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The Hidden World of Insect-Plant Interactions: a review

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ABSTRACT: This review examines the hidden world of plant-insect interactions by emphasizing on the sensory perception and behavior of phytophagous insects, nutritional influence on insect reproduction, host plant resistance, Insects, weed and crop interaction, Insect pollinator plant interaction, tri-trophic interaction, and insect biotechnology. It explores how insects use sensory cues to forage for food, find mates, perceive dangers, and navigate their environment. It also examines the influence of host plants on insect behavior and the use of chemical cues for communication. The potential use of semio-chemicals in pest management for sustainable agriculture is highlighted. Nutritional factors and their impact on insect reproductive success are also discussed, emphasizing the need for balanced diets. The different categories of host plant resistance and their effects on insects are examined. The interdependent relationships between insects, plants, and weeds in agricultural ecosystems are explored, with a focus on the role of insect pollinators. The decline of insect pollinators and the importance of studying them are emphasized. The importance of tri-trophic interactions in maintaining ecological balance and biodiversity is discussed. Moreover, the role of biotechnological techniques like genomics, proteomics, transcriptomics, and epigenetics in understanding insect plant interactions as well as developing insect pest control strategies is discussed. The potential use of natural products produced by plants in environmentally friendly pest control methods is also examined. Overall, this review provides a comprehensive exploration of insect-plant interactions and the potential for sustainable pest control methods.

Keywords/ phrases: Host plant resistance, Insect behavior, Insect biotechnology, Insect plant interaction, Semiochemicals, Tri-trophic interaction

SENSORY PERCEPTION AND BEHAVIOR IN PHYTOPHAGOUS INSECTS

Phytophagous insects are a group of insects which feed on plant material, and some of them are considered as a pest of agricultural crops. They have different feeding habits, such as leaf chewers, sap suckers, fruit borers, or seed feeders. They are highly diverse, with an estimated 500,000 species, representing about 25% of known multicellular animals (Bernays, 2009). The majority of phytophagous insect species are found in the orders Lepidoptera, Orthoptera, Coleoptera, Heteroptera, Hymenoptera, and Diptera (Bernays, 2009). Insects rely on sensory perception to interact with their environment, including when foraging for food, finding mates, perceiving dangers, and navigating. Plant-insect relationships involve complex processes, with phytophagous insects possessing sensory receptors to detect stimuli from plants such as visual, mechanical, olfactory, gustatory, and tactile cues. These cues are integrated in the insect central nervous system to elicit appropriate behavioral responses (Saitta et al., 2023).

Host plants can influence the behavior of phytophagous insects, in a different way. Insects use a number of sensory cues in host selection, including visual, olfactory, gustatory, and tactile stimuli, as well as humidity and light intensity (Heard, 2000). The success of plant defenses against phytophagous insects depends on rapid and specific recognition of the phytophagous threat, and plants trigger a cascade of short-term responses that eventually result in the production of a wide range of compounds with defense properties (Santamaria et al., 2018). Generally, Insects recognize their food or host using sensory inputs such as visual cues, chemical cues, tactile cues, and mechanical stimuli as well as physical characteristics of the plant (Borkakati et al., 2019).

Visual Perception

Insects rely heavily on visual perception for survival and reproduction, playing a significant role in host plant selection (Kooi et al., 2021). Different species of insects use color vision, polarization vision, and motion detection to navigate their environment and locate host plants (Wernet et al., 2023). For example, thrips have color-specific responses for identifying host plants, while Schistocerca is attracted to patterns of vertical stripes (Borkakati et al., 2019). Additionally, phytophagous insects such as aphids, leafhoppers, and whiteflies are attracted to yellow and yellow-green colors, enabling them to recognize crops based on color contrast (Bora & Deka, 2014; Kaiser et al., 2017). Bees are also attracted to flower colors from a distance, utilizing visual cues like nectar guides for locating nectar sources (Borkakati et al., 2019). Yellow color is particularly stimulating to green receptors in phytophagous insects(Lopez-reyes et al., 2022). Insects can detect polarized light for navigation and analyze motion using their sensitive visual systems, with the optomotor response being a characteristic of their motion-processing ability.

Olfactory perception

Insects may use a variety of senses, such as the sense of smell (olfaction), taste, vision, and touch to select the appropriate host. Though the all kinds of senses are important, but olfaction often plays a most important in selection of mates and hosts. In addition to visual cues, insects are famously sensitive to olfactory cues, including those of food. Plants emit a variety of volatiles; these volatiles are often similar or identical to chemicals that can serve as feeding deterrents (Schoonhoven et al., 2005). Because of the general lack of visual factors in insects, olfaction must usually play an important part in arriving and recognizing the food. For many herbivores, plant secondary compounds serve as "token stimuli" for feeding or oviposition (Borkakati et al., 2019). The ability to respond via taste or olfaction to these compounds is conferred by odor and taste receptors.

Gustatory perception

Gustatory action can be defined by the response of an insect to relatively high concentrations of nonvolatile stimulatory components which generally come into contact with the receptors in aqueous solution. So, the gustatory sensilla are also known as contact chemoreceptors and due to which insect may avoid unpalatable food or reject endoparasitic larvae for egg laying. Generally, taste receptors come into contact with the stimulus in a solid or liquid form via a single terminal pore in the receptor. For example, two cells of cabbage butterfly, Pieris brassicae, respond to glucosinolates present on cruciferous vegetable (Borkakati et al., 2019). Contact chemoreceptors commonly occur on the tarsi, and stimulation of tarsi of blowflies and butterflies with sugar leads to extension of the proboscis. In nectar–sucking insects like bee, the strength of these responses increases with the concentration of sugars. Host selection in aphids occurs mainly after alighting when the insect probes the plant with its proboscis.

Tactile perception

Tactile stimuli, in addition to contact reception, also plays a role in host location finding and recognition. The surface characteristics of bark and foliage influence the choice of both feeding and oviposition sites. Bark beetle often displays a preference for rough bark over smooth bark areas. The cereal leaf beetle prefers smooth-leafed wheat over verities that are pubescent (Bora et al., 2013).

Mechanism of host recognition in phytophagous insects

The behavior of insects in host selection involves a sequence of responses, including orientation to food, initial biting response, and continued response. This behavior is seen in parasitoids and phytophagous insects, and is also applicable to blood feeders and parasites. The sensory coding of feeding deterrents in phytophagous insects involves neural responses and chemoreceptors. In addition, odor perception is crucial for the survival of phytophagous insects and is encoded by different classes of receptor neurons. Olfactory systems in these insects help them detect specific chemical cues released by host plants, influencing their host choice and feeding behavior (Coutinho-abreu et al., 2014; Renou, 2014; Silvia, 2008).

INSECTS AND CHEMICAL ENVIRONMENTS OF PLANTS

Plants and insects have evolved to interact with one another in complex and fascinating ways. A key aspect of this interaction is the use of chemical cues, both by plants to attract beneficial insects and deter pests, and by insects to locate and evaluate potential food sources (Prasad, 2022). Insect chemical ecology can be studied from two different perspectives including: Mechanism by which insects defend themselves against array of plant secondary metabolites that are toxic to insect herbivores, and interaction between insects and plants and among themselves (mostly tri-trophic interactions) or semiochemical-based interaction (Prasad, 2022).

Semiochemicals

Semiochemicals are message-bearing chemicals substances or mixtures released by an organism that influence the behaviors of other organism (Beck et al., 2017; El-ghany, 2019). Semiochemicals are used in pest management to control and monitor pests by interfering with their communication and changing or disrupting their normal behavior. They are also used in the biological management of arthropods and can be applied in various ways, such as monitoring, mass trapping, attract-and-kill, push-pull, and disruption strategies (Beck et al., 2017). They are categorized as either intraspecific (transmit signals within the same species) e.g., pheromones, and interspecific (communication between different species) e.g., allelochemicals (Fig.1).

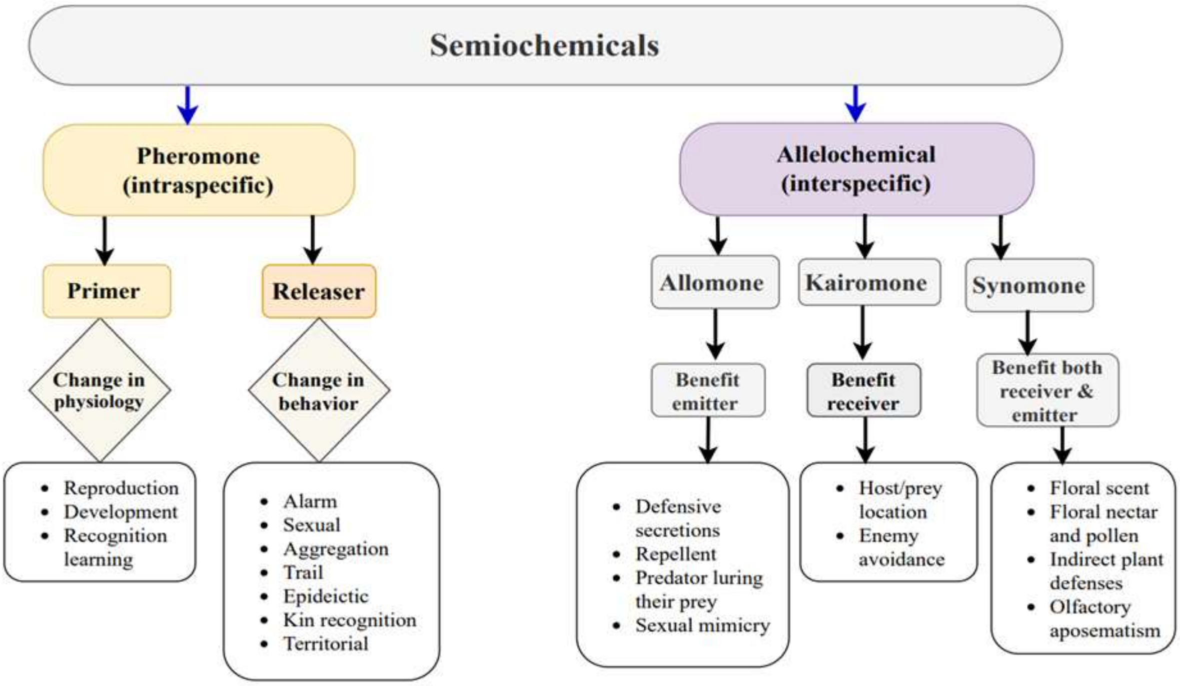

Figure 1: Classifications of Semiochemicals.

