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3. Physiological Changes in Plants in Response to Insect Pests

Kanika Choudhary, Kumari Ruchika, Alka Rana,
Poonam Kumari

Department of Animal Sciences,
Central University
Himachal Pradesh.

Abstract:

Insects and plants are diverse groups with complex relationships that can be classified as mutualistic, antagonistic, or commensalistic. Fossil records and molecular clock concepts can reconstruct historical interactions between plants and insects. Plants produce secondary metabolites to protect themselves from herbivores, and insect chemoreceptors help them recognize specific primary and secondary metabolites in plants. Understanding these secondary metabolites helps quantify plant insect interactions. Plants can be damaged by herbivorous insects, which release volatile compounds called herbivore-induced volatile plants (HIPVs), which pollinate host plants and attract natural enemies. Reactive oxygen species (ROS) and plant hormone signaling are essential components in plants' communication system, enabling them to respond to environmental factors. Insect herbivory significantly impacts photosynthesis, with chloroplast reactions producing various forms of ROS. Stomata play a crucial role in interactions between plants and herbivores, with changes in stomatal dynamics affecting cellular, organismal, and community levels. Overall, the intricate relationships between plants, microorganisms, and environmental factors play a vital role in the overall health and productivity of agricultural systems.

Keywords:

Secondary metabolites, host plants, photosynthetic alterations, ROS, herbivory.

3.1 Introduction:

Insects and plants are highly diverse groups known for their ability to exploit many niches, from the desert to the arctic zone, and also occupy almost all plant species**.** The total number of multicellular organisms is approximately half that of plants and insects. Traditionally, plant-insect interactions have been classified as mutualistic, antagonistic, or commensalistic (Calatayud et al., 2018). It has taken a long time for insects and plants to develop complex relationships. In a recent study, it was shown that fossil records, which contain different types of signals, can be used to reconstruct historical relationships between plants and insects (Schatz et al., 2017). According to Schatz, et al. 2017, phylogeny and molecular clock concepts also provide robust assumptions about the age of insect lines and their relationship to their hosts. A mutualistic relationship has evolved between plants and insects through the process of pollination. Because organisms are part of food webs, direct and indirect interactions between members of an ecosystem are common.

A diverse array of secondary metabolites is produced by plants in order to protect themselves from herbivores (Divekar et al., 2022). The study of secondary metabolites and their role in insect traits has greatly benefited understanding and quantifying plant insect interactions. The majority of insects reject non-hosts or plants that might be harmful to them. Molecular interactions between specific ligands and chemoreceptors play a key role in insect host adaptation and speciation (Nishida, 2014).

Plants can be damaged by herbivorous insects that release volatile compounds called herbivore-induced volatile plants (HIPVs), which pollinate host plants and attract natural enemies. Insects and arthropod predators are among these enemies (Guo & Wang, 2019). As a result of the use of synthetic pesticides and fertilizers in crop production, the environment as well as the health of humans have been negatively affected. Plant diseases are controlled through biocontrol, which is the most eco-friendly used technique. Host plants and Trichoderma species engage in a mutually advantageous symbiotic relationship, where both gets benefit. Trichoderma-based products have been on the market as biocontrol agents (BCAs) to effectively manage various crop pathogens, as well as biofertilizers or growth stimulants that foster plant growth (Alfiky & Weisskopf, 2021). There are several important role of secondary metabolite, that help the cabbage root fly to recognize and locate suitable hosts (Ahuja et al., 2011).

The stomata of plants are proving to be important mediators of interactions between plants and herbivores. Herbivores produce oral secretions that contain enzymes and phytohormones that trigger the closure of the stomata in response to herbivory (Lin et al., 2022). The changes in stomatal dynamics caused by herbivory may affect cellular, organismal, and even community levels since they are linked to interrelated physiological processes.

3.2 Plant Perception and Signalling:

Plants communicate constantly with their environment through volatile organic compounds (VOCs). In order to achieve maximum fitness, plants and the organisms they interact with rely on this communication to coordinate growth, development, defence, propagation, and reproduction (Bouwmeester et al., 2019). Insects use visual cues for locating plants over long distances, especially those that can disperse over long distances (Grunseich et al., 2019). During plant-insect co-evolutionary arms races, plant volatiles play an invisible role. In the ecosystem, they are involved in a variety of Tri-trophic interactions mediated by plants. Insect's advanced olfactory systems enable them to detect and process these complex environmental cues (Binyameen et al., 2021). Species-specific compounds or specific ratios of ubiquitous compounds will be used by insects to recognize a host plant. Phytophagous insects detect volatile organic compounds (VOCs) through olfactory sensilla on their antennae, which provide information about food, mates, and oviposit sites (Riolo et al., 2012). As a direct resistance agent, molecules from volatile plants have a strong ability to penetrate wound sites and act as direct agents of healing (Zhang et al., 2023).

