# Ecology and Evolution of Insect-Plant Interactions

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**Abstract**

Interaction between herbivores and plants is essential for ecosystem functioning. Phytochemical variation in plants is one of the most fascinating yet bewildering properties of the natural world and has important implications for both human health and the functioning of the ecosystem. One of the key aspects of plant phytochemical research is to study the insects that feed on plants which are one of the driving forces behind the development of chemical diversity in plants. Decoding their interaction from molecular to the ecological level is important for developing a comprehensive understanding of their interaction that has shaped their evolutionary history. Applications of advanced technologies and collaborative work between molecular biologists, geneticists, ecologists, evolutionary biologists, and biochemists will unravel their complex interactions for meeting future challenges. In this chapter, we have emphasized on the ecological perspective of the two interacting system and how it has led to evolution of certain traits in them.

**Keywords**

Insect herbivory · Constitutive defense · Induced defense · Secondary metabolites · Coevolution

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# 1    Introduction

Plant-insect interactions are one of the oldest kinds of interactions that nature has been witnessing since the time the two came into existence. The evolution of plants on Earth gave birth to the diverse form of life; most important and the oldest relationship that it has shared is with insects. The association between them probably dates back to 390 million years which is indicated by the molecular dating of the records of a holometabola (Rehm et al. 2011). Due to the preservational artiefact and fragmentary remains, the actual earliest coexistence cannot be ascertained so far. However, with the findings of the first complete insect fossil of Late Devonian, at least their existence during that period is established (Garrouste et al. 2012). Since then, these two organisms are constantly interacting with each other for their own benefit and to develop strategies to overpower the other.

The large diversity of insects, which is estimated to be more than 500,000 known species, is often attributed to their close association with land plants (Kerogoat et al. 2017). Insects derive benefits for their food, shelter, mate selection, and oviposition from plants, and plants, in turn, try to evade the herbivore attack by developing physical and chemical mechanisms (Ehrlich and Raven 1964). It is not just the damage that plants have to face from insects, but they do get benefit from insects in their defense and pollination (Panda and Khush 1995). In doing so, each has to pay the cost or, in other words, be subjected to the pressure of developing strategies to overcome the attack by the insects. Thus the interaction between the two systems exists in dynamicity, which is subjected to variation depending on the kind of pressure exerted by one on the other. Insect feeding impacts both the phenotype of the plant (Kessler and Baldwin 2002; Mithofer and Boland 2012) and the well-defined plant chemistry (Schoonhoven et al. 2005), which in turn impacts plant interactions with its other linked community (Stam et al. 2014). A diverse array of chemicals that are synthesized by plants are usually allocated into primary and secondary chemicals, though the two remain intertwined, and the division is arbitrary and for convenience. The primary metabolites such as carbohydrates, lipids, and proteins are the basic need for plant biological processes and they also serve vital nutrients for herbivorous insects (Scriber and Slansky 1981; Schoonhoven et al. 2005). Plant-derived secondary chemicals, which have recently been termed "specialized metabolites," are the compounds like glucosinolates, alkaloids, terpenoids, tannins, etc. which often not openly intricate in basic plant metabolism but have evolved to cope with heavy herbivory, and they have grown in different plant heredities to help them adjust to specific ecological situations and are essential to improve plant's fitness (Schilmiller et al. 2008; Pichersky and Lewinsohn 2011; de Brito and Martinoia 2018). Diversity of specialized chemicals derived from plants across different species is tremendous and likely exceeds 200,000 (Tissier et al. 2014). Insects also evolved to survive against these metabolites by developing counter mechanisms to detoxify or circumvent plant defense systems. Studies have shown that coevolution is the outcome of community interactions across time and space. Therefore mere understanding of the mechanistic process between the two would provide the base of this relationship, but research in entomological,

ecological, and evolutionary context and genetic and molecular approach would probably give us a panoramic view of this interaction. In the last few years, researchers in both basic and applied sciences have been continually working to decipher the complex interaction existing between the two. This has been revolutionized with the advancement of genomic tools including next-generation sequencing (NGS), gene-editing technology, etc. (Hermsmeier et al. 2001; Hui et al. 2003). In this review, the ecological as well as evolutionary aspects of insect-plant interaction will be dealt with more recent findings.

