# Defense Mechanisms of Plants to Insect Pests: From Morphological to Biochemical Approach

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**Abstract**
Plant defense against insect herbivores is just one of multiple layers of interactions. In addition, plants are being utilized as nutrition source and shelter by parasitizing fungi, bacteria and viruses, along with vertebrates such as birds, lizards and mammals, as well as other invertebrates like worms and snails. Together with plants, these players are involved in complex interaction networks. To elucidate these fascinating interactions both biochemical and ecological studies, and combinations thereof, are required.
**Keywords**:  Insects, Defense mechanisms, Biochemical defense, Secondary metabolites

## 1. INTRODUCTION

Insects are one of the dominant forms of life in terms of the number of species and of individuals. Plants can have different types of interactions with insects, such as antagonistic interactions with herbivores and mutualistic interactions with carnivorous and pollinating insects. . Plants can defend themselves against insects by employing a 'do-it-yourself' strategy and/or by enlisting 'bodyguards' that attack herbivores. These plant strategies can be present constitutively or they can be induced by herbivory. Inducible defenses result in variable plant phenotypes and consequently in variable types of interactions with insects (Dicke M. 2001).

Plants respond to herbivore through various morphological, biochemical, and molecular mechanisms to counter/offset the effects of herbivore attack. According to Oerke (2006), each year there is a huge crop yield loss by different insect pests around the world. Therefore, understanding the defensive systems or mechanisms of plants enables development of resistant crops or pest management systems reducing the need of hazardous pesticides and supporting safer crop production. Another positive effect would be a reduction of the development of pesticide resistant pest strains.

Insect herbivores have traditionally been divided into generalists (polyphagous) that feed on several hosts from different plant families, or specialists (monophagous and oligophagous), which feed on one or a few plant types from the same family. The generalists tolerate a wide array of defenses present in most plants, while they cannot feed on certain plants that have evolved more unique defense mechanisms. Specialists, on the other hand, use a specific range of host plants releasing defense compounds that at the same time may function as feeding stimulants and provide ovipositioning cues (Da Costa and Jones, 1971).

Pegadaraju *et al.* (2005) stated that, the defensive mechanisms in plants operate at different levels. They vary from external defenses like thorns to complicated chemical responses leading to poisoning of the attacker. To overcome the insect attack, plants produce specialized morphological structures or secondary metabolites and proteins that have toxic, repellent, and/or antinutitional effects on the insect pests. In addition, plants also release volatile organic compounds that attract the natural enemies of the herbivores (Usha Rani and Jyothsna, 2010).

Resistance factors for direct plant defense against herbivorous insects comprise plant traits that negatively affect insect preference (host plant selection, oviposition, feeding behavior) or performance (growth rate, development, reproductive success) resulting in increased plant fitness in a hostile environment. Such traits include morphological features for physical defense, like thorns, spines, and trichomes, epicuticular wax films and wax crystals, tissue toughness, as well as secretory structures and conduits for latices or resins. They also include compounds for chemical defense, like secondary metabolites, digestibility reducing proteins, and antinutritive enzymes. All these traits may be expressed constitutively as preformed resistance factors, or they may be inducible and deployed only after attack by insect herbivores. The induction of defensive traits is not restricted to the site of attack but extends to non-infested healthy parts of the plants. The systemic nature of plant responses to herbivore attack necessitates a long-distance signaling system capable of generating, transporting, and interpreting alarm signals produced at the plant–herbivore interface. Much of the research on the signaling events triggered by herbivore has focused on tomato and other solanaceous plants. In this model system, the peptide systemin acts at or near the wound site to amplify the production of jasmonic acid. Jasmonic acid or its metabolites serve as phloem-mobile long-distance signals, and induce the expression of defense genes in distal parts of the plant (Howe and Schaller, 2008).

## 2. HOST PLANT DEFENSES AGAINST INSECTS

Plants respond to insect attack through an intricate and dynamic defense system that includes structural barriers, toxic chemicals, and attraction of natural enemies of the target pests. Both defense mechanisms (direct and indirect) may be present constitutively or induced after damage by the insects. Induced response in plants is one

of the important components of insect pest control in agriculture, and has been exploited for regulation of insect herbivore population.

