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THE ROLE OF PLANT TRICHOMES IN INSECT RESISTANCE : A SELECTIVE REVIEW¹

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ABSTRACT

Trichomes are a common feature on vegetative and reproductive structures in many plant species. They have been used to develop insect resistant cultivars in several agricultural crops. This paper briefly reviews the types of trichomes, their mode of action and the phytophagous arthropods against which they are effective in alfalfa, soybean, chickpea, cotton, sorghum, wheat, potato and tomato. A list of other plant species in which trichomes have been identified as providing a defense against specific arthropod herbivores is given. The role of trichomes as an ovipositional stimulant and a performance barrier to natural enemies is also highlighted.

Key words: Alfalfa, chickpea, cotton, exudate, insect resistance, plant hairs, potato, pubescence, sorghum, soybean, trichomes, tomato, wheat.

INTRODUCTION

Trichomes, or plant hairs, are a common anatomical feature on leaves, stems and/or reproductive structures in all higher plant families. They are considered a primitive characteristic with many independent evolutionary origins. Dicotyledons are generally hairier than monocots, but trichomes can be induced even in glabrous species (Jeffree, 1986). There is often considerable variation in trichome form and function within a species and these genotypic differences have been exploited in the development of insect resistant cultivars.

The fact that trichomes are inducible is an indication of the malleability of this character. Seasonal, habitat and developmental variation can affect the ontogeny and expression of trichomes (Southwood, 1986). At the same time, trichomes are a more common feature in some families and species than in others. This paper briefly reviews the role of trichomes as mechanism for insect resistance in 8 agricultural crops: Alfalfa, soybean, chickpea (Fabaceae), cotton (Malvaceae), sorghum, wheat (Poaceae = Graminae), potato and tomato (Solanaceae). Appendix 1 lists other plant species in which plant trichomes have been reported to provide protection against phytophagous arthropods. Before discussing the specific role of trichomes in these 8 crops, we first summarize the types of trichomes, their functions and the interactions between trichomes and insects.

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TYPES AND FUNCTIONS OF TRICHOMES

Trichomes are either glandular, if they produce, secrete or contain trichomal chemicals, or nonglandular if they do not produce or contain chemicals. The chemicals in and on glandular trichomes may either be toxic or may impede an insect's ability to move, feed and/or survive. Trichomes have also been classified morphologically. Jeffree (1986) lists seven types: 1) simple unicellular, 2) multicellular uniseriate, 3) multicellular multiseriate, 4) 2-5 branched, 5) stellate, 6) dendritic or arboriform and 7) peltate. There is much variation and overlap between types.

Plant trichomes may be purely structural and have only a physiological function (Southwood, 1986). A dense pubescence changes the optical properties of the leaf surface and may reflect or absorb certain wavelengths of light. Another possible physiological function is that by trapping a layer of air against the leaf surface, trichomes could conserve heat and moisture.

The role of trichomes as an insect defense mechanism has been well documented (Levin, 1973; Webster, 1975; Stipanovic, 1983). Trichomes can act as an insect resistance mechanism in one of three ways: 1) as a physical barrier limiting an insect's contact with the plant, 2) by producing toxic compounds which poison the insect through contact, ingestion and/or inhalation and 3) by producing gummy, sticky or polymerizing chemical exudates which impede the insect (David and Easwaramoorthy, 1988; Duffey, 1986). The effectiveness of the first mechanism, as a simple physical barrier to reaching the plant surface, is dependant on the length, density and orientation of the trichome and on the insect's size, mode of locomotion and type of mouthparts (Southwood, 1986). Longer, denser and/or more erect hairs may be inferred to provide a better barrier to insect herbivores. As a purely physical phenomena, trichomes are also known to interfere with the insect digestion (Wellso, 1973). The other two resistance mechanisms pertain to only glandular trichomes. The fluidity and volume of the exudates, whether toxic or sticky, varies with weather, time of day and plant age (Koundal and Sinha, 1981; Rembold *et al.*, 1990).

