1 Insect-Plant Interrelationships

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Abstract

The green plants and insects represent the two dominant groups of living organisms on Earth. The green plants occupy the most capacious segment among all biological organisms, whereas the insects are the most specious group. These two ‘empires’ are interconnected as well as interdependent. Green plants are the primary producers of food, and all animals being heterotrophs depend directly or indirectly on plant-produced food. In turn, nearly three fourths of all angiosperms require the services of insect pollinators. The entomophilic flowering plants and their insect pollinators thus represent the most evident and widely applicable example of mutualism among living organisms. But a wide variety of phytophagous insects also flourishes, diversifies and sustains on these plants. Consequently, the plants have evolved a dizzying array of morphological and biochemical (constitutive as well as induced) barriers for protection against insects and other herbivores. Evolutionary interactions between plants and insects may have contributed to the increased biodiversity and success of both these groups. The study of these interrelationships, as outlined in this chapter, is of great practical significance for the future agricultural production. The development of pest-resistant cultivars of crop plants and progress in integrated pest management both require an intricate understanding of insect-plant relationships.

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State-of-the-art techniques such as mutant analysis, metabolomics, RNAi and proteomics developed during the last three decades have been instrumental in providing improved insight into these interrelationships.

Keywords
Coevolution • Pollinators • Insect pests • Flowering plants • Mutualism • Plant defences

1.1 Introduction

The ‘plant kingdom’ and the ‘class Insecta’ represent the two dominant groups of living organisms, in terms of the abundance of species as well as in the amount of biomass. Green plants are the primary producers of food, and all animals being heterotrophs depend directly or indirectly on plant-produced food (Schoonhoven et al. 2005). In turn, a majority of the 300,000 plant species require the services of insect pollinators for reproduction. Colourful, scented flowers and floral nectarines were in all probability developed by plants for attracting insect pollinators. Flower anatomy ensured that while feeding, the insects also picked up the pollen (Kearns et al. 1998). Consequently, to prevent over-exploitation, the plants have also evolved a dizzying array of structural and biochemical barriers for protection against insects and other herbivores. While some of these barriers are synthesized by plants regardless of the presence of herbivores (constitutive defences), many others are produced only in response to herbivory (induced defences). Only those insect species, which are able to overcome these barriers in one or more plant species by avoidance, detoxification, etc., can access that plant species as food. The insects which damage the economically important plants have been termed as ‘insect pests’ by humans. The important mutualistic and antagonistic interactions between plants and insects are introduced hereunder.

1.2 Mutualistic Interactions: Flowering Plants-Insect Pollinators

The most evident and widely applicable example of mutualism is that between insect-pollinated flowering plants and their insect pollinators. Nearly 80% of all flowering plants are bisexual and bear flowers with stamen and pistils in the same flower. This promotes self-fertilization and consequently inbreeding. The plants avoid self-fertilization either by separating the sexes in time and space (differences in the timing of maturation) or by self-incompatibility. Both mechanisms promote cross-pollination, which is assisted by various agencies e.g. wind, water, and animals, etc. More than three fourths of all flowering plants are wholly or partially insect-pollinated (Faegri and Pijl 1971). The economic value of insect pollinators is enormous. Most of the important oilseeds, pulses, fruits, vegetables, nuts, spices and ornamentals (Hill 1997; Atwal 2000) show improved yields with animal pollination (Klein et al. 2007). It has been estimated that animal pollination has an economic value of €153 billion annually, which is nearly one tenth of global agricultural production (Galai et al. 2009).

Some of the widely accepted estimates of the number of angiosperms pollinated by animals vary from 67% to 96% of all angiosperm species (Axelrod 1960; Nabhan and Buchmann 1997). Ollerton et al. (2011) observed that these estimates are not based on firm data. They compiled data on published and unpublished community level surveys of plant-pollinator interactions and concluded that proportion of animal-pollinated species was 78% in temperate-zone communities and 94% in tropical communities, with a global mean of 87.5% of all flowering plants. The pollinators benefit from rewards in the form of nectar and pollen. Both are nutrient-rich foods with nectar containing 50% sugars and pollen 15–60% proteins and other essential elements (Proctor et al. 1996; Roulston et al. 2000). Together, they provide nourishment for the bees, which are the most important among insect pollinators (Schoonhoven et al. 2005).

The entomophilous flowering plants and the pollinating insects constitute an example par excellence of mutualism. However, the degree of mutualism varies among various plant-pollinator combinations (Schoonhoven et al. 2005). In some cases, there is obligate mutualism, and a species of plant can only be pollinated by a single species of pollinator, which depends on it for food. For instance, figs (*Ficus* spp., Moraceae) are dependent upon fig wasps (Agaonidae, Chalcidoidea) for pollination (Wiebes 1979). Every species of fig is pollinated by a specific wasp species, e.g. the pollination in *Ficus carica* Linnaeus is carried out by the fig wasp, *Blastophaga psenes* (Linnaeus) (Ramirez 1970). Another example of obligate mutualism is observed between yucca moths (Prodoxidae) and yucca plants (Agavaceae). The yucca moths are the sole pollinators for yucca flowers and deposit their eggs in the locule of the ovary of flowers so that the young caterpillars can feed on the developing seeds (Pellmyr and Krenn 2002).

Another interesting example is based on the great naturalist Charles Darwin's prediction. In 1862, while doing research on orchids, Darwin found that the astounding Christmas orchid, *Angraecum sesquipedale* Thouars, had nearly a foot-long green nectary. As this group of orchids was moth pollinated, Darwin predicted that there must be a gigantic moth species with extended proboscis capable of feeding on the long nectary. More than four decades later, Rothshild and Jordan in 1903 described the Morgan's sphinx moth, *Xanthopan morganii* Walker with an extended proboscis length of >12 in., as the only known pollinator of *A. sesquipedale*, which is endemic to Madagascar (Kritsky 2001). However, such reciprocal evolution in plant-pollinator relationships is not widespread. Burkle and Alarcon (2011) observed that most plant-pollinator relationships have a fairly broad range with a high degree of annual turnover of pollinator species, and the relative importance of a pollinator species may vary in different years for pollination of the same plant species.

Insect pollination has undoubtedly contributed to the evolutionary success of angiosperms. The fossil records show that pollination originated around 250 Myr ago (Labandeira 2013). The early angiosperms were probably pollenized both by the wind and animals. In view of the advantages conferred by entomophily, its importance increased over evolutionary time (Cox 1991; Crepet et al. 1991). Entomophilic angiosperms display a diversity of flower size, shape, colour and fragrance which may have been determined by the requirements of the pollinators. The pollen in flowers of such plants may have a sculptured structure and/or is covered with sticky substances which help it to easily adhere to the insect body. The hairs on the insect legs and other body parts also aid in pollen transfer. The bumble bee pollinated flowers in foxglove, *Digitalis purpurea* Linnaeus are bell shaped, while the butterfly pollinated flowers of *Calopheria* spp. have tubular corolla, which is an adaptation to the long probocis (Schoonhoven et al. 2005). In addition, the latter contain higher levels of amino acids than flowers fed on by flies (Baker and Baker 1986). In order to attract pollinators, some plant species produce sterile ‘reward anthers’ which are brightly coloured (Nepi et al. 2003). Flowers of the orchid Mirror of Venus, *Ophrys speculum* Link, imitate the virgin female wasps of their pollinator, *Dasyscolia ciliata* (Fabricius), by releasing the female sex pheromone to entice the male wasps. The attracted male wasps try to mate with the flowers and in doing so act as pollination vectors (Ayasse et al. 2003).

Hymenopterans, especially the Apoidea, are the most important group involved in flower pollination at present, but other groups have been equally important in the past. Basal angiosperms are even now primarily pollenized by the beetles and flies (Thien et al. 2000). Bees are closely adapted to a floral diet (Atwal 2000) and are able to assimilate pollen grains despite the presence of an almost impermeable cuticle (Velthius 1992). Individual honeybees often exhibit flower constancy by preferably visiting flowers of a single species. It improves pollinator efficiency and also helps in reproductive isolation of plant species. The insects’ ability to remember combinations of flower odours and colours plays a central role in flower constancy. Honeybees have been reported to have the capacity to distinguish at least 700 different floral aromas (Schoonhoven et al. 2005).

1.3 Antagonistic Interactions: Herbivorous Insects-Green Plants

Insects are the most diverse and a tremendously successful group of organisms on Earth. The members of a number of insect orders infest plants and obtain food from them. Species in some of the insect orders are almost exclusively (Lepidoptera, Orthoptera, Phasmida) or predominantly (Hemiptera, Thysanoptera) herbivorous. But Coleoptera, Hymenoptera and Diptera are only partly herbivorous and also include numerous carnivorous species (Schoonhoven et al. 2005). Every vascular plant species usually harbours several insect species. There are insect species feeding on all parts of the plant including the roots, stem, bark, shoots, leaves, flowers and fruits. While solid feeders chew plant tissues externally (defoliators) or internally (borers), others suck the sap (aphids, jassids), reduce plant vigour and even act as vectors of plant pathogens, e.g. whitefly.

Most insects usually exhibit a high degree of specialization in their choice of food plants. The monophagous insects feed on only a single or a few closely related species of plants, while oligophagous ones feed on a number of plant species, all of which belong to the same family. In contrast, the polyphagous insects use a wide range of plants from different plant families as food (Panda and Khush 1995). But most insects exhibit some degree of specialization in their host plant choice. Investigation on herbivorous insects has revealed that only around one tenth of these insects have the ability to feed on plants of more than three plant families. The host range of each insect species is constrained by several structural, biochemical and ecological factors. As a generalization, it may be stated that, except for Orthoptera, all other orders of herbivorous insects are largely composed of species specialized to feed on particular plant species (Schoonhoven et al. 2005). According to Bruce (2015), the herbivores have evolved over time to become specialized feeders, even though some of polyphages continue to be important agricultural pests. Insects have the ability to recognize and respond to host cues for feeding and oviposition.

Despite the antagonistic relationships between plants and phytophagous insects presumed to operate in all cases, herbivory has been observed to increase plant growth and fitness in some cases (Owen 1980; Vail 1994; Sadras and Felton 2010). Yield decreases due to arthropod feeding are quite common, but there are examples of increased yield recorded in insect-damaged as compared to undamaged plants (Harris 1974). The compensatory responses to herbivore damage may in some cases more than offset the damage caused. It basically depends on how plants respond to attack by insects or other herbivores.

1.3.1 Plant Defences Against Herbivores

Plants are immobile organisms and have to defend themselves against insects and other herbivores. Most plants in natural ecosystems show little or no obvious damage in spite of the presence of wide variety of phytophagous insects in large numbers. Complete defoliation by phytophagous insects is an exception rather than a rule. It has been estimated that on an average, insects consume only around 10% of all annually produced plant biomass (Barbosa and Schulz 1987). This is primarily due to the fact that plants have evolved a diverse range of structural and biochemical characteristics to protect themselves from herbivores. In contrast, insect pest's damage is usually higher in agroecosystem as many of these characteristics have been lost while breeding plants more palatable to human taste and/or outyielding the traditional plant genotypes. There is a need to study these plant defences to exploit them optimally in commercial agriculture.