Pheromones

Pheromones (Gk. phereum, to carry; horman, to excite or stimulate) are released by one member of a species to cause a specific interaction with another member of the same species. The first semiochemical to be chemically characterized was the sex pheromone of the silkworm moth (Bombyx mori) in 1959 by Adolf Butenandt after sacrificing around 50, 000 female moth and years of hard work. Bombykol is also the first pheromone chemically characterized (EZ-10,12-)-hexadecadienol (Prasad, 2022). The term pheromone was coined by Karlson and Luscher in 1959. The authors defined pheromones as "substances secreted to the outside of an individual and received by a second individual of the same species in which they release a specific reaction." Pheromone can also be called as ectohormone as they are released outside the body of an organism.

There are two distinct types of pheromones: releasers and primers. Releaser pheromones initiate immediate behavioral responses in the receiving organism upon reception, such as alarm, defense, aggregation, attraction, marking of territories, and trail following. Primer pheromones cause change in the receiver's physiology (e.g., endocrine or reproductive system in animals) (Kost, 2008), which eventually modifies the organism's behavior, as seen in case of queen substance released by queen honey bee to arrest the ovarian development in case of worker honey bees. On the basis of interactions mediated, pheromones are again classified as sex pheromone, aggregate pheromone, alarm pheromone, trial pheromone, and host marking pheromone (Prasad, 2022).

Sex Pheromones

The term sex pheromone refers to compounds released by organisms that influence mating or sexual interactions between individuals (Kost, 2008). Female sex pheromones are more common in insects, specifically in the order Lepidoptera, compared to male sex pheromones (Mayer, 2019; Prasad, 2022). Male sex pheromones, also called attractants, are used by insects to attract potential mates, either males, females, or both. These pheromones help male insects find females for mating, while females focus on finding suitable egg-laying sites. Bark beetles and weevil insects are key sources of information on male sex pheromones, with Lepidopteran insects like the cabbage looper also producing them, albeit through different mechanisms. Despite extensive research on female sex pheromones, information on male sex pheromones remains limited.

Epideictic or Dispersion Pheromones

Chemicals produced by insects such as the western pine beetle serve to prevent overfeeding or grazing by attracting large numbers of both sexes to a food source. The aggregation pheromone of the western pine beetle includes myrcene, exo-brevicomin, and frontalin, which attract both males and females (Six & Bracewell, 2013). These chemicals attract beetles to attack host trees like ponderosa pine, where α-pinene and myrcene act as aggregate pheromones. After mating, beetles produce anti-aggregation pheromones like verbenone and ipsdienol to space out and deter further beetles from landing nearby, helping to maintain resources. These host marking pheromones can also be called epideictic pheromones.

Alarm Pheromones

Insects produce alarm pheromones in response to predators to warn conspecific individuals. These pheromones can be released when a predator is detected or after a predator attack. They are found in eusocial insects like ants and honey bees, as well as in other insects like aphids. (Kost, 2008). For example, aphids release (E)-β-Farnesene as an alarm pheromone to alert others, causing them to move away or drop off the plant surface to avoid predators (Basu et al., 2021). Predators and parasitoids sometimes use these pheromones to locate their prey, leading to an evolutionary arms race between insects and their natural enemies.

Host Marking Pheromones

Many phytophagous insects and insect parasitoids use marking pheromones to signal feeding and oviposition sites to other conspecific individuals, reducing competition. These chemicals have been identified in insects from various orders, such as Diptera, Lepidoptera, Coleoptera, and Hymenoptera (Prasad, 2022). In Lepidopteran insects like Pieris brassicae and Pieris rapae, adults avoid sites where conspecific females have already deposited eggs, relying on visual cues and cues from the oviposition site. Not only cues from adult females, but also cues from feeding caterpillar frass can deter conspecific females from depositing eggs. Fruit flies of the Tephritidae family in the Diptera order also use marking pheromones deposited by the ovipositor or present in feces on fruit surfaces to deter conspecific egg deposition (Prasad, 2022).

Trail Pheromones

These pheromones are produced by foraging ants, termites, and larvae of some lepidopteran insects. Dufour's gland, the venom gland, are generally involved in the production of trail pheromones in eusocial insects such as honey bees and ants (Morgan, 2009). They are essentially used to indicate sources of requisites to other members of the colony. Most of the trail pheromones are secreted along with alarm pheromones and mainly used for foraging by conspecific in insects in eusocial insects.

Allelochemicals

Allelochemicals are chemical compounds produced by one species that affect the behavior, growth, or development of another species. They can have both beneficial and detrimental effects on the target organisms and community. These compounds, also known as secondary metabolites, are created by plants, animals, or microorganisms and serve ecological purposes rather than basic metabolism (Hickman et al., 2021; Zhao-Hui et al., 2010). Allelochemicals are nonessential for cell development and are released into the environment. Allelochemicals can be grouped into different categories:

Allomones

Allomones are chemicals that, when received, trigger a behavioral response (releaser effect) or a physiological response (primer effect) in the recipient (Kost, 2008). These responses benefit the sender, but not the receiver, in terms of adaptation. Examples include repellent or toxic compounds for defense, suppressants to inhibit competitors, and venoms to poison prey organisms (Kost, 2008). Allomones can be beneficial, such as plants using chemical cues for mutualistic associations with pollinators. Plants producing secondary metabolites act as allomones by deterring herbivores. Insects also release toxic chemicals or exhibit mimicry as allomones for defense against predators. For example, Eusocial insects like ants, bees, and wasps use poisonous stings as allomones (Prasad, 2022).

Kairomones

A substance produced by the organism when it comes in contact with an individual of another species, evokes a reaction which is favorable to the receiver. Kairomones include the majority of attractants, phagostimulants, and other substances that mediate the positive responses of predators to their prey, herbivores to their food plants, and parasites to their hosts. Most of the male sex pheromones that use host plant or tree compounds discussed erstwhile in this chapter falls under the category of kairomones.

Synomones

A substance produced by an organism, when contacts with individual of another species, evokes in the receiver behavioural reaction that is favourable to both emitter and receiver (Kost, 2008). α-pinene and myrcene which is produced by damaged pine trees are kairomones for species of bark beetles of Dendroctonus as they are attracted for location of feeding sites but the same chemicals are also attractive to pteromalid

NUTRITIONAL INFLUENCE ON INSECT REPRODUCTION

Insects play a significant role in the food chain and ecosystem, especially as a food source for other animals. Reproduction is a key component of insect life cycles, as it ensures the continuity of populations, which influences their significance in the food chain. Insects exhibit a wide range of reproductive strategies, and their reproductive success is highly influenced by nutritional factors (Huck et al., 2021). While various factors affect insect reproduction, diet and nutrition strongly influence an insect's reproductive success and the nutritional value of an insect's diet can impact its fecundity, fertility, longevity, mating behavior, and offspring development (Huck et al., 2021; Lardies & Carter, 2004).

Recent study showed that, food has a double impact on females of predatory ladybirds: qualitative signal effect (the onset of oogenesis) and quantitative nutritional effect (the increase in oogenesis intensity) (Ovchinnikov et al., 2023). Moreover, study conducted by Ormerod et al 2017 demonstrated that, dietary composition can influence and alter development, physiology, behavior, and lifespan of drosophila (Ormerod et al., 2017). Diet can have a profound effect on several metrics for both the larval and adult forms of insects. Understanding the nutritional requirements of insects is therefore crucial for managing pest populations and implementing sustainable pest control strategies. However, despite the growing body of research on the subject, several gaps in understanding remain exists.

Nutritional Requirements for Insect Reproduction

Essential nutrients, including carbohydrates, lipids, proteins, vitamins, and minerals, are vital for insect reproductive biology. Different studies have elucidated the specific roles of these nutrients in various reproductive processes. Lipids contribute up to 40% of an insect egg's dry weight and serve as the primary source of energy for the developing embryo (Fruttero & Leyria, 2017). These findings emphasize the significance of understanding the role of specific nutrients in insect reproductive biology. Different dietary composition is immensely important for survival and reproduction of the blowfly *Lucilia sericata* (Diptera: Calliphoridae) (Alqurashi et al., 2019).

Effects of Macronutrients and Micronutrients on insect reproduction

Nutritionally balanced diets, encompassing adequate macronutrients (proteins, carbohydrates, and lipids) and micronutrients (vitamins and minerals), are essential for optimal insect reproduction (Lee, 2015). Moreover, the ratio of macronutrients like protein and carbohydrate in an insect's nutritional regime can significantly influence its survival, growth, and fecundity (Wang et al., 2018).

