Novelty Journals

ISSN 2394-9716

International Journal of Novel Research in Interdisciplinary Studies
Vol. 8, Issue 3, pp: (15-39), Month: May – June 2021, Available at: www.noveltyjournals.com

REVIEW ON PLANT DEFENSE MECHANISMS AGAINST INSECT PESTS

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Abstract: **As primary producers, plants are under constant pressure to defend themselves against potentially deadly pathogens and herbivores. Insects pose a great threat to plants and plants in turn, withstand to insect attack through a wide diversity of defensive mechanisms. Interactions between plants and insect herbivores are important determinants of plant productivity in agriculture. In response to attack, plants have evolved a range of defenses to reduce the threat of injury and loss of productivity. Plant characters that confer herbivore resistance prevent or reduce herbivore damage through expression of characters that deter pests from settling, attaching to surfaces, feeding and reproducing, or that reduce palatability.**

Plant defensive mechanisms are either produced constitutively or in response to plant damage, and affect feeding, growth, and survival of herbivores. Plant defense mechanisms against insect herbivores are broadly categorized into direct and indirect defense mechanisms. Direct defense is involved both physical and biochemical barriers which synergistically obstruct insect herbivore's growth, development, reproduction, etc. The indirect defense mechanisms have no direct impact on insect herbivores but suppress pests by releasing volatile compounds that attract natural enemies of the herbivores. Overall categories of direct plant defenses against insect herbivores include limiting food supply, reducing nutrient value, reducing preference, disrupting physical structures, and inhibiting chemical pathways of the attacking insect. Major known defense chemicals include plant secondary metabolites, protein inhibitors of insect digestive enzymes, proteases, lectins, amino acid deaminases and oxidases. In this review, the two broad categories of plant defense mechanisms against insect pests: direct and indirect defense mechanisms have been widely discussed.

Keywords: **Insect pests, Herbivory, Plant defence, direct defense, structural defense, biochemical defense, indirect defense, natural enemy.**

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1. INTRODUCTION

Plants can have different types of interactions with insects, such as antagonistic interactions with herbivores and mutualistic interactions with carnivorous and pollinating insects. However, the impact of insect herbivores on their host plants has been known since ancient times (Strong *et al.*, 1984; Herms & Mattson, 1992) and a lot of research has been done on it (Coulson & Witter, 1984; Fernandes, 1987). Due to insect pests, there is a huge yield loss each year around the world (Oerke 2006; Singh and Kaur 2018; Sibanda *et al.*, 2000). Plants and insects have co-evolved continuously since the first appearance of phytophagous insects in the history of life and insect–plant co-evolution has been ongoing for 400 million years (Labandeira 2013).

During the long course of interaction and coevolution with herbivorous insects, plants have evolved a broad range of defense mechanisms to counter insect attacks (Zhao *et al.*,2009; Karban 2011). Today, various morphological, and biochemical, plant defense mechanisms are known (Howe and Jander 2008). Plant defense mechanisms can be preformed (constitutive) and/or inducible. Constitutive defenses include physical and chemical barriers that exist before insect attack, whereas inducible defenses include defensive mechanisms that become activated upon insect attack (Miranda *et al.*, 2007; Steppuhn and Baldwin, 2007). Inducible defense mechanism in plants is one of the important components of pest control in agriculture, and has been exploited for regulation of insect herbivore population (Tibebu, 2018; Howe and Jander, 2008; Agrawal, 2011). Plant defense mechanisms are categorised into direct and indirect defense mechanisms. Direct defense mechanisms are plant characters that directly affect the attacker insects (Kessler, A. and Baldwin, 2001) whereas indirect defense mechanisms are plant characters that do not directly affect the attacker insects but attract natural enemies of the attacker insects which finally leads to suppression of the insect population, and as a result, reduce plant damage caused by the insect **(**Arimura *et al.*, 2009; Karban, 2011)Plant characters that attract natural enemies of herbivore insects arevolatile organic compounds produced and released by plants during insect attack while direct plant defense include various morphological and biochemical plant characters that negatively affect insect preference such as host plant selection, oviposition, feeding behaviour or insect performance such as growth rate, development, and reproductive success; resulting in increased plant fitness in a hostile environment (Dudareva *et al* 2006; Usha and Jyothsna, 2010). Morphological defense mechanisms include structures such as trichomes, surface waxes, tissue toughness, cell walls and cuticle thickening, plant colour, plant shape and size as well as secretory structures and ducts for lattices or resins whereas biochemical defense mechanisms include secondary metabolites, digestibility reducing proteins, and antinutritive enzymes (Hanley *et al.*, 2007; Howe and Jander, 2008; Karban, 2011). Moreover, synergistic effect among different defensive components enhances the defensive system of plants agains insect pests (Tibebu, 2018).

