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The Chemical Ecology of Plant-Insect Interactions

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Abstract

Plants employ a combination of direct and indirect defense strategies to safeguard themselves against insect herbivores. Direct defenses include both physical and chemical barriers that work together to hinder the growth, development and reproduction of these insects. In contrast, indirect defenses discourage herbivores by releasing volatile substances which attract their natural predators rather than directly harming them. This chapter explores the multifaceted connections that exist between plants and insects, emphasizing chemicals, compounds derived from proteins and plant volatiles, while insects employ strategies such as metabolization, sequestration, or avoidance. Consequently, the link between plants and insects is intricate, multi-layered and incorporates a variety of macro and microorganisms in both space and time. Exploring these interconnected relationships offers a complete picture of the natural world.

Keywords Defense mechanism, Insects, Metabolization, Multi-layered, Spatially

1. Introduction

The intricate relationship between plants and insects is a complex association shaped by various living and non-living factors. Within natural ecosystems, plants and insects engage in continuous and complex interactions. Insects play beneficial roles such as defense and pollination, while plants offer essential resources including shelter, oviposition sites and food, which are crucial for insect to thrive and proliferate. The complicated relationships that insects have with their host plants require a comprehensive understanding

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of the roles played by orientation, dietary habits, egg-laying strategies, chemical cues (allomones) and plant nutrition. To fend off insect attacks, plants generate a wide range of chemical substances. Herbivorous insects use the constitutive chemicals that plants always have, even in the absence of stress, to identify their host plants. The metabolism of secondary metabolites is one of the defensive strategies that plants shield themselves against insect herbivory (Kliebenstein *et al.*, 2001), the release of volatiles that attract herbivore predators, the activation of protective proteins (Haruta *et al.*, 2001), the development of chemical and physical barriers and an increase in density of trichome (Fordyce and Agrawal, 2001).

Insects have simultaneously devised techniques to circumvent plant defenses, including detoxifying harmful substances (Scott and Wen, 2001), avoidance strategies, sequestering toxins (Nishida, 2002), modifying gene activity patterns (Silva *et al.*, 2001) and purifying harmful compounds. Plant defense chemicals operate primarily in two ways: they either deter herbivores directly by making tissues of plant harder to digest, or they function as inducible substances evolve when attack by herbivores. A large number of specialist insects have developed tactics to get over both triggered and intrinsic plant protection. This has led to co-evolutionary processes in insect-plant interactions, where each side has evolved ways to resist the other's defenses. Different plant defensive responses are often triggered according to the insect's mode of feeding strategy, aiding to the beginning of different defense mechanisms (Walling, 2000). Phloem-feeder insects (including aphids, leafhoppers and whiteflies) activate genes related with the Jasmonic acid pathway, while chewing insects activate genes relevant to the Salicylic acid pathway, when compared between chewing insects and sucking insects. This finding is in accordance with the theory that phloem-feeding insects inflict little harm on tissue and, as a result, trigger defense signaling pathways that are analogous to those commonly used against infections (which are regulated by salicylic acid).

2. Insect-Plant Interactions

Numerous connections between insects and plants, such as antagonism, commensalism and mutualism, have a substantial effect on production of food in horticulture, forestry and agriculture. In contrast to mutualistic interactions, which mostly entail insect pollination, antagonistic interactions include herbivory, intricate multitrophic interactions and situations in which plants prey on insects. From entire plant communities to the morphological and molecular levels of both insects and plants, these interactions take many different forms (Sharma *et al.*, 2014). Insects and host plants co-evolve, particularly in their analysis of the relationship between monarch butterflies and milkweed plants (Futuyma, 2000). Insect-plant interactions are intricate and essential since plants provide food for insects but also generate a diverse array of secondary metabolites that act as feeding stimulants, deterrents, or be sequestered by insects for their own defense. From locating plants for feeding and oviposition to dealing with plant secondary metabolites, both insects and plants exhibit a range of strategies benefiting from these interactions. Insects can harm plants directly by consuming leaf portion or by piercing and sucking sap (*e.g.*, aphids, jassids) and indirectly by spreading plant diseases or transporting harmful insects between plants. Plants have developed numerous traits to avoid insect attacks, such as phenological escape to evade specific insects (Visser and Holleman, 2001), production of toxic and digestibility-reducing secondary metabolites, emission of volatiles produced by insects that attract herbivores' natural enemies, enhanced release of nectar to aid natural enemies (Heil *et al.*, 2001) and physical characteristics such as trichomes and surface structure. Insects also engage in mutualistic relationships with plants. Most flowering plants depend on insects for pollination, offering nectar and pollen as food in return. Insects' body hairs aid in pollen transfer between flowers. In order to meet their nutritional needs, several carnivorous plants have also developed systems for capturing and digesting insects. As a result, the inter-link between plants and insects are extremely complex and dynamic.