Effect of protein on reproductive performance of insects

Protein is essential for insect development, and studies have shown that protein deficiency negatively affects insect reproduction. A study by (D. Chen et al., 2017) investigated the effects of protein deprivation on the reproductive performance of fruit flies. The researchers observed that the female fruit flies exhibited significantly reduced egg production and size when deprived of protein. Another study by (Lee, 2015) investigated the effect of protein on the reproductive performance of brown plant hoppers. The results showed that protein deficiency significantly reduced the number of eggs produced by the brown plant hoppers. In insects, protein consumption by females enhances fecundity and likewise, protein consumption by males tends to enhance the expression of sexual traits (Macartney et al., 2022). The amino acid-Target of Rapamycin (AA/TOR) and insulin pathways play a pivotal role in reproduction of female insects, serving as regulatory checkpoints that guarantee the sufficiency of nutrients for developing eggs (Smykal & Raikhel, 2016). Therefore, Protein is regarded as an important nutritional element for insect reproduction, particularly in contributing to higher rates of production of offspring by females (Lardies & Carter, 2004; Romeis & Wackers, 2002).

Effect of carbohydrates on reproductive performance of insects

Carbohydrates are the primary source of energy for insects. Previous studies have shown that altering the concentrations of yeast and sugar in the semi-synthetic media has a profound impact on lifespan in Drosophila melanogaster, suggesting that dietary protein: carbohydrate (P:C) balance is the main driver of lifespan and ageing processes (Lee, 2015; Lushchak et al., 2014). Most studies on carbohydrate resources in ants have assumed they are used to fuel worker activity (Wills et al., 2015), aggression, or foraging (Grover et al., 2007). Larval development in ants and other insects is thought to be protein limited, but growing evidence suggests that carbohydrates are also needed for growth, particularly in holometabolous insects (Dussutour et al., 2012; Wills et al., 2015). In general, carbohydrate is the main energy source to support optimum growth, development, and survival of most insects.

Effect of lipids on reproductive performance of insects

Lipids are essential components of insect diets, the primary storage molecules and an essential source of energy in insects during reproduction, prolonged periods of flight, starvation, and diapause (Toprak & Park, 2020). Lipids are important for the development and survival of eggs and larvae in insects. They provide the main energy supply for the developing embryo and account for a 90% of the energy needed for development in mosquitoes like Culex quinquefasciatus (Angel-dapa et al., 2010; Ziegler & Antwerpen, 2006). A lipid deprivation causes a reduction in insect reproductive performance. Another study showed that lipid deprivation have a great effect on the reproductive performance of the fall webworm and as a result the lipid-deprived fall webworm produced significantly fewer eggs than those fed a normal diet (Zhang et al., 2019). Furthermore, another study investigated the effect of lipid on the reproductive performance of the cotton bollworm and the cotton bollworm fed a high-lipid diet produced significantly more eggs than those fed a low-lipid diet (Feng et al., 2016).

Effect of vitamins on reproductive performance of insects

Vitamins are essential nutrients for insect growth and reproduction, functioning as coenzymes in enzymatic reactions. Deficiencies in vitamins can disrupt metabolic functions and increase susceptibility to disease. B vitamins are water-soluble organic micronutrients required for insect survival, with roles in enzyme catalysis and metabolic transformations. As insects cannot synthesize B vitamins, they must obtain them from their diets. Vitamin C is necessary for plant-feeding insects, while β-carotene and vitamin E are important for insect vision and reproduction, respectively. Carotenoids, responsible for insect coloration, must be obtained from diets as insects cannot produce them. Overall, vitamins play crucial roles in insect physiology and reproduction (Douglas, 2017).

Effect of minerals on reproductive performance

Minerals are essential nutrients which play an important role in animal's reproductive physiology and its imbalance causes various problems leading to lowered reproductive efficiency. Therefore, adequate trace minerals supplementation and its absorption are required for various metabolic functions including reproduction and growth. Often correcting an imbalance in mineral levels may improve the reproductive performance, fertility and health of the animals (Ojha et al., 2018).

Most naturally occurring mineral elements are found in insects because they are constituents of the food insects eat. For insects, sodium, potassium, calcium, magnesium, chloride and phosphate are considered essential minerals (Behmer, 2008). As in all animals, iron is the central element in cytochromes and a dietary source is required. Zinc and manganese are also essential and play a part in hardening the cuticle of mandibles in insects. Interestingly, some plants hyperaccumulate heavy metals, such as iron, at levels that greatly exceed nutritional requirements. Behavioral studies show that insects given such plants quickly develop learned aversions to them, but that if they are given no alternative, they will eat these plants and suffer reduced growth and high rates of mortality (Behmer, 2008).

Nutritional Stress and Reproduction

Stressful nutritional conditions, such as limited availability of essential nutrients or unbalanced diets, often lead to decreased reproductive success in insects (Raubenheimer et al., 2016). Nutritional stress can affect various reproductive parameters, including pre-mating behavior, sperm quality, and egg viability. Nevertheless, more research is needed to understand the physiological mechanisms underlying these effects. Furthermore, the amount and quality of nutrients consumed by organisms have a strong impact on stress resistance, life-history traits and reproduction of insects (Sisodia & Singh, 2012). The balance between energy acquisition and expenditure is crucial to the survival and reproductive success of animals. The ability of organisms to adjust their development, physiology or behavior in response to environmental conditions, called phenotypic plasticity, is a defining property of life. One of the most familiar and important examples of phenotypic plasticity is the response of stress tolerance and reproduction to changes in developmental nutrition. Larval nutrition may affect a range of different life-history traits as well as responses to environmental stress in adult.

Maternal Effects and Transgenerational Nutrition

Nutrition is the most important environmental factor that can influence early developmental processes through regulation of epigenetic mechanisms during pregnancy and neonatal periods (Li, 2018). Maternal diets or nutritional compositions contribute to the establishment of the epigenetic profiles in the fetus that have a profound impact on individual susceptibility to certain diseases or disorders in the offspring later in life. Maternal diet can significantly influence offspring quality and reproductive success in insects (Wen et al., 2020). Transgenerational effects of maternal nutrition have been observed on various reproductive traits, such as offspring size, growth rate, and stress resistance. However, the underlying mechanisms behind these effects remain poorly understood.

INSECTS AND HOST PLANT RESISTANCE

Host plant resistance (HPR) is a natural phenomenon based on plant self-defense mechanisms and it is a low-cost, and ecologically friendly pest control method. Host plant resistance is the key component of pest management and one of the most appreciated control tactics in advanced agriculture (El-Dessouki et al., 2022). Resistant plants interfere with insect pests' ability to select a host plant and disrupt their biology, making it difficult for them to successfully develop. In the USA, insect-resistant wheat and apple cultivars were first developed and cultivated in the 18th and early 19th centuries. In France, the control of grape phylloxera was an early successful example of utilizing host plant resistance. The breeding of insect-resistant cultivars began in the 20th century after the rediscovery of Mendel's laws of heredity.

Insects select their host plants based on physical and biochemical characteristics such as color, odor, texture, and nutritional quality. Plants can be categorized as either susceptible or resistant. Susceptible plants are those that harbor a large population of insect pests and show more damage symptoms. On the other hand, resistant plants possess an innate ability to avoid, resist, or tolerate damage by insect pests. Host plant resistance has advantages such as being species specific, compatible with other management methods, cost-effective, eco-friendly, and persistent (Mookiah et al., 2021). However, there are drawbacks such as the time required to develop resistant varieties, genetic limitations, and incompatible resistance characters. Despite these pitfalls, improving plant germplasm to develop resistant genotypes may be an important tool in integrated pest management.

Classification of Resistance

Early classifications were based on the physicochemical resistance, and physiological resistance. Physicochemical resistance focuses on the physical and chemical aspects of the plant, whereas physiological resistance focuses on factors such as vigor and seasonal adaptation (Mookiah et al., 2021). Resistance can be classified based on the degree/intensity of resistance, plant-insect interactions, evolutionary concept, trophic level, and screening conditions.

Based on Degree/Intensity of Resistance

Painter introduced a scale to classify resistance intensity, ranging from immunity to high resistance, moderate resistance, low resistance, susceptibility, and highly susceptibility. These terms are relevant for evaluating resistance levels in field conditions but do not explain the mechanism of resistance.

i. **Immunity-**an immunity variety is one which will never be infested by a specific insect under any known condition. There are few cultivars immune to the attack of specific insect, which are otherwise known to attack cultivars of the same species.

ii. **High Resistance-**this type of variety possesses qualities that result in small damage by a specific insect under a given set of conditions.

iii. **Moderate Resistance-** moderate or intermediate level of resistance results from any of at least three situations: (a) A mixture of phenotypically high and low resistant plants (b) Plants homozygous for genes, which under a given environmental condition produce an intermediate level of injury (c) A single clone, which is heterozygous for incomplete dominance for high resistance.

iv. **Low Resistance-** This type of variety possesses qualities that result in lesser damage/infestation by an insect than the average damage caused by an insect.

v. **Susceptibility-** This type of variety exhibits average/more than average damage caused by an insect.

vi. **High Susceptibility-** The high susceptible variety shows more than average damage by the insect under consideration.

Based on Plant-Insect Interactions

The level of resistance in plants depends on the likelihood of attack and the importance of the organ. Plants regularly attacked by herbivores have more constitutive defenses and less inducible defenses. Resistance can be divided into constitutive, inducible, direct, and indirect categories (M. Chen, 2008; Mithöfer & Maffei, 2016).