2. PLANT DEFENSE MECHANISMS AGAINST INSECT PESTS.

Plants have morphological structures, biochemicals and proteins to defend themselves from herbivore attack. These plant defense mechanisms have toxic, repellent, and/or antinutitional effects on the herbivores (UshaandJyothsna, 2010). Plants defend the herbivores attack both directly by affecting host plant preference or survival and reproductive success and indirectly through other species such as natural enemies of the insect pests (Howe and Jander, 2008; Dudareva *et al.*, 2006; Arimura *et al.*, 2009). Direct defenses are mediated by plant characteristics that affect the herbivore’s biology such as mechanical protection on the surface of the plants or production of toxic chemicalsthat either kill or retard the development of the herbivores (Hanley *et al.*,2007). Indirect defenses against insects are mediated by the release of a blend of volatiles that specifically attract natural enemies of the herbivores and/or by providing food and housing to enhance the effectiveness of the natural enemies (Arimura *et al.*, 2009). Generally, synergistic effect among different defensive components enhances the defensive system of plants against the insect pests (Tibebu, 2018).

2.1. PLANT DIRECT DEFENSE MECHANISMS

The term direct defense is used when plants produce physical barriers against insect herbivores, or compounds that exert repellent, antinutritive or toxic effects on the herbivores themselves. Plants have evolved direct defenses such as biochemicals that could be both inducible and part of the constitutive defense, inducible defense proteins and various morphological features (Tibebu, 2018). Direct defense includes the activation or production of antifeedants, such as toxins and inhibitors of digestion, which negatively affect the growth and/or survival of herbivores (Howe and Jander, 2008).

2.1.1. Morphological defense mechanisms

Structures of plants are the first line of defense against insect pests (Hanley *et al.*, 2007; Agrawal *et al.*, 2009). Plant Structural defenses include morphological and anatomical characters that confer a fitness advantage to the plant by directly deterring the herbivores from feeding (Agrawal *et al.*, 2009. Morphological characters interfere physically with locomotors mechanisms especially with the mechanism of host selection, feeding, ingestion, digestion, mating or oviposition. These may also indirectly cause nutritional imbalances either through restrictive feeding because of texture or shape which would reduce the amount of nutritive material being ingested, or through limiting the digestibility and utilization of food by insects (Howe and Jander, 2008; Hanley *et al.*, 2007; Karban, 2011).

The morphological structures of a plant which confer resistance to pests are trichomes on plant surface, surface waxes, hardness of plant tissues, thickness of cell walls and cuticle, anatomical modifications, silica content, colour, shape and size (Amjad *et al.*, 2009; Chamarthi *et al.*, 2010; Handley *et al.*, 2005).

2.1.1.1. surface waxes

Waxes protect plant surface against desiccation, insect feeding and diseases (Engelberth, 2002). They affect feeding behaviour of insects, particularly the setting of probing insects, acting as phagostimulants or feeding deterrents (Norris and Kogan, 1980) and also increase the slipperiness, which hinder non-specialized insects from populating the leaf surfaces (Schaller and Howe, 2008). It has been reported that due to the presence of waxes on plant surface the sense organs on the insect tarsi and mouth parts receive negative chemical and tactile stimuli from the plant surface resulting in resistance of the plant to insect attack *(*Blenn *et al.*, 2012). It was also reported that leaf epicuticular wax is an important factor that affects the rate and pattern of feeding of flea beetle (*Phyllotreta cruciferae)* in Brassicaceae (Bodnaryk, 1991)and neonate larvae of *Plutella xylostella* had non-preference for leaf wax charcteristic in glossy leaved resistant *Brassica oleracea* L.Eigenbrode and Shelton(1990) displayed that Diamond backmoth (*Plutella xylostella)* larvae had non-preference for leaf wax in glossy-leaved resistant *Brassica oleracea*. Similarly, it has been found that glossy lines of Brassica species had low population of cabbageworm (*Artogeia rapae)*, cabbage aphid (*B. brassicae)* and *P. xylostella* (Stoner, 1990). It has also been observed that in bloom cultivars, the culm is heavily waxed and the neonate larvae face considerable difficulty in climbing because their prolegs stuck in the wax and never reach the feeding site (Bernays *et al*, 1983). Anstey and Moore (1954) reported that broccoli with waxy leaves was more resistant to *Phylotrata olbionica* than broccoli with a glossy leaves. It has also been known that sugar cane stalk surface wax contributed to resistance against sugarcane borer (*Eldana saccharina)*(Rutherford and Staden, 1996).