Jasmonic acid (JA), along with its precursors and derivatives known as jasmonates (JAs), play a crucial role in orchestrating plant reactions and protective mechanisms in response to both biotic and abiotic stress factors (Wang et al., 2021).

Hormone metabolism components and signaling have provided a greater understanding of how plant growth and physiology are regulated (Jang et al., 2020). A study is underway to investigate whether JA signaling influences root exudation in a way that can enhance plant tolerance to biotic stress through the recruitment of microbes (Carvalhais et al., 2017).

A phytohormone is a signal molecule produced by the plant that regulates gene expression and controls its growth and development (Curaba et al., 2014). There are various phytohormones, growth regulators (Abscisic acid and ethylene) stress tolerance (Salicylic Acid and Jasmonic Acid) (Tiwari et al., 2017). Herbivores and pathogenic microbes are effectively and efficiently responded to by the plant when inducible immune responses are activated (Caarls et al., 2015). When an intruder is detected, the organism accumulates signaling substances like salicylic acid (SA) and jasmonic acid (JA) and their related compounds. These molecules play a crucial role in triggering subsequent defensive reactions.

3.3 Induced Defence Mechanisms:

Plants cannot evade the challenges posed by living threats like pathogens, parasites, herbivores, as well as non-living factors such as drought, floods, high or low temperatures, UV radiations, salinity and nutrient deficiencies. Through a combination of structural characteristics and biochemical reactions, which may or may not be present throughout the life of the plant, plants defend themselves against pathogen attack and continue to grow and yield in significant quantities (Shittu et al., 2019). Numerous subcellular structures are essential for orchestrating defense signaling in plants, with key contributions from organelles such as chloroplasts, mitochondria, vacuoles, and the endoplasmic reticulum (ER) (Iqbal et al., 2021). Secondary metabolites in plants are compounds that aren’t crucial for their fundamental growth and development. However, they frequently serve significant functions in protecting against herbivors, pathogens, and environmental stressors.

The phenylpropanoid pathway is a typical route for generating these secondary metabolites (Sharma et al., 2019). This pathway produces compounds like flavonoids, lignins and phenolic acids. Another pathway is the terpenoid pathway, responsible for producing compounds have roles in defense against herbivores (Chen et al., 2018).

As part of the regulation of a wide range of physiological processes in plants, jasmonate phytohormones (JAs) are derived from lipids. These phytohormones regulate growth, development, abiotic stress tolerance, and insect and pathogen defences. JAs are essential for the digestion and benefiting of prey by the carnivorous plants (Pavlovič & Mithöfer, 2019). An inducible systemic acquired resistance (SAR) confers a broad spectrum of immunity against secondary infections beyond the site of infection itself. Researchers have provided a first clue to understanding the molecular mechanism behind these phenomena through studies of wheat and barley NPR1 homologs genes (WANG et al., 2019).

In plants, salicylic acid (SA) is known as a phytohormone that regulates seed germination, photosynthesis, respiration, flowering, and senescence (Rivas-San Vicente & Plasencia, 2011). SA also activates plant defence responses against extreme temperatures, ozone pollution, UV irradiation, heavy metals, droughts, and salinities.

3.4 Photosynthetic Alteration:

Agricultural and indigenous plants encounter various biological challenges stemming from living organisms, spanning from viruses to mammals. Numerous of these detrimental factors influence the process of photosynthesis, either by modifying its core functions such as primary photochemical reactions, electron transport, and Calvin cycle, or by impeding gas exchange and diminishing the available surface area for photosynthesis. Pathogens, including fungi, bacteria, and viral agents, as well as animal pests, on average, lead to a 15% and 18% reduction in crop yield, respectively (Barón et al., 2011) .

Photosynthesis, a vital process in plant physiology, plays a vital role in defending plants contrary to biotic stress. When plants interact with pathogens and pests, it often leads to changes in sugar metabolism and source-sink relationships. These alterations can serve as part of the plant's defense mechanisms, limiting nutrient availability to the invaders. Alternatively, pests may manipulate plant metabolism for their value (Pérez-Bueno et al., 2019). Environmental stressors, such as salinity or salt stress, can have detrimental effects on the process of photosynthesis in plants. These modifications in the cell wall can, in turn, have an impact on the overall structure of plant leaves, ultimately leading to a decrease in the efficiency of photosynthesis (Dabravolski & Isayenkov, 2023).

