complexities of the insect-weed–crop plant interaction. Army cutworm is a common lepidopteran pest in the western Great Plains region of North America in which wheat (*Triticum aestivum* L.) is grown. The larval stage of this insect (Figure 1) feeds aboveground at night, and spends the daylight hours hiding in the soil, so its feeding behavior is poorly documented. Although it is known predominantly as a pest of small grains, it feeds on a large number of plants, including many weeds in preference to grain crops. In Figure 1, the feeding behavior of the army cutworm can be seen in a photograph taken at night; note that they are clustered on pinnate tansy mustard [*Descurainia pinnata* (Walt) Britt.]. Also, the effect of army cutworm feeding on this weed is clearly evident a few days later; in an adjacent photograph, the foliage is completely consumed and only the base of the plant remains. Note that the wheat plants on both sides of the weeds are free of cutworms and cutworm feeding. Indeed, up to this point the army cutworms are beneficial insects, serving to reduce competition by the weeds with the young wheat by killing or severely inhibiting the growth of the tansy mustard plants. However, if the tansy mustard plants (or other weeds) are completely consumed before the larvae reach maturity, the cutworms are forced to feed on the wheat. Thereafter, they are no longer beneficial organisms, but pests.

It is tempting to conclude that the presence of weeds may

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be beneficial to wheat culture because it lures cutworms from the wheat. However, the weeds use soil moisture, a limiting resource in dryland wheat culture, and so wheat farmers apply herbicides to eliminate the weeds. If they apply herbicides before the cutworms are mature, they deprive the larvae of food, forcing them onto the wheat. An enlightened approach, therefore, is to delay herbicide application until after the larvae are mature, reducing or eliminating the herbivory of wheat. This necessitates an extensive soil sampling effort, however, because the cutworms are not easy to detect during the daylight hours. Another approach is to apply insecticide at the same time as the herbicide, and although this also requires some sampling to be sure that the cutworms are present in potentially damaging numbers, it is considerably more economical than having the wheat damaged, or applying insecticide as a separate application at a later date.

Weeds Affect Host-Finding by Herbivores

Weeds can modify the attractiveness of crops to the insect herbivore, thereby affecting the rate of colonization. Both vision and odor play an important role in host location by most insects (Stanton 1983). In the case of vision-based host finding, it is the spectral profile (nonvisible to humans as well as visible) to which the insect responds. In their landmark work with aphids, J. S. Kennedy and collaborators postulated that during the dispersal phase, insects (aphids, for example) were attracted to short-wavelength ultraviolet light, and this tended to take insects upward toward the sky. After a period of flight, they were no longer attracted to ultraviolet light, instead preferring long-wavelength (often heat emanating from the soil or plants) light (Kennedy et al. 1961). Vegetation (weeds vs. bare soil, or weeds plus crop plants vs. crops plus bare soil) could influence the spectral reflectance pattern of a site, thereby affecting the propensity of flying insects to alight. Weeds can also modify the attractiveness of crops to insects by affecting the hue (color) of the foliage; as first demonstrated conclusively by V. Moericke (Kennedy 1976), many herbivorous insects are attracted to yellow or yellowish green during the host-seeking phase, relative to dark green or other colors (Kostal and Finch 1996; Moericke 1969). Thus, light green weeds interspersed among darker green crops could be relatively more attractive to alighting insects. Conversely, rows of crops interspersed with bare soil have sometimes been shown to be more attractive to flying insects than dense stands of vegetation, so weeds in crop fields may also deter alighting. Crop producers sometimes manipulate alighting behavior by mulching the crop with silver plastic mulch to increase the amount of ultraviolet light being reflected, effectively disorienting flying insects and reducing the rate of alighting by airborne insects (Rhainds et al. 2001; Stapleton and Summers 2002; Stavinsky et al. 2002; Summers and Stapleton 2002).

Weeds also affect chemical-based host finding. Many insects do not depend on vision, or they use vision only to identify an appropriate habitat and then use odor to identify a suitable host. Some argue that the host-location process is the other way around, but most agree that both vision and odor are important (Judd and Borden 1992a, 1992b). In many cases, insects using odor for host location tend to be more selective in their feeding habits than insects depending mostly on vision. In other words, chemicals play a more important role in the evolution of specific host-herbivore relations than does vision. When resources are concentrated, as in agricultural monocultures, presumably insects can readily find their host plant due to the concentrated host-produced odors. On the other hand, in polycultural systems or in weedy fields (particularly weeds that are unrelated to the crop plant), the chemical stimuli may be less concentrated or confusing to the potential herbivores. Another hypothesis is that weeds or other noncrop plants may release repellent chemicals that deter insects from alighting or feeding (Stanton 1983).

Finch and Collier (2000) proposed that host-location behavior resulting from visual and chemical orientation was modified by the retention time and behavior of insects in a crop. They postulated that insects may not oviposit upon first encountering a suitable host, instead investigating nearby vegetation. If continuously stimulated by the appropriate stimuli (as would occur in a crop monoculture) the insect would oviposit and begin an infestation. On the other hand, if an unacceptable host was encountered during the investigatory phase (this is more likely in a polyculture or weed-infested crop), or chemical stimuli were inadequate (as in a polyculture or weed-infested crop), the insect would be more likely to move on, thereby reducing the likelihood that a crop would be infested. Despite the well-documented importance of chemicals for host finding among many specialist herbivores, the exact mechanism of population suppression associated with mixed populations of plants is uncertain or variable (Herzog and Funderburk 1986). However, many studies have documented that mixed plantings are less affected by specialist herbivores (Smith and McSorley 2000), so weeds may contribute to reduction in insect damage to crops by interfering with host location in some manner.

