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Review on Genetical, Morphological, Physiological and Molecular Mechanism of Plant to Insect Resistance

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Abstract
Plants and insects have been living together for more than 350 million years. In co- evolution, both have evolved strategies to avoid each other's defense systems. Plants produce specialized morphological structures, genetical, physiological or secondary metabolites, molecular or proteins that have toxic, repellent, and/or anti nutritional effects on the herbivores, to counter the herbivore attack and the insects have also their own weapons. Research on plant-herbivore interactions is one of the most important and multidisciplinary undertakings in plant biology involving various disciplines to describe chemical and ecological processes influencing the outcome of plant - herbivore interactions. Our understanding of how plants communicate with their neighbors, symbionts, pathogens, herbivores, and with their personal "bodyguards"- the natural enemies, both above and below ground, via chemical signals, is still in its infancy. Because of this reviewing of the genetical, morphological, physiological and molecular mechanism of plant to insect resistance are very important in designing crop plants with better protection against the herbivores.
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1. Introduction

Plants and insects have been living together for more than 350 million years. In co- evolution, both have evolved strategies to avoid each other's defense systems. This evolutionary arms race between plants and insects has resulted in the development of an elegant defense system in plants that has the ability to recognize the non-self-molecules or signals from damaged cells, much like the animals, and activates the plant immune response against the herbivores (Howe and Jander ,2008 and Hare,2011). Plants produce specialized morphological structures, genetical, physiological or secondary metabolites, molecular or proteins that have toxic, repellent, and/or anti nutritional effects on the herbivores, to counter the herbivore attack (Rani and Jyothsna ,2010 and War AR etal., 2012).

Plants confront the herbivores both directly by affecting host plant preference or survival and reproductive success (direct defense), and indirectly through other species such as natural enemies of the insect pests (indirect defense)according to (Howe and Jander ,2008).Direct defenses are mediated by plant characteristics that affect the herbivore's biology such as mechanical protection on the surface of the plants (e.g., hairs, trichomes, thorns, spines, and thicker leaves) or production of toxic chemicals such as terpenoids, alkaloids, anthocyanins, phenols, and quinones) that either kill or retard the development of the herbivores (Hanley etal.,2007). Indirect defenses against insects are mediated by the release of a blend of volatiles that specifically attract natural enemies of the herbivores and/or by providing food (e.g., extra floral nectar) and housing to enhance the effectiveness of the natural enemies (Arimura etal.,2009).

Research on plant-herbivore interactions is one of the most important and multidisciplinary undertakings in plant biology involving various disciplines to describe chemical and ecological processes influencing the outcome of plant - herbivore interactions. Our understanding of how plants communicate with their neighbors, symbionts, pathogens, herbivores, and with their personal "bodyguards"- the natural enemies, both above and below ground, via chemical signals, is still in its infancy. This is an enthralling area from an ecological point of view, and has a great potential for utilization in crop protection. Understanding the nature of gene expression of the plant defensive traits will have a tremendous application in designing crop plants with better protection against the herbivores. This in turn will reduce the need for use of harmful pesticides for insect control. However, the arms race between plants and herbivores will continue, and herbivores could co-evolve in response to the resistant plant genotypes. Knowledge of the complex chemical plant-herbivore interactions is required to optimize the production of new crops (War AR etal., 2012).

The Objective of this study is to review the genetical, morphological, physiological and molecular mechanism of plant to insect resistance.

2. Literature Review

2.1 Host plant defenses against insects

Plants respond to herbivore attack through an intricate and dynamic defense system that includes structural barriers, toxic chemicals, and attraction of natural enemies of the target pests (Howe and Jander, 2008). Both defense mechanisms (direct and indirect) may be present constitutively or induced after damage by the herbivores. Induced response in plants is one of the important components of pest control in agriculture, and has been exploited for regulation of insect herbivore population.