Trichomes *per se* do not provide complete protection against all insect herbivores. Highly adapted, specialized phytophagous insects may have developed effective biochemical (e.g. Kennedy *et al.*, 1987) or morphological (e.g. Gregory *et al.*, 1986) responses to negate the impact of the trichomes. In addition, trichomes may reduce the effectiveness of parasites and predators, thereby indirectly favoring specialized herbivores (e.g. Kauffman and Kennedy, 1989 a,b). Dense pubescence can also be an attractive oviposition substrate for some insects, thereby increasing herbivore loads relative to more glabrous cultivars (Renwick and Chew, 1994).

ALFALFA (FABACEAE)

Alfalfa (*Medicago sativa*) is an important forage legume in many parts of the world. Though a number of insects are reported as pests, the role of trichomes as a defense mechanism has been studied most extensively for potato leaf hopper, *Empoasca fabae*

(Taylor, 1956), alfalfa weevil, *Hypera variabilis* (= *postica*) (Danielson *et al.*, 1987), alfalfa blotch leafminer, *Agromyza frontella* (MacLean and Byers, 1983), pea aphid, *Acyrtosiphon pisum* (Shade and Kitch, 1983), spotted alfalfa aphid, *Theriophis maculata* (Ferguson *et al.*, 1982) and alfalfa seed chalcid, *Bruchophagous reddy* (Brewer *et al.*, 1983).

Species of alfalfa possess either simple nonglandular (e.g.: *M. sativa* and *M. neoneana*) or both glandular and non-glandular (e.g.: *M. scutellata* and *M. rugosa*) trichomes (MacLean and Byers, 1983). In general, glandular trichomes confer resistance to insect attack (Shade *et al.*, 1975). They are of two types: erect and procumbent (Kreitner and Sorensen, 1979a). Erect glandular trichomes provide protection against *H. variabilis* in certain annual *Medicago* species. (Shade *et al.*, 1975). Larvae are immobilized by the sticky exudates produced in these trichomes (Johnson *et al.*, 1980a). The exudates increase larval mortality by physical entrapment and by suffocation when the spiracles of the larvae are sealed (Shade *et al.*, 1975). Procumbent hairs of perennial species of alfalfa are ineffective in immobilizing larvae and this may be related to lipid content and therefore, viscosity and hardening of the exudate (Kreitner and Sorensen, 1979b).

Several wild species of alfalfa are also resistant to *E. fabae*. Five such species with glandular hairs were nearly immune to first instar *E. fabae*. Mortality rates of up to 100% in the first stadium were observed in all five species (Shade *et al.*, 1979). One species, *Medicago noeana*, produced 100% adult mortality within 3 days, compared to 53% mortality in *M. sativa* after 9 days. Also, Brewer *et al.* (1986) recorded a decrease in oviposition rate as the glandular hair density increased. *E. fabae* highly prefer the nonglandular hairy-type *Medicago* species for egg laying compared to the glandular haired species. Similarly, Johnson *et al.* (1980 a,b) found that glandular haired annual alfalfa species were resistant to adult *H. variabilis* feeding and oviposition. Perennial alfalfa species (*M. glandulosa*, *M. prostrata*, *M. glutinosa*) have also shown resistance to *H. variabilis* oviposition due to glandular hairs and smaller stem diameter (Danielson *et al.*, 1987).

Glandular trichomes confer resistance to two other alfalfa pests, *A. frontella* and *A. pisum*. MacLean and Byers (1983) concluded that the higher density of glandular hairs prevent *A. frontella* from oviposition. Survival, development and fecundity of *A. pisum* were negatively affected on wild type alfalfa species due to the presence of dense glandular hairs. A nonglandular alfalfa cultivar supported significantly higher *A. pisum* population than the other 6 glandular species studied (Shade and Kitch, 1983). Contrary to these findings, Carter *et al.* (1988) reported that hairy accessions did not adversely affect the survival of *T. maculata*.

SOYBEAN (FABACEAE)

Soybean, originally from East Asia but now cultivated worldwide, is valued for its protein and its oil content. Trichomes have been evaluated as potential resistance

mechanism for potato leaf hopper, *Empoasca fabae* (Wolfenbarger and Sleeman, 1963), Mexican bean beetle, *Epilachna varivestis* (Johnson, 1975), springtail, *Deuterostmiathurus yumanensis* (Turnipseed, 1977), southern green stink bug, *Nezara viridula* (Chaiprasert, 1985), soybean looper, *Pseudoplusia includens*, velvetbean caterpillar, *Anticarsia gemmatilis* (Lambert *et al.*, 1992), corn earworm, *H. zea* (Panda, 1979) and cabbage looper, *Trichoplusia ni* (Khan *et al.*, 1986).

