Chapter 3

Insect-Plant Interaction: A Roadmap to Sustainable Pest Management

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Abstract

The phenomenon of insect-plant interaction is continued since the beginning of lives on earth. The communication between these two categories of organisms is complex and its consistent exploration discloses new and interesting aspects about it. The chapter deals with the various categories of tritrophic interactions between plants, insects and their natural enemies and provides an insight of these relationships. The active communication between different species (plants and insects) exists through secondary compounds released by the plants, however; members of the same species

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communicate through the signals and cues released by the other member (either insects or plants). The communication between intra or inter species because of coevolution develops various kind of resistance wihin the communicating organisms. The mechanism of resistance consists of antibiosis, antixenosis and tolerance. The deep understanding of these semiochemicals, connections and mechanisms between the members of an ecosystem can be exploited to maintain a balance in populations of insect pests and their natural enemies. Sustainable pest management can be efficiently applied by using natural resources and adapting innate traits in breeding programs to maintain the required characteristics in valued crops in agriculture.

Keywords: Insect plant interaction, tritrophic interaction, natural enemies, resistance, insect pests, sustainable pest management, tolerance, antibiosis, antixenosis.

3.1. Evolution and coevolution

The green plants along with their dependents i.e. herbivores have been coevolved since ancient times. Both have developed strategies to overcome the defense of each other and at time, one of these may drive extra benefit than the other. Evolution of plants started from the simplest unicellular form in mid-Paleozoic era, about 480 to 360 million years ago (Kenrick and Crane 1997a). This evolution continued and a wide range of flora has been evolved (Kenrick and Crane 1997b). With the evolution of plant life, the animal life started on the surface of earth and the first terrestrial animal form was reported 450 million years ago (Pisani et al. 2004) followed by the historic association of animals and plants on the earth. The coevolution of plants and animals is continued earth and both are overcoming the defensive traits of each other. The current chapter mainly focuses on the coevolution of plants and insects.

3.2. Insect-plant Interaction

The insect plant interaction is an important constituent of environmental balance on the earth. Their process of coevolution is continued since the beginning of the earth and becoming complex with the passage of time. New races, stains and biotypes have been evolved because of this complex association. Various components are playing a key role in this complex of insect plant interaction leading to various guild types in the ecosystems.

3.2.1. Components of insect-plant interaction

3.2.1.1. Host plants

The plants are one of the important components of insect-plant interactions. Both morphological as well as physiological aspects of a plant stimulate the reaction of the insects. The morphological features of the host plant are mainly responsible for insect attraction. Degree of foliage acceptance and its utilization by insects is totally dependent on the variations in physical conditions of host plants including; size, shape, color and release of various hormonal secretions. e.g., presence of hairy structures (pubescence) and hard leaf tissues often present the insect movement and feeding on the specific host plants.

Similarly, physiological characteristics of plants are responsible for the production of repellent chemicals against the insects. The secondary metabolic processes that are responsible for the production of these chemicals, termed as semiochemicals.

Primary and secondary plant metabolites often seem to be interconnected about their production in plants. The secondary metabolites or chemicals extensively produce in plants and are considered nonessential for primary metabolic processes. However, most of these secondary chemicals take part in the defense mechanisms of plants against herbivores. These metabolites are produced and stored in various plant parts and are secreted from external plant surface.

The release of these secondary compounds depends upon the feeding of herbivores on the target plants. The interaction between chemical response of plants and the insect feeding are of two types. The type of interaction existed among the members of one species is called “pheromones”, however, the interactions among the organisms of different species is called “allelochemicals”.

Allelochemicals are further subdivided into “Allomones and kairomones”. The defensive elements which cause repulsion in insect behavior against their host plants are known as allomones, for example, repellent, oviposition and feeding deterrents along with toxicants are the allomones reported from plant systems. The chemicals which are responsible to increase connectivity between host and herbivores are considered as kairomones. Attractants and arrestants in plant systems are general examples of kairomones.

Host-plant selection by insects usually involves both primary and secondary substances (Plant products). Some theories emphasize and considered secondary metabolites as a main role; however, many pointed out that both play an important role. Host-plant odor or taste for insects comes from nutrients and secondary compounds that are combined to form a complex sensorial input. These inputs are initiated and control by insect central nervous system to determine a given plant as a host. In breeding programs for plant resistance, it is important to understand the nature of insect/plant relationships and their expression in host selection. Such understanding helps to exploit and generate the susceptibility in target plant species and enhances efficient development of resistant cultivars.