1.3.1.1 Structural Defences

1.3.1.1.1 Surface Wax Layer(s)

Surface waxes over the epicuticle protect the plant against desiccation, herbivore feeding and pathogen invasion. Wax layers are variable in thickness and structure, and their amount may reach up to several percent of the dry weight of a plant. Wax crystals often act as structural barriers to insect feeding (Jeffree 1986). Further, the mechano- and chemoreceptors on the insect tarsi and mouth parts receive negative tactile and chemical stimuli from the plant surface covered with a wax layer. For instance, leaf epicuticular wax in Brassicaceae results in non-preference for feeding by the flea beetle, *Phyllotreta cruciferae* (Goeze) in (Bodnaryk 1992).

But wax layer may also have the opposite effect by favouring some insects. In several instances, plants with glossy leaf surfaces (reduced wax layer) have also been shown to be less susceptible to insect pests (Eigenbrode and Espelie 1995). As an indirect effect, wax crystals and wax blooms may also impair the adhesion, mobility and effectiveness of predatory insects resulting in an increase of herbivore populations (Eigenbrode et al. 1999).

1.3.1.1.2 Trichomes

The epidermal surface in plant is usually covered with hair-like structures, which are variable in shape, size, location and function (Werker 2000). The hairs present on the aerial parts of a plant are commonly referred to as trichomes, while the term pubescence refers to the collective trichome cover of a plant surface. The trichomes range in size from a few microns to several centimetres, and the shape varies greatly in different species. The trichomes are of two types: non-glandular and glandular (Payne 1978). Non-glandular trichomes may act as physical barriers against the movements of insects over the plant surface or prevent the herbivores' mouth parts from accessing the feeding tissues of the plant (Ram et al. 2004). Glandular trichomes are specialized to secrete a variety of chemicals (Fahn 2000), which act as important chemical barriers against pests and pathogens (Glas et al. 2012). Hooked trichomes of black bean, *Phaseolus vulgaris* Linnaeus, were found to impale the aphid, *Aphis craccivora* Koch (Johanson 1953), and the leafhopper, *Empoasca fabae* (Harris), leading to wounding and death (Pillemer and Tingey 1978). Interestingly, in some cases, trichome density has been observed to be induced in response to insect feeding. Feeding by the cabbage-white butterfly, *Pieris rapae* (Linnaeus), and the cabbage looper, *Trichoplusia ni* (Hubner), on young black mustard, *Brassica nigra* (Linnaeus) W. D. J. Koch, plants resulted in increased trichome density on newly expanded leaves (Traw and Dawson 2002). Some insect pests have also been reported to have developed morphological or biochemical adaptations to neutralize the effect of trichomes. Trichomes may also have indirect effects on plant resistance by limiting the searching capacity of natural enemies of herbivores. The parasitic wasp, *Encarsia formosa* Gahan, is considerably more efficient in finding its host – whitefly nymphs – on glabrous cultivars than on hairy leaves (van Lenteren et al. 1995).

1.3.1.1.3 Plant Toughness

Coley (1983) observed that leaf toughness was the best predictor of interspecific variation in herbivory rates, in a lowland tropical forest. Plant cell walls strengthened by deposition of macromolecules such as cellulose, lignin, suberin and callose together with sclerenchymatous fibres make a plant resistant to penetration by mouth parts (piercing sucking) and ovipositors (adult females) of insects as well as tearing action of mandibles of chewing insects. In wheat, solid-stemmed cultivars were resistant to stem sawfly, *Cephus cinctus* Norton (Platt and Farstad 1946). In sugarcane, rind hardness was an important factor in reducing internode borer *Diatraea saccharalis* (Fabricius) damage (Martin et al. 1975). Seed damage due to the seed chalcid *Bruchophagus roddi* (Gussakovsky) in alfalfa was less in genotypes with highly lignified pod walls (Springer et al. 1990).

1.3.1.1.4 Plant Architecture

The suitability of a plant to serve as a host for phytophagous insects may vary with plant size and architecture. Plant characteristics such as canopy spacing; stem, leaf and bud shapes and dimensions; and branching angles may affect insect preferences and survival. The increasing size and architectural complexity of plants from monocots through herbs, to bushes and trees, is correlated with an increase in the diversity of the associated insect fauna (Lawton 1983). Indirect effects of plant architecture on herbivores are also mediated through their influence on the natural enemies. In cotton, okra-leaved cultivars suffer less damage by a number of insect pests including bollworms, whitefly and boll weevil as compared to normal-leaved cultivars (Ram et al. 2004). In soybean, cultivars with smaller cotyledons and unifoliate leaves were resistant to the legume seedling fly, *Ophiomyia phaseoli* (Tryon), and these are the parts where the insect lays eggs (Talekar and Tengkano 1993).

1.3.1.2 Biochemical Defences

Plants have evolved a plethora of chemical structures to prevent colonization by insects and other herbivores. While a limited number of chemicals are involved in primary metabolism, many other compounds have been found to repel, deter, kill or prevent insects and other herbivores from utilizing these plants as food sources (Chapman 1974; Harborne 1993; Mithofer and Boland 2012). As phytophagous insects have developed the ability to exploit their hosts, the plants have responded by evolving defensive biochemicals to counteract herbivore attack (Johnson 2011). The chemicals produced by plants, thus, fall into two broad categories: nutrients and allelochemicals.

1.3.1.2.1 Nutrients

The suitability of a plant as a host for one or more insect species is dependent on its ability to supply holistic nutrients for development and multiplication of these insects. From an insect's perspective, the plants usually supply a mixture of nutrients at suboptimal concentrations, which are combined with indigestible structural compounds, such as cellulose and lignin, and a variety of allelochemicals (Schoonhoven et al. 2005). The latter may exert a wide range of behavioural, physiological and growth-inhibiting effects, some of which may even lead to insect mortality.

Most insects have qualitatively similar nutritional requirements, consisting of carbohydrates, amino acids, fatty acids, sterols and a number of micronutrients. Host plants are often nutritionally suboptimal per se. The main groups of primary plant metabolites – amino acids, carbohydrates and lipids involved in fundamental plant physiological processes – serve as essential nutrients for herbivores. Therefore, changes in primary plant metabolites and nutrients greatly affect the survival and multiplication of phytophagous insects (Berenbaum 1995).

Nitrogen is especially important as insects are unable to exploit inorganic nitrogen, and organic nitrogen content of plants is suboptimal for the insects (Schoonhoven et al. 2005). This may constitute a major barrier to successful exploitation of plants by a majority of insect taxa (orders). Interestingly, the herbivorous taxa include nearly half of the total arthropod fauna in less than one-third of insect orders, indicating that once the nitrogen deficiency barrier is breached, these organisms are able to access an abundant supply of food (Strong et al. 1984).

1.3.1.2.2 Selected Examples of Nutritional Factors in Plant Defence Against Insects

The host plant, which is deficient in one or more essential nutrients required by the insect, may prove insect resistant by causing antibiotic and antixenotic effects on the insect. Such effects could also result from an imbalance of available nutrients (Arora and Dhaliwal 2004).

Cotton Cotton genotypes with inbuilt defence based on nutritional factors have been evolved for insects such as the leafhopper, *Amrasca biguttula* (Ishida); whitefly, *Bemisia tabac*i (Gennadius); stem weevil, *Pempherulus affinis* (Faust); and the thrips complex (Uthamasamy 1996). The whitefly *B. tabaci*-resistant genotypes showed higher contents of K, P and Mg and lower of N and Fe as compared to susceptible ones. But the other parameters like sugars, proteins, Ca and Cu did not show significant relationship with whitefly buildup. In another study, it was reported that total sugar content of cotton cultivars was positively correlated with whitefly incidence during the vegetative phase but negatively correlated with it after flowering of the crop (Rao et al. 1990). In the case of leafhopper, *A. biguttula*, highly susceptible genotype Acala 4–42 had higher amount of reducing sugars (2.55%), proteins (18.49%) and free amino acids (10.15 mg/g) as compared to highly resistant BJR 741 containing 1.63% reducing sugar, 13.45% proteins and 6 mg/g free amino acids (Singh and Agarwal 1988).

Rice The thrips, *Stenchaetothrips biformis* (Bagnall)-resistant rice genotypes possessed significantly less reducing sugars and free amino acids in comparison with the susceptible genotypes (Thayumanavan et al. 1990). The occurrence of asparagine in minute quantities in rice variety ‘Mudgo’ was considered to be the primary cause of resistance to brown plant hopper, *Nilaparvata lugens* (Stal). Young females of brown plant hopper caged on variety Mudgo had underdeveloped ovaries containing few eggs, while those caged on susceptible varieties had normal ovaries full of eggs (Sogawa and Pathak 1970). The gall midge *Orseolia oryzae* (Wood-Mason)-resistant varieties PTB 18, PTB 21 and Leuang 152 had higher content of free amino acids and less sugar in their shoot apices than susceptible varieties Jaya and IR8. In the case of stem borer, *Scirpophaga incertulas* (Walker), stems of both the resistant (TKM6) and moderately resistant (Ratna) genotypes had less amino acids and sugars than susceptible genotype (IR8) (Vidyachandra et al. 1981).

Legumes The importance of amino acid concentration in the pea plant on susceptibility to aphid, *Acyrthosiphon pisum* (Harris), was revealed by Auclair (1963). He observed that the concentrations of amino acids in the sap of susceptible genotypes were significantly higher than those in the resistant genotypes. It has been reported that high percentage of non-reducing sugars and low percentage of starch in the seeds of chickpea genotype GL 645 might be responsible for the low incidence of the pod borer *H. armigera* in the test cultivar as compared to the infestor (Chhabra et al. 1990).

Low amino acid, protein and sugar contents and high phenol content induced resistance in pigeon pea cultivars against pod borers. Sugar content was high both in seeds (3.64–4.82%) and in the pod coat (3.66–4.92%) of susceptible cultivars (ICPLI, ICPLS7 and UP AS20). In the resistant cultivars, the total sugar content ranged between 2.86 (ICPLS3024) and 3.51% (HS9–2) in the seeds and 2.91 (ICPLS3024) and 3.44% (HS9–2) in the pod coat. The amino acid content was low in the pod coat (1.40–1.52 mg/g) and seed (1.39–1.55 mg/g) of resistant pigeon pea cultivars tested as compared to the susceptible cultivars (1.89–2.57 mg/g in pod coat; 2.04–2.62 mg/g in seed). Highly significant positive correlation observed between amino acid content and incidence of individual borer species supported the possible role of amino acids in offering resistance to the pod borers (Sahoo and Patnaik 2003).

1.3.1.2.3 Allelochemicals

The plant-produced allelochemicals are mainly secondary metabolites which do not play major role in primary metabolic pathways of plants. While the primary metabolic pathways are common in almost all flowering plants, these secondary substances vary widely in different plant species (Schoonhoven et al. 2005). It was Fraenkel (1959) who first postulated that these substances act to deter insects and other herbivores. It has been observed that the plant produce a dazzling variety of secondary metabolites, and more than 200,000 of these have been identified (Dixon and Strack 2003).