Constitutive Resistance

Constitutive plant resistance is a type of resistance that is always expressed by plants, independent on the presence or absence of an attack (Mithöfer & Maffei, 2016). It involves both physical and chemical defenses such as mechanical barriers and quantitative defenses (Schoonhoven, et al., 2005). Many physical defenses are constitutive as well as toxic compounds that are synthesized and stored in certain plant tissues. These defenses, including trichome density and cell wall lignification, help protect plants from insect pests. Constitutive resistance can also benefit other management practices, as even partial resistance can slow down the development of pests and make them more vulnerable to predators and parasitoids (Mookiah et al., 2021). However, the effectiveness of resistance can be reduced if pests evolve frequently.

Induced Resistance

Induced defenses are activated only, when necessary, i.e., upon attack by an herbivore. Almost all induced reactions belong to chemical-based defenses. In those situations, the plant has to recognize the presence of the attacker quickly and efficiently in order to induce signaling cascades to eventually induce downstream responses. A complex signaling network including intracellular calcium transients as well as the phytohormones jasmonate and salicylate and subsequent gene activations ensures adequate defense (Maffei et al., 2007; Mithofer et al., 2009). If the induced defense response is established fast and very early, it can reduce the magnitude of the herbivore attack and improve the overall fitness of the plant (Agrawal, 2011). However, a substantial redirection of the metabolism from growth toward defense – as is characteristic of induced defenses – is costly for the plants; on the other hand, the constitutive synthesis and storage of toxic compounds is costly as well, but paid continuously. The host plant can respond to insect attack through direct induced resistance by synthesizing defensive compounds, such as antifeeding proteins and insecticidal secondary metabolites, or through indirect induced resistance by producing volatile organic compounds to attract natural enemies of insects. The production of volatile organic compounds (VOCs) to attract natural enemies of insects is known as Indirect induced resistance (Agrawal et al., 2000).

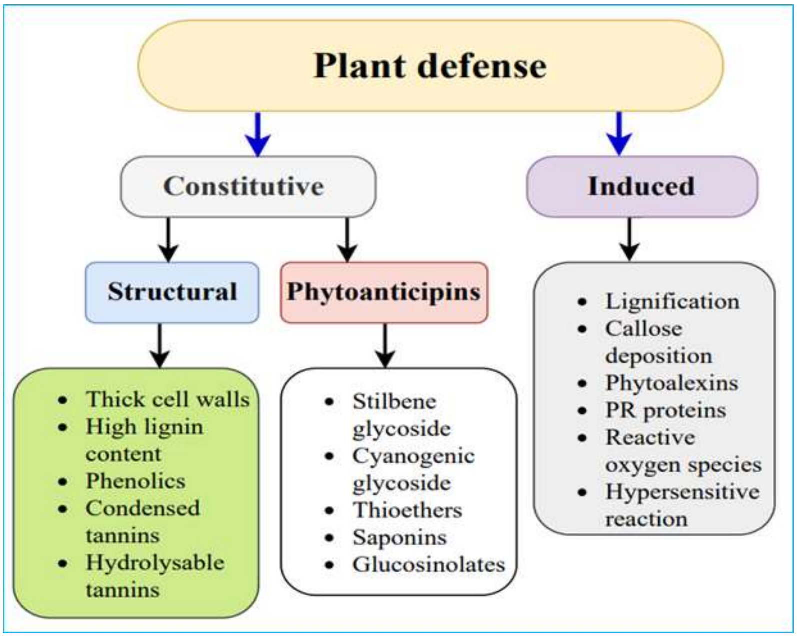

Figure 2: Plant defense based on Insect-Plant Interactions

Based on Evolutionary Concept

Sympatric Resistance

Sympatric resistance is a type of resistance that is acquired through the coevolution of a plant and insect, and it is governed by major genes (Mookiah et al., 2021). This resistance is specific to certain insects and can be influenced by various factors, such as the plant's genetics, environmental conditions, and the interaction between the plant and the insect

Allopatric Resistance

Allopatric resistance is a type of plant defense against insects that is not the result of coevolution. It is caused by genes with pleiotropic effects that are unrelated to the insect pest. Allopatric resistance can be found outside the geographic region where the pest originated and is often polygenic, durable, and provides defense against different types of the insect (Mookiah et al., 2021).

Based on Trophic Level

Intrinsic Resistance

Intrinsic resistance is when a host plant at the first trophic level develops defense mechanisms using biophysical methods like trichomes or toughness, biochemicals such as toxins, digestibility reducers, or nutrient imbalances, or a combination of both, like glandular trichomes or resins.

Extrinsic Resistance

Extrinsic resistance occurs when the natural enemies of insect pests contribute to reducing pest populations, consequently benefitting the host plants. The impact of intrinsic resistance on the third trophic level and factors relating to extrinsic resistance can be either positive or negative.

Based on genetic basis

Vertical host plant Resistance (VR)

This resistance is determined by specific genes and is characterized by being specific to certain biotypes. It is called qualitative resistance because the distribution of resistant and susceptible plants is distinct (Mookiah et al., 2021). The resistance gene can be dominant or recessive depending on the offspring of resistant and susceptible parents. Some plant varieties show resistance while others are susceptible to the same biotype. This resistance, known as vertical resistance, puts significant pressure on the insect but is not long-lasting or stable compared to horizontal resistance.

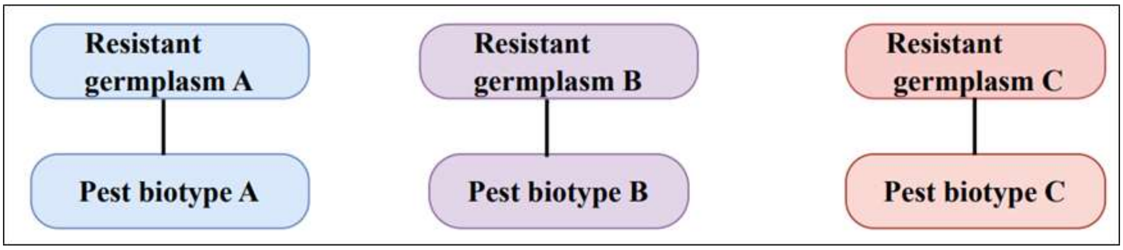

Figure 4: Horizontal Resistance (Mookiah et al., 2021)

Mechanisms of Resistance

Plant resistance is primarily determined by plant genetics. This means that the resistance mechanisms are inherited and preexisting in the plant. However, the extent to which these mechanisms are expressed can also be influenced by environmental factors. Therefore, the classification of resistance mechanisms takes into account both genetics and environmental conditions.

Genetic Resistance

The commonly recognized and widely adopted mechanisms in plant resistance to insect pest studies were proposed by Painter (1941), as preference, antibiosis and tolerance. In 1951, Painter added non-preference with preference as a mechanism of resistance, and in 1968, he started using non-preference alone as a resistance mechanism instead of preference, as it denotes susceptibility. The term 'non-preference' refers to a behavioral response of an insect to a plant, whereas 'antibiosis' and 'tolerance' refer to plant characteristics. Both antibiosis and antixenosis mechanisms are related to insect pests' reaction to host plant characters, whereas the tolerant plants are responding to insect attack.

Antixenosis/ non-preference

Antixenosis is defined as adverse effects on insect behavior, which led to either delayed acceptance or possible outright rejection of a host plant (Smith & Clement, 2012). Antixenosis signifies that the plant is considered as undesirable or a bad host. Non-preference becomes evident when a plant possesses characteristics that make it unattractive to insect pests for feeding, oviposition and shelter (Salim, 2018).

Antibiosis

Antibiosis is the primary, preferred, and long-lasting method of resistance in which it exhibits itself through two main ways: firstly, by directly causing the death of insect larvae, and secondly, by indirectly affecting various stages of the insect's life. Antibiosis encompasses all negative impacts on the insect's life cycle that occur when it consumes a host plant that is resistant to it (Salim, 2018).

Tolerance

The term tolerance in plants refers to the ability to withstand damage from pests without economic loss by compensating and reducing symptom expression. This mechanism is based on the coexistence and coevolution of insects and plants, with various plant traits contributing to tolerance such as growth habit, wound healing, and nutrient regulation. Tolerant varieties have higher economic threshold levels and do not negatively impact insect biology or predator populations. This approach helps maintain yield stability and prevents the development of new pest biotypes (Mookiah et al., 2021).