Soybean leaves possess simple non-glandular trichomes. Morphologically, they have been distinguished into simple long (1-3 mm; cylindrical with 1-3 basal cells) and simple curly (flat and curly) hairs (Singh *et al.*, 1971). Soybean accessions have been grouped into glabrous, normal and densely pubescent based on trichome density on leaves (Lambert and Kilen, 1989). Broersma *et al.* (1972) believed that the orientation of the hairs of soybean are more important for resistance to *E. fabae* than the number of hairs. Johnson (1975) and Turnipseed (1977) observed that in addition to the orientation, the length of the trichomes were important as a resistant factors for *E. fabae* and *E. varivestis*. Size of the insect body also determines the degree of resistance. *E. fabae* (body length= 1.0-4.0 mm) population decreased with increasing trichome length, regardless of trichome density, whereas *D. yumanensis* (body length= 0.2-0.4 mm) population decreased with a increasing trichome density (Turnipseed, 1977). Trichomes of pubescent cultivars produce a highly irregular surface which prevents normal attachment for feeding and oviposition of *E. fabae* (Lee *et al.*, 1986) thereby making the glabrous varieties more susceptible. Accessions with a higher number of trichomes on the pods were recommended for use against *N. viridula* (Chaiprasert, 1985).

Soybean accessions with greater pubescence have shown lower susceptibility to lepidopteran insects. Panda (1979) found pubescence in soybean genotypes a major resistance factor against the damage by *H. zea* in spite of its preference for ovipositing on trichome rich genotypes. Khan *et al.* (1986) established the role of trichomes as a feeding inhibitor against *T. ni* by shaving them and allowing the larvae to feed. Damage intensity was similar to that of unshaven leaves of trichomeless accessions. Plant hairs are an important resistance mechanism against larvae of *H. zea*, *P. includens* and *A. gemmatilis*, though trichomes enhance oviposition by these Lepidoptera (Lambert *et al.*, 1992).

CHICKPEA (FABACEAE)

Chickpea (*Cicer arietinum*) ranks third among pulse crops and is especially important in the traditional vegetarian societies of south Asia. The two most important insect pests are leafminer, *Liriomyza cicerina* in west Asia and pod borer, *Helicoverpa armigera* in south Asia. Trichomes have been found to be important resistance factors to both insects (Rembold *et al.*, 1990).

The green surface of the plant, including the pods, are densely covered with trichomes. Three types have been identified, one nonglandular and two glandular (Cubero, 1987). The glandular trichomes secrete a highly acidic (pH1) exudate,

composed primarily of malic and oxalic acids (Koundal and Sinha, 1981; Rembold and Weigner, 1990). The quantity and composition of the exudate produced varies among genotypes, seasons and time of the day (Santhakumari *et al.*, 1979; Koundal and Sinha, 1981; Rembold *et al.*, 1990).

The amount of malic acid in the exudate has been correlated with the level of resistance to *L. cicerina* and *H. armigera* (Rembold, 1981; Rembold and Winter, 1982; Lateef, 1985; Rembold *et al.*, 1990). The resistance to *H. armigera* provided by trichomal exudates has been shown to be nonpreference and antibiosis (Srivastava and Srivastava, 1990; Weigand and Pimbert, 1993). Recently, Yoshida and Cowgill (In press) incorporated oxalic acid and malic acid separately into semi-synthetic diet and observed an antibiotic effect on *H. armigera* larvae for oxalic acid only.

COTTON (MALVACEAE)

Cotton (*Gossypium* spp.) is attacked by a large and varied group of insects. Trichome rich *Gossypium* lines have been found to be more resistant to boll weevil, *Anthonomus grandis* (Hunter *et al.*, 1965), cotton aphid, *Aphis gossypii* (Kamel and Elkassaby, 1965), Asiatic cottonworm, *Spodoptera littoralis* (Abul-Nasr, 1960; Kamel, 1965), spotted bollworm, *Earias fabia* (Mehta, 1971), green leafhopper, *Empoasca libyca* (Evans, 1965), jassids, *Empoasca (Ambrasca) biguttula* (Sharma and Agarwal, 1983; Tidke and Sane, 1962), *E. devastans* (Sikka *et al.*, 1966; Batra and Gupta, 1970), *E. fascialis* (Reed, 1974), *E. maculata* (May, 1951), pink bollworm, *Pectinophora gossypiella* (Smith *et al.*, 1975), tobacco budworm, *Helicoverpa virescens* (Ramalho *et al.*, 1984), turnipseed plant bug, *Lygus lineolaris* (Meredith and Schuster, 1979) and cotton bug, *Lygus hesperus* (Wilson and George, 1986).