The allelochemicals have been functionally classified into two categories: *allomones* which benefit the producing organism, i.e. the host plant, and *kairomones* – which benefit the organism perceiving it, i.e. the phytophagous insect. The involvement of allelochemicals in various types of insect-plant relationships can determine the status of a plant either as a host (presence of kairomone) and non-host (absence of kairomone) or as resistant (presence of allomone) and susceptible (absence of allomone) (Panda and Khush 1995). Allomones are considered a major

Table 1.1 Major groups of phytochemicals utilized in plant defences

Phytochemical group	Example	Typical plant source	Approximate number of compounds known
Terpenoids	(E)-β-Farnesene cucurbitacins	Ubiquitous	>30,000
Steroids	Phytoecdysteroids	Ranunculaceae	~200
Cardenolides	Digoxigenin	Plantaginaceae	~200
Alkaloids	Nicotine	Solanaceae	>12,000
Fatty acid derivatives	(3Z)-Hexenylacetate	Ubiquitous	Not available
Glucosinolates	Sinigrin	Capparales	~150
Cyanogenic glucosides	Dhurrin	Rosaceae, Fabaceae	~60
Phenolics	Simple phenols, coumarins, lignin, tannin	Ubiquitous	>9000
Polypeptides	Trypsin inhibitor	Ubiquitous	Not available
Nonprotein amino acids	γ-Aminobutyric acid	Fabaceae	>200
Silica	SiO_2	Poaceae	1
Latex	Undefined emulsion	Euphorbiaceae	Not available

Modified from Mithofer and Boland (2012)

factor responsible for plant defence against insects, and these have been exploited to increase levels of resistance in several agricultural crops (Green and Hedin 1986). The various groups of secondary plant metabolites implicated in plant defence against insects (Table 1.1) are briefly discussed here (Rosenthal and Berenbaum 1991; Arora and Dhaliwal 2004; Schoonhoven et al. 2005; Iason et al. 2012).

Nonprotein Amino Acids The nonprotein or unusual amino acids are common in a number of unrelated families of higher plants as well as in some lower plants. At least 600 such amino acids have been elucidated from various plants especially legumes. Nonprotein amino acids may afford protection against predators and pathogens due to their structural analogy to the common nutritionally important amino acids. The biological effects on insects are partly due to the fact that the analogue molecule gets misincorporated into protein synthesis of the insect or through inhibition of biosynthetic pathways (Rosenthal 1991; Huang et al. 2011; Yan et al. 2015). Among these, canavanine, azetidine-2-carboxylic acid, 2,4-diaminobutyric acid, mimosine, 3-hydroxyproline, 5-hydroxynorvaline, β-cyanoalanine and pipecolic acid are significant in causing insect growth disruption (Parmar and Walia 2001, Yan et al. 2015).

Terpenoids Terpenoids are the largest and most diverse class of organic compounds found in plants. They exhibit enormous chemical variety and complexity, but all are formed by fusion of five-carbon isopentane units, and most of them are lipophilic substances (Ruzicka 1953). Terpenoids achieve their greatest structural and functional diversity in the plant kingdom. Nearly 30,000 terpenoids are known in plants, and a majority of them serve as defences against herbivores and pathogens or as attractants for pollinators and fruit-dispersing animals. The terpenoids are constituted of two or more five-carbon units in their structures: monoterpenoids (2xC_5), sesquiterpenoids (3xC_5) diterpenoids (4x C_5), triterpenoids (6xC_5), tetraterpenoids (8xC_5) and polyterpenoids [(C_5) n where n>8] (Gershenzon and Croteau 1991).

Monoterpenoids have been demonstrated to work as toxins and as feeding/oviposition deterrents against a large number of insects. The best known insect toxin among monoterperoids is the botanical insecticide pyrethrum, found in the flowers and leaves of certain *Chrysanthemum* species. The active ingredient in pyrethrum is a mixture of monoterpene esters collectively known as pyrethroids (Casida 1973).

Cotton and related malvaceous plants possess spherical pigment glands in leaves, flowers and most other parts of the plants. In addition to anthocyanin pigments, these pigment glands contain high concentrations of a variety of mono- and sesquiterpenoids especially gossypol. Gossypol is a phenolic, sesquiterpene dimer with two aldehyde residues. Gossypol is toxic to a variety of herbivorous insects, causing significant decrease in the survival, growth and development of a number of important lepidopterous and coleopterous pests. The toxicity of gossypol to herbivores is supposed to result from its binding to proteins in the gastrointestinal tract, causing a reduction in the rate of protein digestion. The proteins in the gastrointestinal tract may be the ingested dietary proteins or the digestive enzymes produced by the insect (Meisner et al. 1977). The sesquiterpene lactone, *beta*-D-glucopyranosyl ester (TA-G), a major secondary metabolite of the common dandelion, *Taraxacum officinale* G. H. Weber ex Wiggers, protects the plant against its major native root herbivore, the common European cockchafer, *Melolontha melolontha* Linnaeus, by deterring larval feeding (Huber et al. 2016).

Triterpenoids (C_{30}) with six-C_5 isoprene units are the largest of terpenoid compounds. The three major groups of triterpenes which have significant roles in plant-herbivore interactions are the cucurbitacins, limonoids and saponins. Cucurbitacins are a group of about 20 extremely bitter and toxic tetracyclic triterpenes, confined mainly to plants in the Cucurbitaceae family. These compounds serve as toxicants and feeding deterrents against a wide range of phytophagous insects (Tallamy et al. 1997). Some specialist insects feeding on cucurbits are, however, able to metabolize or avoid these toxic compounds and even use cucurbitacins as host recognition cues (Abe and Matsuda 2000).

The limonoids are a large group of highly oxygenated substances with a basic skeleton of 26 carbon atoms. Limonoids are found in three closely related families, the Rutaceae, Meliaceae and Cneoraceae. Limonoids are powerful feeding deterrents against insects. Over 100 triterpenoids have been isolated from the neem *(Azadirachta indica* A. Juss.) seeds, and a number of these are active as insect feeding deterrents and antifeedants. Most important of these is the azadirachtin, which is effective at dosages as low as 50 parts per billion. More than 400 species of insects have been reported to be susceptible to neem preparations at various concentrations. In addition to antifeedant effects, neem is reported to affect the survival, growth, development, vigour and fecundity of insects (Schumutterer 1995; Dhaliwal and Arora 2001).

Saponins are common constituents of a large number of plant species and consist of a sugar moiety (glycoside) linked to a hydrophobic aglycone, which may be a triterpene or a steroid, both of which originate from the C_{30} precursor, squalene. Triterpenoid saponins have been detected in common legumes such as soybeans, beans, peas, tea, spinach, sugar beet and quinoa. Steroidal saponins are found in oats, capsicum, peppers, aubergine, tomato seed, allium and asparagus (Francis et al. 2002). Saponins exert a strong insecticidal action against several orders and cause increased mortality, lowered food intake, weight reduction, growth retardation and moulting defects (Geyter et al. 2007).

Alkaloids The alkaloids are a heterogeneous class of natural products that occur in all classes of living organisms but are most common in plants. Alkaloids generally include basic substances that contain one or more nitrogen atoms, usually in combination as part of a cyclic system. Most of them are derivatives of common amino acids, such as lysine, tyrosine, tryptophan, histidine and ornithine (Facchini 2001). Alkaloids are found in some 20% of the species of flowering plants. Generally, each alkaloid-bearing species displays its own unique, genetically defined alkaloid pattern. Numerous alkaloids have been reported to be toxic or deterrent to insects. Because of their nitrogenous nature, many alkaloids interfere with the key components of acetylcholine transmission in the nervous system. Nicotine and nornicotine derived from tobacco plant were popular as botanical insecticides before the advent of synthetic organic insecticides (Dhaliwal and Arora 2001). Several groups of structurally unrelated alkaloids such as pyrrolizidines, quinolizidines, indole alkaloids, benzylisoquinolines, steroid alkaloids and methylxanthines are feeding deterrents to many insects and other herbivores at dietary concentrations over 0.1% (Schoonhoven et al. 2005).

Glucosinolates Glucosinolates form a small group of about 100 sulphur- or nitrogen-containing distinctive secondary compounds, which act as precursors of mustard oils. Glucosinolates occur commonly in the order Brassicales, including the commercially important family Brassicaceae. Glucosinolates appear to contribute to effective chemical defences against a majority of non-adapted phytophagous insects (Fahey et al. 2001). In the thale cress *Arabidopsis thaliana* (Linnaeus) Heynhold genome, at least 52 genes are involved in glucosinolate biosynthesis (Arabidopsis Genome initiative 2000, Halkier and Gershenzon 2006). When herbivores attack plant tissues, glucosinolates are hydrolysed by the enzyme myrosinase into several herbivore-deterring metabolites (Hopkins et al. 2009). On the other hand, a small minority of adapted (Brassica-feeding) insects are able to utilize glucosinolates in host seeking and host recognition behaviour. Glucosinolates and their volatile hydrolysis products are also used as cues by natural enemies of Brassica-feeding insects (Louda and Mole 1991).

Insect Hormone Mimics and Antagonists The endocrine system is critical for the development, growth, survival and multiplication of insects. Although many insect hormones are known, two powerful hormones, the juvenile hormone (JH) and the ecdysone or moulting hormone (MH), are recognized to play a major role in these processes. The analogues of these hormones are called juvenoids and ecdysteroids, respectively. It is presumed that plants may have developed juvenoids and ecdysteroids as subtle defences against insect pests. Plant species having high ecdysteroid content (> 1000 ppm) are avoided by insects. Farnesol, sesamin, juvabione, sterculic acid, bakuchiol and thujic acid are some of the important juvenoids isolated from plants and are known to disrupt metamorphosis, moulting and reproduction in insects (Bowers 1991).

Proteinase Inhibitors Protease inhibitors (PIs) constitute an abundant and important group of compounds in plants, which have a defensive function against herbivores, especially insect pests (Dunaevsky et al. 2005). Recent studies using microarrays and proteomic approaches have revealed that the protein-based plant defences play a more important role against herbivores then previously realized (Felton 2005; Zhu-Salzman et al. 2008). Defence-related proteins such as arginases, polyphenol oxidases and peroxidases may have antimicrobial properties; others such as chitinases, cysteine proteases, lectins and leucine amino peptidases may be toxic (Zhu-Salzman et al. 2008). However, the anti-insect action of plant proteins is easily inactivated by proteases. These proteolysis-susceptible proteins can be protected with PIs (Mithofer and Boland 2012).

The PIs inhibit the activities of various enzymes in insects especially insect peptidases including serine, cysteine and aspartate proteinases and metallo-carboxypeptidases, which are involved in insect growth and development. The PIs also reduce the digestive ability of the insect pests, thus leading to the shortage of important food constituents such as amino acids resulting in slow development and/or starvation. A large number of PIs have been reported in plants (De Leo et al. 2002), which are effective against many lepidopteran and hemipteran insect pests (War and Sharma 2014). For instance, in tomato plants, PIs were positively tested for their trypsin- and *H. armigera* gut proteinase-inhibitory activity in different parts of the plant (Damle et al. 2005).