## 2     Ecological Traits of Insect-Plant Interaction

There are two types of interactions that exists between insects and plants – the plant-pollinator interactions and the herbivore-plant interaction both of which are considered to be specialized interactions (Futuyma and Moreno 1988; Cook and Rasplus 2003). However, plant-pollinator is more generalized in terms of its niche width than herbivore (Fontaine et al. 2009). These two interactions though different as one is greatly mutualistic and the other one is antagonistic but they are important in shaping the way the plants are and for their diversity, which in turn impacts the various adaptive modifications in insects. However, we will deal with the ecological concepts of insect herbivory only as insect-pollinator concept is beyond the scope of this book.

Recognition of the host plant by insect is a complex process involving multiple sensory modalities – olfactory, visual, tactile, and gustatory cues. With the successful input received from these cues, the insect is capable to choose its host. The selection of plants is determined at two levels – oviposition and larval-feeding stages (Schoonhoven et al. 2005). In both the stages, the selection of a plant is dependent on two factors-response of the insects to plant and characteristics of the plants which shapes the insect responses (Saxena 1969). In both situations, chemistry of plants plays a significant role in host plant selection (Schulz 1988) that acts both from a distance and in contact. Once in the vicinity of the plant or in contact with the plant, the physical characteristics of both plant and insects come into play. However, for the first phase of interaction to occur, it is the plant volatiles that are of prime importance. Insect tries to adopt the best of its strategies to overcome the noise of volatile bouquet emanating from different host as well as non-host species in the field (Randlkofer et al. 2010) to be able to focus its senses efficiently to land on the appropriate plant for feeding or oviposition. As a result specialized and sensitive neurons have developed in the insects as an adaptation to the information processing problem (Bernays 1996). This may be one of the factors that largely favors the specialist insect herbivory with reduced diet breadth. Strong specialization is not only seen on specific plant but on specific parts and tissue of that plant (Gutbrodt et al. 2011; Kimmerer and Potter 1987; Gall 1987). This specificity depends on several parameters like the texture of the plant part, its age, morphology, kind of mouthpart insect possesses, etc. (Pecetti et al. 2010; Schoonhoven et al. 2005). Insect tries its best to utilize the resources of the host plant to maximize its fitness. After

landing on the plant, the structural characteristics like trichomes, wax crystals, surface texture, etc. and the chemical profile of the plants play a vital role in final selection of the host by the insects.

## 2.1 Plant Actions to Insect Herbivory

Responses of plants to herbivores are complex. For the plants that are rooted and immobilized, nature has bestowed upon them the plasticity in their morphology, growth, development, etc. to respond to environmental variability. These adaptabilities are the result of their ability to anticipate or detect change in ecological conditions and respond accordingly (Casal et al. 2004). They have developed sensory mechanisms to recognize the danger of herbivory and activate their defense mechanism to respond accordingly. Both physical and chemical defense have developed in plants to counter the attack of insects and pathogens. It is the interplay of these chemical and physical defense mechanisms that defends the plant from herbivory, and these defense systems have complex interactions from molecular or genetic to the level of ecology (Dicke et al. 2009). For understanding such a complex process, researchers adopt a reductionist approach by concentrating on only one level of plant defense either molecular or genetic or ecological and then try to extrapolate their findings to get a comprehensive understanding of this interaction. In short, it can be stated that the interaction of the plant and insects at the ecological level is the outcome of the interactions of the cascade of genes at the molecular level. Herbivore attack results in a cascade of gene activation. With the advancement in molecular approaches, such as whole-genome sequences, microarrays, differential cloning techniques, etc., changes in gene expression profiles in herbivore-damaged plants have been investigated extensively in recent years (Korth 2003; Hermsmeier et al. 2001; Hui et al. 2003). However, the discussion in this chapter is limited to the ecological perspective.