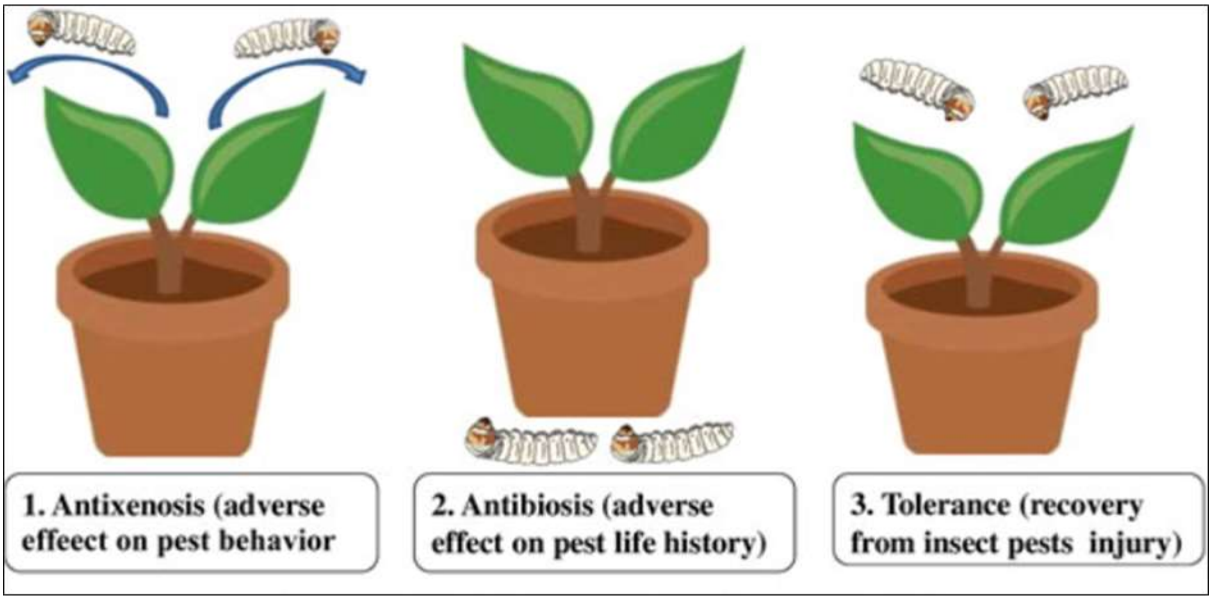

Figure 5: Mechanism of host plant resistance in insects (Kumari et al., 2022).

Ecological Resistance

This type of resistance mostly depends on the environmental conditions where the crops are cultivated than on the crop genetics. The characteristics are temporary, which is the result of transitory characters in the potentially susceptible cultivars. The characteristics are temporary and cultivars involved are potentially susceptible. It must be carefully synchronized with environmental conditions for its effectiveness. Pseudoresistance is generally classified into three broad categories.

Host Evasion or Phenological Asynchrony

Under some situations, certain crop varieties can be able to avoid insect damage by passing the most susceptible stage of the crop rapidly. In this case, the use of early maturing crop varieties or fast fruiting varieties or short season varieties, to provide a long, host-free period, can be followed as an effective pest management strategy. Sometimes, the low infestation may be due to the less population of insect pests at that time. The plants that escape the insect infestation by this mechanism are likely to be infested due to early build-up of insect pest population, e.g. early sowing of paddy in kharif minimizes the stem borer, Scirpophaga incertulas, infestation. Early maturing varieties of paddy escape from brown planthopper (BPH). Sowing of sorghum soon after onset of monsoon in June helps to overcome shoot fly infestation. Short duration cotton varieties escape boll weevil and pink bollworm infestation.

Host Escape

It refers to the lack of infestation or injury on the susceptible host plants, because of transitory circumstances, such as incomplete infestation. If any un infested plant is located in a susceptible population, it does not mean that it is resistant. Even under very heavy infestation, susceptible plants will occasionally escape. The terms host evasion and escape look like synonymous, but host evasion is related to the whole population of the plants under cultivation and absence or insignificant population of insects, while host escape relates to one or a few individuals of the host plant in the presence of insects causing damage to other plants.

Induced Resistance

Is a type of resistant mechanism by which increase in resistance temporarily as a result of some changed conditions of plants or environment such as change in the amount of water or nutrient status of soil.

INSECTS, WEED AND CROP INTERACTION

Agricultural production is more than just a source of food, feed, fiber, and fuel, with insects, weeds, and crops interacting in various ways to produce positive or negative impacts on crop production and pest management (Barbercheck & Wallace, 2021). Weeds and insects are typically seen as non-desirable components of agroecosystems, but weeds can also provide benefits to cropping systems by supporting pollinators and beneficial arthropods (Neher & Barbercheck, 2019). In annual agroecosystems, crop yield loss from weed interference is a significant factor affecting farm profitability, with grain corn and soybean yield loss potentially exceeding 50% without weed control practices (Soltani et al., 2017). Weeds contribute to biodiversity in agroecosystems and support the delivery of regulating ecosystem services by increasing beneficial arthropods involved in pollination and biological control (Storkey & Neve, 2018). Furthermore, plant-feeding insects are a major cause of crop yield losses worldwide and the similarity between weeds and crops can influence the potential for damage to crops by weed-feeding insects (Capinera, 2005). Practices that disrupt the taxonomic link between weeds and crop plants can reduce the movement of specialist and oligophagous insects from weeds to crop plants, ultimately benefiting crop productivity.

Insect-Crop interactions

Insects have a significant impact on crop productivity. Several insect species such as aphids, caterpillars, and thrips can directly damage the plants by feeding on them or causing infections. These insects indirectly impact the growth of a crop by acting as vectors for plant diseases such as viruses and bacteria. Insects can also have a positive impact on the crop's success. For example, the pollination of crops by bees and other insects has a crucial role in the success of crop production. The role of insects in pollination has been highlighted in several studies (Garibaldi et al., 2013; Klein et al., 2007). Insect control methods such as chemical pest control, biological control, and genetic modification are different ways to regulate insects.

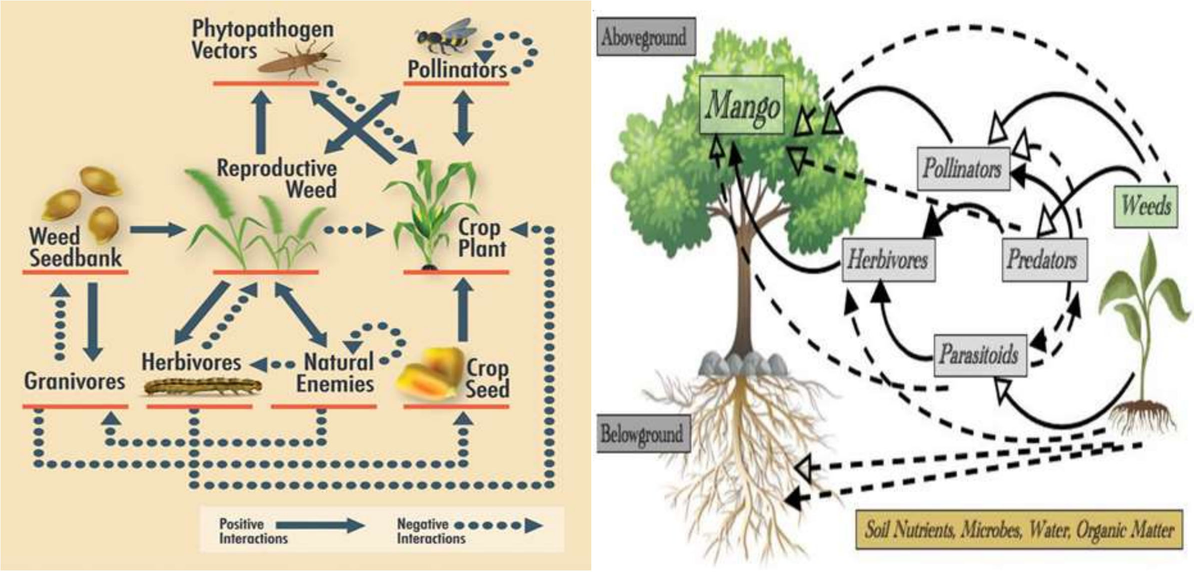

Figure 6: Positive and negative interaction between insect, weed and crop plants. Source: (Barbercheck & Wallace, 2021; Kleiman & Koptur, 2023)

Weed-Crop interactions

Weeds are often viewed as unwanted plants in agriculture. Weeds compete with crops for nutrients, light, and water, which reduces the productivity and quality of crops. Weeds can be classified as broad-leaved, grass-like, and sedge-like based on their structure. The effect of weed-crop interactions on crop growth and productivity is directly proportional to the density and duration of the weed, the type of weed, and the interactions between the weed and crop. Several studies have shown that weed presence has a detrimental effect on crop growth and yield (Barroso et al., 2015). Weed control includes different methods like physical, cultural, and chemical control.

Interaction between Insects and Weeds on Crop

The interaction between insects and weeds has a mixed outcome on the crop growth and productivity. Several weed species can act as a shelter or food source for different insect species. For instance, studies show that weed species like Vicia faba and Fallopia convolvulus act as a host for several insect species that are beneficial for crop growth, such as parasitoids, pollinators, and predators (Bianchi et al., 2006; Haaland et al., 2011) These beneficial insects can help control insect pests that damage crops. However, some weed species can act as a host for insect pests, and their presence can cause damage to crops (Goyal et al., 2012). Several studies analyze the relationship between insects, weeds, and crops (Bianchi et al., 2006; Haaland et al., 2011).

Weeds Are a Food Resource for Insects

Weeds are a primary resource for many phytophagous insects. From the perspective of crop protection, this has both positive and negative aspects. In a positive sense, insect feeding on weeds makes water, soil nutrients, and sunlight more available to crop plants, thereby reducing weed competition with crops. Many insects feed exclusively, or nearly so, on weeds. For example, the sesiid moth Carmenta haematica (Ureta) attacks only snakeweeds, Guteirrezia and Grindelia spp., in the family Asteraceae. Other insects prefer weeds, but may damage crops readily in the absence of attractive weeds. For example, the Colorado potato beetle (Leptinotarsa decemlineata Say) prefers to oviposit on hairy nightshade (Solanum sarrachoides Sendtner) rather than on potato (Solanum tuberosum L.), and eggs are less abundant on potato in the presence of nightshade. This preference for weeds also has been exploited effectively through the introduction of selective herbivores for the biological suppression of adventive (invader) weeds, sometimes with spectacular success (Myers & Bazely, 2003). This process, which strives to reunite a natural predator (in this special case, an herbivorous insect) with its prey (in this case, a weedy plant), is called classical biological control, or introduction biological control.