3.2.1.2. Insect herbivores

Insect herbivores are important constituents of insect plant interaction. Various areas of plant canopy are preferred by insects under the influence of certain physical factors, for example; light, gravity, wind, humidity and temperature. These physical factors play very important role for general habitat selection by insects. These factors are considered the important elements for habitat selection especially for migrant species and intruders.

The other most important requirement is to find the appropriate host plant in the suitable habitat. Sensory receptors particularly visual and olfactory help to sense and response towards host plants in a certain locality. However, the physical factors of the host plants including color, size and shape also responsible for attraction of insects, for example; sucking insects including most of the aphids and whiteflies find their host based on color and are attracted mostly to yellow-green surfaces (Bottrell et al. 1998). Normally, color is due to physiological characteristics and cannot be a part of plant resistance. Red cultivars of cabbage, cotton and oat hold less attraction to insects and can be considered as a good agronomic trait. Some fruit flies, *Ragoletis* spp. locate their host based on shape and size. In these conditions, short range stimuli are responsible for insect's movement towards their host plants. These stimuli can either be of physical or chemical nature.

After finding the proper host, insects take a test bite from it. Some caterpillars take sample bite on the host and decide finally to adopt the plant as a host or not. In monophagous herbivores, for example the silkworm (*Bombyx mori* L.), a series of chemical compositions of their mulberry host help them to continue swallowing and feeding. Major physical factors, for example; leaf structure, plant toughness, pubescence type and densities are involved in acceptance or rejection of a host by a herbivore. These factors play a role in feeding and oviposition of an arthropod on selected hosts.

Finally, the availability of sufficient quantity of nutrients from a host plant prove it as an appropriate host plant. Availability of adequate food without any toxin and threat for the feeding insect, help them to complete their normal developmental period with full potential of longevity and fecundity.

3.2.2. Types of insect-plant interaction

Different ways are used to classify insect-plant interactions. According to Southwood (1973), there are three main categories of basic interaction; exchange of food, shelter and communication between the insect and plant. Gilbert (1979) identified seven different types of interactions based on ecological relationship (Table No. 1). However, litreature review in case of phytophagous insects, points three important classes of interactions:

1) Insects act as predators
2) Insects act as parasites
3) Insects act as mutualists with host plants

Sustainable pest management strategies generally deal with first two categories (predators and parasites) and rarely with the third category (mutualists).

3.2.2.1. Insects as predators and phytophagous

Insect feeding and predation on host plants depend upon various factors such as various life stages of insects feed on different plant parts and different plant stages. Usually, mortality rate of host plant increased because of attack on seeds. In some cases, insects can kill seedling (e.g., reproduction weevils) and mature trees (e.g., spruce budworms and bark beetles). Several groups of insects are present in the category of insect predators including defoliators, tip feeders, flower feeders, root feeders and stalk feeders (Peterson and Higley 2001).

3.2.2.2. Insects as Parasites

In this type of interaction, insects act as parasites on plants and the host is not killed by the parasites. Numerous insects fit into this category, for example; most sap sucking insects, some phloem-feeding insects, wood boring insects and gall forming insects (Peterson and Higley 2001).

3.2.2.3. Insects as mutualists

In this category, both partners are benefited without harming each other. e.g. pollination and predation. In insect pollination, plants obtain benefit through efficient transfer of pollen grains and the insect is benefited with its food (nectar). Predacious ants are attracted as results of secretion of extra floral nectararies of some plants that ultimately limit activity of other herbivores (Stephenson 1982). Production of honeydew because of feeding of aphids attract a wide variety of predacious Hymenoptera (Gilbert 1979).

3.3. Tritrophic relationship

Some insects are pests because they act as a disease vector and/or cause economic losses. These types of insect-plant interactions have occurred in nature for years ago with the presence of and coevolutionary arms race between these categories of real world. Entomologists are interested in insect-plant interactions with reference to sustainable production of agriculture crops. This approach involves the study of plant and herbivores communications in their related food chains. An important review is written by Price et al., (1980) which highlighted the significance of the third trophic level (natural enemies) along the first two trophic levels (plant and herbivore) in the studies of insect-plant interactions.