Over the past few decades, considerable progress has been made in studying induced responses in plants against different stresses, and has become an important topic in evolutionary biology and ecology. Although induced responses have some metabolic costs, (Agrawal etal.,2002) they are very important when aimed at alleviating the stress of immediate concern, as most of these chemicals are produced in response to herbivore attack. 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 herbivores (War AR etal.,2011).

2.2 Morphological mechanism

Plant structures are the first line of defense against herbivory, and play an important role in host plant resistance (HPR) to insects. According to (Hanley etal.,2007 and Agrawal etal.,2009) 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 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 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 herbivory(Hanley etal.,2007).

2.2.1Trichomes or Hairiness

Trichomes play an imperative role in plant defense against many insect pests and involve both toxic and deterrent effects.According to (Chamarthi etal.,2010) there are physico-chemical mechanisms of resistance to shoot fly in sorghum and (Handley etal.,2005) Variation in trichome density and resistance against a specialist insect herbivore in natural populations of *Arabidopsis thaliana.* In addition, dense trichomes affect the herbivory mechanically, and interfere with the movement of insects and other arthropods on the plant surface, thereby, reducing their access to leaf epidermis. 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 (Hanley etal.,2007 and Sharma etal.,2009). Also induction of trichomes in response to insect damage has been reported in many plants(Agrawal,2009).

2.3 Physiological mechanism.

Plant chemicals can be divided into two major categories: primary metabolites and secondary metabolites. Primary metabolites are substances produced by all plant cells that are directly involved in growth, development, or reproduction. Examples include sugars, proteins, amino acids, and nucleic acids. Secondary metabolites are not directly involved in growth or reproduction but they are often involved with plant defense. These compounds usually belong to one of three large chemical classes: terpenoids, phenolics, and alkaloids. 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 (Howe and Jander ,2008).

The secondary metabolites not only defend the plants from different stresses, but also increase the fitness of the plants. It has been reported that secondary metabolites used to corn earworm and sorghum shoot fly resistance (Nuessly etal.,2007 and Chamarthi etal.,2011). Study on secondary metabolites could lead to the identification of new signaling molecules involved in plant resistance against herbivores and other stresses. Ultimately genes and enzymes involved in the biosynthesis of these metabolites could be identified. Role of some of the secondary metabolites in plant defense will be discussed below.

2.3.1 Plant phenolics

Among the secondary metabolites, plant phenols constitute one of the most common and widespread group of defensive compounds, which play a major role in HPR against herbivores, including insects(Rani and Jyothsna ,2010). Phenols act as a defensive mechanism not only against herbivores, but also against microorganisms and competing plants. Qualitative and quantitative alterations in phenols and elevation in activities of oxidative enzyme in response to insect attack is a general phenomenon (War etal.,2011). 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 herbivores, and also decreases the nutritional content of the leaf. Lignin synthesis has been found to be induced by herbivory or pathogen attack and its rapid deposition reduce further growth of the pathogen or herbivore fecundity (Johnson etal.,2009).

2.3.2 Role of phytohormones in induced resistance in plants

Plant defense against herbivore 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 according to (Verhage etal.,2010). A number of plant hormones have been implicated in intra- and inter-plant communication in plants damaged by herbivores. 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.

2.3.3 Herbivore induced plant volatiles (HIPVs)

Volatile compounds act as a language that plants use for their communication and interaction with the surrounding environment. To date, a total of 1700 volatile compounds have been isolated from more than 90 plant families. These volatiles, released from leaves, flowers, and fruits into the atmosphere and from roots into the soil, defend plants against herbivores and pathogens or provide a reproductive advantage by attracting pollinators and seed dispersers. Plant volatiles constitute about 1% of plant secondary metabolites and are mainly represented by terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, and amino acid derivatives (Dudareva etal.,2006 Plants indirectly defend themselves from herbivore feeding by emitting a blend of volatiles and non-volatile compounds. Herbivore-induced plant volatiles (HIPVs) play an important role in plant defense by either attracting the natural enemies of the herbivores or by acting as feeding and/or oviposition deterrent. The HIPV's produced vary according to the plant and herbivore species, the developmental stage and condition of the plants and the herbivores (Arimura etal.,2009). 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 (Gatehouse, 2008).

