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Plants and Insects' Interaction: a Review on the Mechanisms of Plant Defense Against Herbivorous Insects

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Abstract: Insects and terrestrial plants have coexisted for hundreds of millions of years. They have created sophisticated interactions that have an impact on organisms at all levels, from the most fundamental biochemistry to the level of population genetics. While some of these interactions, like pollination, are advantageous to both parties, the majority involve insect predation on plants and plant defense against herbivorous insects. Because of the importance of such interactions in agriculture, especially in pest management, this review was conducted to highlight how plants and herbivore insects interact in an ecosystem and it majorly emphasizes the mechanisms of plant defense against herbivore insects. Herbivorous insects depend on their host plants to live and reproduce, which in turn harms the plants. The plants by their side should defend themselves to survive. Plants have different defense and resistance mechanisms against their herbivore insects. The major mechanisms are non-preference/*anti-xenosis*, antibiosis and tolerance. These mechanisms of host resistance to insects may involve morphological, physiological, or biochemical features of the host plant and in some cases, a combination of the features may be involved. The defense mechanisms are either constitutive or induced after a herbivore attack. The complex interactions between plants and herbivore insects can influence the ecology of herbivorous insects, beneficial insects, predators and resource availability.

Key words: Herbivorous/Herbivore · Co-Evolution · Defensive Response · Interactions · Mechanisms

INTRODUCTION

The history of biological diversity on Earth has been significantly influenced by plant-insect interactions and coevolution. Due to these interactions, both plants and insects have undergone significant diversification, resulting in the vast number of species that exist today [1,2]. A variety of physical and chemical cues are used in the interactions between plants and insects [3]. Insect herbivores have developed techniques to detect and distinguish plants, whereas plants have evolved a variety of defense mechanisms to protect themselves [4-7]. Over time, they have created sophisticated relationships that have an impact on organisms at all levels, from the most fundamental biochemical to the population genetic. Pollination is one of these positive partnerships, but the majority of interactions involve insect predation on plants and plant defense against herbivorous insects (Figure 1) [8]. For example, the evolution of mutualism between pollinating insects and flowering plants could help the diversification of angiosperms [9-11].

According to Howe and Jander [10], in addition to directly impacting host plant selection, survival and reproductive success, plants often fight off herbivores indirectly through interactions with other species, such as natural enemies of insect pests. Plant characteristics that influence the biology of herbivores include mechanical defenses on the surface of the plant, such as hairs, trichomes, thorns, spines and thicker leaves, or the production of toxic chemicals that either kill or postpone the development of herbivores (such as terpenoids, alkaloids, anthocyanins, phenols and quinones). These traits mediate direct defenses [12]. Some examples of indirect defenses against insects include the release of a volatile combination that draws the natural enemies of herbivores, particularly and/or the supply of food like extra flower nectar and shelter to boost the effectiveness of the natural enemies [13].

Plant-herbivore interactions also influence the ecosystem. For instance, ecosystem dynamics, including trophic cascades and community structures, are greatly influenced by plant defenses. Depending on the unique

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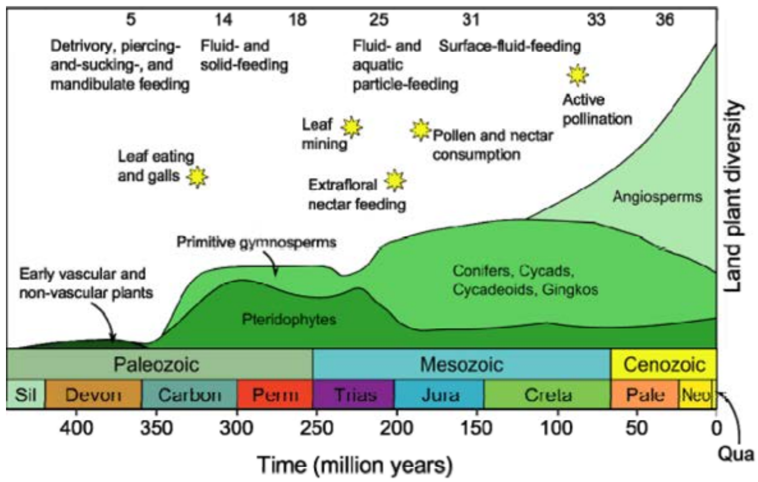