### 2.1.1 Defensive Types

Plants have adapted themselves to insect and pathogen attack by evolving constitutive and induced defense mechanisms. Defenses through constitutive way are inherently present in the plants, and induced defenses are the ones which are activated by the attack of herbivore or pathogens. These defenses can be provided by the mechanical structures like thorns, leaf surface wax, trichomes, etc. which form the primary physical barriers to the ovipositing and feeding herbivore and/or can be provided by the chemical barriers such as nonvolatile chemicals (e.g., antinutritive enzymes, toxins, and deterrents) that form the next barrier defending the plants from their succeeding attack (Kessler and Baldwin 2002; Hanley et al. 2007; Schilmiller et al. 2008; Runyon et al. 2010) or volatile organic chemicals (VOCs) that are released against the attack of herbivore. The physical traits and nonvolatile chemicals are considered as direct defense system as they act directly against the aggressor, whereas the VOCs are considered as the indirect defense system of the plant as they deploy natural predators of herbivore like parasitoids to

manage the populations of the herbivores, and they also serve to pass signals for plant-plant communication (Karban and Baldwin 1997; Dudareva and Pichersky 2008).

Apart from the volatile chemicals, some physical structures of the plants also contribute towards the indirect defense system. Plants, by possessing domatia, provide nesting or refuge sites to predators to get indirect defense from herbivores (Heil 2008). Recently, glandular trichome structures have been found to contribute in the indirect defensive mechanisms (Weinhold and Baldwin 2011). Glandular trichomes emit diversified secondary molecules including terpenoids, flavonoids, and alkaloids that can act as a chemical and structural defense (Hanley et al. 2007; Sharma et al. 2009). Diverse defensive chemicals are plant toxins, so the chemicals for constitutive defense are synthesized and stored separately as inactive precursors, like glycosides, to avoid poisoning themselves (Jones and Vogt 2001), which ensures separation from the activating enzymes.

Both the direct and indirect defenses can be constitutive and induced defense system. In response to herbivory on lima beans (*Phaseolus vulgaris*) and *Acacia* tree, the plants were found to discharge nectar that attracted ants which protected the host from herbivores (Heil et al. 2004; Heil 2004). While volatiles are usually secreted in a programmed manner but the quality and quantity of the VOCs may change under stress from herbivore or pathogen attack (Heil 2008). The herbivore-induced plant volatile (HIPV) contains more than 200 chemicals (Dicke and van Loon 2000) (Fig. 1) which function in an orchestrated manner to defend the plant from the insect herbivory. During quantitative changes, the volatiles existing in the non-induced plants are secreted in higher amounts or the comparative abundance is changed (e.g., Mumm et al. 2003; Bukovinszky et al. 2005). Qualitative changes indicate production of de novo many chemicals in plants resulting in the qualitative modifications of the volatile emissions (Turlings et al. 1998; Dicke 1999; Leitner et al. 2005). Plant genotypes are also associated with the kind of the volatile mixture released after such attack (Halitschke et al. 2000; Fritzsche-Hoballah et al. 2002). Other important factors include light or nutrients (Gouinguene and Turlings 2002; Fritzsche-Hoballah et al. 2002), the mode of damage (Mithöfer et al. 2005), developmental stage of the aggressive herbivores and the species (Ozawa et al. 2000; Heil 2008), kind of the herbivore (Paré and Tumlinson 1997), and egg deposition (Hilker and Meiners 2006). The plant volatile emissions are triggered by the elicitors present in the saliva of the insects but cannot be induced by the mechanical damage of the plant (Truitt and Pare 2004; Schmelz et al. 2006). For example, volicitin (N-(17-hydroxylinolenoyl)-L-glutamine) compound isolated from the oral emissions of caterpillars (beet armyworm) was found to attract parasitic wasps and the natural predators of the caterpillars, but the mechanical injury of the leaves did not attract the natural enemies (Alborn et al. 1997). The HIPVs are also involved in decreasing the rates of oviposition by the herbivores and thus are a part of both direct and indirect defense systems (Dicke and van Loon 2000; Kessler and Baldwin 2001).