Weeds Affect Beneficial Insects

Weeds can directly affect the abundance of beneficial insects, including predators, parasitoids, and pollinators (Al-Doghairi and Cranshaw 2004; Alteiri 1988; Showler and Greenberg 2003). Some predators and parasitoids also feed on weeds. For example, many predatory insects with piercing-sucking mouthparts are facultative predators, feeding preferentially on other insects but imbibing plant sap when necessary to sustain their existence. Predators, and parasitoids during the adult stage, often feed on nectar from flowers or from extrafloral nectaries. Thus, the presence of certain weeds (those with accessible nectar from flowers or extrafloral nectaries) enhances the survival of beneficial insects and assists in biological suppression of pests (Russell 1989; Southwood 1986).

Weeds also can indirectly affect the abundance of beneficial insects. Predators, and to a lesser degree parasitoids, may have several insect host species. The presence of phytophagous insects on weeds may support populations of beneficial insects; elevated populations of generalist beneficial insects will spill over onto crops and help suppress pests. In some cropping situations, weeds or other noncrop plants (called refugia or banker plants) are deliberately planted to foster development of beneficial insects that will affect pest populations on crop plants.

In addition to the benefits of weeds on natural enemies of pest insects, weeds affect the activities of pollinators. Pollinators collect nectar and pollen, and often are not abundant in the absence of weeds. Thus, crops that require pollination (e.g., many fruit crops and cucurbits) may benefit from the presence of a diversity of weeds (Bäckman and Tiainen 2002). On the other hand, if weeds are too attractive, they may inhibit crop pollination by attracting the pollinators away from the crop.

Weeds Are a Source of Diseases

Weeds can serve as a source of diseases, including both diseases of insects and of crop plants. The importance of weeds as refugia for entomopathogenic diseases may be minor, or relatively unstudied, but it certainly exists. For example, weedy areas around crop fields are often the overwintering site for grasshoppers (as eggs in the soil), which initially feed (weeds may be the only source of food early in the growing season) and roost there (preferring the taller weeds for thermoregulation and possibly for nutrition). In the case of summit disease of grasshoppers, caused by the fungus *Entomophaga grylli*, such weeds are sometimes heavily populated by dying grasshoppers that cling to elevated perches even after death (Carruthers et al. 1997). The high grasshopper densities at such sites serve as foci of disease infection, and foster the spread of the insect pathogen in the insect population.

The beneficial effects of weeds on insect pathogens is far overshadowed, however, by the negative effects of weeds on disease; in this case, plant disease. Crop plants, particularly annual crops, start their life fairly disease-free. Weeds, however, often harbor diseases that can be transferred to crop plants by insects feeding first on weeds, and then on the crop (Chellemi et al. 1994). Plant diseases caused by viruses and mollicutes, and to a lesser degree by fungi and bacteria, are commonly transmitted by insects from weeds. Aphids, whiteflies, leafhoppers, and thrips are the most common vectors of plant disease because they have piercing-sucking mouthparts, and in some cases secrete the disease propagules as they feed (Hunter 2004). However, many other insects are implicated in disease transmission, and piercing-sucking insects are not particularly effective in the transmission of fungi and bacteria. The diseases may be introduced into a crop by only a few insects, followed by rapid secondary transmission within the crop. It is difficult to prevent the inoculation of a disease, though secondary transmission can be reduced through effective insect suppression (usually by using insecticides). Because in most cases it is not possible to prevent some disease-bearing insects from alighting and feeding on a crop, and it is usually not possible to cure plants once they have become infected with plant disease, insect-transmitted disease is a formidable problem. Elimination of the source of the disease and vectors is often the most effective approach to management, and this often means weed control (Agrios 1997, 2004).

Effective Weed Management Can Be Key to Insect Management in Crops

I have tried to summarize, from an entomological perspective, some of the benefits and costs of having weeds present in, and adjacent to, crops (see Norris and Kogan 2000 for a more complete discussion). Although there are situations in which certain weeds are beneficial, overall, the presence of weeds in crops is detrimental to insect management. Thus, we need be concerned not only with the direct effects of weeds on crops (e.g., competition for light, water, and nutrients) but also with the effects of weeds on insects, including herbivores (by providing harborage and food for the insects), pollinators (by competing with the crop for pollinators), and plant diseases vectored by insects (by serving as a reservoir for plant diseases). Some considerations associated with weed-insect management issues include the following:

- Weeds that harbor plant diseases are a special concern, and should be eliminated, or controlled at the earliest possible stage before potential insect vectors infest them.
- Weed control must be carefully timed if the weeds are infested with insects that can infest crops, so that they are not driven onto the crop plants.
- Conservation and minimum-tillage fields sometimes have higher weed densities, which can lead to unusual problems with insects and insect-transmitted diseases.
- Weeds and crop residue in out-of-production fields can be a major source of insects and the plant diseases they transmit, so crop placement (location), and area-wide management of the insects, become more important to consider as options in management of insects and insect-transmitted diseases.
- Weeds are a special problem for area-wide insect management programs if they host insects, because the number of insects that must be managed is higher, and the area that must be treated is greatly expanded.