Fig. 1: How plant classes and insect feeding strategies have evolved over time [8].

herbivores available, plants can change the expression of their defenses, improving defenses against various herbivores. This can result in changes in plant characteristics and systems that mediate interactions between herbivores and mutualists, such as pollinators [14]. Phytohormones such as jasmonic acid and salicylic acid are used by plants to defend themselves and this can have an impact on the development, reproduction and density-dependent population increase of herbivores [15, 16]. The importance of intraspecific heterogeneity and evolutionary specialization in multi-trophic interactions is highlighted by the fact that intraspecific trait variation among herbivore lineages with varied host plant specializations can also affect the strength of trophic cascades [17, 18]. Overall, trophic cascades and community structures are influenced by how plants interact with herbivores and other organisms in the ecosystem.

Understanding the nature of gene expression for the plant's protective traits can substantially aid in the design of agricultural plants with increased herbivore resistance. As a result, less harmful pesticides will have to be used to control insects. Because of the ongoing arms race between plants and herbivores, herbivores may co-evolve in response to resistant plant genotypes. It is essential to comprehend the complex chemical interactions between plants and herbivores in order to enhance the production of new crops [7]. This article therefore highlights the genetic, morphological, physiological and molecular aspects behind plant-to-insect resistance.

Plant Defensive Responses to Herbivore Insects: Insect invasion has forced plants to protect themselves since they are unable to escape from herbivore attack because they are rooted to the ground [9]. Plant responses to herbivore attack entail a sophisticated and dynamic defense mechanism that includes structural barriers, toxic substances, reassigning resources and the recruitment of pests that are natural enemies [10, 14, 20-22]. Additionally, they have the ability to emit additional flora nectar and volatiles to entice herbivores' natural predators [23].

Insects, on the other hand, have altered their morphological, behavioral and biochemical properties to generate counter adaptations to plant defensive traits and these adaptations allow herbivores to withstand plant defense pressure [24]. Insect herbivores find the plant environment unpredictably altered by changes in a plant's defense components as a result of an insect attack, which alters the fitness and behavior of the herbivores [6]. Depending on the insect damage (severity of the herbivore harm), direct or indirect defense mechanism can be induced by the plants. Induced responses have been utilized as a component of pest management [25].

The different mechanisms of resistance of host plants to herbivore insects are non-preference, antibiosis, tolerance and avoidance. Non-preference is when host plants exhibit unattractive or unsuitable characteristics for colonization, oviposition, or both by an insect pest. This type of resistance is also termed as non-acceptance and *anti-xenosis*. Antibiosis-type resistance causes an adverse effect when feeding on a resistant host plant, which in turn hinders the development and/or reproduction of the insect pest. In severe cases, it may even lead to the death of the insect pest. Tolerance is the ability of the host plant to withstand the insect population to a certain extent, which might have damaged a more susceptible host. Pest avoidance is the same as disease escape and as such, it is not a case of true resistance [26]. These mechanisms of host resistance to insects may involve morphological, physiological or biochemical features of the host plant; some cases of insect resistance involve a combination of features [7, 27]. The processes might be triggered after an attack or expressed continuously [8, 31].

Morphological Defensive Responses: According to War *et al.*[24], some of the morphological defensive responses include increase in the trichomes, sclerophylly and latex deposition. Plant structures serve as the first line of defense against herbivores and are essential for host plant resistance (HPR) to insects [12, 29]. The structures include features such as spines and thorns (spinescence), trichomes (pubescence) and toughened/hardened leaves (sclerophylly) [12].