2.1.1.2. trichomes

Trichomes are outgrowths from the epidermis of leaves, shoots and roots (Upholf, 1962) and serve as morphological defense against insect pests (Johnson, 1975). They occur in several forms, shapes and sizes: straight, spiral, stellate, hooked, and glandular forms (Uphof, 1962; Johnson, 1975; Hanley *et al.*, 2007). Trichomes are one of the most important morphological adaptations of plants against insect pests(Schaller and Howe, 2008). Trichomes can be divided into two distinct categories, glandu1ar and non-glandular(DE Candole,1841). They affect locomotion, attachment, shelter, feeding and survival of insects. For example, it has been reported that early first instar larvae of cereal leaf beetle (*Oulema melanopa)* were critically affected by trichomesof wheat plants (Schillinger and Gallun, 1968) and this caused greater mortality of the larvae (Kogan,1972). The mortality was owing to the fact that larvae had to eat the hairs to reach the epidermis and thus ingested large amounts of cellulose and lignin and this caused death of the young larvae due to unbalanced diet from cellulose and lignin (Schillinger and Gallun, 1968). In addition to unbalanced diet, the larvae were suffered with undigested hairs, some of which pierced the gut wall of the insect (Kogan, 1972; Webster, 1975).

Trichome density and length play important role in plant defense against insect pests. For instance, research reports indicated that density of hairs on cotton affected the feeding behaviour of cotton aphids (*Aphis gossypii)* by reducing the feeding time and increasing the first non-feeding time and penetration frequency (Jiang andGuo, 1996) and was found that weight gain and leaf feeding capacity of *Spodeptera littoralis and H. armigera* was smaller on hairy cultivars than on the glabrous cultivars (Navon *et al.*, 1991).

Research results showed that, glandular trichomes can play role in defending insect pests. For example, Kisha(1984) stated that *Bimesia tabaci* was trapped and killed by the glandular hairs of tomato leaves. Similarly, Kriha (1984) reported that adults of whitefly (*Bemisia tabaci)* were found trapped by the glandular hairs on tomato leaves where they come in contact with the glandular exudates and become immobile due to the hardening of these exudates (Kriha, 1984)and the exudates accumulated on the tarsi, immobilized and caused others to fall off the plants. Moreover, the biochemicals produced by glandular trichoms inhibit movement of insects on plant surfaces and act as repellents and deterrents, disrupt feeding, affect development, reproduction and survival of insects (Webster, 1975). For example, resistance of wild tomato to *Helicoverpa zea* (Dimochand Kennedy, 1983) and *Leptinotarsa decemlineata* is attributed to high levels of 2-tridecanone present on the tips of trichomes. Similarly, glandular trichomes in *Lycopersicon hirsutum* produce biochemical 2-tridecanone and 2-undecanone which is toxic to *Spodoptera enigua* (Lin *et al*., 1987).

There are also reports that indicate the role of hooked trichomes in plants defense mechanisms against insect pests. For instance, (Mizukoshi and Kakizaki, (1995) reported that mortality of early instar aphids was higher on cultivars with heavily hooked trichomes.In the same way, Richardson (1943) observed that bean leaf hooked hairs immobilized and starved bedbugs to death. Similarly, the hooked trichomes of *Passiflora adenopoda* (Passifloraceae) provide a specific and effective defense against its major class of herbivore, the butterfly larvae (Gilbert, 1971). The host hairs entrap and kill larva by a combination of starvation and loss of hemolymph caused by numerous puncture wounds in the larval integument.

Moreover, Vanduyn *et al*. (1972) reported that trichomes can influence the attachment of insects to plant leaf surface and he observed that the Mexican bean beetle (*Epilachna varivestis)* falls off leaves without trichomes. Other studies have also shown that several insects prefer hairy leaves for attachment (Lukefahr *et al.*, 1970).