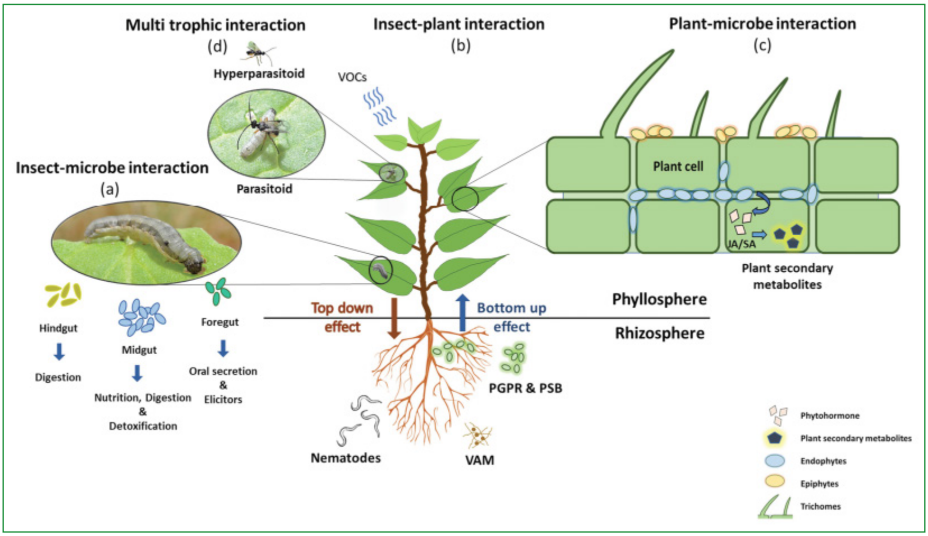

Figure 1: Multilayered interactions between insects and plants (Source: Sharma *et al.*, 2021)

This interaction system operates across four key dimensions:

i) Insect-Microbe Associations, where microbial symbionts within insects play a vital role in modulating herbivory;

ii) Insect-Plant Dynamics, in which plants deploy both structural and chemical defenses in response to insect herbivores;

iii) Plant-Microbe Relationships, where microbial communities in the rhizosphere and phyllosphere, including endophytes and epiphytes, enhance plant systemic resistance;

iv) Multitrophic Networks, involving the ecological interplay among predators, parasitoids and their natural enemies.

3. Insect-Plant Relationships in a Multitrophic Context

Tri-trophic relationships form when an additional element is added to the insect-plant dynamic. These interactions involve insects, plants and either biotic agents, like predators, pathogens, endophytic fungi, endosymbionts and genetic diversity, or abiotic factors such as soil quality, drought stress, light availability, wind velocity, air contaminants and other temporal influences. These additional components are crucial in shaping the nature and outcomes of insect-plant interactions (Shikano *et al.*, 2017). Microbes associated with insects (both herbivores and parasitoids) can enhance insect fitness by inhibiting and purifying plant defenses and phytochemicals. On the other hand, microbes that benefit plants can enhance their growth and alter their nutritional and phytochemical properties, which can subsequently influence insect health either positively or negatively (Raman and Suryanarayanan, 2017).

4. Plant Reactions to Insect Invasion

Constitutive compounds, which deter herbivores by directly attacking or via synthesizing inducible compounds and plant tissues less digestible, which are produced in reaction to herbivore tissue injury, are the two main ways by which plants use chemical defenses. These strategies effectively deter most herbivores, though a small number of insects can adapt to specific plant species. As adaptable defenses against unforeseen biotic invasions, plants use both chemical and physical barriers (epidermal layers, hairs, thorns and trichomes). When an insect makes contact, plants undergo chemical alterations, beginning with changes in cell wall. During this process, signals that the insect releases are perceived by plant receptors, which then generate the plant's immune system. Furthermore, herbivore attacks can also heighten a plant's vulnerability to pathogens like bacteria, fungi and viruses.

Every plant species generally shows a range of defense traits, which differ due to trade-offs in resource allocation among different parts of the plant. Rather than focusing all defensive attributes in a single individual, plant species may distribute different defense traits across multiple individuals. Agrawal and Fishbein (2006) suggested a spectrum of anti-herbivory defenses encompassing three categories: (i) plants that utilize phenological escape mechanisms and have weak defences; (ii) plants with nutritious, palatable leaves that are shielded by physical and chemical defences; and (iii) plants with tough, unpalatable leaves. Chemical volatile compounds in plants serve dual purposes. The poisonous effects of the molecules emitted into the air may repel a variety of herbivores and attract a few specialized pest species. Additionally, these volatiles also serve as an indirect defense strategy by luring parasitic or predatory insects that feed on plants (Birkett *et al.*, 2000). Since evolutionary balance is most likely achieved at modest levels of herbivory suppression and fitness, these costs are essential for the development of resistance. According to Pare and Tumlinson (1999), plant volatiles may act as plant-to-plant signaling, causing nearby healthy plants to mount defenses in response to volatiles from injured tissues.