Predictability of the Weed-Insect Relationship

The weed-insect relationship is complex, and may appear to be unpredictable. However, there are insightful elements of the herbivore-plant relationship, particularly the evolution of insect feeding, that are useful for prediction.

Insects are more selective in their feeding behavior than is commonly believed. Even polyphagous insects have strong and consistent feeding preferences. Part of the problem is due to an inability by many people to accurately identify some insects, and so they do not distinguish among species within groups of related insects (e.g., flea beetles, grasshoppers, white grubs) even though individual species within these groups may have greatly varying host preferences. This leads to the perception that the host range is much broader than is actually the case. Another important issue is that host lists are extremely deceptive. Most insects, on occasion, develop very high populations, over-run their food supply, and are forced to feed on nonpreferred or unacceptable plants. During these periods of population outbreak, insects are observed on plants that are not normally eaten, but in the entomological literature these become recorded as hosts, adding to the perception that these rarely eaten crops are at risk when they probably are not.

What makes insects selective in their feeding habits? Insects are often constrained in their feeding behavior by mouthpart morphology and chemical preferences, and feed on plants within certain families. For example, grasshopper and cutworm larval mandibles, and likely those of most other insects, are often adapted to optimize feeding on certain
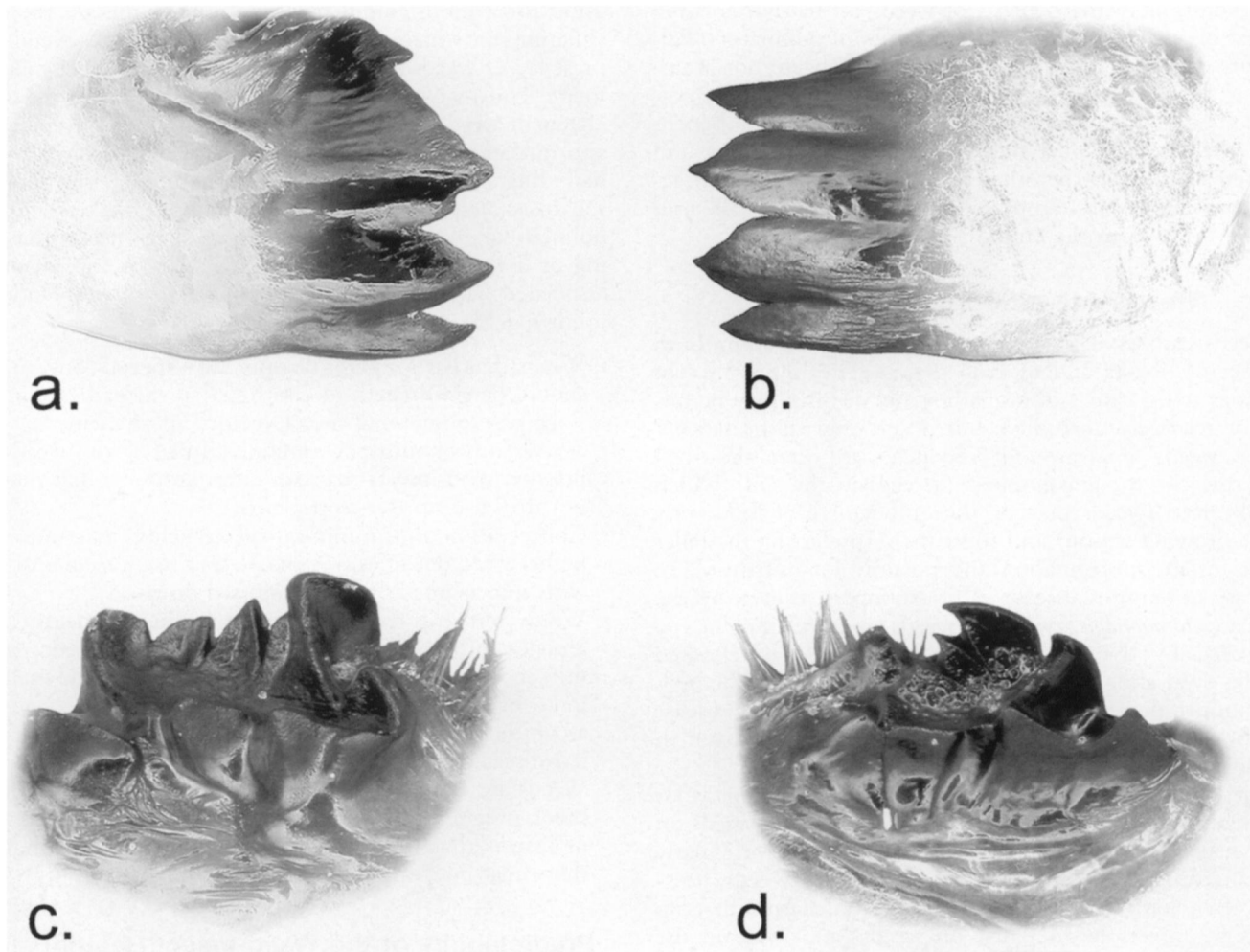
FIGURE 2. The mandibular structure of grasshoppers and other insects reveals adaptations that allow some degree of host-choice predictability. Forb-feeding grasshoppers, such as the grasshopper *Schistocerca ceratiola*, have mandibles with short and pointed incisor teeth, and with the molar teeth irregular and well developed: (a) right incisor region, (b) left incisor region, (c) right molar region, (d) left molar region.

types of plants (Gangwere 1966; Isley 1944; Kang et al. 1999; Patterson 1984).