Three phenotypes are recognized in *Gossypium hirsutum*: Glabrous (smooth leaf, no hairs), hirsute (medium length, normal hair density) and pilose (short, dense hairs) (Meyer, 1957). The level of expression of two genes, H1 for hair length and H2 for hair density, determine which phenotype is expressed (Knight, 1952). When H1 genes fail to express, H2 genes confer a dense pilosity of minute length as observed in the wild Hawaiian species *G. tomentosum* (Knight and Sadd, 1954).

Hairiness in cotton confers resistance to *A. grandis* by preventing easy movement (Cook, 1906). Hair length, density and position are three important qualities to be considered for their resistance (Wannamaker, 1957). Stephens (1957) recorded less damage on pilose than on hirsute types. The pilose traits considerably reduced the proportion of egg laying punctures compared to hirsute traits (Wessling, 1958). Larval development was also slow on hairy buds (Stephens and Lee, 1961). However, Merkle and Meyer (1963) attributed the lower damage to gossypol content and plant appearance in addition to pilosity.

Hairy cottons suppress *P. gossypiella* infestation (Smith *et al.*, 1975). The 1st instar larval movement was less on highly hairy leaves than on glabrous leaves. Larvae paused regularly to head swing and sample the substrate while moving. This resulted in higher

mortality due to starvation or desiccation because of their inability to reach bolls in time. Wilson and George (1986) compared infestation rate among smooth, hirsute and pubescent traits and found smooth leaf genomes more susceptible.

H. freshens (Lukefahr *et al.*, 1975), *L. lineolaris* (Meredith and Schuster, 1979) and the cotton fleahopper, *Pseudatomoscelis seriatus* (Walker *et al.*, 1974) prefer pubescent genotypes for egg deposition. Nevertheless, Ramalho *et al.* (1984) found that *H. virescense* larvae were prone to biotic (predators and parasites) and abiotic (high temperature and insecticides) factors because of slower movement on pubescent genotypes. *L. hesperus* lays more eggs on pilose leaves though, nymphal weight is greater when reared on smooth leaves; nymph survival was 86% on both leaf types (Benedict *et al.*, 1983). Also, glabrous leaves are more vulnerable to *L. hesperus* attack (Wilson and George, 1986). Afzal and Abbas (1943) cautioned against planting glabrous cotton in *Empoasca* spp. prone areas. The hair length is a more important determinant of resistance than hair density (Parnell *et al.*, 1949), though, Ambekar and Kalbhor (1981) indicated both were important. Adults are prevented from egg laying on along the adaxial mid-rib, since the ovipositor is smaller than the mid-vein hair length (Khan and Agarwal, 1984).

SORGHUM (POACEAE)

Sorghum (*Sorghum bicolor*) is an important food and forage crop throughout the world. A large number of insects are reported as pests of sorghum but trichomes have been identified as a resistance mechanism only for shootfly, *Antherigona soccata* (Sharma, 1993).

Wild sorghum species with high trichome densities on the lower leaf surface are immune to shootfly (Bapat and Mote, 1982). These hairs prevent larvae from penetrating and are considered a mechanical resistance mechanism (Blum, 1967). Adults lay eggs on the lower side of the leaves. After hatching the larvae move down the leaf blade and into the culm between the outer sheaths, before finally boring into the growing point (Chapman and Woodhead, 1985). Trichomes may hinder the easy movement of the larvae toward the target site, making the plant less susceptible (Gibson and Maiti, 1983; Raina, 1985). Resistance have also been attributed to ovipositional nonpreference (Blum, 1968) which may be due to the presence of prickle hairs on the leaf surface (Maiti and Bidinger, 1979; Maiti *et al.*, 1980; Bapat and Mote, 1982).