5. Defenses of Host Plants against Insects

The co-evolution of insects and plants dates back hundreds of millions of years, resulting in sophisticated defenses against different insect feeding techniques. In reaction to insect invasions, plants utilize a sophisticated and adaptive defense mechanism that includes structural barriers, harmful chemicals and the attraction of natural predators of the pests. The mechanisms can be both directly and indirectly or either constitutive or induced following insect damage. Damage by insect cascades a variety of internal signaling event in the impacted plant tissues, including systemic and jasmonate-mediated signaling pathways, phosphorylation cascades and calcium ion fluctuations. Unaffected plant sections receive these signals and use them to trigger their own defenses by generating a variety of defensive metabolites with modest molecular weights.

Herbivorous insects may be repelled or poisoned by these bioactive compounds and defense-related proteins may disrupt their digestive systems. Induced responses in plants are a crucial aspect of insect pest management tactics in agriculture and have been utilized to manage insect herbivore populations. Induced defenses provide plants with phenotypic plasticity, lessening the likelihood of insects which adapt to the defense chemicals (War *et al.*, 2012). Alterations in a plant's defensive compounds as a result of insect attacks introduce uncertainty into the plant environment for herbivores, influencing their fitness and behavior. Plants also utilize physical features such as waxes, trichomes and latexes to hinder insect feeding. Additionally, they produce extrafloral nectar, food and refuge sites to support and attract predators of herbivores. Nevertheless, herbivorous insects have developed strategies to overcome plant defenses and in certain instances, capture these compounds for their own protection. In most plant-insect interactions, the metabolic costs of both insect adaptation and plant protection result in a standoff where both the herbivore and the host survive, but with less-than-ideal development.

6. Direct Defenses

"Direct defense" describes the methods plants employ to create morphological obstruction (Thorns, trichomes, wax on the leaf surface and thicker or lignified cell walls) against insect herbivores or to produce compounds that either repel, diminish nutritive value, or are harmful to the insects. By acting as growth inhibitors and poisons, secondary metabolites lessen the digestibility of plant tissues and provide further barriers against future assaults. Furthermore, the synergistic interaction among various defensive components enhances the plant's overall defense system against insect invaders.

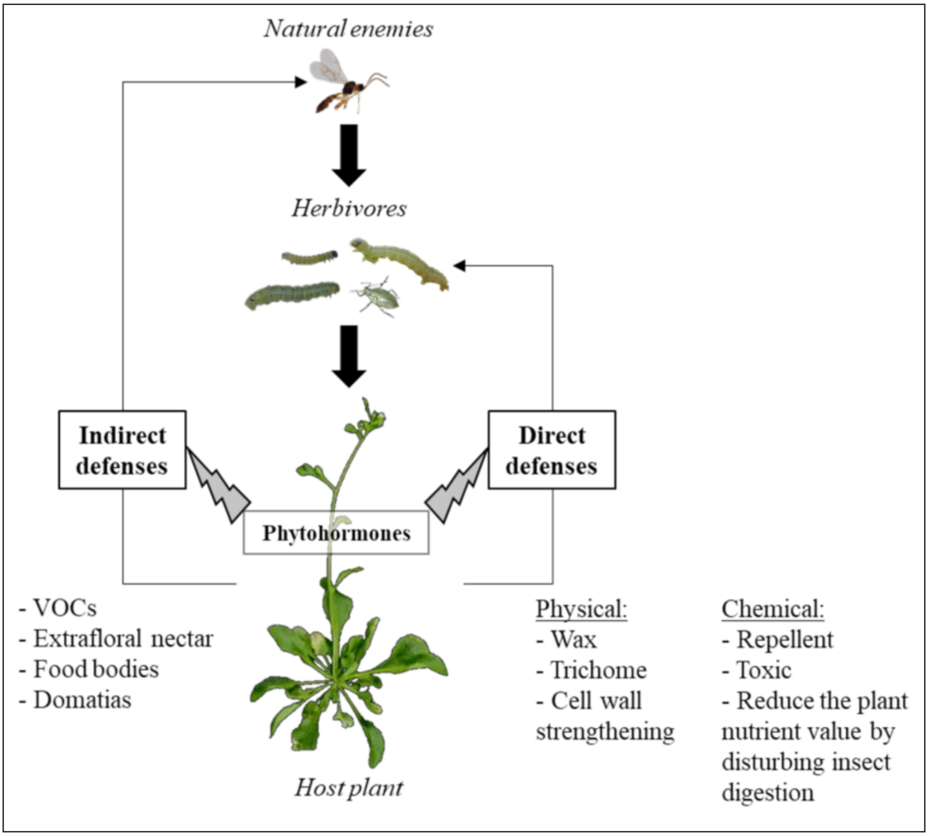

Figure 2: Constitutive vs. inducibe defenses (Source: Ourry, 2019)

7. Morphological Adaptations for Physical Defense

Plants exhibit various structural modifications, such as enhanced trichome production, increased root density and cell wall fortification, to deter insect herbivory. These adaptations disrupt insect feeding, digestion and oviposition. Every part of the plant plays a role in resisting herbivores, from hardening of tissue to intricate glandular trichomes and spines. Additionally, most vascular plants are coated with epicuticular wax films and crystals. Research has shown a positive link between plant-associated microbes and the improved development of these morphological structures (Del *et al.*, 2019). Numerous researches reveal that plant structures serve as the main safeguarding measures against pest insects and are critical for a host plant's resistance. Characteristics that aid plants protects themselves against insect pests include pubescence, trichomes, stiffened leaves (sclerophylly), divaricated branching (generating wiry stems at broad angles) and spines and thorns (spinescence).