Induced defenses make the plants phenotypically plastic, and thereby, decrease the chances of the attacking insects to adapt to the induced chemicals. Changes in defensive constituents of a plant on account of insect attack develop unpredictability in the plant environment for insect herbivores, which in turn, affects the fitness and behavior of the insects. If induced response occurs very early, it is of great benefit to the plant, and reduces the subsequent herbivore and pathogen attack, besides improving overall fitness of the plant. Plants with high variability in defensive chemicals exhibit a better defense compared with those with moderate variability (War *et al*., 2012).

## 2.1. Direct Defenses

Plant structural traits such as leaf surface wax, thorns or trichomes, and cell wall thickness/ and lignification form the first physical barrier to feeding by the insects, and the secondary metabolites such act as toxins and also affect growth, development, and digestibility reducers form the next barriers that defend the plant from subsequent attack. Moreover, synergistic effect among different defensive components enhances the defensive system of plants against the insects' invaders. For example, in tomato, alkaloids, phenolics, proteinase inhibitors (PIs), and the oxidative enzymes when ingested separately result in a reduced affect, but act together in a synergistic manner, affecting the insect during ingestion, digestion and metabolism. In a wild tobacco (*Nicotiana attenuate)*, trypsin proteinase inhibitors and nicotine expression, contributed synergistically to the defensive response against beet armyworm (*Spodoptera exigua)* (War *et al*., 2012). Now we will discussed below the role of morphological and biochemical constituents in host plant resistance (HPR), and induced responses to insect damage.

### 2.1.1. Morphological features for physical defense

Insect herbivores from all feeding guilds must make contact with the plant surface in order to establish themselves on the host plant. It is therefore not surprising that physical and chemical features of the plant surface are important determinants of resistance. All plant parts offer some sort of resistance against herbivory. They range from tissue hardness to highly complex glandular trichomes and spines. Epicuticular wax films and crystals cover the cuticle of most vascular plants. In addition to their important role in desiccation tolerance, they also increase slipperiness, which impedes the ability of many non-specialized insects to populate leaf surfaces. The physical properties of the wax layer as well as its chemical composition are important factors of preformed resistance (Howe and Schaller, 2008).

Based on different findings, plant structures are the first line of defense against insect pests, and play an important role in host plant resistance to insects. The first line of plant defense against insect pests is the erection of a physical barrier either through the formation of a waxy cuticle, and/or the development of spines, setae, and trichomes. Structural defenses includes morphological and anatomical traits that confer a fitness advantage to the plant by directly deterring the herbivores/insects from feeding, and range from prominent protrubances on a plant to microscopic changes in cell wall thickness as a result of lignification and suberization. Structural traits such as spines and thorns (spinescence), trichomes (pubescence), toughened or hardened leaves (sclerophylly), incorporation of granular minerals into plant tissues, and divaricated branching (shoots with wiry stems produced at wide axillary angles) play a leading role in plant protection against insect pests. Sclerophylly refers to the hardened leaves, and plays an active role in plant defense against herbivores by reducing the palatability and digestibility of the tissues, thereby, reducing the herbivore damage.

Spinescence includes plant structures such as spines, thorns and prickles. It has been reported to defend the plants against many insects. Pubescence consists of the layer of hairs (trichomes) extending from the epidermis of the above ground plant parts including stem, leaves, and even fruits, and occur in several forms such as straight, spiral, stellate, hooked, and glandular. Chamarthi *et al*. (2010) reported that leaf glossiness, plumule and leaf sheath pigmentation were responsible for shoot fly (*Atherigona soccata*resistance in sorghum *Sorghum bicolor* (L.) (Moench).

## Trichomes

The plant epidermis is often covered by outgrowths called trichomes. They are found in all major groups of terrestrial plants. They originate from epidermal tissue and then develop and differentiate to produce hair-like structures (Johnson, 1975). Trichomes play an imperative role in plant defense against many insect pests and involve both toxic and deterrent effects. Trichomes density negatively affects the ovipositional behavior, feeding and larval nutrition of insect pests. In addition, dense trichomes affect the insect mechanically, and interfere with the movement of insects and other arthropods on the plant surface, thereby, reducing their access to leaf epidermis. These can be, straight, spiral, hooked, branched, or un-branched and can be glandular or non-glandular. Glandular trichomes secrete secondary metabolites including flavonoids, terpenoids, and alkaloids that can be poisonous, repellent, or trap insects and other organisms, thus forming a combination of structural and chemical defense.