Different research reports indicated that trichomes have both positive and negative effect on oviposition of insect pests (Webster 1975). For instance, females of Hessian fly (*Mayetiola destructor*) laid fewer eggs on the pubescent leaved wheat than on the glabrous leaved (Roberts *et al.*, 1979) and cereal leaf beetle (*O. melanopus*) was found to oviposit less on pubescent wheat than glabrous wheat leaves (Lampert *et al.*, 1983). Moreover, reports has been displayed that wheat varieties with dense and long trichomes were highly resistant to oviposition (Hoxie *et al.*, 1975) and in the same fashin, trichomes on sugarcane plants negatively affected the oviposition of sugarcane borer (*D. saccharalis)* (Sosa, 1988) and it has been also found that the number of trichomes on leaves of maize cultivar deterred oviposition of corn earworm (*C. partellus)* (Kumar, 1992). Similarly, the presence of trichomes on leaf surface of sorghum was related to less frequency of oviposition by shoot fly (*A. soccata)* (Maiti *et al.*, 1980). Likewise, alfalfa varieties with long glandular hairs were resistant to seed chalcid (*Bruchophagus roddi)* (Pierce, 1983) and in this manner, the apple codling moth preferred the glabrous leaf for oviposition over the pubescent leaf surface (Plourde *et al.*, 1985). Likewise, Sharma and Singh(2001) observed that hair density and hair length had negative correlation with the number of eggs laid by leafhopper (*A. biguttula)* on malvaceous plants. In the same way, in okra, *A. biguttula* population decreased with an increase in hair density on lamina and such varieties were less preferred for oviposition.

However, trichomes may in some cases enhance oviposition by some insect species resulting in the build-up of pest population. For example, glabrous cotton strains were less favourable for egg laying than pubescent strains for oviposition by *H. zea and H. virescens* (Stadelbacher and Scales, 1973)

Generallytrichomes have a great role in defending plants against insect pests. For instance, research results showed that resistance in *Brassica juncea* to mustard aphid (*Lipaphis erysimi)* was correlated with hairiness of leaf surface (Lal *et al.*, 1999) and in pigeon pea, resistance of pods to *H. armigera* larvae was due to high density of trichomes (Romies *et al.*, 1999). In the same way, tolerance in plants to flea hopper (*Pseudatomoscelis seriatus)*increased with increase in trichome density. Trichome density on sorghum leaves imparted resistance to shoot flies (*A.soccata)*. Hairiness in cotton increased resistance to a number of insects such as jassid (*Amrasca spp.)* (Evans, 1965), cotton aphid, (*Aphis gossypii)* (Kamel and Elkassaby, 1965), cotton leafworm (*Spodoptera littoralis)* and spider mites (*Tetranychus spp*.)(Abdul Nasr, 1960), bollweevil, (*Anthonomus grandis)* (Stephens and Lee, 1961) and pink bollworm, (*P. gossypiella)* (Smith *et al.*, 1975). In the same way, reports showed that cotton cultivars with trichomes on upper and lower leaf surfaces and petioles provide a mechanism of resistance to movement of newly hatched larvae of tobacco bud worm (*Helicoverpa virescens*) (Ramalho *et al.*, 1994). Hairiness in cotton also confers resistance to *Pectinophora gossypiella*. **2.1.1.3. thickening of cell walls**

Because of the deposition of liginin & celulose on the plant cell walls, tissue of plants become hard and tough and thus become resistant against insect pest teairning by mandibles or penetration by ovipositor of insect pests (Raupp, 2008). The cell walls of leaves are also reinforced during feeding (McNaughton and Tarrants, 1983) through the use of different macromolecules, such as lignin, cellulose, suberin and callose, together with small organic molecules, such as phenolics, and even inorganic silica particles (Schoonhoven *et al.*, 2005). Roots eaten by insect herbivores exhibit extensive regrowth, both in density, as seen in *T. repens* eaten by *Sitona lepidus* (clover root weevil) (Care *et al.*, 2000), and in quantity, as observed in *Medicago sativa* (alfalfa) attacked by clover weevil (*Sitona hispidulus)*(Johnson *et al.*, 2010). Tanton (1962) stated that feeding rates and larval growth of mustard beetle (*Phaedon cochlariae)* was comparatively less on tough turnip and Brussels sprout leaves. Likewise, Seed damage due to alfalfa seed chalcid (*Bruchophagus raddi)* was less in medicago species which had highly lignified pod-walls (Springer *et al*, 1990).It has also been known that sugarcane resistance against top borer (*scirpophaga nivella)* was due to the presence of higher deposition of liginin on its mid-rib (Verma and Mathur, 1950). Similarly, it was reported that the movement of *Chilo partellus* larval on sorghum leaves was resisted by toughness of the mid-rib (Kishore, 1991). Singal and Singh (1985) also reported that in chickpea, resistance to *Callosobruchus maculatus* and *C. Chinensis* was associated with roughness and toughness of the seed coat.