Spinescence encompasses features such as spines, thorns and prickles, whereas pubescence pertains to hair layers (trichomes) on foliar parts of the plant, including stems, leaves and fruits. These trichomes can be straight, spiral, hooked, or glandular. Unlike aboveground insect herbivores, belowground insects interact directly with rhizosphere microbes, influencing root morphological responses (Koricheva *et al.*, 2009). For instance, mycorrhizal associations increase root thickness and density, enhancing resistance against soil pathogens and nematodes (Brundrett, 2002).

7.1. Trichomes

Plants defend themselves either through direct self-defense mechanisms or by recruiting “bodyguards.” These defense strategies are categorized into direct and indirect mechanisms in evolved to herbivore attacks. Trichomes resemble hair-like structures that extend from the plant epidermis, varying in shape and size. They can be microscopic unicellular structures or large multicellular formations, including hairs, scales, buds and papillae, originating from epidermal tissue and developing into diverse forms. Insect pests’ oviposition behavior, eating habits and larval nutrition are adversely affected by high trichome concentrations. Insect mobility on the surface of plant and leaf epidermis might be physically hindered by densely packed trichomes. Based on their morphology and secretory capacities, trichomes are categorized as glandular or non-glandular. They can be straight, spiral, hooked, branching, or unbranched. Glandular trichomes produce, secrete, or contain chemicals that can be toxic or impede an insect’s movement, feeding and survival, while non-glandular trichomes do not. In species like Virginia pepperweed and wild radish, increased trichome density has been observed following insect damage.

7.2. Solidness and Other Stem Character

Insect-plant interactions are greatly influenced by the thickness and hardness of plant stems. Complex polymeric compounds such as cellulose, lignin, callose, suberin and sclerenchymatous tissue are added to plant cell walls to reinforce them. Because of this fortification, the plant surface is protected from piercing-sucking mouthpart penetration as well as mechanical harm by insect mandibles (Raupp, 1985). For instance, since celery leaves (*Apium graveolens*) have a rougher surface than *Chenopodium murale* leaves, the beet armyworm (*Spodoptera exigua*) needs three times as much time to consume them (Hanley *et al.*, 2007).

In response to herbivory, plant roots often exhibit substantial regrowth in both density and quantity. For example, *Trifolium repens* attacked by the clover root weevil (*Sitona lepidus*) shows extensive root regrowth (Care *et al.*, 2000), as does *Medicago sativa* when damage by the clover weevil (*Sitona hispidulus*) (Johnson *et al.*, 2010). It has been found that mustard beetle (*Phaedon cochleariae*) had reduced feeding rates and slower larval growth on tougher leaves of turnip and Brussels sprouts. In chickpeas, resistance to the bruchid (*Callosobruchus maculatus*) is associated with the seed coat's roughness and toughness.

8. Role of Epicuticular Waxes

Plant surfaces are shielded by epicuticular waxes against pathogens, insects and desiccation. Insect pests are deterred both chemically and physically by these waxes, which are esters made by connecting aliphatic alcohols and long-chain fatty acids. Wax builds up on plant surfaces and triggers negative stimuli for insect tarsi and mouthpart sensory organs, which increases plant resistance (Blenn *et al.*, 2012). For instance, in bloom cultivars, the heavily waxed culms hinder neonate larvae from climbing to feeding sites as their prolegs stick in the wax. On the surface of juvenile *Eucalyptus globulus* leaves, epicuticular wax crystals provide a slippery coating that inhibits insect herbivores (psyllids) from sticking to the leaves, lowering their chances of surviving by starving (Chen, 2008).

8.1. Shape and Size of Plants

The shape and size of plants can influence insect behavior, although no specific resistance mechanisms have been reported. For example, *Heliothis virescens* females prefer plants with an erect growth habit for oviposition over those with a procumbent growth habit. In tomatoes, smaller vine sizes correlate with reduced fruit damage by the fruitworm (*Helicoverpa zea*). Additionally, soybean cultivars resistant to *Ophiomyia phaseoli* exhibit significantly smaller cotyledons and unifoliate leaves, which are the preferred egg-laying sites for the insect.

8.2. Plant Color

While plant color does not directly confer insect resistance, genetic alterations of plant color can affect fundamental plant processes. Plant shape can influence insect orientation, but color is a more significant factor. For instance, aphids are attracted to yellow surfaces, which are leveraged in yellow sticky traps for monitoring their numbers. Yellow attracts aphids because it mimics the color of senescing tissue they prefer. The adult *Pieris rapae* prefers green and blue-green surfaces for pre-ovipositional behaviour, while *Brevicoryne brassicae* is less inclined to red Cruciferae (Ellsbury *et al.*, 1992). Similarly, the boll weevil shows less attraction to red cotton plants compared to green ones. Despite these preferences, it is debated whether color can be a reliable resistance mechanism, as its effect may not persist without hosts of the preferred color.