Weeds Affect Host-Finding by Herbivores

Weeds can modify the attractiveness of crops to the insect herbivore, thereby affecting the rate of colonization. Both vision and odor play an important role in host location by most insects (Kooi et al., 2021). In the case of vision-based host finding, it is the spectral profile (nonvisible to humans as well as visible) to which the insect responds.

Weeds Affect Beneficial Insects

Weeds have a direct impact on beneficial insects such as predators, parasitoids, and pollinators, with some insects feeding on weeds and others using them for nectar. Weeds can enhance the survival of beneficial insects, leading to biological pest suppression. Additionally, weeds indirectly support beneficial insects by providing food sources for predators and parasitoids, which can then move to crop plants to control pests. Weeds also play a role in supporting pollinators, which collect nectar and pollen from them. However, while weeds can benefit pollination in some cases, they may also divert pollinators from crops if they are too attractive. (Al-Doghairi & Cranshaw, 2004; Capinera, 2005).

Weeds Are a Source of Diseases

Weeds can serve as a source of diseases for insects and crop plants. Weeds can act as refugia for entomopathogenic diseases, such as summit disease of grasshoppers caused by the fungus Entomophaga grylli. Weeds around crop fields can harbor dying grasshoppers infected with the fungus, serving as foci for disease infection and spread. However, the negative effects of weeds on plant diseases outweigh the beneficial effects on insect pathogens. Weeds can harbor diseases that can be transferred to crop plants by insects feeding on both weeds and crops (Capinera, 2005).

INSECT POLLINATOR PLANT INTERACTION

Insect pollinator interaction with plant species is critical for the survival and reproduction of both plants and pollinators, and it also plays vital roles in the production of food crops and wild fruits. Insect-pollinators provide essential ecosystem services in several environments as they support biodiversity conservation and ecosystem well-being (Elisante et al., 2020; Gemmill-herren & Ochieng, 2008) as well as crop production (Ojija & Leweri, 2022), which enhances food security and human nutrition. In recent years, research on insect pollinator and plant interaction has gained significant attention in various fields, including ecology, agriculture, and environmental conservation (Baldock, 2020; Ires & Aués, 2020).

Importance of Insect Pollinator-Plant Interaction

Pollination is a vital ecosystem service that facilitates plant reproduction and fruit formation. Approximately, 85% of all flowering plant species depend on insect pollination, and insects are the most common and efficient pollinators of plant species (Ollerton et al., 2011b). Besides, insect pollinators also play a significant role in transferring genes, maintaining genetic diversity, and facilitating ecological restoration processes (Winfree et al., 2011). Moreover, insect pollinators contribute to the production of fruits, nuts, seeds, and other agricultural products, which are essential for human food security and economic development (Gallai et al., 2009). Furthermore, insect pollination also affects plant-pollinator mutualistic relationships, generating complex ecological networks that regulate the dynamics of plant and insect communities (Bascompte & Jordano, 2007).

The majority of essential fats and micronutrients derived from plants for human consumption and societal well-being are the result of insect pollination (Gill et al., 2016). Insect-pollinators are therefore vital for the global crop varieties that humans grow and consume (Cane et al., 2007; Chaplin-kramer et al., 2014). About four billion kilograms of fruits, vegetables, and/or seeds are produced by these crops (Cane et al., 2007). Recent study showed that, over 308,000 blooming plant species rely on insect-pollinators as pollen transfer vectors (Ires & Aués, 2020; Ollerton et al., 2011a; Shuttleworth & Johnson, 2009). This implies that the loss of insect-pollinators could result in a decrease in agricultural productivity, particularly in rural African communities whose crops are largely dependent on insect-pollinators (Ojija & Leweri, 2022). Even though insect-pollinators are essential for life on Earth, there is growing concern over their demise (Zattara & Aizen, 2021).

Types of Insect Pollinators

Insect pollinators comprise several orders of insects such as Hymenoptera, Diptera, Lepidoptera, Coleoptera, and Hemiptera. They exhibit various behaviors and preferences while pollinating flowers, such as visiting specific types of flowers, colors, shapes, and aromas, and collecting nectar or pollen rewards (Rader et al., 2016). For example, bees, including honey bees and bumblebees, are the most effective pollinators, as they have specialized structures that allow them to collect and spread pollen efficiently (Goulson et al., 2015). Additionally, butterflies and moths (Lepidoptera) provide pollination services, although they are less effective than bees and other insects. Furthermore, flies (Diptera) and beetles (Coleoptera) also act as pollinators of plants species that exhibit specialized morphological features that enable these insects to obtain pollen and nectar effectively (Kato & Kawakita, 2004).

Threats to Insect Pollinator-Plant Interaction

In recent years, insect pollinator-plant interactions have been threatened by various human activities that have altered their habitats and food resources (Ires & Aués, 2020; Tommasi et al., 2021; Zattara & Aizen, 2021). Causes of global pollinator decline include habitat destruction, pesticides, climate change, deforestation, diseases, invasive species (Ojija et al., 2019; Ramis, 2016; Stiers et al., 2014). In Africa, farming, burning, and grazing activities threaten insect-pollinators (Ojija & Leweri, 2022), leading to altered habitats and floral resources. Habitat loss reduces pollinator diversity and efficiency, while pesticides harm navigation, immunity, and reproduction (Goulson et al., 2015). Climate change disrupts plant-pollinator synchronization, affecting pollination and fruit formation (Hegland et al., 2009). Limited data hinder efforts to assess pollinator declines in Africa (Connal et al., 2009; Tarakini et al., 2020). African data deficits pose challenges for pollinator conservation planning, with little effort to study and characterize African insect-pollinators (Elisante et al., 2020).

INSECT PLANT GOAL INTERACTION

Insect–plant interaction is complicated form of relationship, involving a number of events that are influenced by biotic and abiotic elements specific to each event (Sharma et al., 2021). Insect-plant interactions are characterized by a complex interplay between two trophic levels, with various goals driving these interactions. Plants and insects are constantly engaging in intricate interactions within natural ecosystems. These two creatures are closely related since plants offer food, oviposition sites, and shelter—the three primary requirements for insect proliferation—and insects have various advantageous functions, such as defense and pollination (Mello & Silva-Filho, 2002). However, depending on the severity of the insect attack, herbivores may do great harm to plants, even killing them.

The relationship between plants and insects is a dynamic system that is always changing and evolving. Plants have evolved a variety of defense systems to ward off insect attacks, such as chemical and physical barriers including the induction of defensive proteins and volatiles that draw insect herbivore predators (Haruta et al., 2001) volatiles that attract predators of the insect herbivores (Birkett et al., 2000), secondary metabolites (Baldwin, 2001) and trichome density(Fordyce & Agrawal, 2001). Insects concurrently evolved defense systems against plant barriers such as detoxification of toxic compounds (Scott & Wen, 2001), avoidance mechanisms, sequestration of poison (Nishida, 2002) and alteration of gene expression pattern(Silva et al., 2001).

Categories and forms of insect plant interaction

Insect–plant interactions can be broadly divided into three categories. These are: Mutualistic, Commensalistic and Antagonistic interactions

Insect–Plant Mutualism

Insect-plant mutualism is a symbiotic relationship with various benefits such as pollination, plant guarding, and seed dispersal (Calatayud et al., 2018). Insects assist in plant reproduction by transferring pollen and receiving nectar or pollen as food. Unique types of pollination like Cantharophily and Melittophily involve specialized adaptations for pollinating specific flowers. Ant-mediated seed dispersal enables plant colonization and provides food for insects. Examples like the yucca plant and yucca moth, as well as the Azteca-Cecropia interaction, highlight the importance and advantages of insect-plant mutualism (Marting et al., 2018; Prasad, 2022). This mutualism plays a vital role in shaping ecosystems, supporting plant reproduction, and assisting in seed dispersal and colonization. It establishes a reciprocal relationship where insects and plants depend on each other for survival and reproduction.

Commensalistic insect plant interaction

Commensalism is a type of relationship where one organism benefits without harming the other. An example includes the interaction between ants and aphids, where aphids feed on plant sap and produce honeydew that attracts ants. Ants protect aphids from predators and parasites and stimulate them to produce more honeydew. Aphids benefit from ant protection, while ants' benefit from the food source, but the plant is unaffected.

Antagonistic insect plant interaction

Antagonistic insect-plant interactions refer to interactions where insects act as antagonists or adversaries to plants (Sharma et al., 2021). It can be categorized as antagonistic herbivory: where herbivorous insects consume plant tissues for nutrition and antagonistic insectivory: where plant eat insects. This can lead to reduced photosynthesis, altered metabolism, and plant death. Plants have evolved defense mechanisms such as thorns, toxins, and attracting natural enemies to protect themselves. Some plants, known as carnivorous plants, have adapted to capture and digest insects through traps and pitfalls. Trapping mechanisms can be active or passive, including pitfall traps, flypaper traps, snap traps, bladder traps, and lobster-pot traps.

Cobra plant

Slender pitcher plant

Raffles' pitcher plant

Sundews plant

Venus flytrap

Bladderwort

Figure 7: Antagonistic plant insect interaction

Association of plant insects with other organisms

Both insects and plants are associated with numerous organisms, and the outcome of insect feeding on a plant is determined by these multi-layered relationships. Furthermore, studies on the microbiome of plants and insects have provided us with a new perspective on this relationship and established that these interactions are more complex than meets the eye (Eberl et al., 2020; Frago et al., 2012). The interaction involves four aspects: (a) insect–microbe interaction, where insect endosymbionts play a crucial role during herbivory; (b) insect–plant interaction, where plant induces chemical and morphological responses against insect attack; (c) plant– microbe interaction, where the phyllospheric and rhizospheric microbiota including endophytes and epiphytes help in inducing induced systemic resistance in plants; (d) multitrophic interaction, that involves parasitoids and predators as well as their enemies.