2.1.1.2. laticifers and oleoresins

Several plants contain networks of channels in vascular tissues called laticifers and resin ducts. Latex and resins are stored under internal pressure, and when the channels are broken, they are secreted and might entrap or intoxicate the herbivore.

Latex laticifers are found in more than 10% of the angiosperms, and are especially common in the tropics (Agrawal and Konno, 2009). Of the more than 50 latex producing plant families, *Asclepias* (milkweeds) is the one most studied. For instance, the latex of *Cryptostegia grandiflora* (rubber wine) may be transported 70cm upwards to the wounding site and when it is exposed to air it coagulates and then traps small insect larvae (Dussourd and Hoyle, 2000). Apart from its stickiness, *A. cannabinum* also has toxic or antinutrive properties due to its complex composition of specialized bioactive natural products, such as alkaloids, terpenoids, phenolics and protein inhibitors (Mithöfer and Boland, 2012).

2.1.1.3. plant colour

Plant colour affects host selection behaviour of insect pests (Norris and Kogan, 1980). Although plant shape may have some effect on insect orientation the most important remote factor is plant colour.The attraction of aphids to yellow reflecting surfaces (Kennedy *et al.*, 1961) is now well known and has been utilized in the construction of yellow sticky traps for monitoring aphid numbers. Yellow is thought to be attractive because it is the colour, or the wavelength of the colour, associated with the senescing tissue favoured by aphids. Adult Pieris rapae prefer green and blue green surfaces for preovipositional displays (Ilse, 1937), the cabbage aphid Brevicoryne brassicae is less attracted to red Cruciferae (Ellis *et al.,* 1996) and the boll weevil is attracted less to red cotton plants than green (Stephens, 1957). The work of Prokopy *et al.* (1983) has shown the importance of the leaf colour for the visual selection of plants by Delia radicum. More females landed on mimics coloured as radish leaves than on green or red mimics of cabbage. Although these differences in preference occur, it is debatable whether such characters can be used as a mechanism of resistance since it is unlikely that the resistant effect of colour will persist in the absence of hosts having a preferred colour. Also little can be done by way of genetic manipulation to affect plant colour without affecting some fundamental physiological plant process (Norris and Kogan, 1980).

2.1.1.4. accumulation of minerals in plant cuticle

Resistance of plants against insect pests can be attributed to the accumulation of certain minerals in plant cuticles that can act as feeding barrier (Pathak, 1969). For example, deposits of silica and calcium carbonate were found in a number of plant species (Martin and Juniper, 1970). Calcified and silicified hairs exist on many plants (Uphof, 1962). Silica contents absorbed by the plants get deposited in the tissues of several plant species and in certain species contribute to resistance against insect attack (Lanning *et al.*, 1980). For instance, it has been found that resistance in sorghum cultivars against shoot fly (*atherigona soccata)* was because of the presence of high silica content in 4-6 leaf stage (Bothe and Pokarhar, 1985). Hanifa *et al*, (1974) showed that there was strong resistance in rice cultivars against stripe stem borer (*chilo suppressalis)* owing to silica content of the stem of the cultivars and Ukwangwa and Odebiyi, (1985) also reported that the same result was found against *chilo zacconius.* Likewise, it has been observed that in rice, a highly significant negative correlation was recorded between silica content of the stem and the susceptibility to the stripe stem borer (*Chilo suppressalis* (Hanifa *et al.*, 1974) and *Chilo zacconius)* (Ukwangwa and Odebiyi, 1985). Similarly, Mandras (1991) reported that susceptibility in rice cultivars to yellow stem borer (*Scirpophaga incertulas)* was seenbecause of lack of silica in their stems. It has also been observed that young cuticle is usually preferred over mature cuticle by certain species of insect pests for feeding and oviposition. Forexample, bayberry whitefly (*Parabemisia myricae)* could not feed on mature lemon leaves due to inhibitory properties of mature cuticle (Walker, 1988) and it has also been proved that mature leaves of citrus were repellent to probing by aphids (Zettler *et al.*, 1969). Correspondingly, younger leaves of lemon were preferred for probing, oviposition and survival of *P. myricae* over mature leaves (Walker and Aitken, 1985).