Previous research gives an insight into the plant acute sensory capacity highlighting the mechanism of chemoreception in plants (Mescher and de Moraes
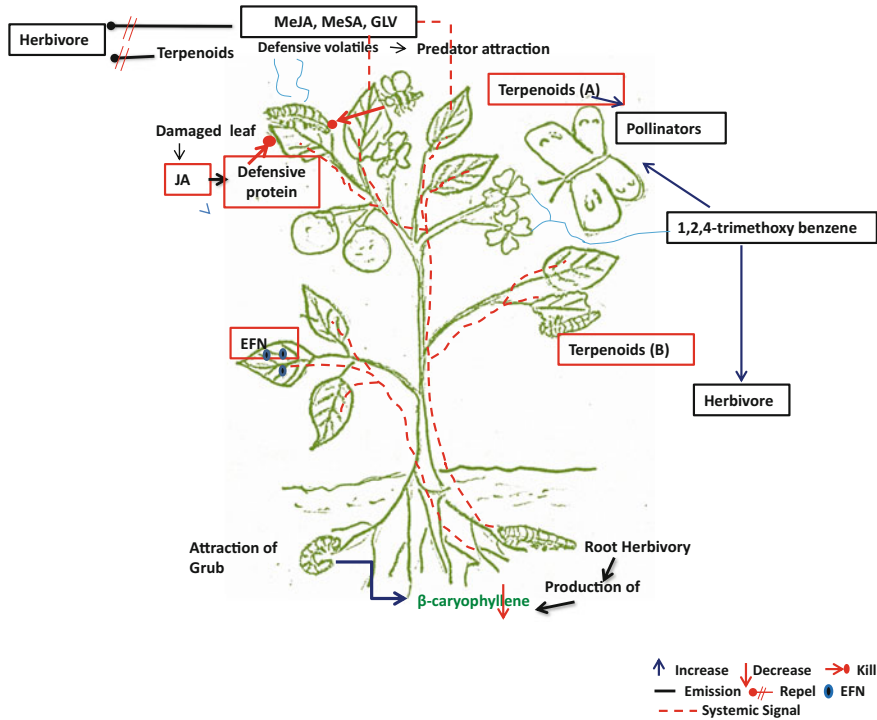
**Fig. 1** Communication between plants and insects. Root herbivory results in production and increase of β-caryophyllene, which attracts beetle larvae. Herbivory-damaged leaves work in two ways – firstly by release of defensive volatiles [terpenoids (A), MeJA (methyl jasmonic acid), MeSA (methyl salicylic acid), and GLV (green leaf volatiles)] that attract the predator and secondly by the release of jasmonic acid (JA), defensive proteins, and terpenoids (B) which will repel the insects from further attack. Other volatiles like 1,2,4-trimethoxy benzene from the plants serve to attract both the pollinators and herbivores, but the terpenoids (B) stored in glandular trichomes will serve to repel the herbivore. Root herbivory also increases EFN (extrafloral nectar) (Das et al. 2012)