Price et al., (1980) highlighted the following elements:

1) Plants in the ecosystems are an important constituent of land communities which are collectively made of three interconnecting trophic levels (Begon et al. 1986)
2) Third trophic level is an important constituent of the theory of “Insect-Plant Interaction” and without considering it, no practical approach can be successful (Price et al. 1980)
3) Natural enemies as a third trophic level should be an ultimate part of natural plant defense complex (Poppy 1997)

3.3.1. Why study tritrophic systems

The ecosystem is a setup based on interaction of organisms belonging to the various trophic levels. These interactions control the physiological, ecological and behavioral features of collaborators. Due to these multiple responses between plants and herbivores, the behavioral and ecological scientists studied the multitrophic relationships between insect and plants. While multitrophic approach is currently dominated by tritrophic interactions. It is recognized that now-a-days, the fourth trophic level, enemies of natural enemies, is of great importance due to its influence on whole chain of tritrophic system.

3.3.2. Components of tritrophic interactions

Parasitoids and herbivore can affect each other through direct and indirect forces. For example; affecting host suitability are the indirect or negative effects; however, providing food and shelter and influence the source searching processes are direct or positive effects. The predatory effectiveness of any biocontrol agents can be influenced indirectly by plant mediated chemical and physical responses (Price 1981).

The major perspective of every constituent of trophic interaction is to maintain or increase its population and to find suitable host for its offspring can complete their dependent life span. The important factors in trophic interactions are host and its habitat, host acceptance by the next trophic levels, suitability of the selected host and its regulatory and nutritional requirements.

Usually, third trophic level particularly parasitoids use their visual and odour cues to search the proper habitats instead of the host habitat. The host/guest population dynamics is also influenced by the spatial distribution of host plant species in the habitat (Read et al. 1970).

Besides the host plants, other plants within the habitat may also offer food and shelter to the parasitoids; however, some parasitoids are only dependent on particularly plants for their food (Jervis and Kidd 1996) and try to depend on any plant as a host in certain locality (Powell 1986). The higher parasitoid population in an area may also be due to the availability of nectar and pollen. Parasitoid longevity, fecundity and mortality are increased by nectars and pollens produced by plants. For example; *Microplitis croceipes* C., a parasitoid prolonged its life span and parasitizing efficiency on larvae of *Helicoverpa zea* L. feeding on the nectaries of cotton plants compared to those larvae fed on nectarless cotton plant (Stapel et al. 1996). So, for the support of biological control, the habitat should be managed as an important tool (Powell 1986).

When parasitoids reached at their habitat, they still need to find their appropriate hosts just like herbivores (Sec. 3.2). They cannot find their proper host by random searching. Parasitoids use visual and particularly chemical cues to find their host location. These chemical cues are known as infochemicals, which regulate the message between the constituents of various trophic levels in certain environments. When parasitoids use these infochemicals to find their hosts, they face the "reliability-detectability problem" (Vet and Dicke 1992), however; these signals produced by the hosts are reliable but are not very easily detectable by the parasitoids (Turlings et al. 1993).

Vet and Dicke (1992) and Turlings et al. (1993) suggested three ways through which the problems of low detectibility of reliable cues can be diminished or overcome;

1) Chemical signals from various host stages should be practiced that are more discernible.

2) Go with easily detectable chemical cues among the signal complex.
3) Induced defense signals are more detectable over undamaged host plant cues.

Herbivore-induced plant volatiles (HIPV) are the substances released by the plants after the herbivore attack. They can easily be detected by noticing the wind direction. One of the examples of HIPVs is bean plants that induce response against aphid infestation (Du et al., 1996). Normally these induced volatiles are released from all leaves of the plant instead of only damaged leaves. Furthermore, the production of induced volatiles is dependent on amount of damage and aphid population, for example; in the case of bean plants, 40 aphids for 72 hours are required for a plant to induce parasitoid response (Guerrieri et al. 1996).

3.3.3. Chemical facilitated tritrophic interaction

In an ecosystem, all the living organisms are biochemically linked in a relationship which connects them in various food combinations. At least three trophic levels are present in a simplest connection of food chain. Each trophic level in this connectivity is evolved from the cost of higher energy level (Price et al. 1980). Furthermore, symbiotic relationship at each level of tritrophic interaction is present in every food chain. The biocontrol agents favor plants by reducing the herbivore populations and in return, plants favor them by making herbivores more vulnerable to them by altering the food chemistry of herbivores. Different factors are involved in such tritrophic interactions; the most important one is semiochemicals. These semiochemicals bring behavioral and physiological changes in the receiver (herbivores) and as a result the interaction are developed (Nordlund 1981). Moreover, these changes cause attraction, repulsion, arrest and detraction types of responses in herbivores (Ruther et al. 2002).