Trichomes: Trichomes, which are tiny protrusions of plant epidermal cells, protect plants against insect herbivores. They offer defense by serving as physical obstacles, obstructing access to plant tissues and entangling herbivores' legs. Trichomes can also emit poisonous substances that repel herbivores and can act as entry points for diseases. Trichomes can also prevent herbivores from ascending by diverting their movements away from the tops of the plants. Trichomes can provide microbiological habitats for microbes while also acting as entry routes for pathogens, which can have positive and negative effects on plants [30-32]. Reports indicate that such physicochemical mechanisms of resistance to shoot flies have been observed in sorghum [27, 33]. They have also reported this defense mechanism and the variation in trichome density in wild populations of Arabidopsis thaliana. Dense trichomes affect herbivory mechanically by restricting insect and other arthropod movement on the plant surface and preventing them from accessing the leaf epidermis. The release of secondary metabolites by glandular trichomes, such as flavonoids, terpenoids and alkaloids that can poison, ward off, or trap insects and other organisms, creates a combination of structural and chemical protection [12, 29, 34].

Sclerophylls: According to the definition in Zhu *et al.* [39], sclerophylly is small, comparatively thick leaves. All tissues in the lamina, including the cuticle and outer epidermal walls, thicken as a result of this leaf thickening and a hypodermis is frequently present. It lessens the taste and digestibility of plant tissues, minimizing herbivore harm.

Latex Deposition: Latex, a sticky emulsion produced by specialized cells called *laticifers* [36]. It contains great varieties of defense chemicals and defense proteins that exert strong defense activities against herbivorous insects by transporting a system to the point of damage [37].

Physiological Defensive Responses: As a result of insect herbivores, plants have developed a variety of physiological defense mechanisms. These reactions include the constitutive or post-infestation synthesis of secondary metabolites, which might impact herbivore growth and development [38]. In reaction to herbivory, plants also produce volatiles that may attract insects' natural predators [39]. Plants have the ability to stimulate internal signals that result in the creation of defensive chemicals, such as calcium ion fluxes and jasmonate signaling [8]. These defensive substances can frighten or repel insects, impede their digestion and make eating more challenging [40]. In order to accommodate and feed herbivore predators, plants can also create extra floral nectar, food sources and nesting or refuge locations [41].

The creation of primary metabolites, which directly support growth, development, or reproduction, occurs in all plant cells. Examples include amino acids, proteins, carbohydrates and nucleic acids. Despite typically playing a defense role for plants, secondary metabolites don't directly affect growth or reproduction. These chemicals often fall into one of three major chemical categories: terpenoids, phenolics, or alkaloids. Secondary metabolites are chemicals that lessen the flavor of the plant tissues in which they are produced without interfering with a plant's normal growth and development [10]. The secondary metabolites not only shield the plants from various threats but also improve their fitness. According to reports [42], sorghum shoot fly and corn earworm resistance have been decreased by using secondary metabolites. Studies on secondary metabolites may lead to the discovery of new signaling molecules involved in plants' resistance to herbivores and other stressors. Some of the secondary metabolites that help plants defend themselves are discussed below.

Plant Phenolic: Plant phenolics, including polyphenols and phenolic glycosides, are essential for plant defense against insects that consume herbivorous plants. These secondary metabolites function as anti-feedants, poisons, feeding deterrents and chemicals that decrease digestibility in both direct and indirect ways [20, 43, 44]. Plant-based natural compounds with insecticidal and insect deterrent properties often contain polyphenols, which are extensively present in blooming plants [45]. In response to biotic and abiotic stressors, plants produce phenols, particularly phenolic glycosides, which prevent the growth of fungus and restrict pathogen adhesion and invasion [46]. These substances are also engaged in interactions between plants and herbivores, affecting insect physiology and regulating how much different herbivore feeding guilds are exposed to plant defenses. In general, plant phenolics function as adaptive traits that have developed as a chemical deterrent against insect herbivores. Phenols are used by plants as a defensive mechanism not just against herbivores but also against rival plants and microorganisms. In reaction to insect bites, phenols frequently undergo qualitative and quantitative changes and the activity of oxidative enzymes rises [47]. The phenolic heteropolymer lignin is a crucial component of a plant's defense mechanism against infections and pests. By physically preventing them or hardening the leaf, it restricts pathogen penetration. This lowers herbivore damage and the leaf's nutritional value. When an infection or herbivore attacks, lignin is produced and its quick deposition stops the infection or herbivore from spreading further [48].