Induction of trichomes in response to insect damage has been reported in many plants (Agrawal, 1999). This increase in trichomes density in response to damage can only be observed in leaves developing during or subsequent to insect attack, since the density of trichomes of existing leaves does not change.  A given authors reported that damage by adult leaf beetles (*Phratora vulgatissima)* in *Salix cinerea* plant induced higher trichome density in the new leaves developing thereafter. Likewise, increase in trichome density in *S. cinera* in response to coleopteran damage has also been reported. Increase in trichome density after insect damage has also been reported in *Lepidium virginicum* L. and *Raphanus raphanistrum* L. In black mustard, trichomes density and glucosinolate levels were elevated after feeding by small white butterfly *(Pieris rapae)*. Furthermore, change in relative proportion of glandular and non-glandular trichomes is also induced by insect.



## Leaf and Root Toughness and Quantity

Leaf toughness interferes with the penetration of plant tissues by mouthparts of piercing-sucking insects and increase mandibular wear in biting-chewing herbivores (Raupp, 2008). The cell walls of leaves are also reinforced during feeding through the use of different macromolecules, such as lignin, cellulose, suberin and callose, together with small organic molecules, such as phenolics, and even inorganic silica particles.

Roots eaten by insect herbivores exhibit extensive regrowth, both in density, as seen in Trifolium repens

eaten by Sitona lepidus (clover root weevil), and in quantity, as observed in Medicago sativa (alfalfa) attacked by clover weevil (Sitona hispidulus). The former might be caused by additional lignification that could increase the toughness of the roots. In addition, genotypes with long fine roots suffered less from herbivory compared to genotypes with short and thick roots.

## 2.1.2. Secondary metabolites for chemical defense of plants

Plants produce a large and diverse array of organic compounds that appear to have no direct functions in growth and development i.e. they have no generally recognized roles in the process of photosynthesis, respiration, solute transport, translocation, nutrient assimilation and differentiation. These compounds or chemicals play a significant role in direct defense impair herbivore performance by one of two general mechanisms: these chemicals may reduce the nutritional value of plant food, or they may act as feeding deterrents or toxins. There has been considerable debate as to which of these two strategies is more important for host plant selection and insect resistance. An important part of this debate concerns the extent to which variation in the levels of primary and secondary metabolites has evolved as a plant defense (Berenbaum, 1995). Plant primary metabolism, which is shared with insects and other living organisms, provides carbohydrates, amino acids, and lipids as essential nutrients for the insect.

Secondary metabolites are the compounds that do not affect the normal growth and development of a plant, but reduce the palatability of the plant tissues in which they are produced. The defensive (secondary) metabolites can be either constitutive stored as inactive forms or induced in response to the insect or microbe attack. The former are known as phytoanticipins and the latter as phytoalexins (antimicrobial compounds synthesized by plants that accumulate rapidly at areas of pathogen infection). The phytoanticipins are mainly activated by β-glucosidase during herbivory, which in turn mediate the release of various biocidal aglycone metabolites. The classic examples of phytoanticipins are glucosinolates that are hydrolyzed by myrosinases (endogenous β-thioglucoside glucohydrolases) during tissue disruption. Other phytoanticipins include Benzoxazinoids (BXs), which are widely distributed among Gramineae. Hydrolyzation of BX-glucosides by plastid-targeted β-glucosidases during tissue damage leads to the production of biocidal aglycone BXs, which play an important role in plant defense against insects. Phytoalexins include isoflavonoids, terpenoids, alkaloids, etc., that influence the performance and survival of the insects. The secondary metabolites not only defend the plants from different stresses, but also increase the fitness of the plants. It has been reported that maize to corn earworm, Helicoverpa zea is mainly due to the presence of the secondary metabolites C-glycosyl flavone maysin and the phenylpropanoid product, chlorogenic acid. Compound, 4, 4- dimethyl cyclooctene has been found to be responsible for shoot fly resistance in sorghum (Chamarthi, 2011).

Study on secondary metabolites could lead to the identification of new signaling molecules involved in plant resistance against insect pests. Ultimately genes and enzymes involved in the biosynthesis of these metabolites could be identified. Some of the secondary metabolites in plant defense will be the following.

## Plant Phenolic compounds

Among the secondary metabolites, plant phenols constitute one of the most common and widespread group of defensive compounds, which play a major role in host plant resistance against insects. Phenols act as a defensive mechanism not only against insects, but also against microorganisms and competing plants.

Lignin, a phenolic heteropolymer plays a central role in plant defense against insects and pathogens. It limits the entry of pathogens by blocking physically or increasing the leaf toughness that reduces the feeding by insects, and also decreases the nutritional content of the leaf. Lignin synthesis has been found to be induced by insect or pathogen attack and its rapid deposition reduce further growth of the pathogen or insect fecundity.