Lectins Lectins or phytohaemagglutinins are proteins with a capacity to reversibly bind to the carbohydrate moieties of complex carbohydrates without altering the covalent structure of any of the recognized glycosyl legends. Lectins are distributed universally throughout the plant kingdom, where they constitute 6–11% of the total plant proteins. The cotyledons of the seeds of legumes are especially rich in lectins. Lectins are associated with the defence of plants against insects and phytopathogens (Liener 1991). *Arisaema helleborifolium* Schott lectin exhibited anti-insect activity towards the second instar larvae of melon fruit fly, *Bactrocera cucurbitae* (Coquillett) (Kaur et al. 2006).

Phenolics Phenolics are aromatic compounds with one or more hydroxyl groups and are ubiquitous in plants (Harborne 1994). Examples of relatively simple phenolics include hydroxybenzoic acids like vanillic acid, the hydroxycinnamic acids like caffeic acid and the coumarins (Schoonhoven et al. 2005). Coumarins possess a 5,6-benz-2-pyrone skeleton and may be variously hydroxylated, alkylated, alkoxylated or acylated. Coumarins can deter feeding as well as interfere with development of insects. The simple coumarin, bergamottin, is ovicidal to the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), while mammein is toxic to the mustard beetles. Coumarins appear to act as kairomones for certain insects that are specialized for feeding on coumarin-containing plants (Berenbaum 1991b).

Among the phenolics, flavonoids are found in nearly all higher plants, and most plants show their own distinctive flavonoid profile. The flavonoids share a basic C_6-C_3-C_6 structure, which is linked to a sugar moiety to form a water soluble glycoside. Common examples of flavonoids isolated from plants are catechin, botanical insecticide rotenone and phaseolin, all of which act as feeding deterrents against insects (Schoonhoven et al. 2005).

Tannins are polyphenolic compounds commonly found in higher plants. The phenolic hydroxyl groups of tannins bind to almost all soluble proteins, producing insoluble copolymers. Proteins bound to tannins are indigestible and thus decrease the nutritional value of plant tissues (Schoonhoven et al. 2005).

Latex Latex is present in specialized cells called laticifers and consists of chemically undefined milky suspensions or emulsions of particles in an aqueous fluid (Agrawal and Konno 2009). Laticifers have a defensive function. Small insects may be physically trapped in latex or their mouthparts may get glued together, and chemical constituents in latex including proteins and toxins affect insect development (Dussourd 1995). Wounding of laticifers by insects results in leakage at wound site (Mithofer and Boland 2012). In the milkweed, *Hoodia gordonii* (Masson) Sweet ex Decne, both larval feeding and adult oviposition by *T. ni* was deterred when latex was added to artificial diet or painted on the leaves of the host plant (Chow et al. 2005).

1.3.1.2.4 Selected Examples of Allelochemicals in Plant Defence Against Insects

Maize Maize, the world's most productive grain crop, is attacked by a diverse range of insect pests. Well-studied anti-herbivore defences in maize include small molecules such as benzoxazinoids (Frey et al. 2009), chlorogenic acid (Cortes-Cruz et al. 2003) and maysin (Rector et al. 2003) in addition to defence-related proteins (Chuang et al. 2014). Xie et al. (1992) analysed several maize lines resistant to western corn rootworm, *Diabrotica virgifera* Le Conte, for hydroxamic acid levels. All the root extracts were found to contain four major hydroxamic acids: 2,4-dihydroxy-7methoxy-l,4-benzoxazin-3-(4H)-one (DIMBOA), 2,4-dihydroxy-7,8dimethoxy-l,4-benzoxazin-3(4H)-one (DIM2BOA), 2-hydroxy,7-methoxy,1,4-benzoxazin-3(4H)-one (HMBOA) and 6-methoxy-benzoxazolinone (MBOA). These chemicals adversely affected the survival development, weight and head capsule width of rootworm larvae. Wiseman et al. (1992) reported a highly significant negative relationship between weights of corn earworm, *Helicoverpa zea* (Boddie), as well as the fall armyworm, *Spodoptera frugiperda* J. E. Smith, larvae and maysin concentration in the silks of a large number of corn entries.

Cotton The allelochemical compounds known to exert adverse effects on insect pests in cotton include gossypol, gossypurin, heliocides, hemigossypolone, tannins, anthocyanins, flavonoids and phenolics. Gossypol was first reported to confer resistance to cotton bollworm *Heliothis zea* by Bottger et al. (1964). Most commercial cotton cultivars have a gossypol content of about 0.5% in squares. Vilkova et al. (1988) reported that high gossypol cotton cultivars (No.1 6482, 6501 and Termez-14) had detrimental effects on insect development, viz. increasing incubation period, causing greater mortality among young larvae and lowering larval weight compared with low gossypol cultivars. They further stated that antibiotic effect of high gossypol reduced the fecundity of *H. armigera* by more than 50%. Gossypol is known to adversely affect the nutritional quality of bolls by forming complexes with amino acids, proteins and enzymes. The tree cotton *Gossypium arboreum* Linnaeus genotypes with high gossypol-gland density on ovary surface suffered lower incidence of bollworm complex including *H. armigera*, *Earias vittella* (Fabricius) and *Pectinophora gossypiella* (Saunders) (Mohan et al. 1994).

In the case of cotton stem weevil, *P. affinis*, when the healthy test plants were assayed, the concentration of tannins was low in susceptible MCU5 and high in the resistant accessions. The concentration increased in the gall region when the plants were infested, and the increase was more in resistant accessions compared to the susceptible MCU5. There was no variation in the total phenolic content in the healthy stem of resistant and susceptible accessions. However, when infested, the concentration of total phenolics increased in the gall regions significantly, the increase being more in resistant accessions. It could thus be inferred that increased tannin and phenolic concentrations might provide a protective mechanism against the stem weevil (Uthamasamy 1996).

Vegetables Potato glycoalkaloids are known to act as natural resistance factors in *Solanum* species against the Colorado potato beetle (CPB), *L. decemlineata*, and the potato leafhopper, *E. fabae*. Several wild *Solanum* species have shown a positive correlation between total leaf glycoalkaloid content and resistance to species of *Leptinotarsa.* Leptine is a very effective feeding deterrent totally inhibiting feeding, while tomatine and demissine are intermediate in activity, followed by solanine and chaconine (Tingey 1984). The field resistance of tetraploid potato *(Solanum tuberosum* L.) selection ND 2858-1 and its backcross progeny against the Colorado potato beetle is caused by antibiosis. Neonates of CPB developed slowly in detached-leaf assays on resistant genotypes, and larval weight gain after 4 days was inhibited by 75% relative to larval development and weight gain on susceptible genotypes. Foliar glycoalkaloids of resistant genotypes included low levels of leptines I and II (Lorenzen et al. 2001).

The wild species of tomato, *Lycopersicon hirsutum* and *L. hirsutum* f. *glabratum*, showed antibiosis against the tomato fruit borer *H. zea*. The chemicals responsible for antibiosis were identified as L-tomatine, 2-tridecanone, phenolics and iron and zinc (Ferry and Cuthbert 1975; Dimock and Kennedy 1983; Kashyap 1983). The allelochemic 2-tridecanone was acutely toxic to *H. zea, Manduca sexta* Linnaeus and *L. decemlineata.* High phenolic content has also been reported to confer resistance to the related species, *H. armigera* (Banerjee and Kalloo 1989), while high tomatine content is inimical to the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Steehius and van Gelder 1985).

The protease inhibitor and chlorogenic acid were responsible for aphid resistance in tomato (Felton et al. 1989). The sesquiterpene carboxylic acids (SCA), (+) E-α-santalen-12-oic, (−)-E-endo-α-bergamoten-12-oic and (+)-E endo-β-berqamoten-12-ion acids were produced in glandular trichomes of *Lycopersicon hirsutum* f. *typicum* accession (LA) 1777, which is highly resistant to pests commonly damaging commercial tomato, *L. esculentum.* Both the tomato fruitworm, *H. zea*, and the beet armyworm, *Spodoptera exigua* (Hubner), larvae exhibited reduced feeding, slow development rates and low survival in presence of these compounds. Sublethal effects were observed at concentrations as low as 2 mg SCA/g of diet, and a concentration of 60 mg SCA/g in diet proved lethal to the larvae (Frelichowski and Juvik 2001).

1.3.1.3 Types of Plant Defences

The plant defences may be classified into: *constitutive*, which are always present in the host plant irrespective of the presence of insect or noninsect pests, and *induced*, which are produced in response to various abiotic and biotic stressors.

1.3.1.3.1 Constitutive Defences

Plants have evolved a plethora of structural and chemical defences that are incorporated into their tissues irrespective of the presence or absence of herbivores. These constitutive defences can deter, repel, intoxicate or disrupt the feeding, development or multiplication of insects (Arora and Dhaliwal 2004; Ram et al. 2004; Mithofer and Boland 2012). These defences include the texture and composition of the plant surface (Johnson 1975); the presence of anatomical structures such as thin veins, thorns, silica, trichomes or resin ducts (Hanover 1975); the absence of essential nutrients (House 1961); the presence of hormone-like substances that disrupt insect development (Williams 1970); unsuitable pH or osmotic pressure (Beck 1965); or the accumulation of secondary metabolites (Chapman 1974). The secondary metabolites are diverse, ranging from amino acids to alkaloids, terpenes, phenolics, steroidal, cyanogenic and mustard oil glycosides (Mithofer and Boland 2012). In addition plants may also convert nitrogen to compounds which are not available to insects (White 1978). The advantage of such constitutive defences to insects is that these are produced during high metabolic periods and can be utilized over an extended period of time. Such defences work well against a diverse group generalist herbivores, but continuous exposure to these chemicals exerts strong selective pressure on the phytophagous insects, which may result in evolution of specialist feeders. Thus, even the best defended species are attacked by a few specialist herbivores.

1.3.1.3.2 Induced Defences

Induced defence is activated in presence of herbivores and enables the plant to resist pest feeding and colonization (Sadras and Felton 2010). Initiation of insect feeding activates several defence signals, leading to suitable defence responses (Wu and Baldwin 2010; Hogenhout and Bos 2011; Bruce 2015). The plants have also been reported to respond to insect oviposition in a similar fashion (Hilker and Meiners 2006). Plant-released volatile organic chemicals (VOCs) have been found to attract natural enemies of pests (Tamiru et al. 2011; Fatouros et al. 2012) or induce direct defences so that insect growth rates are reduced on plants harbouring eggs (Gieselhardt et al. 2013).