9. Chemical Defense in Plants: The Role of Secondary Metabolites

Secondary metabolites are byproducts of basic metabolic activities in plants and don't aid in the growth and development of the plant, rather they serve various physiological roles, including UV protection, nitrogen storage and transport and attraction of pollinators and seed dispersers. Their primary function, however, is to act as defensive compounds against pathogens and herbivores (Mao *et al.*, 2007; Tiku, 2018); while primary metabolites support growth, development and reproduction, secondary metabolites are crucial for plant defense against herbivory and disease. These substances have the ability to both attract specialized insects and repel generalist ones.

9.1. Role of Alkaloids

Plants are the primary source of alkaloids, a broad class of bioactive substances known to have significant effects on mammals and ward off insect herbivores (Howe and Jander, 2008). Examples of these drugs include nicotine, morphine, caffeine and cocaine. Alkaloids are synthesized from amino acids in the plant roots and are found in approximately 20% of all vascular plants, with around 15,000 different types identified. True alkaloids are produced in the root tissues and then travel through the phloem and xylem to gather in the plant's aerial portions (Courdavault *et al.*, 2014). Herbivore attack can cause an increase in the production and transport of these chemicals, even though they are routinely generated at baseline levels. By interacting with cellular components including DNA, membranes and enzymes, alkaloids have considerable biological activity and become toxic to a variety of creatures, including arthropods (Wink *et al.*, 1998).

9.2. Role of Phenolics

One important class of secondary metabolites present in plants are phenols, which are widely distributed defense mechanisms against insects and other herbivory. Lignin, a phenolic heteropolymer that is essential to plant defensive mechanism, is a member of this group which physically obstruct pathogen entry, enhancing leaf toughness and reducing nutritional content, which decreases herbivore feeding (Barakat *et al.*, 2010). Lignin is synthesized when attacks by insects or pathogens and its quick deposition aids in preventing additional infection growth or insect reproduction (Johnson *et al.*, 2009). Furthermore, phenolics help to lower reactive oxygen species (ROS), including hydrogen peroxide, hydroxyl radicals, superoxide anions and singlet oxygen, which activate defensive enzyme cascades (Maffei *et al.*, 2007). In willow plants under light and nutrient stress, which contain significantly fewer phenolics than non-stressed plants, there is an increased attraction for leaf beetles (*Galerucella lineola*), in comparison to controls (Larsson *et al.*, 1986). Additionally, salicylates and other simple phenolics on Salix leaves serve as antifeedants for insect herbivores like *Operophtera brumata*. Although salicylic acid (SA) serves as a phytohormone more significantly than as a deterrent, its levels negatively correlate with larval growth.

9.3. Role of Terpenoids

Terpenoids, the most diversified class of naturally occurring bioactive substances found in plants, have about 40,000 different structural variations. Synthesized from acetyl-CoA, these compounds are crucial for plant defense. They function as active components in resins, volatiles, repellents and toxins and can also affect herbivore development (Aharoni *et al.*, 2005). Monoterpenes and sesquiterpenes, such as limonene found in citrus plants, are notable for forming essential oils those exhibit repellent and toxic properties towards insects. Bark beetles and other insects are affected by monoterpenes found in conifers such as pine and fir (Trapp and Croteau, 2001). When an herbivore damages the plant, these ducts rupture, releasing the resin which entraps insects such as stem-boring bark beetles. Combining terpenoids can result in much stronger protection; for example, a mixture of citronellal and trans-anethole and thymol shows a tenfold increase in efficiency against *Spodoptera litura* (Hummelbrunner and Isman, 2001).

9.4. Role of Flavonoids

Flavonoids are vital compounds that serve multiple roles in plant biology, particularly in mediating interactions with their environment. They help safeguard plants from a range of biotic and abiotic stressors, including insect pests, microbial pathogens and exposure to UV (Treutter, 2006). Known for their cytotoxic properties, flavonoids can bind to and complex with various enzymes. Both flavonoids and their subgroup, isoflavonoids, contribute to plant defense by impacting insect behavior, development and growth which encompasses compounds such as anthocyanins, flavones, dihydroflavonols, chalcones, aurones, flavans and proanthocyanidins *etc.*