Phytohormones: Plant hormones are essential for protecting plants against insect herbivores. Herbivore attacks cause plants to activate signaling pathways that cause the synthesis of protective chemicals. Jasmonic acid (JA) is a significant hormone that plays a role in this process [20]. When an insect feeds, JA is produced, which causes the development of poisonous secondary metabolites, volatile organic compounds and anti-digestive proteins that either ward off or sedate the insects. In order to deter herbivores and attract predators, plants produce volatiles when they are attacked by them [40]. By acting as a deterrent to herbivory, these hormones and defense substances make it more challenging for insects to feed [50, 51]. To counteract plant defenses, however, herbivorous insects have also developed strategies and some even sequester the chemicals for their own defense. The interaction between plant hormones and herbivore insects is complex and involves metabolic costs for both parties, resulting in a standoff where both host and herbivore survive, although their development may be suboptimal.

Plant defense against herbivore attacks involves numerous signal transduction pathways that are mediated by a network of phytohormones. According to Verhage *et al*. [52], plant hormones are necessary for regulating a plant's growth, development and defense mechanisms. Several plant hormones have been connected to intra- and inter-plant communication in plants damaged by herbivores. The main signal-transduction pathways that are activated by jasmonic acid, salicylic acid and ethylene are plant defense responses to insects. These pathways cause specific defense-related gene groups to be activated in response to damage or insect feeding. These hormones may react singularly, collectively, or antagonistically, depending on the attacker.

Herbivore-induced Plant Volatiles (HIPVs): Herbivore-induced plant volatiles (HIPVs) are a diverse group of small-molecule volatile chemicals produced by plants. Depending on the plant's species and cultivar, these chemicals have different identities. HIPVs can be used as cues by the natural enemies of many plant pests to find afflicted plants and, by extension, their prey or host. HIPVs are consequently an indirect defense mechanism since they attract predatory or parasitic insects that harm the plant pest [28]. HIPVs production is influenced by the types of plants and herbivores, their developmental stages and their general health (Figure 2) [13]. By attracting pollinators and seed dispersers, these volatiles give plants an advantage during reproduction while defending them from herbivores and pathogens. In addition to being released from roots into the soil, they are also released from leaves, flowers and fruits into the atmosphere. Plant volatiles, which make up the majority of terpenoids, phenyl propanoids/benzenoids, fatty acid derivatives and amino acid derivatives, account for about 1% of plant secondary metabolites [53]. Plants release a volatile mixture that is unique to that insect-plant system when an insect attacks, including any natural adversaries and neighboring plants. The HIPVs mediate interactions between plants and bacteria, unharmed plants nearby, unharmed spaces inside the plant and interactions between plants and arthropods [54].

Elicitors: Plants recognize cues in the insect's oral secretion/saliva and in the ovipositional fluid. Insect oral secretions contain specific elicitors such as fatty acid conjugates, which stimulate plant defense. According to Alborn *et al*. [55], the first plant defense elicitor identified from the oral secretions of beet armyworm, *Spodoptera exigua,* was volicitin (N-(17-hydroxylinolenoyl)-L-glutamine), whose application on maize wounds resulted in the emission of a blend of volatiles that attracted natural enemies of the pest. Different elicitors result in various types of defenses, depending on the underlying biological processes and the elicitor in question [56].