In the case of grasshopper mandibles, there are two important regions: the distal incisor region and the proximal molar region. These regions slice and crush the excised leaf material, respectively. In the case of grasshoppers that feed on forbs (broad-leaf plants, with netlike veins), the incisor teeth are short and pointed, and the molar teeth are irregular and well developed. In distinct contrast, grasshoppers that feed on graminoids (narrow leaf blades, with parallel veins) have long but blunt incisor teeth, and a molar region with ridges and furrows rather than teeth. These are adapted for slicing through, and feeding parallel to, the tough parallel veins of graminoids (primarily grasses). Mixed-feeding species (feeding on both forbs and graminoids) have intermediate arrangement of the mandibular structures. Thus, examination of the mandibles (Figures 2 and 3) can provide considerable information on the feeding behavior of these insects. Grasshoppers and cutworm larvae are not readily identifiable by many plant protection specialists, and these insects tend not to be identified to the species level (for which specific feeding habits are known), so the damage potential of the insects is commonly uncertain. Yet, simple examination of the mandibles will allow some predictive ability relative to their tendency to damage crops. Even better, of course, would be species-level identification of the insects, but this is not always possible.

Preferences based on plant chemistry similarly are not fully appreciated by plant protection specialists. Many insects, but particularly those more selective in their feeding habits, are influenced by allelochemicals, also known as secondary plant compounds or secondary metabolites (Hanson 1983; Harborne 1982). Plants synthesize a variety of allelochemical compounds of differing chemical structure (terpenoids, flavonoids, alkaloids) that affect selection and suitability of the plant by the insect. Although most of these chemicals can be classified as toxins, they need not be truly toxic, but only distasteful (distasteful compounds are often classified as repellents or deterrents), to deter herbivory. From an evolutionary perspective, it is not even essential that a plant be distasteful; lack of adequate nutrition and the inability of an insect to survive and reproduce (e.g., due to the presence of tannins) can be adequate over time.

Of interest, a compound that is toxic or repellent to one species of insect can be an attractant to another species. This is due to the coevolutionary process that sometimes
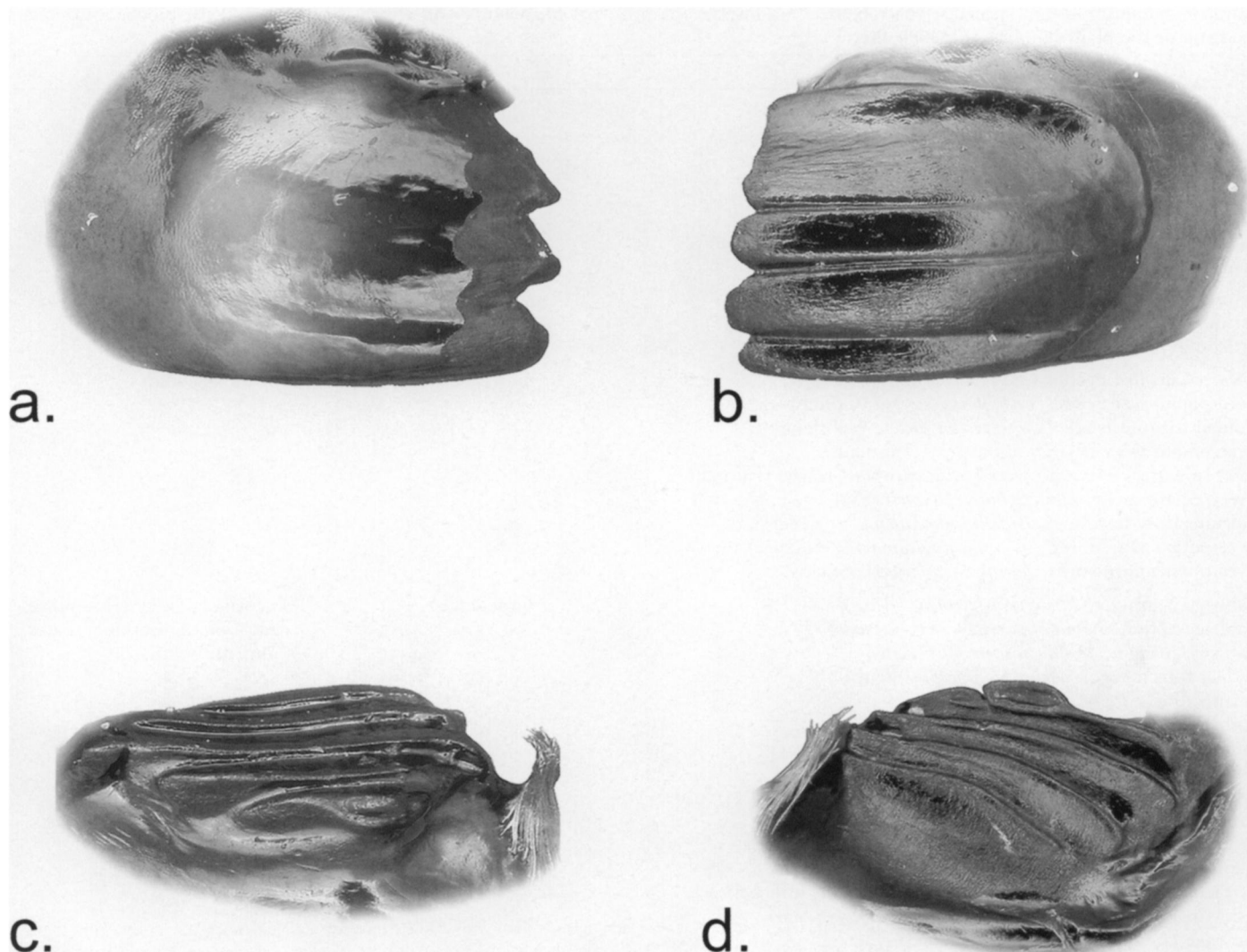
FIGURE 3. Grasshoppers that feed on graminoids, such as the grasshopper *Amblytropidia mysteca*, have long but blunt incisor teeth, with a molar region consisting of ridges and furrows rather than teeth: (a) right incisor region, (b) left incisor region, (c) right molar region, (d) left molar region.