9.5. Role of Lectins

Lectins, a specific class of carbohydrate-binding proteins present in many species of plant, exhibit entomotoxic properties. These glycoproteins play a protective role against various pests by binding to carbohydrate moieties on insect cells (Chakraborti *et al.*, 2009). Their insecticidal properties have been harnessed as natural insecticides (Saha *et al.*, 2006). The first identification of anti-insect properties in lectins was based on their detrimental effects on bruchid beetle larvae, specifically *Callosobruchus*. One notable characteristic of lectins is their stability within the digestive systems of herbivores, which increases their insecticidal effectiveness (Vandenborre *et al.*, 2011). They function as anti-nutritional or detrimental agents by binding to glycosyl groups on the digestive tract membrane, leading to detrimental systemic reactions. Lectins have shown promise against varied insect orders, including Homoptera, Lepidoptera and Coleoptera (Macedo *et al.*, 2007). Plant lectin production can be induced by elicitors such as jasmonic acids, which activate lectin genes like NICTABA in *Nicotiana* leaves, affecting insects like Cotton leafworm, Tobacco hornworm and Two-spotted spider mite. Different insect feeding behaviors trigger the expression of specific lectins; for instance, the phloem-feeding aphid *Rhopalosiphum padi* induces production of HFR3 and HFR2 sequentially, while larvae of *Spodoptera frugiperda* primarily induce HFR2 in monocots (Giovanini *et al.*, 2007). Through genetic engineering, the application of these insecticidal proteins in crop protection may be made possible by improving our understanding of how stressors like herbivory activate plant lectins.

9.6. Role of Proteinase Inhibitors

Proteinase inhibitors (PIs) represent most prevalent defensive protein classes in plants which accounts for 1-10% of the total protein content in storage portion like seeds and tubers, where they are most prevalent. These proteins are essential for protecting against insect herbivory because they work by blocking several enzymes (Dunse *et al.*, 2010). In response to hinder the activity of digestive enzymes in the insect stomach and impede the digestion of proteins, proteinase inhibitors (PIs) bind to these enzymes leading to amino acid shortages and subsequent developmental delays or starvation in insects (Azzouz *et al.*, 2005). The most common targets are serine proteases, prevalent in Coleoptera, Lepidoptera and Orthoptera possessing neutral to alkaline gut pH. Cysteine and aspartic proteases, found in Hemiptera, Diptera and Coleoptera, are adapted to acidic gut pH, while metalloproteinases, the smallest group, are less common. Phloem-feeding herbivores lack digestive proteinases and rely on free amino acids from phloem sap. Inhibitors that target proteinase classes are produced by plants and may hinder larval growth without really killing them. Insects can inactivate ingested PIs or produce PI-insensitive proteases to combat PIs, which can diminish PI effectiveness and increase plant damage (Steppuhn and Baldwin, 2007; Zhu *et al.*, 2008). The success of transgenic crops that produce proteinase inhibitors (PIs) emphasizes the importance of understanding the processes and interactions of various PIs as well as insects' adaptive responses.

9.7. Role of Enzymes

Environmental stresses, including insect herbivory, significantly impact crop production by triggering various plant biochemical processes involved in stress tolerance. Studies have highlighted the crucial function of plant oxidative enzymes in defending against biotic stress from herbivores. Essential enzymes that disrupt nutrient absorption in insects include peroxidases (PODs), polyphenol oxidases (PPOs), ascorbate peroxidases and other peroxidases. These enzymes convert mono- or dihydroxyphenols into reactive o-quinones, which are electrophilic and can polymerize with nucleophilic protein groups (such lysine's -SH or ε-NH_2) (Gulsen *et al.*, 2010). More and more recent studies have focused on the overexpression of antioxidant enzymes in response to herbivory (Chen *et al.*, 2005).

9.8. Role of Polyphenol Oxidases (PPOs)

Plant enzymes known as polyphenol oxidases (PPOs) are crucial for defense against biotic and abiotic stressors and have an essential influence on the feeding, growth and development of insect pests (He *et al.*, 2011). PPOs are metalloenzymes that catalyse the oxidation of monophenols and O-diphenols (such as chlorogenic acid) to form highly reactive quinones. These quinones readily polymerize and react with nucleophilic amino acid side chains, cross-linking proteins and reducing their nutritional value for insects (Bhonwong *et al.*, 2009). Through alkylation processes, PPOs aid in the oxidation of ortho-dihydroxyphenolic compounds, producing quinones that have the capacity to damage or spontaneously polymerize proteins, amino acids and nucleic acids (Constabel and Barbehenn, 2008). While PPOs accumulate in various plant tissues, including leaves, roots, stems and flowers, young and vulnerable tissues exhibit more pronounced induction. The defensive role of PPOs is shown by the fact that they are frequently elevated after injury. For example, PPO activity has been interlinked to resistance to Lepidopteran larvae (Felton *et al.*, 1992), *Melanoplus species* and the *Leptinotarsa decemlineata* (Alba-Meraz and Choe, 2002). Additionally, PPOs can create a "super glue" effect that ensnares tiny insects by reacting with particular phenolic substrates present in glandular trichomes (Falco *et al.*, 2001).