## Plant defensive proteins

Ecologically, in insect-plant interaction, interrelationship between two is important for the survival of the both. Insects always look for a true and healthy host plant that can provide them proper food and could be suitable for mating, oviposition and also provides food for the offspring's. The nutritional requirements of insects are similar to other animals, and any imbalance in digestion and utilization of plant proteins by the insects' results in drastic effects on insect physiology. Alteration of gene expression under stress including insect attack leads to qualitative and quantitative changes in proteins, which in turn play an important role in signal transduction, and oxidative defense. Many plant proteins ingested by insects are stable, and remain intact in the mid gut, and also move across the gut wall into the hemolymph. An alteration in the protein's amino acid content or sequence influences the function of that protein. Likewise, anti-insect activity of a proteolysis-susceptible toxic protein can be improved by administration of protease inhibitors (PIs), which prevent degradation of the toxic proteins, and allows them to exert their defensive function. Better understanding of protein structure and post-translational modifications contributing to stability in the insect gut would assist in predicting toxicity and mechanism of plant resistance proteins. Recent advances in microarray and proteomic approaches have revealed that a wide spectrum of plant resistance protiens is involved in plant defense against insects.

## Plant lectins

Lectins are carbohydrate-binding (glyco) proteins, have protective function against a range of pests. The

insecticidal activities of different plant lectins have been utilized as naturally occurring insecticides against insect pests. One of the most important properties of lectins is their survival in the digestive system of insects that gives them a strong insecticidal potential. They act as antinutritive and/or toxic substances by binding to membrane glycosyl groups lining the digestive tract, leading to an array of harmful systemic reactions. Lectins are stable over a large range of pH and damage the luminal epithelial membranes, thereby interfere with the nutrient digestion and absorption.

### Flavonoids
Flavonoids are cytotoxic and interact with different enzymes through complexation. Both flavonoids and isoflavonoids protect the plant against insect pests by influencing the behavior, and growth and development of insects.

### Tannins
Tannins have a strong deleterious effect on phytophagous insects and affect the insect growth and development by binding to the proteins, reduce nutrient absorption efficiency, and cause mid gut lesions. Tannins are astringent (mouth puckering) bitter polyphenols and act as feeding deterrents to many insect pests. They precipitate proteins nonspecifically (including the digestive enzymes of insects), by hydrogen bonding or covalent bonding of protein $NH_2$ groups. In addition, tannins also chelate the metal ions, thereby reducing their bioavailability to insects. When ingested, tannins reduce the digestibility of the proteins thereby decrease the nutritive value of plants and plant parts to insects. Role of tannins in plant defense against various stresses and their induction in response to insect damage has been studied in many plants.

### Proteinase inhibitors
Proteinase inhibitors (PIs) cover one of the most abundant defensive classes of proteins in plants. Higher concentration of PIs occurs in storage organs such as seeds and tubers, and 1 to 10% of their total proteins comprise of PIs, which inhibit different types of enzymes and play an important role in plant defense against insect. PIs bind to the digestive enzymes in the insect gut and inhibit their activity, thereby reduce protein digestion, resulting in the shortage of amino acids, and slow development and/or starvation of the insects. The defensive function of many PIs against insect pests, directly or by expression in transgenic plants to improve plant resistance against insects has been studied against many lepidopteran and hemipteran insects. The success of transgenic crops in expressing PIs against insect pests has accentuated the need to understand the mechanisms, and interactions of multiple PIs with other defenses, and the adaptive responses of the insects.