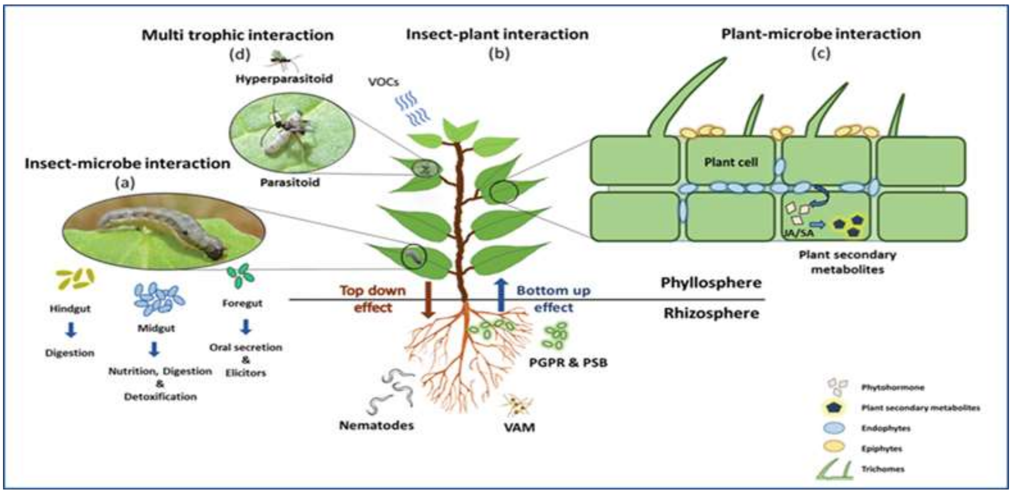

Figure 8: The association of insects-plant with other organisms (Sharma et al., 2021)

Ecological significances of insect-plant interactions

Insect-plant interactions play a crucial role in maintaining ecological balance and promoting biodiversity. One significant ecological significance of these interactions is pollination. Insects such as bees, butterflies, and beetles are important pollinators that facilitate the transfer of pollen from the stamen to the stigma of flowers. This process is essential for the reproduction of flowering plants and the production of fruits and seeds. It is estimated that about 80% of flowering plants rely on insect pollinators for reproduction. Without these interactions, many plant species would not be able to reproduce, leading to a decline in plant diversity and the loss of important food sources for wildlife.

Another ecological significance of insect-plant interactions is herbivory. While it may seem counterintuitive, herbivorous insects play a vital role in maintaining ecosystem health. By feeding on plant tissues, they help regulate plant population sizes and prevent overgrowth. In addition, herbivores can selectively feed on certain plant species or parts, which can influence the competitive balance between plant species and shape plant community composition. Furthermore, herbivory can induce plants to produce chemical defenses, such as toxins or repellents, which not only protect the plants from further herbivory but can also influence the behavior and survival of other organisms in the ecosystem. Overall, insect-plant interactions, particularly herbivory, contribute to maintaining species diversity, promoting plant adaptation, and influencing ecosystem dynamics.

TRITROPHIC INTERACTION AMONG PLANTS HERBIVORE AND THEIR NATURAL ENEMIES

Tri-trophic interactions involve a plant, an herbivore, and a predator or parasitoid(Price et al., 2011). Plant defenses against herbivores can be induced or constitutive and are influenced by factors like herbivore type and environmental conditions (Hahn et al., 2018). Plants can produce chemicals to deter herbivores and attract natural enemies (Kessler & Baldwin, 2016). Herbivorous insects may feed on young leaves with fewer defensive compounds and avoid older leaves with higher concentrations (Schoonhoven et al., 2005). Natural enemies like predators and parasitoids help control herbivore populations by targeting and consuming them effectively (Hoover & Newman, 2017). The tri-trophic interaction is complex and can be influenced by environmental stressors affecting plant defenses and natural enemy efficiency (Hahn et al., 2018).

Plant conditions and its direct and indirect impact on the natural enemy's interaction

Direct defenses include physical barriers such as thorns, trichomes, and cell wall thickness, as well as secondary metabolites such as toxins that affect the herbivore's growth, development, and digestibility. Aljbory & Chen, 2018 discuss the concept of indirect defenses in plants, which involve attracting natural enemies of herbivores to reduce plant loss. One-way plants achieve this is through inducible indirect defense, where plant traits slow herbivore growth and make them more vulnerable to predators and parasitoids. The study tested this theory using soybean varieties, Mexican bean beetles as herbivores, and predatory bugs, showing that slower-growing herbivores were more effectively regulated by predators. Other factors such as digestibility reducers, plant characteristics, and induced resistance also play a role in influencing herbivore-natural enemy interactions. Induced resistance can have lasting effects on herbivores and their natural enemies, impacting interactions for varying durations.

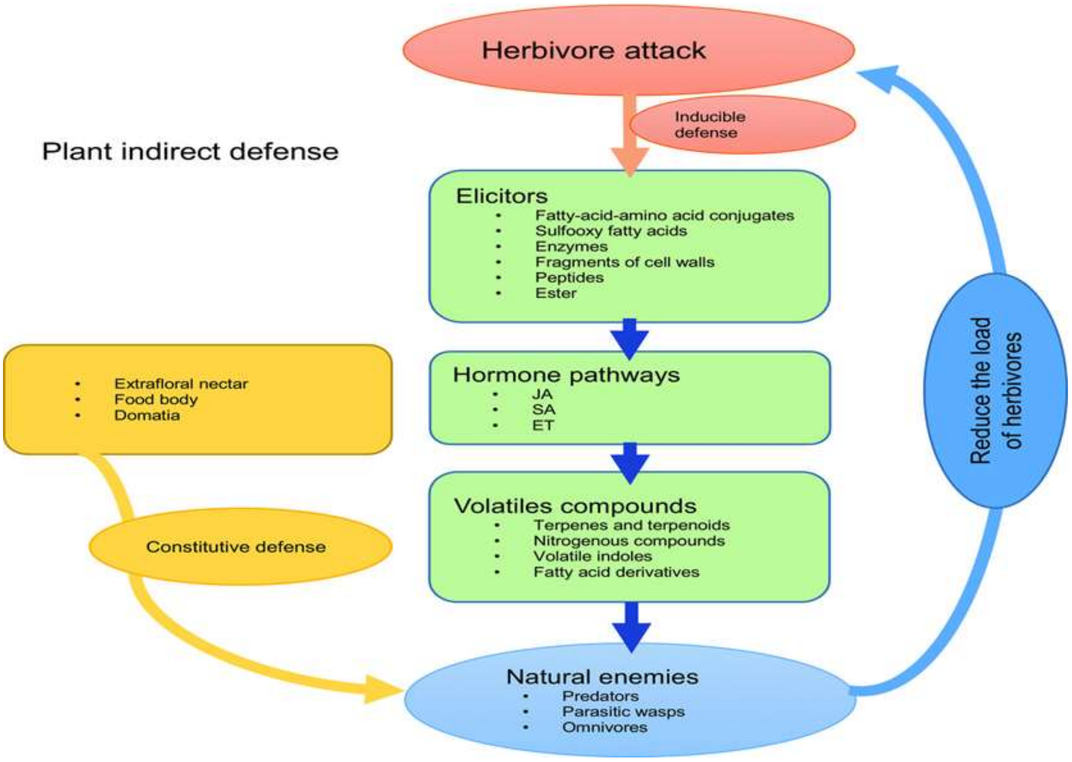

Figure 9: Indirect defense of plants (Aljbory & Chen, 2018)

The importance of dietary specialization in determining the interactions between herbivores and their natural enemies

Specialist herbivores are better equipped to handle plant defenses, such as toxins, compared to generalist herbivores. The interaction between the nicotine in tobacco, specialist herbivore Manduca sexta, generalist herbivore Trichoplusia ni, and pathogenic bacterium Bacillus thuringiensis demonstrates this. Specialist herbivores benefit from higher toxin levels, as they are more protected against natural enemies. Furthermore, specialists are better adapted to the defenses of their prey/host compared to generalists. This example highlights how tritrophic interactions also involve pathogens of herbivores. Additionally, the dietary specialization of parasitoids can impact their response to plant toxins, with specialist parasitoids being less affected than generalists. Overall, plants emit complex blends of volatile organic compounds when under attack by herbivores, which attract natural enemies (Dicke et al., 2009; Snoeren et al., 2009).

BIOTECHNOLOGY AND NATURAL PRODUCT IN INSECT PLANT INTERACTION

Biotechnology plays a crucial role in understanding and manipulating the intricate interactions between insects and plants. Biotechnology techniques like genomics, transcriptomics, and proteomics are used to identify the genes and molecular mechanisms involved in the interaction between insects and plants. These techniques help researchers gain insights into the insect's ability to locate, feed on, and reproduce on plants, as well as the plant's defense mechanisms. The contributions of biotechnology in insect plant interaction includes: the development of genetically modified (GM) crops with resistance against insect pests, exploring the chemical communication between insects and plants, producing plants that emit synthetic or enhanced versions of volatile compounds which can attract or repel insects beneficially, and the development of environmentally friendly approaches for insect pest control. For instance, researchers can use biotechnology to identify and isolate beneficial microorganisms or natural enemies of insect pests. These biocontrol agents can be used to reduce insect populations, protect crops, and serve as a sustainable alternative to chemical pesticides.