10. Indirect Defense Mechanisms

Indirect defenses refer to plant strategies where plants attract, support, or shelter other organisms to mitigate herbivore pressure. Emission of volatile chemicals, secretion of extrafloral nectar, provision of food bodies and establishment of nesting or refuge places are some of these tactics. Herbivores face threats from natural enemies like parasitoids and predators which are attracted to or kept by indirect defenses (Sabelis *et al.*, 2001) and are crucial for plant protection against herbivory (Belete, 2018). These defenses may be elicited by herbivore elicitors or constitutive, resulting from mechanical injury. By secretion of volatiles and extrafloral nectar (EFN), plants facilitate interactions with natural enemies that help reduce herbivore populations (Dudareva *et al.*, 2006). Recent research has increasingly focused on induced indirect defenses, exploring their genetic, biochemical, physiological and ecological aspects (Arimura *et al.*, 2009). Belowground, indirect defenses also take place. For example, when *Diabrotica virgifera* larvae attack maize roots, the roots emit the volatile β-caryophyllene, which draws entomopathogenic nematodes that prey on the beetle larvae (Rasmann *et al.*, 2005).

11. HIPVs: Linking Plant Defense to Trophic Interactions

Herbivore-induced plant volatiles, or HIPVs, are vital for plant defense because they either attract herbivores' natural enemies or deter feeding and egg-laying. In reaction to insect damage, these HIPVs, which are lipophilic compounds with high vapor pressure, are produced from leaves, flowers, fruits and roots. The particular combination of HIPVs generated differs depending on the kind of plants and insects involved, as well as their developmental stage and general condition (Maffei, 2010). These volatiles are tailored to the specific insect-plant interactions, including communication with natural enemies and neighbouring plants (Engelberth *et al.*, 2004). HIPVs aid in association between plants and various organisms, including arthropods, microorganisms and neighbouring plants and can signal undamaged plant parts (Karban, 2011). Diverse insect pest feeding patterns cause the generation of particular volatile chemicals, which in turn leads to activation of diverse defense signaling pathways (Walling, 2000).

12. Plant Hormones as Key Modulators of Resistance Responses

Phytohormones are vital signaling molecules that control plant physiological development and response to various environmental pressures (Verma *et al.*, 2016). Plants use intricate signal transduction pathways facilitated by a network of phytohormones as part of their defense mechanisms against herbivore attacks. These hormones are crucial in controlling plant's reaction to biotic and abiotic stress (Verhage *et al.*, 2010). During an attack, the levels of specific phytohormones increase to initiate a cascade of signaling events. After herbivore damage, a number of plant hormones play important roles in triggering defensive mechanisms within and between plants. Of these, ethylene, salicylic acid and jasmonic acid (JA) are crucial (Gill *et al.*, 2010).

12.1. Salicylic Acid (SA)

Salicylic acid (SA), a monohydroxybenzoic acid derived from cinnamate through the action of phenylalanine ammonia lyase, is a vital endogenous plant growth regulator (Chen *et al.*, 2009). It modulates various metabolic and physiological processes, including defense, growth and development (Pieterse and Van Loon, 2004). The release of volatiles that aid in directing plant defense mechanisms is facilitated by SA signaling pathways (Diezel *et al.*, 2009). It is the regulatory protein Non-expressor of Pathogenesis-Related Genes1 (NPR1) that determines how effective salicylic acid (SA) is. Compared to chewing insects, SA is especially effective against piercing and sucking insect infestations. Additionally, it causes systemic resistance through methyl salicylate (MeSA), a bioactive derivative. Jasmonic acid and Salicylic acid; however, frequently behave antagonistically; SA can inhibit JA activity and vice versa. Predatory arthropods are drawn to MeSA in field conditions as a result of its volatile signal function, which initiates induced defenses such as the release of HIPVs. In response to damage by chewing insects, the JA pathway is activated, leading to the conversion of SA to MeSA through methylation. A synergistic impact between SA and JA is produced by the conversion and emission of MeSA, which improves indirect defensive mechanisms.

12.2. Jasmonic Acid

One important phytohormone that mediates indirect plant defenses is jasmonic acid (JA). Through a sequence of biochemical processes involving phospholipase, lipoxygenases, allene oxide cyclases and synthases, JA is produced from linolenic acid (Wasternack and Hause, 2013). This hormone, which comes from the octadecanoid pathway, builds up in plant tissues when evolve to herbivory injury (Zhang *et al.*, 2008). It influences the expression and activity of Calcium-Dependent Protein Kinases (CDPKs) in potato plants. CDPKs, which include a vast portion of serine/threonine kinases, are crucial for plant defense against a range of biotic and abiotic stresses through signaling pathways (Ludwig *et al.*, 2004). According to Pauwels *et al.* (2009), jasmonates, which include JA, cause a range of defensive reactions, including the synthesis of extrafloral nectar, proteinase inhibitors, volatile organic compounds, alkaloids and antioxidative enzymes.

Numerous genes associated in defense against herbivores are regulated by JA (Shivaji *et al.*, 2010). Herbivore-associated elicitors that activate the JA pathway have been identified in various species, such as *Spodoptera frugiperda* and *Manduca sexta* (Schafer *et al.*, 2011a). Methyl jasmonate (MeJA), JA-IIe and 12-oxophytodienoic acid (OPDA), a precursor to JA, are among the active forms of JA that can be transformed from it (Woldemariam *et al.*, 2012). MeJA-treated plants emit more volatile chemicals and are more successful at luring in natural predators compared to those treated with herbivore elicitors (Bruinsma *et al.*, 2009).