A few genotypes also have pronounced lingular hairs and the larvae may become trapped in these hairs (Taneja and Woodhead, 1989). However, the relative contribution of trichomes and/or other traits to lower shootfly damage has not been analyzed.

WHEAT (POACEAE)

Wheat (*Triticum* spp.) is second only to rice in worldwide production and consumption. Trichomes on *Triticum* spp. have been shown to provide resistance to cereal leaf beetle,

Oulema melanopus (Schillinger, 1969; Webster *et al.*, 1973; Wellso and Hoxie, 1982), Hessian fly, *Mayetiola destructor* (Miller *et al.*, 1960; Roberts *et al.*, 1979), bird cherry oat aphid, *Rhopalosiphum padi* (Roberts and Foster, 1983) and frit fly, *Oscinella frit* (Peregrine and Cutling, 1967).

The trichomes on wheat leaves are nonglandular and unicellular (Ringlund and Everson, 1968). *O. melanopus* females lay fewer eggs on genotypes with highly pubescent leaves compared to glabrous leaved cultivars (Gallun *et al.*, 1973; Schillinger and Gallun, 1968). Smith *et al.* (1971) induced greater leaf pubescence on *Triticum aestivum* and observed greater resistance to *O. melanopus*, relative to wheat grown under natural conditions. Their damage potential was considerably reduced on pubescent lines and larval survival and weight gain was lower (Webster and Smith, 1971; Wellso, 1973). These varieties suffer less damage and produce higher yields relative to less pubescent varieties (Webster *et al.*, 1972).

Hoxie *et al.*, (1975) reported that both oviposition and larval survival in *O. melanopus* were lower on cultivars with relatively longer and/or denser trichomes, though trichome length was of greater importance than trichome density. In contrast, Kolarov (1988) recorded moderate resistance as a consequence of a greater trichome density rather than greater trichome length. Papp *et al.* (1992) investigated trichome length and density in seedlings and on flag leaves and their relationships to *O. melanopus* resistance. On flag leaves, trichome length provides reliable information about the level of resistance while in seedlings, trichome density is a better indicator of resistance. In addition, trichomes also provide protection from *M. destructor* and *R. padi*. Both of these pests produce fewer eggs and have lower survivorship on pubescent compared to glabrous cultivars (Roberts *et al.*, 1979; Roberts and Foster, 1983).

POTATO (SOLANACEAE)

Commercial potato (*Solanum tuberosum*) cultivars are susceptible to attack by a wide range of pests including Colorado potato beetle, *Leptinotarsa decemlineata*, potato leafhopper, *Empoasca fabae*, green peach aphid, *Myzus persicae* and potato aphid, *Macrosiphum euphorbiae* (Tingey, 1991; Yencho and Tingey, 1994). The wild species of *Solanum* have been found to be resistant to *L. decemlineata* and to the species of leafminer, *Liriomyza*, tuber moth, *Phthorimaea*, aphids, *Macrosiphum*, *Myzus*, leafhopper, *Empoasca* and flea beetle, *Epitrix* due to glandular exudates (Gibson, 1971; Ave *et al.*, 1987; Neal *et al.*, 1989; Tingey, 1991; Yencho and Tingey, 1994). Hybrid potatoes obtained by crossing *S. berthaultii* with the cultivated species resist *E. fabae*, *L. decemlineata* and the species of *Macrosiphum*, *Myzus* and *Epitrix* (Tingey, 1981; Tingey *et al.*, 1982; Plaisted *et al.*, 1992).

The leaves and stems of *S. berthaultii* possesses two types of glandular trichomes (Tingey, 1985). The so called Type A trichome is short with a tetralobulate, membrane bound gland at its apex. Its exudate is only released after rupture (Tingey and Laubengayer, 1981). The longer and simple Type B trichome is elongate with an ovoid gland at the tip, which continuously exudes a viscous fluid.

as observed for several egg and larval parasitoids of *H. zea*, *H. virescens* and *M. sexta* on the wild tomato, *L. hirsutum* f. *glabratum* (Farrar and Kennedy, 1991; Farrar *et al.*, 1994; Kauffman and Kennedy, 1989a, b). Kashyap *et al.* (1991) reported that *Trichogramma* species get stuck in these exudates.