2.1.1.5. mimicry and camouflage

Mimicry refers to adaptive similarity between a mimic organism and a model. Camouflage is used by organisms to disguise their appearance which blends with their surroundings. Organisms use camouflage to mask their location, identity and movement. This allows prey to avoid predators, and for predators to sneak up on prey. The woody vine *Boquila trifoliolata* mimics the leaves of its supporting trees in terms of size, shape, color, orientation, petiole length, and tip spininess to escape the attack of some weevils and leaf beetles (Gianoli and Carrasco-Urra 2014). The bracts of a woodland plant *Monotropsis odorata* functioned as camouflage, making the plant blend in with its surroundings avoiding herbivores. These are brown colored that resembles the leaf litter from which cover the pinkish-purple colored buds and deep purple stems (Hund 2017). Heliconiines larvae are important defoliating agents of *Passiflora* spp. A number of *Passiflora* species have several distinct structures on their leaves. These structures mimic the presence of Heliconius butterflies yellow eggs on their leaves. Female butterflies are less likely to lay their eggs on plants that already have butterfly eggs. This is due to fact that larvae of many Heliconius feed on congeneric eggs and larvae and females exhibit great care in inspecting oviposition sites (Williams and Gilbert 1981).

2.1.2. Biochemical defense mechanisms

Plants produce biochemical compounds called primary and secondary metabolites. The primary metabolites are used for growth, development and reproduction whereas secondary metabolites are used to protect the plant against herbivory and pathogens (Engelberth, 2006). They can perform as repellents for generalist insects and as attractants for specialist insects (Fraenkel, 1959). Toxic compounds will intoxicate generalist herbivores, while specialists are forced to invest resources in detoxification mechanisms, and their growth and development will therefore slow down (Kessler and Baldwin, 2002).

2.1.2.1. alkaloids

Alkaloids are heterogeneous biochemicals that occur in all living organisms but are most common in plants (Levin, 1976). Theyare widely distributed in vascular plants and are commonly found in the *leguminosae*, *liliaceae*, *solanaceae*, and *amaryllidaceae* species and they maybe evolved as defense against insect herbivory (Howe andJander, 2008). The true alkaloids are biosynthesized from amino acids in the roots,followed by phloem and usually xylem transports(Courdavault *et al.*, 2014) and accumulated above ground. Alternatively, the final steps of their de novo biosynthesis can take place above ground (Miettinen *et al.*, 2014). Alkaloids are constitutively present in plants, but their production and transport can increase upon herbivory (Baldwin, 1988). They can react with DNA, membranes and enzymes, and are therefore potent toxins for many organisms, including arthropods (Wink *et al.*, 1998). Interestingly, the nectar of some plants contains sub-lethal amounts of alkaloids, which not only protects them from nectar robbers (Kessler *et al.*, 2008), but also improves their reproductive success by manipulating the behaviour of their natural pollinators (Kessler *et al.*, 2012a). They contain nitrogen in a heterocyclic ring. The ring structure includes pyridines, pyrroles, indoles, pyrrolidines, isoquinolines and piperidines (Fattorusso and Taglialatela-Scafati, 2007). Alkaloids derived from quinolizidine, such as cytisine and sparteine, are efficient feeding deterrents against a number of herbivores (Petterson *et al.*,1991).

Pyrrolizidine alkaloids are derived from ornithine or arginine and occur naturally in many plants as non-toxic *N*-oxides. However, as soon as they reach the often alkaline digestive tracts of some insect herbivores, they are quickly reduced and forms toxic, uncharged, hydrophobic tertiary alkaloids, which can easily pass through membranes (Hartmann, 1999). Furthermore, pyrrolizidine alkaloids were found to be very potent antifeedants and extremely toxic to the aphid *Rhopalosiphum padi* and the Milkweed bug *Oncopeltus fasciatus*.

2.1.2.2. benzoxazinoides

Grammeae spp., such as maize, rye and wheat, produces the defense-related secondary metabolites 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside (DIBOA-Glc) and dihydroxy-7-methoxy- 1,4-benzoxazin-3-one-glucoside (DIMBOA-Glc, Figure 8b) from indole-3-glycerol phosphate. The conversion is catalyzed by BX1-BX9, of which BX1 cleaves off the glycerol phosphate, BX2-BX5 (cytochrome P450s CYP79C1-4) catalyze the reactions forming DIBOA, BX8/BX9 add the stabilizing glucosyl group, and BX6-BX7 assists in the conversion from DIBOA-Glc to DIMBOA-Glc (Dutartre *et al.*, 2012).