3.3.4. Types of semiochemicals

Semiochemicals are mainly divided into two classes, pheromones and allelochemicals. Pheromones are categorized as intraspecific semiochemicals, which mediate interactions between the organisms of same species, such as interaction between insects or between plants. These are further classified into different types based on their performance, for example; sex pheromones, alarm pheromones, aggregating pheromones etc. (Nordlund 1981). However, allelochemicals are interspecific semiochemicals, having great importance for communicating the organisms of different species and play a significant role in tritrophic interactions. These are further classified into allomones, kairomones and synomones. According to Ruther et al. (2002), allomones are the chemicals which are released and performed in favor of emitter, however; the chemicals that are favorable for both, the donor and the recipient are known as Synomones, whereas the chemicals released in favor of receiver only are known as kairomones.

According to Nordlund (1981), these categories of allelochemicals can be used interchangeably depending upon the receivers and emitters, including plants, herbivores and natural enemies. The terpenoids released by pine trees act as allomones for plant itself (Smith 1963) whereas same chemical cues are used by bark beetle for finding its food, hence may be considered kairomones for beetles and synomones for the predators of bark beetle which are being attracted using the same chemicals (Wood 1982). Furthermore, these semiochemicals can be categorized into plant produced and insect produced based on their sources.

3.3.4.1. Plant-based volatiles

Semiochemicals which are produced by plants act as intrinsic defense against herbivores. Although, third trophic level may also be affected by these chemicals which result in tritrophic interaction (Ahmad et al. 2004). The plant volatiles, food and floral scent are used as synomones by beneficial insects especially pollinators (Leius 1967; Pellmyr and Thien 1986). The predators locate their potential host, a herbivore, which is also feeding on the same plant with the help of these cues. Nectar is one of the major reasons to attract some parasites and predatory ants (Bentely 1977; Smiley 1978). Plant odors are also a significant feature in tritrophic relationships (Read et al. 1970; Vinson 1984). The coccinellid predator of pine aphid, *Anatis ocellata* L., used the odor of infected pine needles to locate its prey (Kesten 1969).

Mostly natural enemies are omnivores throughout their lives feed on herbivores during their immature stages and use plant nectars as food during adult stages (Hagen 1986). This feeding division of natural enemies is advantageous for plants as well as for themselves (Hespenheide 1985). However, the efficiency of natural enemies to find their hosts at any life stage depends upon the quality of food and cues offered by host plants and preys (Sundby, 1967; Foster and Ruesink 1984). The Mustard aphid, *Brevicoryne brassicae* L. and its parasitoid *Diaeretiella rapae* M. is a known example of tritrophic interaction mediated by compound, sinigrin released by mustard plant (Read et al. 1970).

Therefore, quality of the interaction is affected by the physical factor of the emitter, such as size, vigor, growth and survival rate of the hosts (Ahmad et al. 2004). In case of plants, secondary metabolites are responsible for deterrent effects on insect pests and in result increase the efficacy of natural enemies of that particular herbivore. *Aphytis melinus* D., a predator of Californian red scales, *Aonidiella aurantii* M., can utilize host of about 0.39 mm^2 and larger, while *Aphytis linginanenis* D. can feed the prey size of 0.55 mm^2 and larger (Luck and Podoler 1985).

3.3.4.2. Herbivore-based volatiles

Herbivores are the main component of tritrophic interaction that links the upper and lower level in a chain. Hence, in case of tri/multitrphic interaction, herbivores face the intrinsic and extrinsic defenses by plants and their natural enemies at the same time. Therefore, plants release the secondary chemicals that are not only used in plant defense against herbivore but also enable predators and parasitoids to search their prey. The chemicals produced by Lycaenid butterfly larvae and aphids that intimate an association between herbivore and predator also act as synomones for predatory ants to protect the herbivores from natural enemies, so a mutualistic interaction is developed between ants and the aphids (Way 1963; Atsatt 1981; Pierce and Mead 1981).

Volatiles (kairomones) are produced by plant feeders and are perceived by natural enemies. These cues may be in form of body smell or order to become a source of attraction for the biocontrol agents particularly parasitoids (Loke and Ashley 1984; Noldus and van Lentern 1985). These kairomones may also be released in form of sex pheromones (Sternlicht 1973; Kennedy 1984), aggregation pheromones (Wood 1982), excretory products (Lewis and Jons 1971; Nordlund and Lewis 1985), body scales (Loke and Ashley 1984) and eggs (Jones et al. 1973). One of the significant examples of body odour detection is found in bee wolf, *Philanthus triangulum* F., a predatory wasp that detect the bees through their body smell and is an example of foraging pheromones (Longhurst and Howse 1978; Howse 1984; Ruther et al. 2002).