Phytophagous insects are a significant challenge in agriculture, leading to substantial economic losses. While synthetic insecticides have been effective, their efficacy has diminished over time due to various factors:

3.4.1 Plant Primary Metabolism in Response to Insect Herbivory:

Photosynthesis, the primary process through which green plants generate carbohydrates, plays a pivotal role in the carbon allocation response to herbivory. The adjustment of photosynthesis and carbon fixation in the face of herbivory has generated divergent theories. Firstly, it's suggested that photosynthetic activity might increase in response to herbivory. This could occur because the synthesis of defensive compounds relies on carbon fixation. Furthermore, plants can respond to the loss of leaf area by increasing photosynthesis in the remaining parts of the plant. In certain situations, insects may influence the plant’s metabolic processes to encourage carbon fixation for their own advantage (Appel et al., 2014). Conversely, another theory posits that photosynthetic activity could decrease. This could be due to the energy-intensive nature of producing the photosynthetic machinery. In exchange for enhanced defensive substances, there could be a potential compromise in the efficiency of photosynthesis (Coppola et al., 2013). Additionally, localized insect feeding can lead to leaf senescence and reduced photosynthesis. Reduced carbon assimilation might limit the carbohydrates available for herbivores.

In plant-herbivore interactions, plant amino acids play a dual role. They function as crucial nutrients necessary for the growth of plants, while also serving as building blocks for the synthesis of various defensive compounds in plants. When plants are attacked by herbivores, they are believed to respond by enhancing their production of amino acids (Appel et al., 2014). Plants that are infested by herbivores are believed to increase their amino acid production in order to facilitate the creation of protective substances.

While plants increase amino acid production for defense, they also aim to restrict herbivores' access to free amino acids. This limitation is important because herbivores depend on free amino acids as nutrients (Steinbrenner et al., 2011).

3.4.2 The Central Role of ROS Signaling in Plant–Insect Interactions:

Reactive oxygen species (ROS) and plant hormone signaling are crucial components of the communication system that enables plants to respond to various environmental factors. It's not surprising, therefore, that ROS play a well-established role in how plants react to insects, including aphids. Insect herbivory significantly impacts photosynthesis, both through physiological mechanisms and changes in the expression of genes related to photosynthesis (Fujita et al., 2006).

In the presence of light, photosynthesis serves as the primary generator of ROS, where chloroplast reactions yield different types of ROS, such as singlet oxygen, superoxide, and hydrogen peroxide, even when conditions are optimal (Nabity et al., 2009).

ROS accumulation in plants is not immediately evident after feeding by insects like *S. littoralis* or *Tetranychus urticae*. It is detected 24 hours after caterpillar damage or leaf yellowing. Arabidopsis experiences a delay in ROS accumulation after phloem-feeding aphids, with up-regulation of genes related to oxidative stress.

This suggests that ROS accumulation may not be essential for redox signaling pathways, but can be activated through secondary events like increased cellular antioxidant turnover rates (Fujita et al., 2006).

3.4.3 Roles for ROS and Antioxidants in Plant Defenses against Insect Herbivores:

Research shows that reactive oxygen species (ROS) are crucial for plant defense responses against insect herbivores. Insects have evolved mechanisms to detoxify these radicals within their gut, with studies showing a connection between tannin tolerance and gut antioxidant function. Tannin-tolerant *Orgyia leucostigma* and tannin-sensitive *Malacosoma disstria* caterpillars exhibited higher levels of antioxidant enzyme activity compared to tannin-resistant species. However, the addition of dietary ascorbic acid mitigated this effect in *Orgyia leucostigma* but not in tannin-sensitive *Malacosoma disstria* (Barbehenn et al., 2001).

Furthermore, *Orgyia leucostigma* exhibited notably higher levels of glutathione within its midgut compared to its diet, suggesting active secretion of this compound by this species. Furthermore, electron paramagnetic resonance spectroscopy (EPR) identified fluctuating quantities of semiquinone radicals derived from tannins and ascorbyl radicals within the midguts of these caterpillar species.

In essence, these findings suggest that ROS are involved in inducing plant defenses against herbivorous insects, and the differences in the antioxidant capacities of insect guts may influence their ability to tolerate specific plant compounds like tannins.