### Enzymes
Enzymes also one of the important aspects of host plant resistance against insects is the disruption of insect's nutrition. The enzymes that impair the nutrient uptake by insects through formation of electrophiles includes peroxidases, polyphenol oxidases, ascorbate peroxidases, and other peroxidases by oxidizing mono or dihydroxyphenols.
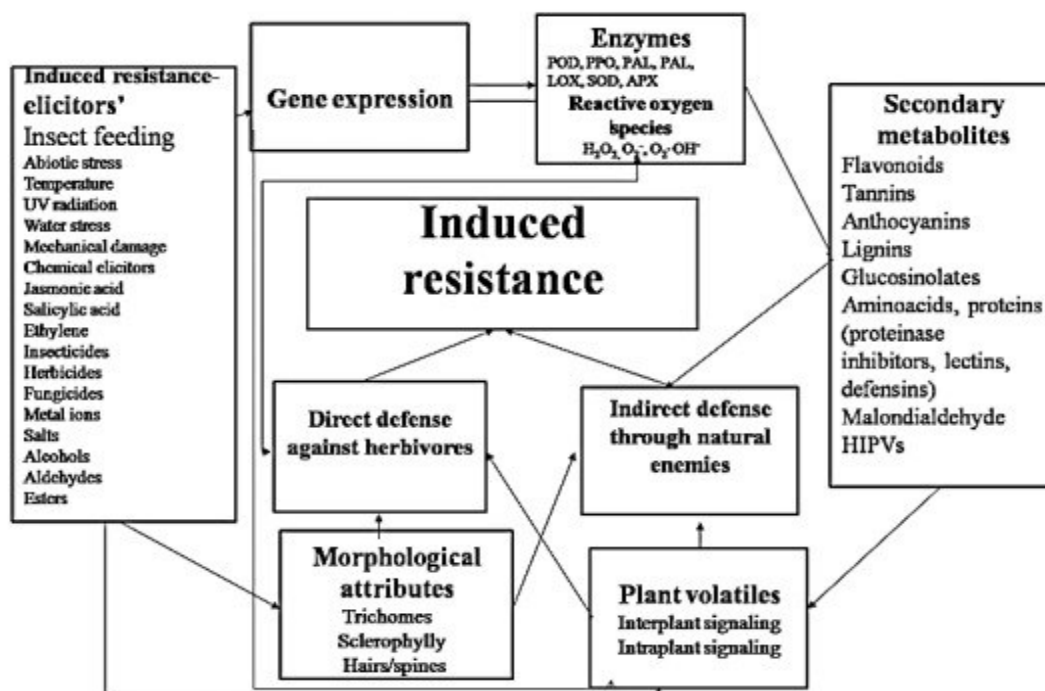


**Figure 1.** Mechanism of induced resistance in plants

## 2.2. Indirect Defenses Methods

The defensive response in plants to attract natural enemies of insects plays a pivotal role in protecting the plants against insect attack. Indirect defenses can be constitutive or induced as a result of combined action of mechanical damage and elicitors from the attacking herbivore. Production of volatiles and the secretion of extra floral nectar mediate interactions of plants with natural enemies of the insect pests (i.e., parasitoids or predators), which actively reduce the numbers of feeding herbivores. Induced indirect defenses have received increasing attention recently and have been studied on the genetic, biochemical, physiological, and ecological levels.

### 2.2.1. Herbivore induced plant volatiles (HIPVs)

In this case plants indirectly defend themselves from insect feeding by emitting a blend of volatiles and non-volatile compounds. Insect induced plant volatiles (HIPVs) play an important role in plant defense by either attracting the natural enemies of the insects or by acting as feeding and/or oviposition deterrent. HIPVs are the lipophilic compounds with higher vapor pressure which are released from the leaves, flowers, and fruits into the atmosphere, and into the soil from the roots by plants in response insect attack. The HIPV's produced vary according to the plant and insect species, the developmental stage and condition of the plants and the insects. An optimum quantity of volatile compounds is normally released by the plants into the atmosphere, whereas a different blend of volatiles is produced in response to insect. The volatile blend released by plants in response to insect attack is specific for a particular insect-plant system, including natural enemies and the neighboring plants. The HIPVs mediate the interactions between plants and arthropods, microorganisms, undamaged neighboring plants, or intraplant signaling that warns undamaged sites within the plant. Depending upon the modes of feeding of insect pests, different defense signaling pathways are activated, which induce the production of specific volatile compounds (Walling, 2000)

### 2.2.2. Defense elicitors (insect oral secretion)

Plants undergo a dynamic change in transcriptomes, proteomes, and metabolomes in response to herbivore-induced physical and chemical cues such as insect oral secretions and compounds in the oviposition fluids. It is generally believed that insect-induced plant responses are mediated by oral secretions and regurgitates of the herbivore. The defenses generated by various elicitors differ based on the type of the elicitor and the biological processes involved. A potential elicitor of herbivore-induced plant volatiles from the regurgitate of *Pieris brassicae* L. larvae has been identified as β-glucosidase which results in emission of a volatile blend from mechanically wounded cabbage leaves that attract the parasitic wasp, *Cotesia glomerata* (L.) (Steppuhn, 2007).