2015). Mechanical response like sudden closure of leaves of *Mimosa pudica* on touch is commonly alleged to function as a herbivory defense, possibly by startling or physically displacing herbivores, decreasing the leaf apparency, or promoting the defensive thorn display (Braam 2005), which is again a type of direct defense of plants. Similarly, vibrations linked with herbivore mastication result in the release of defensive chemicals in *Arabidopsis*, even over less distance from the wounding site (Appel and Cocroft 2014). Such vibrations along with other phytohormonal signalling pathways like jasmonic acid or salicylic acid pathway cause a systemic response in the plants. The vibrations also travel between plants through stems or roots, sending the distress signals to the nearby plants, signalling them for the herbivore presence and triggering the defense processes in them (Cokl and Virant-Doberlet 2003).
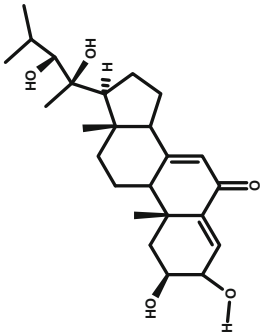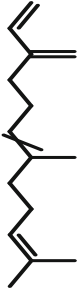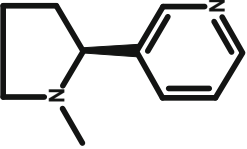
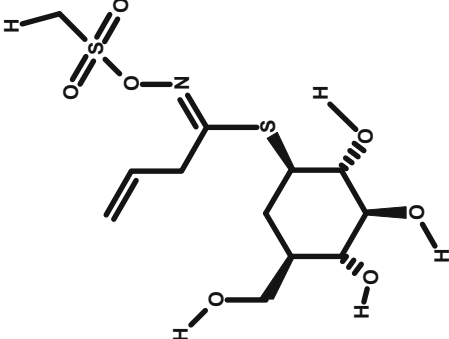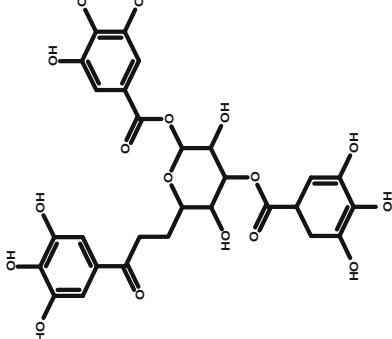### 2.1.2    Plant Specialized Metabolites Against Insect Herbivores

Chemical defense in plants is provided by the specialized metabolites that work against insects and pathogens (Fraenkel 1959) besides their role to mediate interactions with other biotic components and abiotic stresses (Sharkey et al. 2001; Munné-Bosch 2005; Karban et al. 2006; Heil and Karban 2010; Lucas-Barbosa et al. 2011). So far, >1700 chemicals have been isolated from different families of plants (Pichersky and Gershenzon 2002). Their diversity in terms of number, functionality, structure, etc. makes it difficult to draw a clear classification system. However, a simple classification system widely followed divides these metabolites into three main groups: the terpenoids (composed almost entirely of carbon and hydrogen), nitrogen-containing alkaloids, and phenolics (Schoonhoven et al. 2005). The specialized plant chemicals which are found active against insect herbivores are listed in Table 1.

These metabolites have variable impacts on the fitness of the insects as well as their behavior and physiology. Only the effects of a few representative chemicals are discussed in this chapter being dealt with in detail. Terpenoids are the chief group of all known secondary derived compounds and exhibit extreme structural diversity and as a result diverse chemical properties and functionality (Nagegowda 2010). Monoterpenes among them are the most abundant volatile terpenoids that play a crucial role in herbivore defense. They act as feeding deterrents largely but are also reported to affect the oviposition behavior of the insect (Mumm et al. 2008). Another group of secondary metabolites, glucosinolates, present in plants belonging to Brassicaceae family are important component in plants' constitutive defense system (Hopkins et al. 2009).