Predators are similarly hindered by glandular and nonglandular trichomes. The walking speed of larvae of several coccinellid species are inversely related to the density of trichomes (Banks, 1957; Obrycki, 1986; Obrycki *et al.*, 1983). On wild tomato, Barbour *et al.* (1993) recorded a lower consumption of *H. zea* eggs and an increased mortality for two predators, coccinellid, *Coleomegilla maculata* and the big-eyed bug *Geocoris punctipes*. This lower efficiency was directly related to the abundance of methyl ketones, the major component of the glandular trichome exudate on the tomato foliage.

The negative effects of glandular trichomes on natural enemies may not be as strong under field conditions as often observed in greenhouses. Obrycki and Tauber (1984) suggested that dust, wind and rain adversely affect the adhesiveness of glandular trichome exudates.

Oviposition is positively correlated with increasing trichome density in many herbivorous species. In cotton, Benedict *et al.* (1983) found the oviposition of *Lygus hesperus* increased with increasing trichome density. A similar effect was recorded by Lukefahr *et al.* (1975) for *Helicoverpa* which use trichomes as well as leaf veins as 'footholds' (Callahan, 1957). *Earias fabia* and *E. vitella* also prefer hirsute over smooth cotton genotypes for oviposition (Mehta and Saxena, 1970). On soybean, *Laspeyresia glycinivorella*, prefers to oviposit on hairy pods compared to smooth pods (Hsu Ching-Fung, 1965). Length and/or density of trichomes on the lower surface of soybean plants was found to be highly correlated with several ovipositional traits of *Ophiomyia phaseoli* (Chiang and Norris, 1983). Hirsute surfaces can also positively alter egg and larval development and survival of herbivores by ameliorating environmental factors (Ramaswamy, 1988).

CONCLUSIONS

This brief review has highlighted the role of plant trichomes as an effective physical and/or chemical barrier to insect herbivores. The distribution, length, density and type of plant trichomes influence insect herbivore loads and the relative amount of damage they cause. Small bodied insects are in general more affected than larger ones. This also includes many natural enemies whose efficacy is reduced thereby enhancing the survival of some herbivores.

Trichomes are an especially effective defense against homopteran pests, because in addition to being small and soft bodied, these insects feed with piercing and sucking mouthparts and must be on or near the plant surface. Growth and development of large bodied insects may be retarded due to feeding hinderance and/or antibiosis. For many Lepidoptera, there is an apparent tradeoff: moths prefer pubescent plant surfaces for oviposition, but early instar larvae may suffer higher mortality.

Trichomes may offer a potential insect resistance mechanism for glabrous crops and/or genotypes. Wild relatives are often a good source of pubescence and have been utilized in several successful breeding programmes (e.g. alfalfa, potato and tomato). Both conventional breeding and biotechnology might be used to transfer such characters between species.

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Plants in which trichomes are reported to be a defense mechanism against arthropod herbivores.

	Arthropod Affected	Order	Reference
	<i>Brevicoryne brassicae</i>	Homoptera	Stoner, 1992
	<i>Pieris rapae</i>	Lepidoptera	Stoner, 1992
	<i>Homoeosoma electellum</i>	Lepidoptera	Rogers <i>et al.</i> , 1987
Leguminales	<i>Philaenus spumarius</i>	Homoptera	Hoffman and McEvoy, 1985
	<i>Diaphania</i> sp.	Lepidoptera	Elsley and Wann, 1982
	<i>Bemisia tabaci</i>	Homoptera	El Khidir, 1965
	<i>Curculio elephas</i>	Coleoptera	Popova, 1960
Leguminales	<i>Bemisia</i> spp.	Homoptera	Bilderback and Mattson, 1977
Leguminales	<i>Boophilus microplis</i>	Acarina	Sutherst and Wilson, 1986
	<i>Empoasca kerri</i>	Homoptera	Dwivedi <i>et al.</i> , 1986
	<i>Acyrtosiphon pisum</i>	Homoptera	Wogerek and Dunajska, 1964
	<i>Empoasca fabae</i>	Homoptera	Wolfenbarger and Sleeman, 1963
	<i>Liriomyza trifolii</i>	Diptera	Quiring <i>et al.</i> , 1992
	<i>Acyrtosiphon pisum</i>	Homoptera	Lampe, 1982
	<i>Empoasca kraemeri</i>	Homoptera	Lyman and Cardona, 1982
	<i>Boophilus microplis</i>	Acarina	Sutherst <i>et al.</i> , 1982
	<i>Porthesia taiwana</i>	Diptera	Talekar <i>et al.</i> , 1988
	<i>Helicoverpa armigera</i>	Lepidoptera	Talekar <i>et al.</i> , 1988
	<i>Ophiomyia phaseoli</i>	Diptera	Uengprasertporn, 1985
	<i>Maruca testulalis</i>	Lepidoptera	Oghiakhe <i>et al.</i> , 1992
	<i>Clavigralla tomentosicollis</i>	Heteroptera	Chiang and Singh, 1988
	<i>Maruca testulalis</i>	Lepidoptera	Jackai and Oghiakhe, 1989
	<i>Acyrtosiphon solani</i>	Homoptera	Walters <i>et al.</i> , 1991
	<i>Tetranychus</i> spp.	Acarina	Gerhold <i>et al.</i> , 1984