A homologue to BX1, indole-3-glycerol phosphatase lyase (Seigler, 1991) catalyzes the formation of free indoles in maize, and is activated by volicitin (Frey *et al.*, 2000). DIMBOA has been shown to confer resistance to *Ostrinia nubilalis* (first-brood European corn borer), northern corn leaf blight *Helminthosporium turcicum* (*Helminthosporium turcicum*), and maize plant louse(*Rhophalosiphum maydis*) (Niemeyer, 1988). However, DIBOA and DIMBOA may also be used as feeding cues by specialist herbivores. *D. virgifera* is attracted to DIMBOA (Robert *et al.*, 2012) as well as one of its degradation products MBOA (Bjostad and Hibbard, 1992). DIMBOA-Glc may be further converted into 2-β-D-glucopyranosyloxy-4,7-dimethoxy-1,4-benzoxazin-3-one (HDMBOA-Glc) through the action of a JA induced 4-*O*-methyltransferase (Oikawa *et al.*, 2002). Interestingly, HDMBOA that is formed following deglycosylation by β-glycosidase acts as a strong deterrent to both the generalist *S. frugiperda* and the specialist *S. littoralis* (Glauser *et al.*, 2011).

2.1.2.3. cyanogenic glucosides

The cyanogenic glucosides (CNglcs), are found in more than 2600 species from more than 550 genera and 150 families, covering all vascular plant classes including angiosperms, both monocotyledons and dicotyledons, as well as gymnosperms and pteridophytes (Seigler, 1991; Orcutt and Nilsen, 2000; Lindberg Møller, 2011). CNglcs are amino acid derived glucosides, originating from aromatic or branched-chain amino acids, such as tyrosine (dhurrin in *Sorghum bicolor*, sorghum (Dustan and Henry, 1902), valine and isoleucine (linamarin and lotaustralin in *Lotus japonicus* (lotus) and *Manihot esculenta* (cassava) (Forslund *et al.*, 2004; McMahon, 1995) and phenylalanine (amygdalin and prunasin in Rosaceae), the rose family, including apples, plums, cherries, peaches and strawberries (Sánchez-Pérez et al., 2008).

Many plant species accumulate cyanogenic glucosides (ahydroxynitrile glucosides) which protect them against herbivores because they can release volatile hydrogen cyanide (HCN), which inhibits cellular respiration (Brattsten, 1983; Way, 1984). Because plants are vulnerable to high concentrations of HCN as well, cyanogenic glucosides are stored in vacuoles, whereas the HCN-liberating enzymes b-glucosidase and a-hydroxynitrile lyase are localized in plastids. (Vetter, 2000; Thayer and Conn, 1981), the apoplast (Frehner and Conn, 1987) or in intracellular protein bodies (Swain *et al.*, 1992). Upon herbivory, the cyanogenic glucosides become exposed to b-glucosidases. Depending on the pH, the resulting a-hydroxynitriles will either dissociate spontaneously into HCN or will be enzymatically converted to it by a-hydroxynitrile lyases (Siritunga *et al.*, 2004). Other roles proposed for CNglcs are as nitrogen storage compounds (Forslund and Jonsson, 1997) or as osmoprotectants (Kamp Busk and Lindberg Møller, 2002). The presence of CNglcs in *M. esculenta* tubers increases resistance towards the generalist cassava burrower bug(*Cyrtomenus bergi*) (Bellotti and Arias, 1992). Furthermore, bitter almond plants containing amygdalin and prunasin are resistant to the larvae of flatheaded woodborer(*Capnodis tenebronis*) (Malagón and Garrido, 1990). Another example is the larvae of alfalfa weevil(*Hypera postica*), which prefer feeding on the acyanogenic leaves of *Trifolium repens* (Ellsbury, *et al.*, 1992). It is also known that CNglcs may act as phagostimulants or oviposition cues for specialist herbivores.

2.1.2.4. glucosinolates

Glucosinolates (GSL) are derived from amino acids Hopkins *et al.*, 2009) and thus, they are sulphur and nitrogen containing defensive metabolites found extensively in *Brassicaceae* and *Capparales* (Halkier and Gershenzon, 2006). GSL are more abundant in roots than shoots. Indol-3-ylglucosinolate is most dominant in shoots, while its methoxyderivatives and aromatic 2-phenylethyl GSL is the major GSL in roots. This tissue specificity is believed to be due to difference in volatility, stability in soil and membrane permeability (Dam *et al.*, 2009). In roots, the GSL levels are mainly constitutive, while they are inducible in shoots, probably a consequence of difference in selection pressure above and below ground (Karban *et al.*, 1999). Similarly, CNglcs, the GSL are located in the vacuole (Grob and Matile, 1979) where they are protected from thioglucosidases called myrosinases. Glucosinolates can be activated by the enzyme myrosinase (Husebye *et al.*, 2002), from which they are separated by compartmentalization. Herbivory mixes the two (Barth and Jander, 2006), thereby triggering the production and release of various reactive hydrolysis products, mainly isothiocyanates and nitriles (Bones and Rossiter, 1996), which can be directly toxic and repellent to herbivores (Bennett and Wallsgrove, 1994) but also attract specialist herbivores (Beran *et al.*, 2014) and serve as attractants of parasitoids (Mumm *et al.*, 2008). Consistently, glucosinolate biosynthesis can be induced by herbivory (Hopkins *et al.*, 2009) and is controlled by JA, SA and ethylene (Schweizer *et al.*, 2013). Glucosinolates also appear to contribute to effective chemical defenses against a majority of nonadapted phytophagous insects. On the other hand, a small minority of adapted (curcifer-feeding) insects are able to utilize glucosinolates in host seeking and host recognition behaviour.