2.3.4 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 (OS) 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 (Pauwels etal.,2009).

2.4 Molecular mechanism of plant resistance to insect or defensive proteins.

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 (*Rani etal.,2010 and Gulsen etal.,2010*).

Extensive rearrangements in gene expression occur in plants in response to herbivory with hundreds, and even up to several thousands of genes getting up- or down regulated as (Chen etal.,2009) and (Zheng and Dicke ,2008) reported ecological genomics of plant-insect interactions. Advances in genomics and transcriptomics including availability of whole-genome sequence data, expressed sequence tags (ESTs), and microarrays, has led to better understanding of the changes in gene-expression profiles in response to insect attack. (Kanchiswamy etal.,2010) also reported regulation of *Arabidopsis* defense responses against *Spodoptera littoralis* by CPK-mediated calcium signaling.

Gene expression levels have also been used to analyze the differences in transcriptional profiles of different genotypes within a plant species (Wang etal.,2008) ,while the aphids regulate the expression of genes involved in cell wall modifications, oxidative stress, calcium-dependent signaling, and glucosinolate synthesis. Different plants respond differently to the same herbivore, e.g., two white cabbage cultivars differ considerably in gene expression in response to feeding by *P. rapae* (Broekgaarden etal., 2007). Combination of various technologies such as genetic, genomic tools including microarrays, deep sequencing, and transcriptional profiling tools and proteomics through mass spectrometry will advance our understanding of molecular mechanisms of plant defense against insect herbivores to a greater extent.

Many plant proteins ingested by insects are stable, and remain intact in the midgut, 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 herbivore gut would assist in predicting toxicity and mechanism of plant resistance proteins (PRPs). Recent advances in microarray and proteomic approaches have revealed that a wide spectrum of PRPs is involved in plant defense against herbivores. According to (Chen H etal.,2005 and Chen Y etal.,2009) plant defensive proteins against insect pests are:-

2.4.1 Plant lectins

Lectins are carbohydrate-binding (glyco) proteins, ubiquitous in nature, and 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 (Saha etal.,2006). One of the most important properties of lectins is their survival in the digestive system of herbivores that gives them a strong insecticidal potential. According to (Vandenborre etal.,2011) plant lectins used as defense proteins against phytophagous insects.They act as ant- nutritive 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. Disruption of lipid, carbohydrate, and protein metabolism causes enlargement and/or atrophy of key tissues, which in turn alters the hormonal and immunological status, threatening the growth and development of insects (Chakraborti etal.,2009) .

2.4.2 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 herbivory (Dunse etal.,2010). 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(Azzouz etal.,2005). 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 herbivores.

2.4.3 Enzymes

One of the important aspects of HPR against insects is the disruption of insect's nutrition. The enzymes that impair the nutrient uptake by insects through formation of electrophiles includes peroxidases (PODs), polyphenol oxidases (PPOs), ascorbate peroxidases, and other peroxidases by oxidizing mono- or dihydroxyphenols, that lead to the formation of reactive o-quinones, which in turn polymerize or form covalent adducts with the nucleophilic groups of proteins due to their electrophilic nature (e.g., -SH or e-NH_2 of Lys) (Bhonwong etal.,2009). Other important antioxidative enzymes include lipoxygenases, phenylalanine ammonia lyase, superoxide dismutase, etc. Induction of antioxidative enzymes in plants following herbivory has received considerable attention in recent years,According to (Rani and Jyothsna ,2010) Biochemical and enzymatic changes in rice is mechanism of defense.