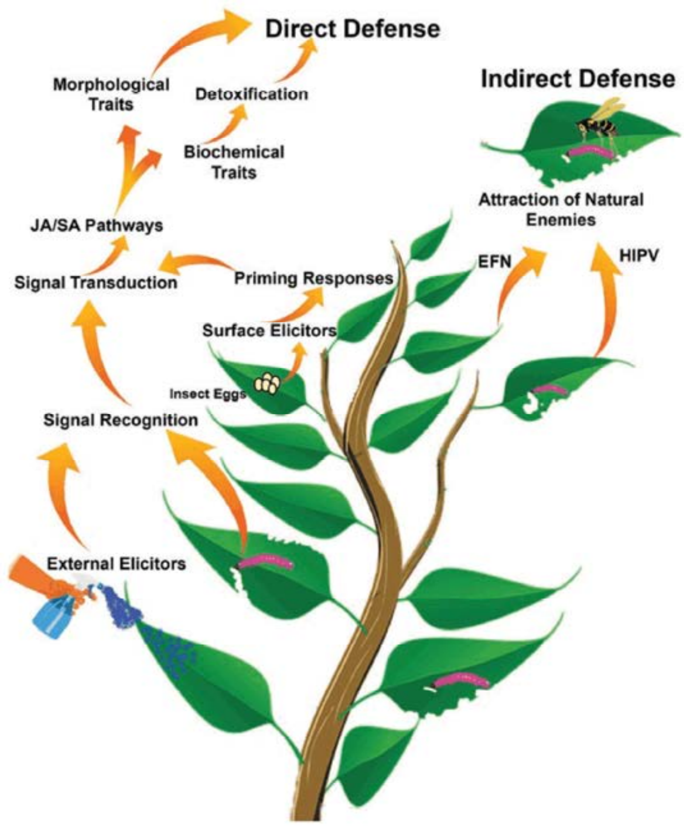

Fig. 2: Plant defense against insect pests (EPF = extra floral nectar; HIPV = herbivore induced plant volatiles; JA = jasmonic acid; SA = salicylic acid) [24].

Molecular Defensive Responses/mechanisms: For oxidative defense and signal transduction, changing gene expression during stressful situations, such as insect attacks, causes changes in protein quality and quantity [6, 57]. According to Chen *et al.* [58] and Zheng and Dicke [59], in response to herbivory, plants undergo substantial gene expression changes, with hundreds and potentially as many as thousands, of genes being up- or down-regulated. Among other advancements in genomics and transcriptomics, the availability of whole-genome sequence data, expressed sequence tags (ESTs) and microarrays has increased our comprehension of the changes in gene-expression profiles in response to insect bites. The report in Kanchiswamy *et al.* [60] indicated the modulation of Arabidopsis defense responses against *Spodoptera littoralis* by creatine phosphor kinase (CPK)-mediated calcium signaling.

Aphids regulate the expression of genes related to glucosinolate production, calcium-dependent signaling, oxidative stress and cell wall changes. Moreover, the changes in transcriptional patterns of several genotypes within a plant species have been examined using gene expression levels [61]. Different plants respond differently to the same herbivore. For instance, distinct cultivars of cabbage had substantially diverse gene expression patterns in response to *Pieris rapae* feeding [62]. By combining a number of technologies, such as genetic and genomic tools like microarrays, deep sequencing, transcriptional profiling techniques and proteomics through mass spectrometry, a deeper knowledge of the molecular pathways driving plant defense against insect herbivores is possible.

Many plant proteins eaten by insects are stable and maintain their integrity in the midgut in addition to crossing the gut wall and entering the hemolymph. Changes to a protein's amino acid sequence or composition have an impact on how well it functions. Similar to this, the use of protease inhibitors (PIs), which prevent toxic proteins from degrading and allow them to fulfill their defense role, can improve a hazardous protein's ability to repel insects. With a better understanding of protein structure and post-translational modifications that lead to stability in the herbivore gut, it may be possible to predict the toxicity and mechanism of plant resistance proteins (PRPs). A wide variety of PRPs are involved in plant defense against herbivores. According to Chen *et al.* [58] and Chen *et al.* [63], the following are plant defense proteins against insect pests.