Furthermore, allomones an important constituent of tritrophic interaction work against either plants or natural enemies and in favor of insect herbivores. Several compounds can be derived from herbivores that to utilize as allomones.

3.3.4.3. Predator-based volatiles

Chemical compounds released by natural enemies cannot be ignored in these interactions of plant and insects as these volatiles play a vital role in altering the plant physiology according to the requirement. For example, *Piper cenocladum* (family: Piperaceae) responds to synomones released by third trophic level (predators) and perceives the presence of obligatory ants, *Pheidole bicorins* F. then produces food bodies (Risch and Rickson 1981).

Natural enemies also produce some kairomones and allomones (Ruther 2002). When these kairomones are detected by herbivores, they run away from the source to avoid their enemies (Dicke and Grostal, 2001). Large number of predatory hymenopterans like ants, wasps and bees respond to kairomone, formicid, to avoid predatory ants in dry-land ecosystem (Chadab 1979). In the same way, some chemicals perform the function of allomones and are used by the predators to mimic the body of their preys (Vander Meer and Wojcik 1982).

3.3.5. Phenomena of plant-mediated interactions between insect herbivores

3.3.5.1. Induced resistance

Herbivores feed on host plants and thus plants produce allelochemicals to resist their feeding (Karban and Baldwin 1997; Constabel 1999). These allelochemicals are defensive in function and include phenolics, terpenoids, alkaloids and glucosinolates (Karban and Baldwin, 1997; Constabel, 1999).

Moreover, herbivores colonization at early stages of plants can induce changes in plant morphology such as leaf structure, trichomes, bud formation and branching structure (Karban and Baldwin 1997). These herbivores induced structural changes in host plant after insect feeding may have positive or negative effects on the subsequent feeders. For example, trichomes in leaf (Agrawal 1998, 1999; Traw and Dawson 2002) and variation in floral patterns and size (Strauss 1997) produce adverse effects on subsequent feeding insects. So, these morphological alterations in plant structure can be further utilized for discouraging the herbivore feeding on the specific host plants.

The herbivore feeding on plants also mediate the nutritional imbalance in the food source for plants and cause the malnutritioning for herbivores. In return, herbivores stop feeding on these plants. Moreover, their initial feeding on host plant stimulates plant defensive system that ultimately attracts the natural enemies at the specific site and location (Vinson 1998; Pare et al. 1999).

3.3.5.2. Induced susceptibility

In this phenomenon, host plant chemicals repel one type of herbivore, while attract other. For example, *Pieris rapae* L. larvae induce glucosinolates and some other volatiles while feeding on wild reddish that are used by the monophagous flea beetle, *Phyllotreta* sp. to locate its host (Agrawal and Sherriffs 2001). In the same way, changing plant structure after herbivore feeding can also help to attract the other herbivores for food and shelter (Ohgushi 2005).

Therefore, induced changes after herbivore feeding can be utilized to repel the one kind of herbivores and attract the any other specialist herbivore on the same host plants.

3.4. Host-plant resistance

3.4.1. Resistance mechanism to insects

The resistance is either a constitutive or an induced mechanism (Painter 1951; Karban et al. 1997; Karban and Agrawal 2002; Traw and Dawson 2002). Generally, based on physiological function, the resistance in insects can be classified into three major categories that are antixenosis (nonpreference), antibiosis and tolerance (Painter 1951).

3.4.1.1. Antixenosis

Antixenotic mechanism of resistance is employed by the host plants that deter the insects from oviposition (Painter 1951; Valencia 1984; Karban et al. 1997; Afzal et al. 2009), feeding, seeking shelter (Dabrowski and Kidiavai 1983; Woodhead and Taneja 1987; Sharma and Nwanze 1997) and establishment (Dhaliwal and Arora 2003). This mechanism makes the plants undesirable or likely not to be the hosts for insect invasions (Bazzaz et al. 1987; Dhaliwal and Arora 2003). Antixenotic characteristics develop in a plant due to certain morphological characters, allelochemicals (Kogan 1982; Rhoades 1983; Edelstein 1986; Edelstein and Rausher 1989; Adler and Karban 1994; Morris and Dwyer 1997; Thaler 1999; Afzal et al. 2009) or interactions between these factors (Panda and Khush 1995). These features result in one or more breaks in the continuous responses of insect oviposition and feeding (Panda and Khush 1995; Dhaliwal and Arora 2003). Following are types of no preference found in litreature:

Allelochemical nonpreference

This is a much-known phenomenon among plants and sometimes makes them non-preferred by herbivores. Some examples include spotted cucumber beetle, *Diabrotica undecimpunctata howardi* M., and other *Disbrotica* species found on cucurbits show allelochemic nonpreference. In this type of insect plant relationship, cucurbits release a chemical, cucurbitacins which acts as attractant and feeding initiating for few coleopterans. In this way, only few beetles are attracted and plants receive low level of damage compared to the plants with more feeding by beetles on them which lack or less levels of specific cucurbitacins (Pedigo and Rice 2009).