Alkaloids, another important secondary metabolites, are natural organic compounds containing a heterocyclic ring with nitrogen, which serve as plant growth inhibitors as well as feeding deterrents (Saunders et al. 1992). Studies have shown that alkaloids exhibit high feeding deterrency to *Lymantria dispar*, *Spodoptera litura,* and *Lipaphis erysimi* (Shields et al. 2008; Ge et al. 2015). Plant phenols are another common group of plant defense playing a chief role in host resistance and are effective on both herbivore insects and microorganisms (War et al. 2012). Synthesis of lignin, a phenolic heteropolymer, is induced by herbivory, and it results in increasing the toughness of the leaf, thereby reducing the herbivore feeding (Johnson et al. 2009). Flavonoids and isoflavonoids also provide protection against the pests as they are potent antifeedants and have effects on the development and growth of the insects. Approximately, more than 5000 flavonoids have been characterized in plants. For example, flavonoids extracted from Tephrosia..T. vogelii were found to be a strong feeding deterrent against Spodoptera sp. (Simmonds et al. 1990). Overexpression of transcription factor, which manages major flavonoid synthesis in *Arabidopsis* was found to confer resistance against *Spodoptera frugiperda* (Johnson and Dowd 2004). Tannins, another secondary metabolite, reduced the growth rate of pests (Schoonhoven et al. 2005), act as feeding deterrent (Feeny 1968; Bernays 1981), and affect the composition of insect communities (Whitham et al. 2006).
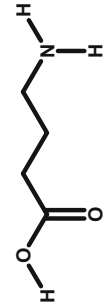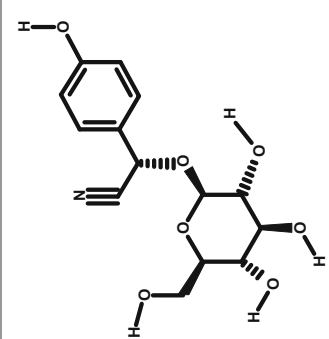
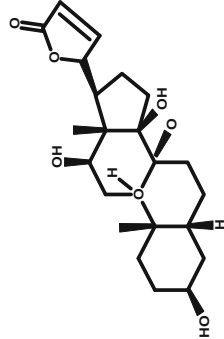**Table 1** List of some of the common secondary plant metabolites

| Source | Compounds | Plant family | Chemical structure | References |
|---|---|---|---|---|
| Steroids | Phytoecdyson | Ranunculaceae |  | Bakkali et al. (2008) |
| Terpenoids | (E)-Beta-farnesene | Ubiquitous |  | Aharoni et al. (2003) |
| Alkaloids | Nicotine | Solanaceae |  | Mithofer and Boland (2012) |

| Glucosinolates | Sinigrin | | Capparales |  | Hopkins et al. (2009) |
| Phenolics | Tannin | | Ubiquitous |  | Coley (1986) |

**Table 1** (continued)

| Source | Compounds | Plant family | Chemical structure | References |
|---|---|---|---|---|
| Amino acids | γ-Aminobutyric acid | Fabaceae |  | Huang et al. (2011) |
| Glucosides | Dhurrin | Rosaceae |  | Vetter (2000) |
| Silica | Silicon dioxide | Poaceae |  | Reynolds et al. (2009) |
| Cardenolides | Digoxigenin | Plantaginaceae |  | Mithofer and Boland (2012) |

## 2.2      Insect Responses to Plant

Insects have developed various ways to enable them to exploit their hosts (Panda and Khush 1995). Insects are dependent on plants, and therefore their community composition is largely influenced by the plant morphology, physiology, chemistry, and genetics (Bukovinszky et al. 2010; Ohgushi 2008). These attributes of plants influence the behavior of insects on their settlement, feeding, growth and development, oviposition, etc. However, it is evident that whatsoever strategies plants evolve to evade insect attack, insects also developed ways to overcome them and are one of the most successful organisms in terms of variety of species and their geographical distribution (Price 1997).

Generalist insects are mostly highly sensitive to defensive compounds of the plants, while specialist insects will utilize these compounds as cues of recognition (Ali and Agrawal 2012; Gols et al. 2008; Schoonhoven et al. 2005). The difference in the responses of the two groups is due to the fact that insects have adapted to plant chemicals through specific sequestration or detoxification mechanism, whereas generalist insects are either incapable to grow or show reduced survival on these plants (Ali and Agrawal 2012; Hopkins et al. 2009). Insects have developed a wide array of enzymes as defense against the various compounds produced by the plants. One of the strategies adopted by insects is to detoxify the plant chemicals by reduction, oxidation, conjugation, or hydrolysis of the compounds (Scott and Wen 2001). Largely the detoxification of plant compounds by insects is done by cytochrome P450 (CYP450)-dependent monooxygenases (Mello and Silva-Filho 2002). In some cases, insects sequester the toxic compound in a manner that enable them to use it for their own defense against parasitoids (Nishida 2002) or feed on those part of the plants that lack this compound (Zangerl 1990). In the tobacco hornworm, insects are able to store the nicotine of the plant which is otherwise toxic to other pests, and they utilize the sequestered nicotine as parasitoid deterrents (de Bruxelles and Roberts 2001).