occurs between insects and plants. Insects that can overcome a particular chemical barrier (usually by possessing the ability to detoxify the chemical) produced by a plant have an important competitive advantage in feeding, as they are able to feed on the plant with impunity. Thus, it is useful to be able to detect that chemical barrier (which is not really a barrier to feeding for insects possessing the proper detoxification mechanism, but a very effective barrier for those lacking the detoxification mechanism). This results in an important pattern of selective feeding because the smell or taste of a plant that is repellent to most herbivores is a signal to others that this is a good food resource. Soon, in a coevolutionary sense, insects that are attracted to a plant's smell or taste may feed only on those plants with the particular chemical which was (and remains for some insects) a barrier to feeding (Futuyma 1983; Kogan 1986).

Many chemical compounds found in plants are common to a group of plants, often most, or all of, the members of a plant family. Some examples of insect herbivores, and the plants on which they feed, are shown in Table 1. These were selected to show that these insects feed on a single family

of plants, although there are other examples in which an insect feeds more selectively (e.g., the silkworm moth, *Bombyx mori* (L.), on white mulberry, *Morus alba* (L.); or the rosemary grasshopper, *Schistocerca ceratiola*, on Florida rosemary, *Ceratiola ericoides* Michx.) or more broadly (e.g, Japanese beetle, *Popillia japonica* Newman, with about 400 species from many plant families recorded as hosts; or green peach aphid, *Myzus persicae* (Sulzer), which feeds on plants from 40 plant families).

Using Knowledge of the Weed-Crop-Insect Relationship to Increase Effectiveness of Insect Management

Despite the tendency of some insects (generalists) to feed broadly on host plants from several families, many show distinct preference for certain plant families. Bernays and Graham (1988), for example, estimated that less than 10% of phytophagous insects feed on plants in more than three different plant families. Thus, taxonomic similarity between the weed and crop plant becomes an important element in predicting damage to crops by weed-feeding insects. Insects

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TABLE 1. Some important specialist vegetable-feeding insects, the principal plant family on which they feed, and the biochemicals characteristic of the plant families on which they feed.[a]

Insect	Plant family[b]	Chemical(s)
Onion maggot, *Delia antiqua* (Meigen)	Alliaceae	Organosulfur compounds
Spinach flea beetle, *Disonycha xanthomelas* (Dalman) Striped flea beetle, *Phyllotreta striolata* (Fabricius) Beet leafminer, *Pegomya betae* Curtis Sugarbeet root maggot, *Tetanops myopaeformis* (Röder) Sugarbeet root aphid (summer host), *Pemphigus betae* Doane Hawaiian beet webworm, *Spoladea recurvalis* (Fabricius)	Chenopodiaceae[1]	Phytoecdysteroids
Lettuce aphid (summer host), *Nasonovia ribisnigri* (Mosley) Lettuce root aphid, *Pemphigus bursarius* (Linnaeus) Artichoke plume moth, *Platyptilia carduidactyla* (Riley)	Compositae[2]	Sesquiterpene lactones, flavonoids, phenolic acids
Sweetpotato flea beetle, *Chaetocnema confinis* Crotch Sweetpotato leaf beetle, *Typophorus nigritis* (Crotch) Golden tortoise beetle, *Charidotella bicolor* (Fabricius) Sweetpotato weevil, *Cylas formicarius* (Fabricius) West Indian sweetpotato weevil, *Euscepes postfasciatus* (Fairmaire) Sweetpotato sawfly, *Sterictiphora cellularis* (Say) Morningglory leafminer, *Bedellia somnulentella* (Zeller) Sweetpotato vine borer, *Omphisa anastomasalis* (Guenée) Sweetpotato hornworm, *Agrius cingulatus* (Fabricius)	Convolvulaceae	Tropane alkaloids
Cabbage leafminer, *Liriomyza brassicae* (Riley) Cabbage aphid, *Brevicoryne brassicae* (Linnaeus) Cabbage maggot, *Delia radicum* (Linnaeus) Radish root maggot, *Delia planipalpis* (Stein) Turnip root maggot, *Delia floralis* (Fallén) Turnip aphid, *Lipaphis erysimi* (Kaltenbach) Imported cabbageworm, *Pieris rapae* (Linnaeus) Mustard white, *Pieris napi* (Linnaeus) Southern cabbageworm, *Pontia protodice* (Boisduval and LeConte) Cabbage webworm, *Hellula rogatalis* (Hulst) Cross-striped cabbageworm, *Evergestis rimosalis* (Guenée) Diamondback moth, *Plutella xylostella* (Linnaeus) Purplebacked cabbageworm, *Evergestis pallidata* (Hufnagel) Yellowmargined leaf beetle, *Microtheca ochroloma* Stål Cabbage curculio, *Ceutorhynchus rapae* Gyllenhall	Cruciferae[3]	Glucosinolates, cysteine sulfoxide, volatile isothiocyanates, and thiosulfinates
Pickleworm, *Diaphania nitidalis* Stoll Melonworm, *Diaphania hyalinata* Linnaeus Squash beetle, *Epilachna borealis* (Fabricius) Squash bug, *Anasa tristis* (De Geer) Squash vine borer, *Melittia cucurbitae* (Harris)	Cucurbitaceae	Cucurbitacins
Corn blotch leafminer, *Agromyza parvicornis* Loew Northern corn rootworm (larva), *Diabrotica barberi* Smith and Lawrence Western corn rootworm (larva), *Diabrotica virgifera* LeConte Southern corn billbug, *Sphenophorus maidis* Chittenden Corn leaf aphid, *Rhopalosiphum maidis* Fitch Corn leafhopper, *Dalbulus maidis* (DeLong and Wolcott) Corn delphacid, *Peregrinus maidis* (Ashmead) Armyworm, *Pseudaletia unipuncta* (Haworth) Striped grass looper, *Mocis latipes* (Guenée) Southern cornstalk borer, *Diatraea crambidoides* (Grote) Southwestern corn borer, *Diatraea grandiosella* Dyar Sugarcane borer, *Diatraea saccharalis* (Fabricius) Grass thrips, *Anaphothrips obscurus* (Müller)	Graminae[4]	Hydroxamic acids
Bean leaf beetle, *Ceratoma trifurcata* (Förster) Mexican bean beetle, *Epilachna varivestris* Mulsant Pea leaf weevil, *Sitona lineatus* (Linnaeus) Pea aphid, *Acyrthosiphon kondoi* Shinji Bean leafroller, *Urbanus proteus* (Linnaeus) Green cloverworm, *Hypena scabra* (Fabricius) Limabean pod borer, *Etiella zinckenalla* (Treitschke) Pea moth, *Cydia nigricana* (Fabricius)	Leguminosae[5]	Isoflavonoids, flavonoids, and alkaloids