Biotechnological approaches to study Insect-Plant interactions

Biotechnological tools have revolutionized the study of insect-plant interactions and the development of pest control strategies (Barbero & Maffei, 2023; Khan et al., 2023; Kumari et al., 2022). Genomics has enabled the sequencing of insect and plant genomes, facilitating the identification of genetic adaptations in insect-plant interactions (Sai Reddy et al., 2022). Transcriptomics allows for the study of gene expression patterns during interactions (I. K. Singh & Singh, 2021), offering valuable insights for developing pest-resistant crops. Metabolomics studies the metabolites produced during interactions, aiding in the discovery of bioactive compounds (Jansen et al., 2009; Maffei et al., 2011). Proteomics helps understand the proteins involved in interactions, revealing molecular defense mechanisms and enzyme activities (Liu et al., 2019; Mittapelly & Rajarapu, 2020).

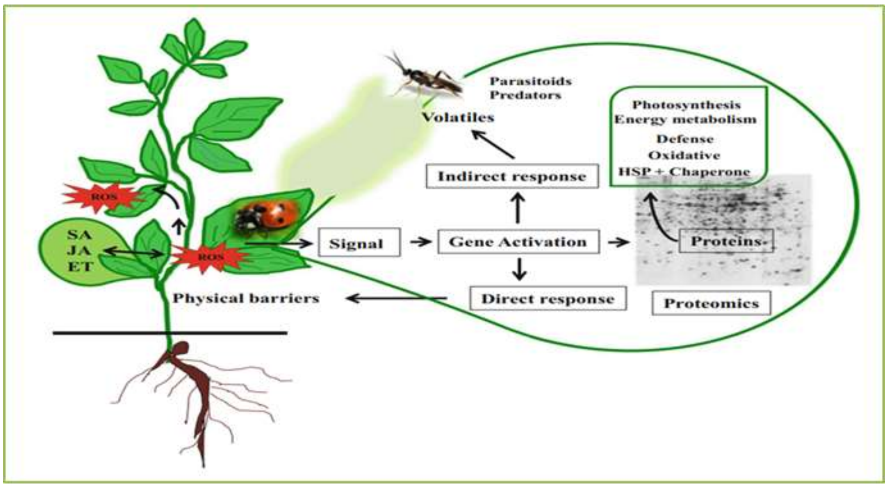

Figure 11: Plant signaling in response to insect infection and use of proteomics to study insect–plant interaction (S. Singh et al., 2021).

***Molecular markers and genetic engineering*:** Molecular markers, such as DNA markers, can be used to identify specific genes or genomic regions that are associated with insect resistance or susceptibility in plants. These markers can help breeders develop crops with improved resistance to insect pests (Dong et al., 2021). Furthermore, genetic engineering techniques can be used to introduce genes into plants that confer insect resistance or alter insect behavior. Potential application of biotechnology in plant defense against insects involves the use of plant-derived insecticidal proteins, such as Bacillus thuringiensis (Bt) toxins. These toxins are toxic to several pests, including the cotton bollworm and the fall armyworm. Bt toxins have been incorporated into transgenic plants, providing a convenient way to develop pest-resistant crops (Samir & Abbas, 2018).

Epigenetics: Epigenetic modifications refer to changes in gene expression that are not caused by changes in the DNA sequence itself. Epigenetic mechanisms can play a role in regulating insect-plant interactions by influencing gene expression in response to environmental cues. Tools that study epigenetic modifications, such as DNA methylation and histone modifications, can help researchers understand the underlying mechanisms of insect-plant interactions. Epigenetic mechanisms have a great role in the plant response to biotic stressors such as bacteria, viruses, fungi, parasites, insects, and weeds by controlling the expression of several resistance genes (Ernst et al., 2012).

RNA interference (RNAi) and plant defense mechanisms

Biotechnology has also been used to manipulate plant defense mechanisms and develop new approaches for pest control. One of the most promising methods involves the use of RNA interference (RNAi). RNA interference (RNAi) is a powerful tool that can be used to manipulate plant defense mechanisms against biotic stress, including defense against insects (Maksimov et al., 2021). RNAi is involved in the safe transport of double-stranded RNA (dsRNA) to the targeted mRNA(s) in the biotic stress-causing agents (for example, fungi and insects) and saves the plant from damage, which is a safer approach compared to the use of chemical pesticides (Ali et al., 2020).

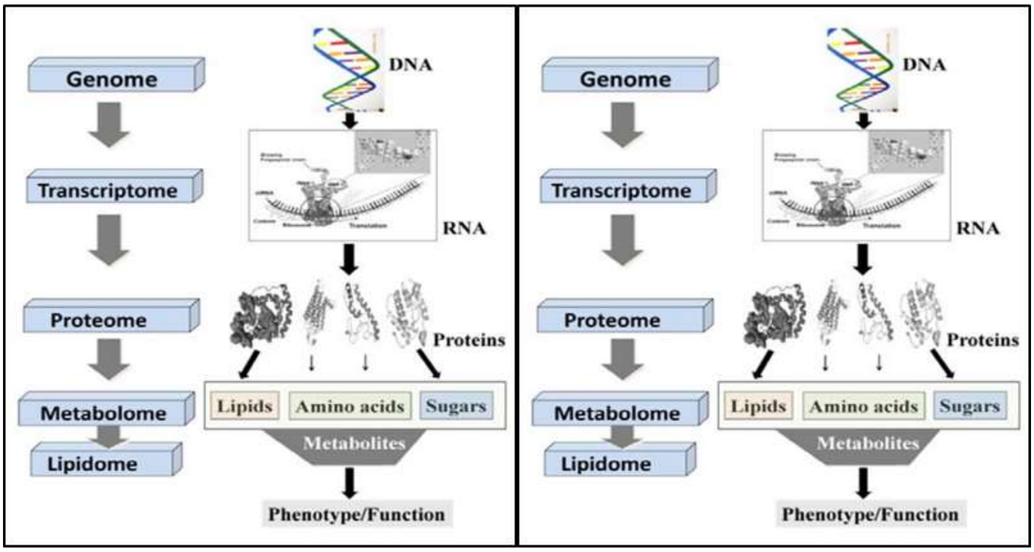

Figure 12: Biotechnological techniques (Seyler et al., 2020)

Natural Products and its role in Insect-Plant Interactions

Natural products are compounds produced by plants that play a critical role in plant survival and defense against herbivores. Natural products play a significant role in plant-insect interactions. These interactions involve the production and use of natural products by plants and insects for various purposes such as defense, communication, and feeding. For example, some herbivorous insects consume and sequester plant toxins within their tissues to provide protection from predators, while plants have evolved defenses against various insect feeding strategies, which are counterbalanced by the ability of insects to detoxify plant chemicals or to react specifically to plant compounds (Gordon-Weeks & Pickett, 2009). In addition, natural products such as plant and petroleum oils can be used to control insects by killing them upon contact or causing them to stop feeding (Borden et al., 2022). Therefore, the study of natural products in insect-plant interactions is important for understanding the ecological and chemical mechanisms underlying these interactions.

Plants have developed various natural products to defend against insects. These defensive compounds can be constitutive or induced in response to plant damage, and they affect feeding, growth, and survival of herbivores (War et al., 2012). Some examples of these natural products include:

***Secondary metabolites*:** Plants produce a diverse array of secondary metabolites as chemical barriers against herbivores. Many phytophagous insects are highly adapted to these allelochemicals and use them for their own protection or as pheromones (Nishida, 2014).

***Toxins*:** Plant secondary metabolites play a key role in plant-insect interactions, whether constitutive or induced. Anti-herbivore defenses can act as repellents, deterrents, growth inhibitors, or cause direct mortality (Ibanez et al., 2012).

***Volatile organic compounds* (VOCs):** VOCs are effective chemical signals in plant-insect interactions. They can attract natural enemies of insect pests, such as parasitoids and predators (War et al., 2018).

***Phenols*:** Phenols are a type of secondary metabolite that can play a role in plant defense against insect herbivory. They can be induced in response to insect infestation or the application of plant defense elicitors (War et al., 2018).

Plant toxins: These compounds can be as effective as synthetic insecticides and have been shown to be extremely toxic to insects (Divekar et al., 2022)

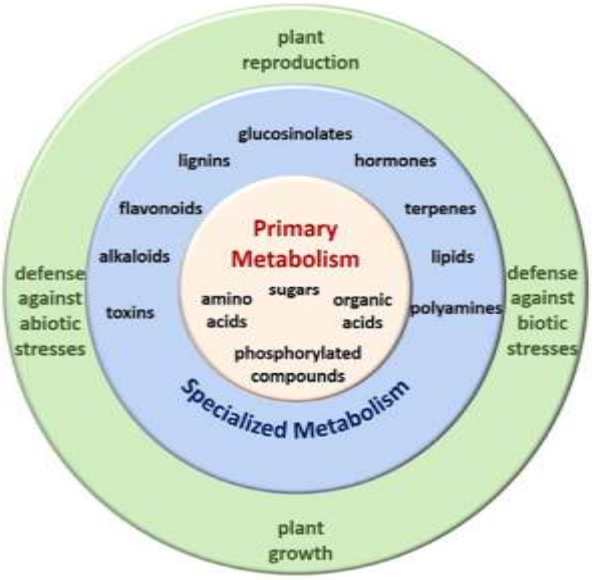

Figure 13: Natural products in plant insect interaction (Castro-moretti et al., 2020).

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