12.3. Ethylene

Ethylene is a crucial phytohormone responsible for plant defense against various insects. Plant defense mechanisms against herbivores and pathogens rely on the ethylene signaling pathway for both direct and indirect effects. S-adenosylmethionine synthetase, 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase sequentially convert methionine into ethylene (Wang *et al.*, 2002). It has been recorded that insect oral secretions and elicitors cause plants like tomatoes and pines to produce excessive amounts of ethylene. The interaction between ethylene and jasmonic acid can either be synergistic or antagonistic, influencing plant defense responses. For instance, in tomatoes, ethylene and jasmonic acid work together to enhance the expression of proteinase inhibitors.

13. Pest Management

Plants employ both direct and indirect mechanisms to deter insect pests, which are regulated by intricate signaling pathways involving phytohormones (Rustagi *et al.*, 2021). Insects, in turn, adapt to these defensive signals, resulting in a co-evolutionary process that is crucial for managing agricultural losses due to pest infestations. Evidence suggests that cross-resistance may develop when herbivorous insects adapt to strong host plant defenses, leading to increased resistance to insecticides. Studies have shown a correlation between the level of insecticide resistance and the insect's diet, including specific dietary components. Therefore, managing insecticide resistance is a critical strategy in plant-insect interactions, as resistance can spread rapidly across insect populations.

14. Advances, Future Perspectives and Challenges

Agricultural systems and insect interactions exhibit a spectrum of relationships, ranging from antagonistic to mutualistic or commensalistic. Effective management of agro-ecosystems necessitates the integration of conservation strategies, including ecologically sustainable pest control methods, to benefit both agricultural productivity and insect conservation. Over the past thirty years, research has extensively investigated insect-plant interactions, with a particular focus on plant biochemistry and evolutionary dynamics. Advances in molecular ecology have deepened our understanding of these interactions, particularly regarding the identification and role of symbionts in plant-feeding insects, as well as differences in symbiont populations across insect orders, including holometabolous and hemimetabolous species. Recent advancements in network analysis tools have improved our capacity to examine how these mechanisms integrate into larger ecological networks. Nevertheless, further research is necessary to fully understand the role of microorganisms in multitrophic interactions, the connection between plant defense and reproduction and the practical applications of these discoveries for pest management and biological conservation (Giron *et al.*, 2018).

Future research aims to elucidate both the beneficial and detrimental aspects of these interactions, considering the combined effects of multiple factors and incorporating historical perspectives into contemporary studies. Although advanced techniques are now available for omics and chemical ecology studies, challenges remain in metabolomics due to the vast array of plant secondary compounds and their biosynthetic pathways. A significant challenge is integrating research approaches that address various biological levels and their ecological functions (Snoeren *et al.*, 2007). The dynamic nature of insect-plant systems, characterized by temporal and spatial variability, underscores the need for continued exploration. While progress has been made in areas such as resistance development, the role of symbionts in pest host range and survival (Hansen and Moran, 2014) and reduced-risk insecticides, several aspects remain underexplored. A more thorough molecular understanding of the advantages of plant diversification, the safe application of novel methods (such gene editing), the participation of plant breeders and the incorporation of "omics" technology at every level of the research process are among the urgent research needs (Giron *et al.*, 2018). Continued research on the differences between insects that are polyphagous, oligophagous and monophagous, as well as their evolution and host specificity and the integration of various research streams into current agricultural practices are crucial for advancing our understanding and management of insect-plant interactions.

15. Conclusion

Direct plant defenses against insect herbivores are often cumulative and can vary significantly across different plant-insect interactions. Typically, multiple defensive mechanisms are employed against a single insect species and factors that are crucial for one species may be of minor importance or ineffective for another. A comprehensive understanding of these interactions and their regulatory mechanisms is vital for developing sustainable agricultural practices that enhance crop health and productivity while preserving ecological balance. Integrating ecological principles into selective breeding and crop management can help balance yield, flavor and pest resistance, leading to more resilient and sustainable agricultural systems.

Habitat restoration initiatives may also improve plant-insect interactions. For example, planting native flowering plants or providing bee nesting places may create or restore habitats for beneficial insects. Promoting conservation and strengthening agro-ecosystem management practices can improve plant-insect interactions. Additionally, research should focus on how specific insect infestations affect plant microbiomes and the resulting impacts on soil microbial communities, identifying key microbial species that influence plant resistance or susceptibility to herbivory. Further investigation is needed on how various herbivores affect nutrient release, soil fertility and plant-microbe competition in different agro-ecosystems, including the effects of plant litter quality and quantity. Advances in technologies such as genomics, proteomics, chromatography, mass spectrometry, chemical purification and monitoring systems have significantly aided researchers in biology and ecology will encourage comprehensive study on plant defense systems in relevance to insect herbivores, including direct and indirect and offer useful information for managing pests.

16. References

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