Lectins: Plant lectins are a class of proteins that play a role in plant defense against herbivorous insects. These lectins can reduce the nutrient value of plant material or interfere with insect metabolism, making them potential tools for pest control strategies [64, 65]. Lectins can bind to sugars and have different molecular structures and specificities [65]. Some lectins are constitutively expressed, while others are inducible in response to herbivory [8]. The mode of action and target sites for lectins in the insect body are still being studied [66]. It is important to consider the effect of plant lectins on non-target organisms and human/animal consumers.

Because of their insecticidal qualities, certain plant lectins have been employed as naturally occurring insecticides against insect pests [67]. One of the lectins' most important properties is their capacity to endure throughout the digestive systems of herbivores, which grants them a major insecticidal capability. According to Vandenborre *et al.* [64], proteins called plant lectins are utilized as defenses against insects that feed on plants. They serve as toxic or anti-nutritional compounds and have a number of negative systemic consequences of adhering to the membrane glycosyl groups lining the digestive tract. A disruption in the metabolism of lipids, carbohydrates and proteins causes hormonal and immunological alterations that endanger the growth and development of insects [68].

Inhibitor Proteins: Inhibitor proteins defend plants against herbivore insects through various mechanisms. Plant inhibitory proteins (PIs) such as protease inhibitors, á-amylase inhibitors, lectins, arcelins and ribosome inactivating proteins (RIPs) play a crucial role in plant defense mechanisms [69]. These proteins inhibit the digestive proteases of herbivorous insects, limiting their ability to digest plant tissues and obtain nutrients [70]. Additionally, PIs can reduce the preference of insects for certain plants by disrupting their physical structures and inhibiting chemical pathways [71]. Plants also produce defense chemicals such as secondary metabolites, proteases, lectins, amino acid deaminases and oxidases, which have direct toxic effects on herbivores [8]. Furthermore, plants may release volatiles to repel herbivores, attract predators, or induce defense responses [66].

One of the most prevalent kinds of protective proteins in plants is known as a proteinase inhibitor (PI). A plant's defense against insect herbivory depends on PIs, which inhibit a number of enzymes and make about one to ten percent of the total proteins in storage organs like seeds and tubers [72]. Storage organs like seeds and tubers contain higher levels of PIs. When PIs bind to the digestive enzymes in an insect's gut, they prevent them from functioning properly and reduce protein digestion, which causes the insect to starve or slowdown in its development. The defensive function of various PIs against insect pests has been investigated in a variety of lepidopteran and hemipteran insects, either directly or by expression in transgenic plants to increase plant resistance to insects [73]. Understanding the mechanisms, interactions and adaptive responses of herbivores as well as other defenses and various PIs has become more important as a result of the success of transgenic crops in producing PIs to ward off insect pests.

Enzymes: The interruption of insects' nourishment is one of the key effects of HPR against insects. The oxidation of mono- or di-hydroxy phenols by peroxidases (PODs), polyphenol oxidases (PPOs), ascorbate peroxidases and other peroxidases results in the formation of reactive o-quinones, which in turn polymerize or form covalent adducts with the nucleophilic groups of proteins due to their electrophilic nature [74]. Enzymes such as lipoxygenases, phenylalanine ammonia-lyase and superoxide dismutase are additional significant antioxidant enzymes. Recently, there has been a lot of interest in how plants produce antioxidant enzymes after being eaten by herbivores [6].