TABLE 1. Continued.

Insect	Plant family[b]	Chemical(s)
Colorado potato beetle, *Leptinotarsa decemlineata* (Say) Tobacco flea beetle, *Epitrix hirtipennis* (Melsheimer) Tuber flea beetle, *Epitrix tuberis* Gentner Pepper weevil Tomato hornworm, *Manduca quinquemaculata* (Haworth) Tobacco hornworm, *Manduca sexta* (Linnaeus) Potato flea beetle, *Epitrix cucumeris* (Harris) Eggplant tortoise beetle, *Gratiana pallidula* Boheman Potato stalk borer, *Trichobaris trinotata* (Say) Pepper maggot, *Zonosemata electa* (Say) Eggplant lace bug, *Gargaphia solani* Heidemann Eggplant leafminer, *Tildenia inconspicuella* (Murtfeldt) Potato psyllid, *Paratrioza cockerelli* (Sulc) Potato tuberworm, *Phthorimaea operculella* (Zeller) Tomato pinworm, *Keiferia lycopersicella* (Walsingham)	Solanaceae	Alkaloids
Carrot weevil, *Listronotus oregonensis* (LeConte) Carrot rust fly, *Psila rosae* (Fabricius) Parsnip leafminer, *Euleia fratria* (Loew) Parsnip webworm, *Depressaria pastinicella* (Duponchel) Carrot root aphid, *Dysaphis foeniculus* (Theobald) Willow-carrot aphid, *Cavariella aegopodii* Scopoli Black swallowtail, *Papilio polyxenes* Fabricius	Umbelliferae[6]	Furanocoumarins, polyacetylenes, and diterpenes

[a] Host data from Capinera (2001).

[b] Also known as [1] Amaranthaceae, [2] Asteraceae, [3] Brassicaceae, [4] Poaceae, [5] Fabaceae, [6] Apiaceae.

with a narrow host range (specialists) are likely to be pre-adapted to accept crops in the same family as the weeds on which they feed (Capinera 2002). Various cropping practices can cause shifts in weed composition within crop fields (Bárberi and Mazzoncini 2001; Tworkoski et al. 2000). Also, herbicides can display taxonomic discrimination, favoring survival of weed populations that are related to the crop plant. Therefore, continuous cropping of the same crop in the same field and repeated application of the same herbicides can lead to shifts in weed populations, including shifts to weeds that are taxonomically related to the crop. For example, use of 2,4-D for control of broadleaf weeds increases frequency of grass weeds in corn (*Zea mays* L.) and wheat. Increase in grass weed incidence sets the stage for insects that are attracted to these weeds to also feed on the crops. Nearby areas, including irrigation ditches, fencerows, and fallow fields are likely similarly infested with these taxonomically related weeds due to the abundance of weed seed and herbicide drift.

It is imperative that the taxonomic link between the weeds and crop plants be broken if insect management is to be optimized. This is especially important for selective insects; those with a narrow host range. So how can we disrupt this taxonomic link? There are several possibilities, including the following:

- Crop rotation;
- Use herbicides more selectively, or implement herbicide/tillage/cover crop practices that eliminate reservoir weeds;
- Seek out important weeds and selectively eliminate them from noncultivated areas.