2.5 Genetical mechanism of plant to insect resistance.

Host Plant Resistance (HPR) "Those characters that enable a plant to avoid, tolerate or recover from attacks of insects under conditions that would cause greater injury to other plants of the same species" (Painter,1951). "Those heritable characteristics possessed by the plant which influence the ultimate degree of damage done by the insect" (Maxwell,1972). Based on number of genes genetic resistance divided into three (monogenic, oligogenic,polygenic) resistance. They controlled by single, few and many genes respectively.

Also when it is major gene resistance it is controlled by one or few major genes (vertical resistance) and when it is minor gene resistance controlled by many minor genes said to be horizontal resistance The inheritance of insect resistance may be governed in three ways, by 1) Oligogenes, 2) Polygenes, and 3) Cytoplasmic gene (Wiseman, 1985).

2.5.1 Transgenerational induced resistance to herbivores

Biotic and abiotic stresses in plants have been found to induce resistance not only in the maternal plants, but also in the offspring's. This maternally induced resistance (transgenerational immunity) has been found to protect the progeny of plants exposed to herbivory from insect pests, besides producing vigorous seeds and seedlings (Agrawal ,2001). However, there are a few reports on transgenerational immunity of plants against insect pests. Wild radish plants, *Raphanus raphanistrum* damaged by *P. rapae* or treated with JA produce offspring's with high levels of induced resistance to this insect according to (Agrawal, 2002). Arabidopsis plants exposed to stresses such as, cold, heat and flood, resulted in a higher homologous recombination frequency and increased genome methylation, which in turn induced the resistance to stress in the progeny (Boyko etal., 2010).

However, further studies are required to understand the genetic and molecular mechanisms of such signaling interactions. Furthermore, research on plant-insect interactions should be focused not only to genetic effects, but also toward the epigenetic regulation of plant defense pathways and insect responses, because a substantial body of evidence has been demonstrated for mobile silencing induced RNA signals and inheritance of DNA methylation based changes in gene expression changes. There is much need for in-depth studies on this subject to exploit it for pest management by manipulating the maternal ecology. An understanding of transgenerational induced resistance might answer some of the intricate questions regarding the ability of plants to withstand herbivore damage (Boyko etal., 2010).

3. Conclusion

Plants respond to through various morphological, genetical, physiological and molecular mechanisms to counter/offset the effects of herbivore attack. The physiological mechanisms of defense against the herbivores are wide-ranging, highly dynamic, and are mediated both by direct and indirect defenses. Direct defenses are mediated by plant characteristics that affect the herbivore's biology such as mechanical protection on the surface of the plants (e.g., hairs, trichomes, thorns, spines, and thicker leaves) or production of toxic chemicals such as terpenoids, alkaloids, anthocyanins, phenols, and) that either kill or retard the development of the herbivores.

The defensive compounds are either produced constitutively or in response to plant damage, and affect feeding, growth, and survival of herbivores. Indirect defenses against insects are mediated by the release of a blend of volatiles that specifically attract natural enemies of the herbivores and/or by providing food (e.g., extra floral nectar) and housing to enhance the effectiveness of the natural enemies.These strategies either act independently or in conjunction with each other. However, our understanding of these defensive mechanisms is still limited. Induced resistance could be exploited as an important tool for the pest management to minimize the amounts of insecticides used for pest control. Host plant resistance to insects, particularly, induced resistance, can also be manipulated with the use of chemical elicitors of secondary metabolites, which confer resistance to insects.

By understanding the mechanisms of induced resistance, we can predict the herbivores that are likely to be affected by induced responses. The elicitors of induced responses can be sprayed on crop plants to build up the natural defense system against damage caused by herbivores. The induced responses can also be engineered genetically, so that the defensive compounds are constitutively produced in plants against are challenged by the herbivory. Induced resistance can be exploited for developing crop cultivars, which readily produce the inducible response upon mild infestation, and can act as one of components of integrated pest management for sustainable crop production.

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