Morphological nonpreference

The morphological nonpreference occurs because of plant features and structures that cause disturbance and interruption in the normal behavior of insect feeders. For example; *Helicoverpa zea* L. (corn earworm), prefers pubescent surfaces for oviposition. Furthermore, litreature shows that cotton varieties with no hairs are suffering less damage by many insect species because of lower rates of oviposition compared to those varieties having hairs on the leaves and other plant parts (Pedigo and Rice 2009).

Some other examples of morphological nonpreference are; husk tightness in corn, stem density and node tissues in wheat and woody stem in cucurbits that help to reduce injury by corn ear worms in maize, by wheat stem sawfly (*Cephus cinctus* N.) in wheat and by squash vine borer, *Melittia cucurbitae* H. in cucurbits respectively (Pedigo and Rice 2009).

3.4.1.2. Antibiosis

Antibiosis occurs when the physiochemical qualities of the plants cause decrease in life history such as survival, egg laying capacity reproduction and developmental rates of the arthropods. Heavy pubescence, increased cuticle thickness and sticky masses on various plant structures that slow down the feeding and continuous growth of the arthropod are some of the physical reasons of antibiosis. Presence of secondary compounds such as allelochemicals or lack of nutrients needed by the arthropod, such as essential amino acids etc. is some physiological antibiotic reasons in plants (Painter 1951).

Normally, allelochemicals and antibiosis are interconnected. The cyclic hydroxamic acids in corn (DIMBOA, 2, 4-dihydroxy-7-methoxy-1, 3-benzoxazin-3-one), gossypol compounds in cotton, steroidal glycosides in potato, and saponins in alfalfa are few important examples of antibiotic compounds examples in various plant species (Pedigo and Rice 2009).

Primary metabolites, their quality and quantity play very important and significant role in determining the antibiosis in any plants. Most importantly, sugar and amino acids imbalance cause malnutrition in insects feeding on that particular plant. For example, resistance is observed in pea cultivars due to low amino acid levels and higher sugar contents against the pea aphid, *Acyrthosiphon pisum* H. Reduced reproductive and egg laying capacities is observed in the brown planthopper, *Nilaparvata lugens* against the rice cultivars with low asparagines (an amino acid) (Pedigo and Rice 2009).

3.4.1.3. Tolerance

Tolerance is defined in numerous ways and researchers have argued whether it is truly a part of host plant resistance, because no deleterious effects have been produced in the insects. Painter (1951) categorized the resistance mechanisms as tolerance, antibiosis and nonpreference (now antixenosis) for the first time (Kogan and Ortman 1978). He defined tolerance as "a basis of resistance in which the plant shows an ability to grow and reproduce itself or repair injury to a marked degree despite supporting a population approximately equal to that damaging a susceptible host" (Painter 1951).

In case of tolerance, the level of feeding or damage by sucking and chewing insects, do not cause any expression but it is a response of plant to a given level of damage. Rapid foliage growth in Lucerne (*Medicago sativa*) after the attack of alfalfa weevil (Dogoer and Hansonc 1963) and speedy tiller production in sorghum followed by the attack of sorghum shoot fly (Doggett et al. 1970) are the examples of tolerance, like the development of secondary and thick roots in maize (*Zea mais*) followed by the damage of corn root worm (Owens et al. 1974).

Tolerance is basically the effect of insect on plant (the less damage means the higher level of tolerance). As the recovery after insect injury is also a *plant* response, that is why it is a part of tolerance. However, recovery from injury has been investigated very little. A rare exception is the work of Morgan et al. (1980). Tolerance should be more useful in a pest management program than antibiosis or antixenosis because of compatibility with other control strategies and biotype considerations.

3.4.2. Genetic basis of resistance

3.4.2.1. Epidemiological types of resistance

A lot of work of plant pathologists on this classification of resistant types has been done to express its the effectiveness and stability against a pest population. Plants genes are used to determine the effectiveness and stability of different resistant varieties. Resistance and the insect genes which allow the resistance to be overcome are conferring by these plant genes (Pedigo and Rice 2009).