Plants respond to elicitors derived from oral secretion of insect herbivores, mechanical damage and/or the exogenous application of inducers. Insect oral secretion/regurgitant contains a number of elicitors of plant defence, the important ones being fatty acid conjugates (FACs). The FACs are composed of two moieties: a fatty acid and an amino acid. It has been observed that the fatty acid and amino acid originate from the plant and the insect, respectively, and are synthesized in the insects' midgut. Expressing the unique insect-plant interaction, the FACs not only serve as important elicitors for plants to perceive insect attack but are also involved in insect nitrogen metabolism. The first FAC isolated from oral secretion of the beet armyworm *S. exigua* larvae was N-(17-hydroxylinolenoyl)-L-glutamine (volicitin), and it stimulates maize plants to produce volatiles, which attract natural enemies of the pest (Alborn et al. 1997). Similarly, regurgitant of the tobacco hornworm, *M. sexta*, contains N-linolenoyl-glu, a potential elicitor of volatile emissions in tobacco plants. In addition, some FACs activate mitogen-activated protein kinase (MAPK) pathway, producing a number of plant defensive compounds having a role in signalling transduction in response to various stresses including drought, pathogen and insect attacks. MAPK signalling is a well-conserved pathway in eukaryotes, and its critical role in plant signalling especially for pathogen stresses is well established. The central role of MAPK in regulating plant transcriptomes has been demonstrated (Wu and Baldwin 2010). Some FACs induce accumulation of 7-epi-jasmonic acid, which activates herbivore-defence genes in tobacco plants. Furthermore, FACs also induce nicotine and proteinase inhibitors (PI) in the coyote tobacco, *Nicotiana attenuata* (Torr. ex S. Watson) (Wu and Baldwin 2010; War and Sharma 2014).

The plant plasma membrane is exposed to the environment and initiates a cascade of events following recognition of pest attack. The changes in cell membrane potential (Vm) induced by herbivory are followed by fast electrical signals, which are systematic in nature. Calcium ions ($Ca+^2$) function as a second messenger in several plant signalling pathways. The signal may appear a few seconds after herbivore attack as a single transient oscillation or repeated spikes with specific subcellular localisation lag time, amplitude and frequency. The $Ca+^2$ signals activate calmodulin and other calcium-sensing proteins. This promotes a cascade of downstream effects, like altered protein phosphorylation and gene expression patterns (Furstenberg-Hagg et al. 2013).

Herbivory leads to the accumulation of phytohormones in plants, the important ones being salicylic acid (SA), jasmonic acid (JA) and ethylene. The phytohormones mediate various signal transduction pathways involved in plant defence against various biotic and abiotic stresses. The main transduction pathways involved in plant defence against herbivorous insects are phenylpropanoid and octadecanoid pathways mediated by SA and JA, respectively. These pathways lead to synthesis and accumulation of toxins at the feeding site or in other parts, which are then transported to the feeding site. In addition, antioxidative enzymes involved in plant defence accumulate in plant tissues on account of insect damage (Wu and Baldwin 2010). Yan et al. (2015) reported accumulation of nonprotein amino acid 5-hydroxynorvaline in leaves of maize inbred line B73 following herbivory by the corn leaf aphid *Rhopalosiphum maidis* (Fitch) and the beet armyworm *S. exigua*, as well as in response to treatment with methyl jasmonate, salicylic acid and abscisic acid.

Both constitutive and induced defences can be either direct or indirect. Direct defences target the herbivores, while indirect defences act via recruitment of natural enemies of insect pests in the aid of plants. Certain volatile organic compounds (VOCs), containing terpenoids, fatty acid derivatives and a few aromatic compounds, serve to attract natural enemies of phytophagous insects (Mithofer and Boland 2012).

1.3.2 Counter-Defences of Insects to Plant Defences

Plants defend themselves from herbivore damage through a plethora of structural and chemical defences. These defences may have exerted enormous selection pressure on the insects resulting in evolution of counter-defences (adaptations) in herbivorous insects. The insect adaptations to plant defences can be physical, behavioural or biochemical and comprise of various mechanisms such as penetration barriers, special excretions, sequestrations, temporary binding with carrier proteins and storage of toxins in adipose tissue, enzymatic detoxifications and target-site mutation. It is important to gain an understanding of these insect adaptations to plant defence to minimize their effects on stability of resistance in plants to insects. The important counter-defence strategies of insects to plant defences are briefly introduced hereunder (War and Sharma 2014; Bruce 2015).

1.3.2.1 Adaptations to Physical and Structural Defences

The slippery wax layer presents a serious obstacle to the movement of insects on plants, and many insects have developed special devices to overcome the problem. For instance, the minute setae on tarsal pulvilli of some chrysomelids excrete an adhesive material for good attachment (Gorb and Gorb 2002). Leafhoppers of *Empoasca* species can use their tarsal pulvilli as suction cups (Lee et al. 1986), while many lepidopteran caterpillars glue a silk thread ‘rope ladder’ to the plant surface to serve as a ‘foot hold’ (Eigenbrode 2004). To overcome the problem of trichomes on the plant surface, the aphid *Myzocallis schreiberi* Hille Ris Lambers & Stroyan has specialized structure in the form of claws and flexible empodia that serve to get a good grip on the short woolly trichomes on the leaves of its host, the Holm oak, *Quercus ilex* Linnaeus (Kennedy 1986).

Leaf toughness has been found to reduce herbivory. As an adaptation to food hardness, in caterpillars of *Pseudaletia unipuncta* Haworth, the head and chewing musculature are twice as large when fed on hard grass as on soft artificial food, even though body mass is similar (Bernays 1986). Water lily beetles *Galerucella nymphaeae* (Linnaeus) feeding on the ‘hard’ water lily have disproportionally bigger mandibles than conspecifics feeding on the great water dock grin, *Rumex hydrolapathum* Huds., another host plant with softer leaf tissues (Pappers et al. 2001).

1.3.2.2 Adaptations to Protease Inhibitors

Production of protease inhibitors is induced in some plants in response to insect damage. Herbivore attack on *N. attenuata* rapidly increases the production and accumulation of trypsin PIs; *M. sexta* and *S. exigua* larvae performed better on Trypsin PI-deficient plants as compared to similar plants producing PIs (Zavala et al. 2004; Steppuhn and Baldwin 2007). However, many insect pests have adapted to plant PIs, which increases damage to the host plants. This counter-defence of PIs by insect pests is a major barrier to the manipulation and utilization of PIs for a stable plant defence and thus warrants an understanding of the mechanisms by which insects counteract the PI-based plant defence. Two types of resistance or adaptation to protease inhibitors have been observed in insect pests. One of these depends on having the alternative proteases that are resistant to PIs (Parde et al. 2010). These insensitive proteases can occur constitutively in the plant and/or are induced when the other proteases are inhibited to compensate their loss (Jongsma et al. 1995; Parde et al. 2012). *S. exigua* has been reported to adapt to potato proteinase inhibitor II by induced gut proteinase activity, which is not inhabited by the PIs. Further, when fed on the soybean proteinase inhibitor (SPI)-containing diet, larval proteases showed insensitivity to the inhibitor (Brioschi et al. 2007). Trypsins insensitive to plant PIs have been characterized from *Agrotis ipsilon* (Hufnagel), *T. ni* and *H. zea* (Volpicella et al. 2003).

The second mechanism of resistance to PIs in insects involves the synthesis of specific proteases, which are able to degrade the protease inhibitors so as to reduce their inhibitory activity. Proteolytic inactivation is an important adaptation developed by insects to withstand the proteolytic inhibition by PIs. A new trypsin-like enzyme is produced by S. *frugiperda* (J.E. Smith) larvae when fed on artificial diet with soybean PIs (Brioschi et al. 2007). The diamondback moth, *Plutella xylostella* Linnaeus, larvae have been found to be insensitive to mustard trypsin inhibitor 2 (MTI2). This insensitivity has been attributed to degradation of MTI2 by the pest, thus avoiding the effect of the PI (Yang et al. 2009).

1.3.2.3 Adaptations to the Glucosinolate-Myrosinase System

The glucosinolate-myrosinase system, also known as the 'mustard oil bomb', present in Brassicales (Brassicaceae, Capparidaceae, Tropaeolaceae) constitutes the most effective and well-studied defence system in these plants against insect pests. Under normal conditions, glucosinolates are compartmentalized and thus protected from their hydrolysing enzyme – a thioglucosidase – myrosinase. While the glucosinolates are distributed in many plant tissues, the myrosinase is localized in scattered cells only. Upon tissue damage, the myrosinase and glucosinolate come into contact producing the unstable aglycones, which spontaneously rearrange into various active compounds, mainly nitriles and isothiocyanates (Li et al. 2000; Hopkins et al. 2009).

It has been revealed that high glucosinolate- and myrosinase-containing lines of *Brassica juncea* (Linnaeus) Czern. are more defensive against *Spodoptera eridania* (Cramer) larvae than the ones with lower content of these two chemicals (Li et al. 2000). The larvae of *T. ni*, a lepidopteran generalist, avoided *A. thaliana* ecotypes that produced isothiocyanates upon glucosinolate hydrolysis and, instead, fed on ecotypes that produced nitriles (Lambrix et al. 2001). Further, certain parasitoids use glucosinolates that are released by feeding herbivores to detect their host insects. In such cases, glucosinolates have a dual function for the attacked host plant, in direct as well as in indirect defence (Hopkins et al. 2009).

Some insect pests even use glucosinolates for their own defence. *Myzus persicae* (Sulzer), *Athalia rosae* (Linnaeus) and *P. rapae* sequester glucosinolates into their hemolymph and body tissues (Muller and Brakefield 2003; Kazana et al. 2007; Bridges et al. 2002). When a predator attacks, the haemolymph oozes out glucosinolates that deter the predators such as ants and predatory wasps (Muller and Brakefield 2003). Some aphids especially *Brevicoryne brassicae* (Linnaeus) and *Lipaphis erysimi* (Kaltenbach) sequester glucosinolates from the phloem sap (Kazana et al. 2007, Bridges et al. 2002). Furthermore, Pierinae caterpillars such as *P. rapae* detoxify the glucosinolates from their host plants by converting these otherwise toxic breakdown products to inert metabolites through a nitrile-specifier protein (NSP). The NSP activity in the gut of *P. rapae* modulates the hydrolysis of glucosinolates and leads to the formation of nitriles instead of toxic isothiocyanates (Wittstock et al. 2004).

1.3.2.4 Adaptations to Tannins

Tannins are the polyphenolic compounds that strongly bind to proteins or to digestive enzymes in the gut, thereby reducing their digestibility by insect pests and thus affecting insect growth and development. In addition, tannins also act as feeding deterrents to many insects because of their astringent (mouth puckering) nature (Barbehenn and Constabel 2011). Tannins form hydrogen or covalent bonds with the protein amino groups, which leads to precipitation of proteins and the digestive enzymes of herbivores. Furthermore, chelation of metal ions in insects by tannins reduces their availability to the insect pests, thus affecting growth and development. Tannins have also been reported to inhibit feeding and cause midgut lesions and pharmacological toxicity (Bernays and Chamberlain 1980). However, insects have developed several adaptive mechanisms to avoid the toxicity of tannins. The potential mechanisms insects use to avoid toxicity of tannins include alkaline gut pH, tannin absorption through peritrophic membrane, polymerization and excretion of the polyphenols after concentration (War and Sharma 2014). The surfactants formed as products of lipid digestion in the gut lumen prevent precipitation of proteins (Martin et al. 1987). Oxygen levels in foregut also play an important role in toxicity of tannins. At higher pH, oxygen levels are low and reduce autoxidation of tannins, thereby lowering their toxicity. The antioxidative system of insects also plays an important role in reducing the tannin toxicity. For example, ascorbate reduces the oxidation of tannins and formation of reactive oxygen species (ROS) in insect gut (Krishnan and Sehnal 2006). The grasshoppers possess a strong midgut antioxidative defence, which enables them to withstand tannins. This antioxidative defence mainly comprises of glutathione, α-tocopherol and ascorbate. The tolerance to tannins, and its association with peritrophic membrane in *S. gregaria*, has been attributed to the ultrafiltration of tannins. In some species including *Melanoplus sanguinipes* (Fabricius), tannic acid does not bind to the peritrophic membrane. In addition, peritrophic membrane protects the insect epithelium against lesions and damage by ROS by adsorbing highly reactive ferrous ions (Barbehenn 2003).