3.4.4 Chloroplast’s Integration of ROS and Hormonal Signaling in Response to Insect Herbivores:

Extensive research has confirmed the vital functions of plant hormones like JA, SA, and ethylene in protecting plants from herbivorous insects. These hormones are major players in the plant's response to herbivore attack (Kessler & Baldwin, 2002). Extensive research has revealed intricate crosstalk between reactive oxygen species (ROS) and hormonal signaling pathways in plants, influencing their responses to various stressors. This communication involves a wide range of plant hormones, such as auxin, abscisic acid, jasmonate, salicylate, ethylene, gibberellins, and cytokinins. ROS, with singlet oxygen, superoxide, and hydrogen peroxide (H_2O_2), interact with these hormonal pathways, coordinating plant development and stress responses (Mittler et al., 2011).

Additionally, studies have unveiled connections between hormonal signaling and light signaling pathways related to the photosynthetic electron transport chain. In high-light conditions, this chain generates oxidants like singlet oxygen, superoxide, and H_2O_2, which further contribute to the intricate signaling network in plants (Pastori & Foyer, 2002). This interplay between ROS, hormones, and light signaling is crucial for plants to adapt and respond effectively to environmental challenges, including herbivore attacks and varying light conditions. These elements are integral components of the light signaling pathways within chloroplasts, and research has demonstrated their connection to both the fundamental and adaptive immune responses in plants.

3.5 Systemic Acquired Resistance:

Plants develop heightened resistance to pathogen attacks after being infected by necrotizing pathogens, known as systemic acquired resistance (SAR). SAR is a form of plant memory that allows plants to recall past experiences of pathogen encounters, triggering their defense mechanisms more quickly and effectively when confronted by a pathogen for the second time. SAR has been recognized since the early 20th century, and research has shown diverse induced disease resistance processes in plants (Conrath, 2006).. Pathogens that produce tissue necrosis can cause a hypersensitivity response or illness symptoms, activating SAR. SAR is famous for establishing stronger resistance in plant organs that haven't been immunized far from the infection site. SAR has broad-spectrum efficacy against various pathogens, providing long-lasting protection lasting weeks to months or even a season (Ryals et al., 1996). SAR's functioning implies that plants have a form of "memory" that allows them to recall past experiences, making it a prime example of plant memory and signal transduction (Yakura, 2020).

3.5.1 Systemic Acquired Resistance Signalling:

Early grafting studies demonstrated that an infected plant's primary leaf emits a systemic signal that induces systemic acquired resistance (SAR) in remote tissue (Kessmann et al., 1994). The exact identity of this long-distance signal was initially unclear, with some suggesting salicylic acid as the translocated signal (Jirage et al., 1999). Recent studies using Arabidopsis mutants suggest that wild-type DIR1 may contribute to the production and transmission of this mobile SAR signal. In Arabidopsis mutants with defects in putative lipases, SAR activation is compromised, suggesting a role for lipid signaling. H_2O_2 has been proposed as a signaling role in SAR. Recent studies have revealed that the release of gaseous methyl salicylate, a volatile compound generated within tobacco leaves, acts as an airborne signal, inducing disease resistance in both affected and unaffected tissues, as well as in nearby plants (Ryals et al., 1996). The long-distance signaling involved in SAR is complex and may involve various signals, with the specific contribution varying depending on the plant species.

3.5.2 Salicylic Acid: Endogenous Signal for SAR:

Salicylic acid (SA) is known to play a critical role in generating systemic acquired resistance (SAR) in distant plant tissues, despite the fact that the precise long-distance signal responsible for SAR is yet unknown. Transgenic tobacco and Arabidopsis plant research provided the first strong support for this theory. These plants were genetically modified to constitutively express a bacterial SA hydroxylase, which prevented them from accumulating significant amounts of SA. As a result of the SA signal being broken, they did not develop systemic resistance when exposed to necrotizing infections (Delaney et al., 1994; Gaffney et al., 2018). The role of SA as a crucial signal in SAR has been further validated by more recent study using Arabidopsis mutants that are impaired in either SA production or SA signaling. Additionally, it was discovered that excessive SA synthesis increased the disease resistance of transgenic tobacco and Arabidopsis plants.(Lawton et al., 1996). These findings collectively emphasize the pivotal role of SA in SAR, even though the exact nature of the long-distance signal involved in SAR remains a subject of ongoing investigation.