Genetic Defensive Responses/mechanisms: Host plant resistance (HPR) is a plant's capacity to fend off, withstand, or recover from insect attacks in situations where doing so would affect other members of the same species more severely [75]. The hereditary features that the plant carries affect how much damage the insect finally causes. Based on the number of genes involved, genetic resistance is divided into three types: monogenic, oligogenic and polygenic. Each of them is controlled by a single gene, a few genes, or many genes. Major gene resistance (vertical resistance) is controlled by one or a limited number of major genes, whereas minor gene resistance (horizontal resistance) is controlled by many minor genes [26].

Transgenerational-induced Resistance to Herbivores: It has been found that both biotic and abiotic plant stimuli can foster resistance in both the mother plant and its offspring. This maternally induced resistance (transgenerational immunity), in addition to producing healthy seeds and seedlings, protects the offspring of plants from insect pests [76]. There are a few studies on plants' transgenerational immunity to insect pests. Agrawal [76] claims that *Pieris rapae*-damaged or jasmonic acid-treated wild radish plants produce offspring with a high level of induced resistance to this pest. In Arabidopsis plants exposed to extremes including cold, heat and flooding, high homologous recombination frequency and increased genome methylation resulted in progeny that were more resistant to stress [77]. Knowledge of transgenerational-induced resistance may provide answers to certain difficult questions surrounding plants' ability to endure herbivore damage [77].

Genetic engineering of plants for induced resistance has been a major focus in crop improvement programs. Strategies such as the synthesis of dual salicylic acid and jasmonic acid-responsive promoters have been developed to enhance plant resistance to a broad spectrum of pathogens [78]. Another approach involves the expression of *Bacillus thuringiensis* toxins in transgenic food crops, which has proven to be effective against a wide range of pests [79]. Overexpression of hydrolytic enzymes that degrade the cell wall of invading fungi has also been used to enhance crop resistance [80]. Protein- and nucleic acid-mediated resistance, as well as the role of host plant genes, plant hormones and ribosome-inactivating proteins, have been explored for developing resistance against plant viruses [81]. These advancements in genetic engineering provide opportunities to engineer plants with multi-mechanistic resistance to various pathogens, contributing to crop protection and food security.

The Ecological Interactions Between Plants and Herbivore Insects: Ecological interactions between insects and plants are complicated and dynamic [19]. Plant relationships with other animals, such as beneficial insects and nearby plants, are significantly influenced by plant defense mechanisms against herbivore insects. Because a lack of water tends to increase a plant's ability to fight and escape from herbivores, water availability is a critical factor in determining how plants and herbivores interact [82]. It has significance for insect-plant co evolution that insects have evolved the capacity to selectively store plant defensive chemicals through sequestration [83]. Depending on the specific herbivore present, plants may change how they exhibit their defense and depending on the predominant herbivore pressure, they may invest in different defense methods [84]. Predators can indirectly increase the productivity of a given system by reducing the negative effects of herbivores on plant biomass, resulting in a world that is green with plant material rather than denuded by herbivory [85]. Given that these substances can have both negative and positive impacts on insect species, it is imperative to comprehend the biochemical and molecular cascades involved in these interactions [27].

CONCLUSION

A number of morphological, genetic, physiological and molecular processes are used by plants to respond to herbivore attacks. Both direct and indirect defenses are used as a part of physiological systems that are extensive and highly dynamic in order to protect against herbivores. Direct defenses include mechanical barriers on a plant's surface, such as hairs, trichomes, thorns, spines and thicker leaves, as well as the creation of poisonous substances like terpenoids, alkaloids, anthocyanins and phenols that either kill or postpone the growth of herbivores. The defensive compounds are either produced constitutively or in response to plant damage and they have an effect on herbivore eating, growth and survival. Categorically, the major defense mechanisms are non-preference/*anti-xenosis*, antibiosis and tolerance. These defense mechanisms are important in agriculture, especially in pest management. Since ecological systems are interlinked and complex, the interactions between plants and herbivore insects can influence the ecology of herbivorous insects, beneficial insects, predators and resource availability.

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