Crop rotation can help to reduce the herbicide-based selection for weeds that are related to the crop. Although the weed seed reservoir can persist for many years, and weeds related to the crop may emerge annually, there will be years when excellent chemical weed suppression is attainable, helping to eliminate those related weeds. Another useful approach is to use alternatives to chemical weed control, principally tillage, or perhaps cover crops. Although chemical weed suppression may be more economical in the short run, it may be logical to use selected tillage or other practices to interfere with development of insect problems or to disrupt the weed seed reservoir, leading to long-term economic advantages. In some cases, herbicides are selective, so use of such products may provide benefits to both insect and weed management, and may be a good choice even if it comes at a premium price. Finally, the vagility of insects must be considered. Insects more commonly invade crop fields from nearby areas than emerge from within crop fields (Figure 4). There are some insects that overwinter in the soil within crop fields, of course, but most insect pests are crop field invaders, overwintering in wooded or waste areas, sometimes including suburban areas (ornamental plants and trees can be an important source of certain overwintering insects) or abandoned crop fields (destruction of crop residue is vital for management of some insects).

Agriculturalists are faced with many decisions, and some choices have far-reaching effects that extend well beyond the proximate issue. Weed management is one of those; the decisions sometimes influence insect pests as well. Although the relationships are sometimes complex, and decisions difficult to make, they are most successful if based on knowledge of weed-insect relationships, particularly the relatedness of weeds and crops, and the feeding behavior of insects.

Acknowledgments

FIGURE 4. The vagility of insects complicates integrated pest management, making it important to consider insect and weed populations growing near the crop field or other source areas. Shown here is strip-cropped wheat, with the area labeled (a) containing wheat stubble and weeds, (b) is an area where grasshoppers have consumed the young wheat, and (c) is undisturbed young wheat plants. The grasshoppers in this field sought shelter in the stubble-weedy area at night, flying daily to the margin of the wheat field where they ate the wheat plants down to the soil surface. Each day the damaged area grew wider as the grasshoppers were forced to fly farther and farther from their shelter to find food. Damage to field margins is the most common form of crop damage by grasshoppers.

images and David Thompson the pictures of army cutworm damage. This is published as Florida Agricultural Experiment Station Journal Series J-R-10285.

Literature Cited

Agrios, G. N. 1997. Plant pathology, 4th ed. San Diego: Academic Press. 635 p.

Agrios, G. N. 2004. Transmission of plant disease by insects. Pages 2290–2317 *in* J. L. Capinera, ed. Encyclopedia of Entomology. Dordrecht: Kluwer Academic.

Al-Doghairi, M. A. and W. S. Cranshaw. 2004. The effect of interplanting of nectariferous plants on the population density and parasitism of cabbage plants. Southwest. Entomol. 29:61–68.

Altieri, M. A. 1988. The dynamics of insect populations in crop systems subject to weed interference. Pages 433–451 *in* E. A. Heinrichs, ed. Plant stress-insect interactions. New York: Wiley-Interscience.

Bäckman, J.-P. C. and J. Tiainen. 2002. Habitat quality of field margins in a Finnish farmland are for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). Agric. Ecosyst. Environ. 89:53–68.

Bárberi, P. and M. Mazzoncini. 2001. Changes in weed community composition as influenced by cover crop and management system in continuous corn. Weed Sci. 49:491–499.

Bernays, E. and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892.

Capinera, J. L. 2001. Handbook of vegetable pests. San Diego: Academic. 729 p.

Capinera, J. L. 2002. North American vegetable pests: the pattern of invasion. Am. Entomol. 48:20–39.

Carruthers, R. I., M. E. Ramos, T. S. Larkin, D. L. Hostetter, and R. S. Soper. 1997. The *Entomophaga grylli* (Fresenius) Batko species complex: its biology, ecology, and use for biological control of pest grasshoppers. Mem. Entomol. Soc. Can. 171:329–353.

Chellemi, D. O., J. E. Funderburk, and D. W. Hall. 1994. Seasonal abundance of flower-inhabiting *Frankliniella* species (Thysanoptera: Thripidae) on wild food plant species. Environ. Entomol. 23:337–342.

Cordo, H. A., C. J. DeLoach, and R. Ferrer. 1995. Host range of the Argentine root borer *Carmenta haematica* (Ureta) (Lepidoptera: Sesiidae), a potential biocontrol agent for snakeweeds (*Gutierrezia* spp.) in the United States. Biol. Control 5:1–10.

Finch, S. and R. H. Collier. 2000. Host plant selection by insects—a theory based on 'appropriate/inappropriate landings' by insects of cruciferous plants. Entomol. Exp. Appl. 96:91–102.

Futuyma, D. J. 1983. Selective factors in the evolution of host choice by phytophagous insects. Pages 227–244 *in* S. Ahmad, ed. Herbivorous insects: Host-seeking behavior and mechanisms. New York: Academic.

Gangwere, S. K. 1966. Relationships between mandibles, feeding behavior and damage inflicted on plants by the feeding of certain acridids (Orthoptera). Mich. Entomol. 1:13–16.

Goeden, R. D. and L. A. Andres. 1999. Biological control of weeds in terrestrial and aquatic environments. Pages 871–890 *in* T. S. Bellows and T. W. Fisher, eds. Handbook of biological control. San Diego: Academic.

Hanson, F. E. 1983. The behavioral and neurophysiological basis of food plant selection by lepidopterous larvae. Pages 3–23 *in* S. Ahmad, ed. Herbivorous insects: Host-seeking behavior and mechanisms. New York: Academic.