3.5.3 Systemic Acquired Resistance (SAR), Activators:

Systemic acquired resistance (SAR) is a well-documented phenomenon in plants, and priming, which leads to enhanced activation of defense responses, is a crucial component of this process. In the primed state, plants acquire the ability to activate their defense mechanisms more rapidly and effectively when faced with biotic or abiotic stress (Lawton et al., 1996). Understanding the primed state at molecular, biochemical, and physiological levels contributes to a deeper comprehension of signal transduction in plants and opens doors to harnessing the natural defense capabilities of plants in practical agricultural settings (Thulke & Conrath, 1998). Researchers like Kauss and Conrath have made valuable contributions to our understanding of priming and SAR, which enables plants to prepare for future battles and mount quicker and more effective defense responses when faced with subsequent pathogen attacks (Conrath, 2006; Kauss et al., 1992). This heightened readiness contributes significantly to their overall resistance against pathogens.

3.6 Biotechnological Implications and IPM Strategies:

Biotechnology has significantly advanced plant resistance to insect pests, revolutionizing agricultural practices. This field has employed various strategies, including gene transformation, genome editing, RNA interference, marker-assisted selection, anther culture, embryo culture, protoplast fusion, and somaclonal variations (Talakayala et al., 2020). Transgenic crops have been developed to express insect-resistant genes, reducing the reliance on chemical pesticides.

Insect-resistant crops, such as cotton and maize, have become widely integrated into global agriculture, leading to a decrease in pesticide use and lowered production costs (Brookes & Barfoot, 2005; Toenniessen et al., 2003).

Plant lectins, proteins that provide resistance against phytophagous insects, have been explored in various crops, offering a natural defense mechanism against pests. Lectins are carbohydrate-binding proteins present in numerous plant species, particularly in families such as Solanaceae, Fabaceae, and Poaceae. They have entomotoxic properties, discouraging a wide array of insects and animals that consume plants. Recent developments have seen the emergence of insect-resistant plants, paving the way for the use of plant lectins in pest management strategies (Caroline et al., 2022).

Intrinsic defenses have also been discovered through biotechnology research, which are integral to the plant's inherent defense mechanisms and can be modifiable for increased efficacy. Plants have evolved a sophisticated and adaptable defense system in response to herbivore attacks, which can be constitutive or induced (Klauser et al., 2016). Induced responses in plants come at some metabolic costs but are crucial for mitigating immediate stress, as most chemicals are produced in response to herbivore attacks.

RNA interference (RNAi) technology has the potential to control a wider range of insects, including sap-sucking insects, which transgenic crops have struggled to manage. RNAi technology employs two main delivery methods, HIGS (host-induced gene silencing) and SIGS (spray-induced gene silencing), to ensure that the target genes are silenced in the pest population (Christiaens et al., 2020). However, there are challenges in efficiently delivering dsRNA to insects and the inherent instability of RNA in unfavorable environmental conditions limit the effectiveness of SIGS approaches (Liu et al., 2020). Overall, biotechnology has the potential to provide eco-friendly solutions for managing agricultural pests and protecting crop yields.

3.7 Future Directions and Conclusion:

The investigation into the physiological alterations that plants undergo in response to insect pests is a vital realm of inquiry with extensive implications for agriculture and pest control. The forthcoming paradigm of pest management revolves around integrated methods. Scientists should concentrate on forging comprehensive IPM strategies that encompass physiological insights. This may encompass amalgamating biological control practices, pest-resistant plant varieties, and precision pesticide applications grounded in pest-plant interactions. By employing genomics, transcriptomics, proteomics, and metabolomics can yield profound insights into plant reactions to insect pests. Given climate change's impact on pest dynamics, forthcoming research should delve into how shifting climatic conditions impact plant-insect interplays. This encompasses scrutinizing how modified temperature and precipitation patterns influence pest lifecycles and plant responses.

Biotechnology proffers promising avenues for heightening plant resilience to insect pests. Sustained exploration in this domain should contemplate the development of genetically modified plants endowed with enhanced resistance traits. Also, research into the allelopathic effects of plants on insect pests can provide sustainable pest control options.

The comprehension of the physiological adaptations in plants when confronted with insect pests holds pivotal importance for sustainable agriculture. Subsequent research should pivot towards multidisciplinary approaches, integrating technological innovations and cognizant of the evolving challenges posed by climate change. This wisdom will empower us to formulate efficacious, eco-friendly pest management strategies, thus securing food sustainability for posterity.

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