The gene-for-gene relationship

Several pest populations include those individuals which have virulent genes that allow a pest species to overcome resistance and further attack a plant. Effect of one or more plant genes responsible for resistance overcome with the order of an individual that has one or more virulent genes. This principle has been called the gene-for-gene relationship (Pedigo and Rice 2009).

In this type of relationship, plant cultivars are resistant because resistant alleles are present at gene locus responsible for avirulence (susceptible) at a specific locus in the insects. Even the resistant cultivar is effective against several insects present in the population. Pedigo and Rice (2009) explained that avirulent allele is absent in an insect, it has only virulent allele. For example; host plants having resistant genes may code for a protein toxic to the insect, and insect having a respective virulent gene may code for an enzyme which are used to detoxifies that specific toxin present in the plant. By this situation, virulent individuals attack the other resistant plant and avirulent genotype can be replaced by virulent genotype for a long-time period. The effectiveness of the resistant cultivar ultimately would minimize (Pedigo and Rice 2009).

Different populations of an insect species which differ in their virulence to the cultivar are known as Biotype. The Hessian fly, *Mayetiola destructor* S. has several biotypes. The term biotype is often used for certain insect populations that overcome plant resistance (Pedigo and Rice 2009).

To date, most insect biotypes have developed in aphid. Spotted alfalfa aphid, *Therioaphis maculate* B. on alfalfa; corn leaf aphid, *Rhopalosiphum maidis* F. on sorghum and corn; greenbug, *Schizaphis graminum* R. on wheat and sorghum and pea aphid, *Acyrthosiphon pisum* H. on peas and alfalfa are the well-known examples (Pedigo and Rice 2009).

3.4.2.2. Vertical and horizontal resistance

Van der Plank (1963) recognized two types of resistance based on effectiveness of a resistance i.e. vertical and horizontal resistance. Vertical resistance refers to the cultivars having resistance limited to one or a few pest genotypes. Horizontal resistance refers to those cultivars that express resistance against a wild range of genotypes.

Some authorities have debated against vertical resistance in breeding programs because of the potential development of biotypes. But in case of Hessian fly on wheat, this type of resistance is successful and is simplest to incorporate into new varieties compared to horizontal resistance. It has been suggested in case of managing insects by using vertical resistance, identification of resistant genes in plants is necessary and may be incorporated into varieties and then released when biotypes appear (Pedigo and Rice 2009).

Horizontal resistance has low heritability and has many difficulties in incorporation for plant breeders. However, some success stories of horizontal resistance are observed such as cultivars of corn with high resistance to both generations of the European corn borer, *Ostrinia nubilalis* H. Moreover, due to stability of horizontal resistance, it is the most desirable type of resistance which is used in management of pests (Pedigo and Rice 2009).

3.4.3. Resistance classes on inheritance

Plant resistance can also be distinguished based on mode by which it is inherited. Three major categories of resistance are recognized by Day (1972) which are; oligogenic resistance, polygenic resistance and cytoplasmic resistance.

3.4.3.1. Oligogenic resistance

This type of resistance is also known as "major-gene resistance" and carried by one or more genes. Vertical resistance is produced by this type against insects and may be inherited through dominant or recessive genes. Single-gene dominant resistance has been incorporated into varieties of different crops such as cotton, apple, rye, raspberry, sweet clover and rice. Single-gene recessive resistance can be found in corn lines which are resistant to the Western corn rootworm and wheat resistant to the greenbug. Another example of oligogenic resistance is wheat resistantance to the Hessian fly, nevertheless, resistance is conferred by a series of dominant or partially dominant genes, as well as by numerous recessive genes. Resistance is often considered oligogenic in this example because a well-understood gene-for-gene relationship exists between resistance genes in wheat and the corresponding virulence genes in the Hessian fly (Pedigo and Rice 2009).

3.4.3.2. Polygenic resistance

This type of resistance conferred by many genes and each have the resistance effect. For this reason, this is also known as "minor-gene resistance". Resistance inherited through the polygenic mode is usually very complex and may be associated with such quantitative traits as plant vigor and yield. Horizontal resistance is usually polygenic. An example of polygenic resistance, as already mentioned, occurs in corn varieties resistant to the European corn borer (Pedigo and Ricw 2009).

3.4.3.3. Cytoplasmic resistance

This type of resistance is conferred by mutable substance (capable or liable to mutation) substances in cell cytoplasm. Cytoplasmic inheritance is maternal because most cytoplasm of the zygote comes from the ovum. Although cytoplasmic inheritance is very important in resistance to pathogenic microorganisms, it has not been a factor in resistance to insects (Pedigo and Rice 2009).