Appendix 1. (Contd.)

Plant Species	Arthropod Affected	Order	Reference
Malvaceae			
<i>Abelmoschus esculentus</i>	<i>Empoasca (Amrasca) devastans</i>	Homoptera	Uthamasamy, 1985
Passifloraceae			
<i>Passiflora adenopoda</i>	<i>Heliconius erata</i>	Lepidoptera	Gilbert, 1971
	<i>H. melpomene</i>	Lepidoptera	Gilbert, 1971
Poaceae			
<i>Oryza sativa</i>	<i>Chilo suppressalis</i>	Lepidoptera	Patanakamjorn and Pathak, 1967
	<i>C. agamemnon</i>	Lepidoptera	Abd-El-Rahman and Salsh, 1993
	<i>Nephotettix impicticeps</i>	Homoptera	Petinez, 1986
	<i>N. apicalis</i>	Homoptera	Petinez, 1986
	<i>Nilaparvata lugens</i>	Homoptera	Petinez, 1986
	<i>Cnaphalocrocis medinalis</i>	Lepidoptera	Dakshayani <i>et al.</i> , 1993
<i>Lolium</i> spp.	<i>Listronotus bonariensis</i>	Coleoptera	Barker, 1989
<i>Avena</i> spp.	<i>Oscinella frit</i>	Diptera	Peregrine and Catling, 1967
	<i>Oulema melanoplus</i>	Coleoptera	Smith and Webster, 1974
<i>Saccharum officinarum</i>	<i>Aleurolobus barodensis</i>	Homoptera	Agarwal, 1969
	<i>Diatraea saccharalis</i>	Lepidoptera	Sosa, 1990
	<i>Melanaspis glomerata</i>	Heteroptera	Agarwal, 1969
	<i>Scirpophaga nivella</i>	Lepidoptera	Verma and Mathur, 1950
	<i>Diabrotica virgifera</i>	Coleoptera	Hagen and Anderson, 1967
<i>Zea mays</i>	<i>Chilo zonellus (partellus)</i>	Lepidoptera	Kumar, 1992
Rosaceae			
<i>Fragaria chiloensis</i>	<i>Otiorhynchus sulcatus</i>	Coleoptera	Doss and Shanks, 1988
Solanaceae			
<i>Solanum melongena</i>	<i>Amrasca biguttula</i>	Homoptera	Schreiner, 1990
	<i>Trialeurodes vaporariorum</i>	Homoptera	Malausa <i>et al.</i> , 1988
<i>Solanum mammosum</i>	<i>Aphis gossypi</i>	Homoptera	Sambandam <i>et al.</i> , 1969
	<i>Epilachna vigintioctopunctata</i>	Coleoptera	Sambandam <i>et al.</i> , 1969
<i>Nicotiana tobaccum</i>	<i>Myzus persicae</i>	Homoptera	Abernathy and Thurston, 1969
	<i>Manduca sexta</i>	Lepidoptera	Thurston, 1970
	<i>Rhopalosiphum padi</i>	Homoptera	Thurston and Webster, 1962
	<i>Acyrtosiphon pisum</i>	Homoptera	Thurston and Webster, 1962