### 2.2.3. Role of phytohormones in induced resistance in plants

Plant defense against insect attack involves many signal transduction pathways that are mediated by a network of phytohormones. Plant hormones play a critical role in regulating plant growth, development, and defense mechanisms. A number of plant hormones have been implicated in intra- and inter-plant communication in plants damaged by insects. Most of the plant defense responses against insects are activated by signal-transduction pathways mediated by jasmonic acid, salicylic acid, and ethylene. Specific sets of defense related genes are activated by these pathways upon wounding or by insect feeding. These hormones may act individually, synergistically or antagonistically, depending upon the attacker.

Jasmonic acid is the most important phytohormone linked to plant defense against insects and activates the expression of both direct and indirect defenses. Jasmonic acid is derived from linolenic acid through octadecanoid pathway and accumulates upon wounding and herbivory in plant tissues. Chewing of plant parts by insects causes the dioxygenation of linoleic acid and linolenic acid.

Jasmonic acid has also been reported to affect calcium-dependent protein kinases (CDPK) transcript, and activity in potato plants. CDPKs comprise of a large family of serine/threonine kinases in plants (34 members in Arabidopsis) and play an important role in plant defense against a variety of biotic and abiotic stresses through signal transduction (Ludwig *et al*., 2004. In addition to the role played by jasmonic acid in direct resistance against insect pests through the induction of various defensive compounds, its role in indirect resistance has also been well established.

Ethylene is an important phytohormone, which plays an active role in plant defense against many insects. Ethylene signaling pathway plays an important role in induced plant defense against insects and pathogens both directly and indirectly. Ethylene signaling pathway works either synergistically or antagonistically, with jasmonic acid in expression of plant defense responses against pathogens and herbivorous insects. It has been reported that Ethylene and jasmonic acid work together in tomato in proteinase inhibitors expression.

Generally, different plant elicitors induced in plants upon herbivory undergo different signal transduction pathways. For example, Calcium ions ($Ca^{2+}$), reactive oxygen species, etc.

## 3. CONCLUSION

In all natural habitats, plants are surrounded by an enormous number of potential enemies (biotic) and various kinds of abiotic environmental stress. Nearly all ecosystems contain a wide variety of bacteria, viruses, fungi, nematodes, mites, insects, mammals and other herbivorous animals, greatly responsible for heavy reduction in

crop productivity. By their nature, plants protect themselves directly by developing different morphological structure and by producing some compounds called as secondary metabolites. Plant mechanical defenses act negatively on herbivores insects, diminishing their larval and adult performance. Generally, a plant character may present two or more roles at least in some phase of a plant's life history. I discussed a few cases where pubescence, tissue texture, crystals, latex, waxes and resins are effective against insect herbivores. Secondary metabolites, including terpenes, phenolics and nitrogen (N) and sulphur (S) containing compounds, defend plants against a variety of herbivores and pathogenic microorganisms as well as various kinds of abiotic stresses.

An understanding of induced resistance in plants can be utilized for interpreting the ecological interactions between plants and herbivores and for exploiting in pest management in crops. Since the biochemical pathways that lead to induced resistance are highly conserved among the plants, the elicitors of these pathways could be used as inducers in many crops. The future challenge is to exploit the elicitors of induced defense in plants for pest management, and identify the genes encoding proteins that are up and/or down regulated during plant response to the herbivore attack, which can be deployed for conferring resistance to the herbivores through genetic transformation. However, before using an elicitor effectively in agricultural systems, it is important to understand the chemical changes they induce in the plant, the effect of these chemicals on the herbivores especially in the field, and to see if there is any alteration in plant growth and yield. The Eco-genomic approach which includes association and correlation studies, natural selection mapping, and population genomics enables the estimation of variable selection at loci, and differentiates this from processes acting on the whole genome, such as migration and genetic drift.

From a biotechnological, food-developmental, and breeding point of view, understanding the defense systems of plants and learning how to apply the knowledge is of course of huge interest. For instance, modifications of the jasmonic acid pathway has been proposed (Grant, 2013). However, due to the extensive crosstalk with other hormone signaling pathways, increased resistance against one certain insect herbivore might result in susceptibility towards another. Furthermore, some defense responses might have negative effects on the environment and humanity as well, as they involve toxic bioactive natural products and proteins reducing digestibility of plant material. Still, reducing the need for synthetic insecticides, by developing crop plants resistant to insect herbivores, would be of significant gain for the food and production industry, both at an economical and environmental level.

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