Harborne, J. B. 1982. Introduction to ecological biochemistry, 2nd ed. London: Academic. 278 p.

Herzog, D. C. and J. E. Funderburk. 1986. Ecological bases for habitat management and pest cultural control. Pages 217–250 *in* M. Kogan, ed. Ecological theory and integrated pest management practice. New York: Wiley-Interscience.

Horton, D. R. and J. L. Capinera. 1990. Host utilization by Colorado potato beetle (Coleoptera: Chrysomelidae) in a potato/weed (*Solanum sarrachoides* Sendt) system. Can. Entomol. 122:113–121.

Hunter, W. B. 2004. Plant viruses and insects. Pages 1762–1768 *in* J. L. Capinera, ed. Encyclopedia of entomology. Dordrecht: Kluwer Academic.

Isley, F. B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers. Ann. Entomol. Soc. Am. 37:47–67.

Judd, G.J.R. and J. H. Borden. 1992a. Influence of different habitats and mating on olfactory behavior of onion flies seeking ovipositional hosts. J. Chem. Ecol. 18:605–620.

Judd, G.J.R. and J. H. Borden. 1992b. Aggregated oviposition in *Delia antiqua* (Meigen): a case for mediation by semiochemicals. J. Chem. Ecol. 18:621–635.

Kang, L., Y. Gan, and S. L. Li. 1999. The structural adaptation of mandibles and food specificity in grasshoppers on Inner Mongolian grasslands. J. Orthop. Res. 8:257–269.

Kennedy, J. S. 1976. Host-plant finding by flying insects. Pages 121–123 *in* T. Jermy, ed. The host-plant in relation to insect behaviour and reproduction. New York: Plenum.

Kennedy, J. S., C. O. Booth, and W.J.S. Kershaw. 1961. Host finding by aphids in the field. III. Visual attraction. Ann. Appl. Biol. 49:1–21.

Kogan, M. 1986. Plant defense strategies and host-plant resistance. Pages 83–134 *in* M. Kogan, ed. Ecological theory and integrated pest management practice. New York: Wiley-Interscience.

Kostal, V. and S. Finch. 1996. Preference of the cabbage root fly, *Delia radicum* (L.), for coloured traps: influence of sex and physiological status of the flies, trap background and experimental design. Physiol. Entomol. 21:123–130.

Metcalf, R. L. and R. A. Metcalf. 1993. Destructive and useful insects; their habits and control. 5th ed. New York: McGraw-Hill.

Moericke, V. 1969. Hostplant specific color behaviour by *Hyalopterous pruni* (Aphididae). Entomol. Exp. Appl. 12:524–534.

Myers, J. H. and D. R. Bazely. 2003. Ecology and control of introduced plants. Cambridge, Great Britain: Cambridge University Press. 313 p.

Norris, R. F. and M. Kogan. 2000. Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. Weed Sci. 48:94–158.

Patterson, B. D. 1984. Correlation between mandibular morphology and specific diet of some desert grassland Acrididae. Am. Midl. Nat. 111:296–303.

Rhainds, M., J. Kovach, E. L. Dosa, and G. English-Loeb. 2001. Impact of reflective mulch on yield of strawberry plants and incidence of damage by tarnished plant bug (Heteroptera: Miridae). J. Econ. Entomol. 94:1477–1484.

Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and its parasitoids. Environ. Entomol. 18:590–599.

Showler, A. T. and S. M. Greenberg. 2003. Effects of weeds on selected arthropod herbivore and natural enemy populations, and on cotton growth and yield. Environ. Entomol. 32:39–50.

Smith, H. A. and R. McSorley. 2000. Intercropping and pest management: a review of major concepts. Am. Entomol. 46:154–161.

Southwood, T.R.E. 1986. Plant surfaces and insects—An overview. Pages 1–22 *in* B. Juniper and T.R.E. Southwood, eds. Insects and the plant surface. London: Edward Arnold.

Stanton, M. L. 1983. Spatial patterns in the plant community and their

effects upon insect search. Pages 125–157 *in* S. Ahmad, ed. Herbivorous insects: Host-seeking behavior and mechanisms. New York: Academic.

Stapleton, J. J. and C. G. Summers. 2002. Reflective mulches for management of aphids and aphid-borne virus diseases in late-season cantaloupe (*Cucumis melo* L. var. cantalupensis). Crop Prot. 21:891–898.

Stavinsky, J., J. Funderburk, B. V. Brodbeck, S. M. Olson, and P. C. Andersen. 2002. Population dynamics of Frankliniella spp. and tomato spotted wilt incidence as influenced by cultural management tactics in tomato. J. Econ. Entomol. 95:1216–1221.

Strong, D. R., J. H. Lawton, and R. Southwood. 1984. Insects on plants: Community patterns and mechanisms. Cambridge, MA: Harvard University Press. 330 p.

Summers, C. G. and J. J. Stapleton. 2002. Use of UV reflective mulch to delay the colonization and reduce the severity of *Bemisia argentifolii* (Homoptera: Aleyrodidae) infestations in cucurbits. Biol. Control 21: 921–928.

Tworkoski, T. J., W. V. Welker, and G. D. Vass. 2000. Weed community changes following Diuron, Simazine, or Terbacil application. Weed. Technol. 14:197–203.

Zherikhin, V. V. 2002. Ecological history of the terrestrial insects. Pages 331–388 *in* A. P. Rasnitsyn and D.L.J. Quicke, eds. History of insects. Dordrecht: Kluwer Academic.