3.5. Case study

In studying plant-insect-interaction, the Hessian fly, *Mayetiola destructor* S. offers the best example of several aspects of insects and plants and co-evolution. This insect illustrates the classical example of genetic variation both in the insect and the plant. For example, wheat is known for having resistant genes against this insect. However, it was not until the genetic components of resistance in the plant and virulence genes in the insect were identified that the first clear evidence for the gene-for gene relationship was described. Gallun (1977) was the first to show that the relationship that Flor (1942) identified for a pathogen in flax was true for an insect in wheat. Most genes for resistance to the Hessian fly are major genes, also referenced as antibiosis genes also known as vertical genes. These resistance genes provide the basis for strong selection advantage for those insects with low frequency of virulence genes. After several generations, there is a shift in local populations to point that insects with the virulence genes are predominant. In lay terms, the insect population has now overcome the resistance genes in the wheat plant. Hence, the value of the resistance in the plant is minimized and the breeders must release new resistance genes in the plant that can withstand the local populations of the insect in "niches" or fields. Resistance in the plant is controlled by a dominant gene; however, avirulence in the insect is controlled by a recessive allele in the fly, hence virulence in the insect confers susceptibility in the plant. This is the classical gene-for-gene relationship in plant insect interaction.

The expression of resistance in host plants has been affected by both biotic and abiotic factors. In soybeans, plant resistance has been shown to be both constitutive and inducible. For example, insect abrasion or injury by any mechanical means may induce resistance in many crop plants (Smith 1989). Such as, induced resistance in soybeans, *Glycine max* has been documented (Kogan and Fisher 1991). Mechanical damage to soybean foliage also causes to induce the resistance against the soybean looper. Wound induced resistance in soybean has been shown to retard the development and growth of both the Mexican bean beetle and soybean looper as well. The induced resistance has been shown to be correlated with raised levels of several plant natural products.

3.6. Conclusion

The complexity of Plant-Insect-Interaction makes it difficult to concise a single chapter. The main relationships between insects and plants from Paleozoic to present times are discussed. Arthropods, more specifically insects make up the major portion of plant feeders. The concept of coevolution was first raised by Ehrlich and Raven (1964). Some authors express that this may be a pre-adaptation by plants.

Plants, mostly green plants, are the major source of energy for most food chains. In phytophagous species, it is difficult to find most advantageous form, monophagy or polyphagy. It is true that polyphagous species have a much greater choice of host plants. True phytophagous insects account for about 50% of the living insects. Toxic plants transmit their toxicity to insects and protect them indirectly. However, that toxicity of plants is not always responsible for toxicity of insects to their predators. Host plant selection in insects is dependent on many factors like visual, olffactive, gustative and chemical reasons. Additionally, the quality of the plant, life stage and rapidity of the development and vigor of the insect also effect the host plant selection.

Clearly, food selection has a strong influence on a species. Selection is often the function of existing pre-adaptation to a given diet (host). Regarding choices, polyphagous species have more chances to evolve quickly than monophagous species. However, this is not a hard-fast rule as illustrated by biotypes of insects on resistant crops cultivars where coevolution has been amply demonstrated numerous times and where we frequently have referred to the gene-for-gene in the insect and the plant. This concept has gone under some strong critiques and now the prevalent thinking is that this co-evolution is more complex than was earlier thought. During the evolution of a crop plant and the host insects, equilibrium exist at some time between the plant and insect, if both were to survive. This co-evolution must have occurred between the plant and the insect as the host plants accumulated genes for resistance and the insects accumulated genes for virulence.

The chemical cues produced by the plants and intercepted by the insects can be utilized in generating the phenomenon of pest management in a specific site. The artificial synthesis of these compounds or manipulation of naturally produced chemicals can play a dynamic role in this field of sustainability of pest management. Keeping in view the interactions among the trophic levels discussed in various sections of the chapter, the proper utilization of these interactions and associations in this domain can be whole success with reduced use of risk carrying chemical control methods.

Table 1 Categories of Insect-Plant Interactions

Insects	Plants
Predators, parasitoids	Prey
Parasites	Host
Pollinators, seed dispersal agents	Provide a reward
Allelopathic agents, antiherbivore defense force	Provide a reward and a certificate of residence
Nutrient gatherers	Certificate of residence
Host	Parasites
Prey	Predators

Source: Gilbert (1979)

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