1.3.2.5 Detoxification of Plant Metabolites

Enzymatic detoxification of toxic chemicals mediates the adaptation of insects to plant allelochemicals and thus helps the herbivores to overcome plant chemical defences. Insects react strongly to the toxic allelochemicals, when provided with the natural host plant diet or incorporated in the artificial diet, by increasing the metabolic mechanisms that result in the production of detoxifying enzymes, such as monooxygenases and glutathione-S-transferases (GST) (Nitao 1989, Wadleigh and Yu Wadleigh and Yu 1988). The mechanisms of detoxification that operate in insects depend on the host plant chemistry, and its levels are generally influenced by concentration of the allelochemicals in the plant (War and Sharma 2014). Insects deploy various enzymes for detoxification of pesticides and plant allelochemicals, and some systems are thought to be ubiquitous (Francis et al. 2005; Scott et al. 2010). The best known is the system of polysubstrate monooxygenases (also called mixed-function oxidases). The terminal component of this system is cytochrome P-450, so called because it absorbs light maximally at around 450 nm when complexed with carbon monoxide. Cytochrome P-450 combines with the substrate (which may be a toxin) and with molecular oxygen, catalysing the oxidation of the substrate. Cytochrome can combine with many different lipophilic substrates and exists as several isozymes that vary in their substrate specificity (Feyereisen 2006).

The P450s are regarded as one of the important players in insect-plant coevolution, since these are used by the plants to produce toxins and by the insects for detoxification of phytochemicals (Schuler 1996). The desert dwelling species of *Drosophila mettleri* Heed feeding on cactus containing toxic allelochemicals possess inducible amounts of P450 involved in the metabolism of these toxins (Danielson et al. 1997). The metabolism of isothiocyanates such as 2-phyenylethylisothiocyanate, indole-3-carbinol and indole-3-acetonitrile in

S. frugiperda midgut microsomes is Cyt P450 dependent (Yu 2000). Adaptation of lepidopteran insects to plant secondary metabolites such as furanocoumarins has been attributed to P450s. Black swallowtail, *Papilio polyxenes* Fabricius, feeding on plants containing furanocoumarins tolerates up to 0.1% xanthotoxin in diet (Berenbaum 1991a), which is detoxified by P450 monooxygenases (Bull et al. 1986). A clearer picture of involvement of P450 in detoxification of plant allelochemicals came after the sequencing of *CYP6B1* from *P. polyxenes*, which codes for P450s. Expression of *CYP6B161* and *CYP6B162* coding for P450s is induced in lepidopteran cell lines, indicating the involvement of P450s in metabolism of linear furanocoumarins, such as xanthotoxin and bergapten (Ma et al. 1994). A number of P450s involved in detoxification of phytochemicals have been isolated from herbivores, for instance, from parsnip webworm, *Depressaria pastinacella* Duponchel (Cianfrogna et al. 2002), *M. sexta* (Stevens et al. 2000) and *Helicoverpa* species. Furthermore, the conversion of dihydrocamalexic acid to camalexin, which are the major *Arabidopsis* phytoalexins, is catalysed by cytochrome P450 PAD3 (Schuhegger et al. 2006). Aphid resistance to glucosinolates is attributed to the CYP81F2, which is a downstream part of the indolic glucosinolate pathway (Pfalz et al. 2009).

P450s have also been characterized from many other insects where they serve to metabolize the host chemicals. For example, in *Musca domestica* Linnaeus, CYP6A1 metabolizes the terpenoids (Andersen et al. 1997); in *H. armigera*, P450 monooxygenase CYP6AE14 detoxifies gossypol (Mao et al. 2007); in *Anopheles gambiae* Giles, CYP6Z1 metabolizes xanthotoxin and bergapten (furanocoumarins), furanochromones and natural myristicin, safrole and isosafrole (Chiu et al. 2008), while CYP6Z2 metabolizes xanthotoxin, lignin, piceatannol and resveratrol (McLaughlin et al. 2008); and in *Diploptera punctata* Eschscholtz, CYP4C7 hydroxylates sesquiterpenoids (Sutherland et al. 1998). Bark beetles such as *Ips pini* Wood & Bright and *Ips paraconfusus* Lanier detoxify the monoterpenes, sesquiterpenes and diterpenoid resin acids by P450s (Seybold et al. 2006).

The glutathione-S-transferase (GST) is another enzyme system involved in insect resistance to host plant defence by detoxification of xenobiotics and catalysation of the conjugation of electrophilic molecules with the thiol group of reduced glutathione, which results in their rapid excretion and degradation (Francis et al. 2005). This family of enzymes has been implicated in neutralizing the toxic effects of insecticides that are neurotoxic and/or affect insect growth and development. These include spinosad, diazinon, DDT, nitenpyram, lufenuron and dicyclanil (Sintim et al. 2009). Several studies have advocated the role of GST in insect adaptation to plant glucosinolates or other plant secondary metabolites incorporated into the artificial diet in *S. frugiperda*, *S. litura, T. ni, M. persicae*, *Aulacorthum solani* (Kaltenbach) and *A. pisum* (Enayati et al. 2005). The overproduction of GST in *M. persicae* has been attributed to insect adaptation to glucosinolates and isothiocyanates in members of Brasicaceae, although there is no direct confrontation of isothiocyanates, because aphids directly insert their stylets into the phloem (Francis et al. 2005; Kim et al. 2008).

1.3.2.6 Insect Gut Symbionts in Counter-Defence

The induction of plant defences in response to herbivore attack has been observed to be modulated by crosstalk between jasmonic acid (JA)- and salicylic acid (SA)-signalling pathways. Herbivores possess diverse microbes in their digestive tracts, and these symbionts can modify plant-insect interactions (Hogenout et al. 2009). Chung et al. (2013) reported that Colorado potato beetle, the *L. decemlineata*, grubs exploited gut bacteria in their oral secretions to overcome anti-herbivore defences in tomato. The antibiotic-untreated larvae decreased the production of JA and JA-responsive anti-herbivore defences but increased SA accumulation and SA-responsive gene expression. The downregulation or plant defences resulted in enhanced larval growth. The gut bacteria belonging to three genera (*Stenotrophomonas, Pseudomonas* and *Enterobacter*) were implicated for defence suppression in this study.

Hammer and Bowers (2015) recently proposed the 'gut microbial facilitation hypothesis', which proposes that variation among herbivores in their ability to consume chemically defended plants can be due, in part, to variation in their associated microbial communities. These hypotheses have drawn support from molecular studies on gut bacteria. The gut bacteria in Japanese common stink bug, *Megacopta punctatissima* (Montandon), is capable of decarboxylating oxalate, a common plant secondary metabolite (Nikoh et al. 2011). The mountain pine beetles harbour gut bacteria associated with terpene detoxification (Adams et al. 2013) and are capable of metabolizing terpenes in vitro (Boone et al. 2013). The *Acinetobacter* species from the midguts of gypsy moth larvae are capable of metabolizing dietary phenolic glycosides (Mason et al. 2014). Given the widespread occurrence of gut bacteria in oral secretions of insects, these may be associated with hijacking of plant defence responses in other cases of insect-plant interactions as well.

1.4 Human-Induced Plant Defences and Insect Counter-Defences: Case Study of Hessian Fly-wheat Interactions

The Hessian fly (HF), *Mayetiola destructor* (Say) (Cecidomyiidae: Diptera), is a serious pest of wheat with a long history of pestilence in the USA. The HF is distributed in North Africa, Europe, West and Central Asia, North America and New Zealand (Buntin and Chapin 1990). The pest has been successfully managed through release of a series of insect-resistant cultivars carrying HF-specific R-gene(s). However virulent biotypes of HF are capable of overcoming resistance in about 6–8 years (Chen et al. 2009; Stuart et al. 2012). Following egg hatch, the neonate HF larva on the upper surface of leaf crawls to the base of the seedling, wherein it establishes a sustained feeding site in susceptible genotypes but fails to do so in resistant ones. Virulent HF biotypes on a susceptible cultivar result in a compatible interaction favouring pest establishment, while a virulent biotype on the resistant cultivar results in incompatible interactions and pest mortality in 3–5 days (Subramanyam et al. 2015) (Table 1.2).

Table 1.2 Variations in responses of wheat and Hessian fly during compatible and incompatible interactions

Compatible interaction	Incompatible interaction
Larval growth completed in 10–12 days	Larvae die within 5 days of attack
	No larval growth
	Gut shows signs of toxin exposure
Seedling apical shoot meristem death	Seedling survival
Shorter plants, fewer heads, fewer seeds	
Increased cell permeability at attack sites	Localized cell death
	Accumulation of reactive oxygen species
Creation of nutritive cells	Adjacent living cells fortified
Cell wall breakdown	Transient increase in permeability
	Epicuticular waxes accumulate
Membrane permeability increases	Toxin production increases
Stress-related proteins increase	Class III peroxidases increases
C/N ratio shift favours N (52% change)	Phenylpropanoid metabolism increases
Nutrient metabolism and transport increases	
Cell wall metabolism decreases	Cell wall and lipid metabolism increases. Nutrient metabolism and transport suppressed
Basal defence response suppressed	Fatty acid degradation suppressed
Phenylpropanoid metabolism suppressed	Phospholipid metabolism suppressed
Histones and structural proteins decrease	Stress-related protein decrease

Modified from Stuart et al. (2012)

As many as 35 distinct resistance genes (*H1-H3*, *h4, H5-H34* and *Hdic*) from wheat and related plants have been characterized and incorporated in commercial wheat cultivars (Chen et al. 2006; Stuart et al. 2012). The HF-wheat system is considered a model system for study of gene-for-gene (GNG) interaction between host plants and insect pests (Hatchett and Gallun 1970; Subramanyam et al. 2015). In the case of resistant cultivars carrying R genes, the plants respond to attack of HF larvae by accumulation of reactive oxygen species (Liu et al. 2010) and production of enzyme inhibitors (Wu et al. 2008), lectins (Williams et al. 2002; Subramanyam et al. 2008) and secondary substances (Liu et al. 2007). On the other hand, the compatible interactions are characterized by increased nutrient availability at the site of attack along with an accumulation of nitrogen-rich molecules (Liu et al. 2007; Williams et al. 2011). It has been revealed that the HF is able to overcome resistance through recessive mutations in corresponding avirulence (HF*Avr*) genes (Aggrawal et al. 2014). The HF*Avr* genes code for proteins (called effectors) that are injected with the saliva in to the plant tissue during feeding (Hogenhout et al. 2009). The plants carrying R genes are able to recognize these secretions and stimulate the defence pathways (Chisholm et al. 2006). In virulent HF biotypes, the Avr proteins are modified to avoid either detection by the plant or a failure to trigger the defence pathway (Chen et al. 2016).