## 3      Evolution of Insect-Plant Interaction

Unraveling the evolutionary relationship between insects and plants has been a matter of extensive research in the biologist community. Different workers have given different theories to underline the evolutionary relationship between them. The most common perspective is that of coevolution (Ehrlich and Raven 1964), which explains the diversity of insects as a filler of niches resulted due to diversification of the plants, which was, in turn, the result of the development of the defensive chemicals in plants in response to herbivory. However, the term "coevolution" being very broad is used in different perspectives like *co-speciation and reciprocal adaptation* and as a concept of "*escape and radiation*" to explain the evolutionary processes that have modelled the insect and plant diversity.

According to Janzen (1980) and Futuyma and Slatkin (1983), coevolution can be explained by the process of reciprocal adaptation where evolutionary changes in a

species bring about changes in evolution in another species through the natural selection. The account of co-speciation of plants and insects can be well understood by studying the interaction that exists between *Ficus* and agaonine wasps (Herre et al. 1996). In plant-insect herbivore interaction, the insect is the only one that is dependent on its partner, unlike in plant-pollinator interactions, which can be better explained by phylogenetic tracking evolution (escape and radiate) rather than co-speciation (Kerogoat et al. 2017).

Secondary plant metabolites present in plants are important from defense point of view (Fraenkel 1959) and are the result of the coevolutionary war between insects and plants that resulted in subsequent increase in the variety of different defensive compounds in plants (Ehrlich and Raven 1964). In an insect attack, the plants suffer by undergoing tissue damage and also by investing energy for the development of resistance. These defense systems come with the cost of investing energy for the toxin synthesis and sequestration, developing resistance against the insect pests or self-toxicity (Gershenzon 1994; Baldwin and Preston 1999; Purrington 2000). These costs are a crucial component for the resistance evolution since an evolutionary equilibrium needs to be maintained for herbivory reduction and plant fitness (Paul et al. 2000). One way to reduce the investment by the plants is by developing inducible defenses whereby plant will invest in defense only (Agrawal 2000). Plants that are rarely attacked have therefore evolved the mechanism to reduce the cost involved by synthesizing defensive chemicals only upon a herbivore or pathogen damage (induced defense). In contrast, those plants which are likely to get frequent attack are better off in investing energy in constitutive defensive system (Wittstock and Gershenzon 2002). Review by Becerra (2015) highlights the macroevolutionary intensification of chemicals in plants as a result of selection pressure exerted by insect herbivore. Such pressures are responsible for escalation in varied chemical compounds and biosynthetic pathway through time in plants which in some cases have resulted in the addition of novel synthetic pathway, consequently delaying the counter adaptation by the herbivore indicating the *escape and radiate* kind of evolution (Ehrlich and Raven 1964; Kerogoat et al. 2017). Phylogenetic analysis based on character evolution and association is important to understand the underlying evolutionary trends of insect-plant interactions (Wanntorp et al. 1990; Harvey and Pagel 1991; Mitter et al. 1991). Studies comprising geographical variations in these interactions may provide an insight for such processes (Thompson 1999). The interaction between the two systems is very diverse and complex in true sense and needs more and more multidisciplinary research to understand the evolution of plant resistance and defense (Futuyma 2000).

## 4    Future Prospect of Understanding Insect-Plant Interactions

Understanding the complex interactions existing between plants and insects at the different multitrophic level has a significant implication in the field of agriculture and forestry. Communication between them which initiates at the molecular level

and reflected ultimately at the ecological level gives us an insight about their diversification and speciation process. Both the systems have tremendous role in the ecosystem; in fact it would not be exaggerating to say that the life system on the Earth revolves around the interaction and the functionality of the two. Research in this direction has revealed a lot of information between the two interacting systems, but with advancements in the molecular technology, more insights need to be developed that can be utilized for the more pertinent issues like ecological balance, food security, and sustainable development.

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