1.5 Theories on Evolution of Insect-Plant Interrelationships and Their Role in Diversification

As early as 1859, Darwin in his magnum opus *On the Origin of Species* wrote of 'Coadaptations of organic beings to each other…'. Every living organism interacts with others of the same as well as another kind. Coevolution refers to genetic change in two interacting species. In other words, coevolution is reciprocal evolutionary change in interacting species. The term was originally used by C.J. Mode in 1958 for the coevolution of obligate parasites and their hosts. Ehrlich and Raven (1964) were the first to extend its relevance to insect-host plant coevolution based on their study of Monarch butterfly-milkweed (host plant) interactions.

A plant is neither susceptible to all the phytophagous insects nor any insect species is a pest on all the species of plants it encounters in nature. Further, less than one third of all insect orders contain exclusively (Lepidoptera, Orthoptera, Phasmida), predominantly (Hemiptera, Thysanoptera) or partially (Coleoptera, Diptera, Hymenoptera) phytophagous species. But such species comprise nearly half of all insect species. This is attributed to the fact that all plants have developed a dazzling array of structural and biochemical defences (constitutive as well as induced) against herbivores. Only those species which are able to breach these defences in one or more plant species can access such plants for food (Arora 2012). The insects thus keep on developing strategies for detoxifying or otherwise overcoming these defensive mechanisms.

The extant phytophages and their host plants are the result of a coevolutionary process that has been ongoing for nearly 400 Myr (Labandeira 2013). Insects have acquired a sensitive system for perceiving their external environment, analysing the sensory input and responding to it suitably (Martin et al. 2011). Successful host finding and acceptance are primarily controlled by chemical cues. The insect responses are dependent on a combination of host and environmental cues (Riffell et al. 2009; Webster et al. 2010). Concomitantly, the plants have also evolved numerous structural and chemical defences for protection against insects and other herbivores. The insects in turn have evolved to avoid or overcome these defences. A number of theories have been propounded to explain this evolutionary arms race between these two interdependent groups of organisms.

1.5.1 Theory of Coevolution

This theory was elaborated by Ehrlich and Raven (1964) and later supported by Berenbaum (1983). According to this theory, many plant taxa manufacture a prototypical phytochemical that is mildly noxious to phytophages and that may have an autecological or physiological function in the plant. Some insect taxa feed upon plants with only this and other, similarly mild, phytochemicals, thus reducing plant fitness. Plant mutation and recombination cause novel, more noxious phytochemicals to appear in the plants. The same chemical can appear independently in distantly related plant groups. Insect feeding is reduced because of toxic or repellent properties of the novel phytochemical; thus plants with more and more potent defences are preferred by the pressure of insect herbivory. In response, the insects have evolved the capacity to avoid or neutralize the effective chemical and even utilize the same compound as well as the plant producing it for their own benefit. An insect can specialize in feeding upon plants with the novel compound. Here it would be free to diversify due to a lack of competition from non-adopted herbivores. The cycle may be repeated, resulting in more phytochemicals and further specialization of insects.

Some supporting evidence for the theory is available from species-level studies on taxa of selected insects and their host plants. Closely related *Phyllobrotica* species feed monogamously on closely related *Scutellaria* species as revealed by the cladograms of the two groups (Farrell and Mitter 1990). Evidence is also available at the level of populations. An analysis of different populations of wild parsnip, *Pastinaca sativa* Linnaeus, and its specialist herbivore pest the parsnip webworm, *Depressaria pastinacella* Duponchel, revealed trait matching between furanocoumarin-based chemical defences in the plants and cytochrome P450 monooxygenase-based insects' detoxification profiles (Berenbaum and Zangerl 1998, Zangerl and Berenbaum 2003).

An interesting example of coevolution is that involving the brassicaceous plants and the pierid butterflies. The glucosinolate-myrosinase system evolved by Brassicales (Sect. 1.3.2.3) around 90 Myr represents a key step in anti-herbivore defences by plants. But shortly thereafter, the Pierinae butterflies which utilized Fabales as host plants came up with a detoxifying system in the form of nitrile-specific protein (NSP) and started colonizing the Brassicales. This resulted in increasing the species diversification rates in Pierinae as compared with that of their sister clade Coliadinae, whose members did not colonize Brassicales, thus lending strong support to the coevolutionary theory (Wheat et al. 2007; Edger et al. 2015).

1.5.2 Theory of Sequential Evolution

The theory of sequential evolution (Jermy 1976, 1984) proposes that evolution of herbivorous insects follows the evolution of plants, without however significantly affecting plant evolution. According to this theory, reciprocal selective interactions between plants and herbivorous insects have not been proved so far. Plants undeniably cause evolutionary changes in phytophagous insects, whereas the latter exert selective pressure on the plants only in rare cases and even in these only weakly. The insects choose their host plants largely based on perception of chemical cues. Therefore, any changes in chemical composition of host plants or their chemosensory perception by insects may lead to emergence of new insect-host plant relationships. However, contradictory paleontological evidence in the form of insect familial diversification preceding the major diversification of angiosperms contradicts this theory. As a consequence, speciation in herbivorous insects may be mediated by plants, but speciation in plants has not been proved to occur as a consequence of interaction with herbivorous insects.

Further evidence in support of the theory was presented by Labandeira (1998) and Janz et al. (2006), who showed that species richness in butterfly family Nymphalidae was strongly correlated with diversity of host use.

1.5.3 Theory of Diffuse Coevolution or Community Coevolution

The theory of diffuse coevolution proposes that, instead of the pairwise reciprocal evolutionary interactions, coevolution must be considered in a community context and not simply as a reciprocal two-species interaction. Every plant may be affected by a diversity of herbivores, plant pathogens, competing conspecifics, plants of other species including alternate host plants of insect pests and organisms at higher tropic levels (Fox 1988). This theory is thus only an extension of the coevolutionary theory.

1.5.4 The Geographic Mosaic Theory of Coevolution

This theory states that the coevolutionary process operates at the level of populations rather than at species level. Thompson (1994, 1999, 2005) propounded that interspecific interactions commonly differ in outcome among populations. These differences result from the combined effects of differences in the physical environment, the local genetic and demographic structure of populations and the community context in which the interaction occurs. As a result of these differences in outcomes, an interaction may coevolve some populations (coevolutionary hot spot), affect the evolution of only one of the participants in other populations (coevolutionary cold spot) and have no effect on evolution in yet another local population (again coevolutionary cold spot). In addition, populations differ in the extent to which they show extreme specialization to one or more species. Some populations may specialize on and sometimes coevolve locally with only one other species, other populations may specialize on and perhaps coevolve with different species and yet others may coevolve simultaneously with multiple species. These interpopulational differences in outcome and specialization create a geographic mosaic in interactions. Gene flow among populations, random genetic drift, selection for novel traits and extinction of some demes reshape the geographic mosaic of coevolution as the adaptations and patterns of specialization developed locally spread to other population or are lost. The result is a dynamic geographic pattern of coevolution between any two or more species.

The coevolutionary relationship between the obligate seed predator, the camellia weevil, *Camellia japonica* Linnaeus, and its host plant, the Japanese camellia, *Camellia japonica* Linnaeus, represents an interesting example of geographic mosaic across the Japanese islands (Toju and Sota 2006, Toju et al. 2011). The thickness of camellia pericarp through which the female weevils bored to lay eggs into seeds correlated with the length of rostrum in females. Further, the pericarp was significantly thicker on islands with weevils than on islands devoid of weevils, and the trait was heritable.

1.6 Practical Applications of Insect-Plant Interrelationships Research

An intricate understanding of insect-plant relationships has immense practical significance for future agricultural production. As consumers of plant products, humans wish to minimize crop losses caused by all other organisms including insect pests and maximize crop productivity. The mechanisms underlying insect-plant interactions are the key to achieve these objectives in the following ways.

1.6.1 Breeding Insect-Pest-Resistant Crops

Insect-resistant cultivars represent one of the most environmentally benign, economically feasible and ecologically sustainable options for management of insect pests. The breeding of arthropod-resistant plants has been undertaken for more than a century and blossomed as a field of research in the first half of the twentieth century with the work of Prof R H Painter at Kansas State University, Manhattan, Kansas, USA (Painter 1951). An outstanding early success in utilizing host plant resistance in pest management was the control of the grape phylloxera *Daktulosphaira vitifoliae* (Fitch) in France by grafting European grapevines onto resistant North American rootstocks (Painter 1951). In India, the early work of Hussain and Lal (1940) led to hairy cotton varieties resistant to jassid, and by 1943 resistant varieties such as Punjab 4F, LSS and 289 F/43 covered extensive areas, where jassid had posed a serious threat. Over the past 70 years, breeding stress-resistant crops has gained increased importance with the involvement of national and international agricultural research centres as well as private sector seed producers. Hundreds of insect-resistant crop cultivars have been developed worldwide and are grown extensively for increasing and stabilizing the crop productivity (Panda and Khush 1995). In economic terms, the arthropod resistance genes deployed in global agriculture currently save us more than US$2 billion annually (Smith and Clement 2012).

Identification of the mechanism of resistance to insect pests followed by isolation and cloning of gene(s) responsible for production of the desired chemical/characteristic is likely to fast-track the production of insect-resistant cultivars. An improved understanding of plant defence responses to herbivory is also essential for further exploitation of induced resistance and plant-released volatiles for development of insect-resistant genotypes (Sandhu and Arora 2013). Exploitation of insect-resistant genes from unrelated organisms (mainly microbes) and their incorporation into elite germplasm is another fruitful approach which has found widespread application. A total of 20 Bt genes from the soil bacterium, *Bacillus thuringiensis*, imparting resistance to lepidopteran and coleopteran pests have been incorporated into cotton, corn, soybean, potato and other crop plants (Shera and Arora 2015).

1.6.2 Cultural Control of Insect Pests

The manipulation of crop production and management techniques for reducing or avoiding pest damage is known as cultural control. An understanding of crop plant-insect pest relationship is useful to modify the crop environment against the pest or in favour of the natural enemies. For instance, early sowing/planting has been found to reduce gall midge and leaf folder damage in rice, shoot fly and headbug damage in sorghum and millets, white grubs' damage in groundnut and aphid damage in crucifers in Northern India (Dhaliwal and Arora 2006).

Increasing intra-field diversity through intercropping, trap cropping or planting of hedge rows results in reduced damage by several species. Tomato intercropped with cabbage has been reported to reduce incidence of diamondback moth. Trap crop of African marigold lowers the incidence of fruit borer *H. armigera* in tomato (Srinivasan 1994). Napier grass and Napier millet serve as trap crops for lowering the incidence of stem borer *C. partellus* in maize and sorghum (Khan 1999; Dhaliwal and Arora 2006).

The parasitoids and predators of insect pests may attain higher population densities in polycultures than in monocultures, because polycultures often offer additional food sources, such as honeydew, nectar and pollen, and more refuges where insects can shelter in the shade (Coll 1998). More than half among the 130 natural enemy species surveyed reached higher population densities in polycultures, than in monocultures, whereas in less than 10% of the cases, lower population densities were observed (Andow 1991).

1.6.3 Botanical Insecticides

Plants have developed pathways to a diverse array of chemicals to prevent their exploitation by insects and other herbivores over millions of years. These chemicals exert behavioural, physiological and biochemical effects on insects, and some of these may even cause mortality in susceptible insects. Botanicals insecticides, as these plant-derived products are known, have been utilized by humans since ancient times. Neem, pyrethrum, *Tephrosia*, tobacco, derris, *Ryania*, sabadilla and many other plants have been used to protect agricultural crops, grains and other commodities from the ravages of insects and noninsect pests in different parts of the world for centuries (Dhaliwal and Arora 2001).

Phytochemicals have also served as prototypes for synthesis and development of novel groups of insecticides. For instance, pyrethrum, derived from the dried flowers of *Chrysanthemum cinerariaefolium* Linnaeus, has been used as an insecticide since ancient times. It is a potent toxicant against insects and comparatively safe to mammals. But it is highly photolabile (Casida 1973). Therefore, the chemical structure of pyrethrum was elucidated to develop synthetic analogues with improved photostability. Many of these chemicals like fenvalerate, deltamethrin, fluvalinate and cyfluthrin became popular insecticides during the 1980s (Dhaliwal and Arora 2006). Similarly synthetic analogues of nicotine, another popular botanical insecticide obtained from tobacco, called neonicotinoids are currently widely used against a broad range of sucking insect and mite pests (Simon-Delso et al. 2015). Thus, botanical insecticides have not only proved useful directly in pest control but have also served as models for generation of new classes of synthetic insecticides. Since plants contain tens of thousands of such chemicals, the scope of their utilization in insect pest management is almost endless.

1.6.4 Biological Control of Insect Pests

The importance of studies on tritrophic and multi-trophic interactions for enhancing the efficiency of natural biological control and integrated pest management can hardly be over-emphasized. Plant-produced volatiles are known to attract natural enemies of insect pests (Weseloh 1981). Ramachandran et al. (1991) reported that the parasitoid *Microplitis demolitor* Wilkinson was attracted by the volatile 3-octanone released by the soybean plant which hosts the soybean looper, *P. includens*. The parasitoid was markedly more arrested by the volatile guaiacol, which was found only in its hosts' frass. But all such interactions may not favour the natural enemies. Hare (1992) found the spectrum of interactions between natural enemies and crop resistance to range from synergistic, to additive, to none apparent, through to disruptive or antagonistic. Dhaliwal et al. (2004) conducted a meta-analysis of 27 studies on interaction of resistant crop cultivars and biocontrol of insect pests. Antagonism was recorded in 29.6%, synergism in 25.9% and additive relationship in 33.3% of cases. In the remaining three cases, the form of relationship varied with resistant level of the cultivars employed. As knowledge of these multi-trophic interactions expands, researchers and IPM practitioners need to exploit it for management of insect pests (Verkerk 2004).

1.6.5 Behavioural Manipulation in Insect Pest Management

Insect behaviour is elicited in response to olfactory, visual, tactile, acoustic and gustatory-sensory information from the host plant as well as the surrounding environment. An improved understanding of cues utilized by insects for feeding and oviposition preference on host plants can help in manipulation of such behaviour, leading to reduced crop damage (Foster and Harris 1997).

The attract and kill method is by far the most popular behavioural manipulation utilized in pest management. The Japanese beetle *Popillia japonica* Newman is successfully managed by a combination of the female sex pheromone, with a food lure (a mixture of phenethyl propionate, eugenol and geraniol) (Ladd et al. 1981). Foods baits have also been found useful for monitoring and controlling tephritids. Protein-hydrolysate-baited traps containing insecticides have been successful against the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann, in the USA

(Chambers 1978). An innovation of the ‘attract-annihilate method’ has worked against the apple maggot fly, *Rhagoletis pomonella* (Walsh). The female flies locate host trees and suitable oviposition sites on apple through olfactory and visual stimuli. Wooden spheres in red colour and covered with a sticky substance at one trap tree^{-1} afforded good protection of fruits from *R. pomonella* (Aluja and Prokopy 1993; Foster and Harris 1997).

1.6.6 Push-Pull Strategy for Management of Insect Pests

An innovative manipulation of the behavioural approaches is the push-pull IPM or stimulo-deterrent approach in pest management. It involves utilization of attracting (pull) and repelling (push) components in tandem to divert the pest away from the main crop and towards the trap crop, from where these may be subsequently removed (Khan et al. 1997; Cook et al. 2007). The technology has been successfully applied for management of several species of stem borers (*C. partellus, Eldana saccharina* Walker, *Busseola fusca* Fuller, *Sesamia inferens* Hampson) infesting maize and sorghum in Eastern and Southern Africa. The ovipositing female moths of borers are repelled from the main crop by repellent non-host intercrops, particularly molasses grass, silverleaf desmodium or greenleaf desmodium (push), and prefer to oviposit on attractive trap plants, primarily Napier grass or Sudan grass (pull). Intercropping of molasses grass with maize increased parasitization by *Cotesia sesamiae* Cameron in addition to lowering the incidence of stem borer (Khan et al. 2011). Push-pull strategies have also been effectively demonstrated against *Helicoverpa* in cotton, *L. decemlineata* in potato, striped pea leaf weevil *Sitona lineatus* (Linnaeus) in beans, rapeseed pollen beetle *Brassicogethes aeneus* (Fabricius) in oilseed rape, onion maggot *Anthomyia antiqua* (Meigen) in onions, western flower thrips, *Frankliniella occidentalis* (Pergande) in chrysanthemum and bark beetles (Scolitidae) in conifers, in addition to several veterinary and medical pests (Cook et al. 2007).

1.6.7 Managing Insect Biotypes

The continuous growing of insect-resistant cultivars exerts selection pressure on the targeted pest, which responds by developing new physiological and behavioural mechanisms to enable feeding and development on the resistant cultivars. Insect biotypes refer to populations within an insect species that can survive on and destroy varieties that have genes for resistance (Heinrichs et al. 1985). Biotype selection is one of the major constraints encountered in breeding programmes for varietal resistance. The concept of biotypes involves gene-for-gene relationship between the gene for resistance in the host plant and the gene for virulence in the insect pest. Aphids comprise 18 of the 39 insect species in which 2 or more biotypes have been reported (Sandhu and Arora 2013). Brown plant hopper, *Nilaparvata lugens* Stal, on rice (Brar et al. 2015) and Hessian fly, *M. destructor* on wheat are the major pests in which biotype development has led to breakdown of resistance in the field (Aggrawal et al. 2014; Subramanyam et al. 2015). The durability of insect resistance can be increased by sequential release of cultivars, gene pyramiding/stacking and gene rotation (Sandhu and Arora 2013). An improved understanding of insect-plant interactions is crucial for efficient management of insect biotypes resulting in greater stability of resistant genotypes.

1.6.8 Biological Control of Weeds

The losses caused by weeds are estimated to be higher than those caused by insect pests to agricultural crops and the global use of herbicides exceeds that of insecticides in crop protection (Oerke 2006). In view of the widespread problems caused by extensive use of herbicides, there is an urgent need to strengthen biological control of weeds. Exotic weeds may be successfully managed by introducing monophagous or oligophagous insect species from the plants' place of origin. Important successful examples include management of shellmound prickly pear, *Opuntia stricta* (Haworth) Haworth, in Australia through releases of the small Argentinian moth, *Cactoblastis cactorum* Berg (Dodd 1940), and of giant salvinia, *Salvinia molesta* D. S. Mitchell, in Papua New Guinea by releasing the weevil *Cyrtobagous salviniae* Calder & Sands imported from Brazil (Room 1990). In Hawaii extensive programmes on biological control of weeds through releases of herbivorous insects as well as pathogens have been undertaken, resulting in complete control of 7 out of 21 target weed species and significant partial control of another 3 species (Gardner et al. 1995; McFadyen 2003).

In some cases, the native insects have also been artificially multiplied and released or otherwise manipulated for the control of native weeds. Native coccids, *Austrotachardia* sp. and *Tachardia* sp., are used for the control of *Cassinia* sp., native woody shrubs in Australia (Holtkamp and Campbell 1995). Conservation/augmentation of the stem-boring agromyzid, *Phytomyza orobanchia* Kaltenbach, has been utilized for managing the parasitic weeds, *Orobanche* spp. in the southern USSR (Kroschel and Klein 1999).

1.6.9 Pollinator Conservation for Improving Crop Productivity

Insect pollinators are essential for successful pollination and reproduction by a vast majority of terrestrial flowering plants. Even self-pollinating crop species may show yield enhancement in vicinity of a good pollinator habitat. Coffee shrubs, for instance, show significant yield increases in regions with stable native or introduced bee populations (Roubik 2002). Most studies on plant-pollinator systems have focused on a single plant species and usually one or a few closely associated visitor taxa. But recent studies have revealed that pollinator complexes are relatively generalized, due to spatiotemporal variation in pollinator visits (Herrera 1996; Waser 1998; Burkle and Alarcon 2011). It is important to understand the bases of spatial and temporal variation in plant-pollinator interactions to answer questions in community structure and function. It will also help in formulating optimal conservation strategies (Burkle and Alarcon 2011). Climate change may disrupt the synchrony between the flower production season of plants and the activity period of pollinating insects. A shortage of nectar and pollen during critical periods may also lead to a decline in population of pollinators (Hoover et al. 2012; Sharma et al. 2014). A precise understanding of the flowering plant-pollinator interactions may help in arresting pollinator decline and maintaining agricultural productivity.

1.7 Conclusions

Insects and green plants, the two dominant life forms in the terrestrial ecosystem, are bound together by intricate relationships. A majority of the angiosperms require the services of pollinating insects for successful reproduction. The shape, size, colour and scent of flowers all serve to attract pollinators, which mostly feed on nectar and pollen produced by these plants. Further, nearly half of all insect species are herbivorous and depend on plants for food, shelter (at least for a part of life cycle) and oviposition sites. Consequently, the plants have evolved a staggering variety of structural and biochemical barriers to protect themselves from insects and other herbivores, as well as pathogens. The insects which are able to overcome these barriers (through avoidance, detoxification, sequestration, etc.) can gain an abundant supply of food with very little competition from other herbivores. Reciprocal adaptation and counter-adaptation between plants and insects have, thus, been an important mechanism driving a steady increase in biodiversity of both these groups of organisms over the last more than 400 million years.

The study of these interrelationships between insects and flowering plants is of great practical importance for future agricultural production. We are only just beginning to understand the intricacies of these relationships. The new techniques of molecular biology including genomics, proteomics and RNAi offer exciting opportunities for further exploration and precise understanding of insect-plant interactions, which is essential for conserving ecosystem biodiversity and developing insect-resistant crop plants, as well as for sustainable management of insect pests and weeds.

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