2.1.2.5. nonprotein amino acids

Many plants, especially Leguminosae produce high concentrations of toxic non-protein amino acids (D’Mello,1994). Both tree and forage legumes contain the arginine analogue canavanine which together with its breakdown product canaline is effective substrates for enzymes utilizing arginine and ornithine. For instance, the arginyl-tRNA synthase of most organisms cannot distinguish between arginine and canavanine, resulting in incorporation of canavanine into proteins, which leads to deleterious effects (Rosenthal, 1991). However, some insects, such as bruchid beetle(*Caryedes brasiliensis*) and curculionid weevil(*Sternechus tuberculatus)* have an arginyl-tRNA able to distinguish between protein and non-protein amino acids (Rosenthal, 1991). Another example is the aromatic amino acid mimosine found in the tropical forage legume *Leucaena leucocephala.* It is usually degraded into toxic dihydroxypyridone (DHP) by ruminant gut bacteria. However, in Central America where *L. leucocephala* is native, the gut bacteria *Synergistes jonesii* is capable of fully metabolizing mimosine and DHP (Huang *et al.*, 2011).

2.1.2.6. phenolics

Among the secondary metabolites, plant phenols constitute one of the most common and widespread group of defensive compounds, which play a major role in host plant resistance against herbivores, including insects (Usha and Jyothsna, 2010). The properties of phenolics are very diverse, some are soluble in organic solutions, some are water-soluble carboxyl acids and glycosides, and some, like the condensed tannins, are large insoluble polymers (Engelberth, 2006). Phenolics serve as defense compounds by repelling feeding herbivores and inhibiting enzymes, by attracting pollinators and fruit dispersers, by absorbing harmful ultraviolet radiation, as mechanical support in the plant, and by reducing the growth of nearby competing plants (Cheeke, 1989). Qualitative and quantitative alterations in phenols and elevation in activities of oxidative enzyme in response to insect attack is a general phenomenon (Barakat *et al.*, 2010).

There are a number of examples of phenolics used in defense against insect herbivores. wheat cultivars containing phenolics are much less attractive to cereal aphid(*Rhopalosiphum padi*) (Leszczynski, 1995). Itwas also reported that light and nutrient stressed willow plant *(Salix dasyclados)*, containing three times less phenolics than non-stressed plants, were significantly more attractive to leaf beetle (*Galerucella lineola)* compared to the controls (Larsson *et al.*, 1986). Furthermore, benzoic acid derived salicylates in Salix leaves halt the growth and development of larvae of oak moth *(Operophtera brumata)* (Ruuhola *et al.*, 2001). Leaves of Fragaria (strawberry) contain catechol based phenolics that provide resistance to two-spotted spider mite(*Tetranychus urticae*) (Luczynski *et al.*, 1990), because the phenolics covalently bind to the mites digestive enzymes and inactivate them.

2.1.2.7. terpenoids

The most diverse class of bioactive natural products in plants is terpenoids, with approximately40,000 structures. Terpenoids are synthesized from acetyl-CoA and play a role in plant defense,can act like active compounds in resin or as volatiles, repellents, and toxins, or can modify developmentin herbivores (Aharoni *etal.*, 2005). Another characteristic in monoterpenes and sesquiterpenes is its abilityto form essential oils, like limonene in citrus plants; these essential oils have repellent andtoxic effects on insects (Cherrett, 1972). Many terpenoids can have synergistic effects upon release(Hummelbrunner and Isman, 2001).

2.1.3. Plant protein defense mechanisms

Plants can also defend themselves by producing proteins that reduce the nutrient value to the attacking insect or causes physical damage to the insect digestive tract. The major classes of such defense proteins are: α-amylase inhibitors, lectins, chitinases, polyphenol oxidases and proteinase inhibitors (Falco *et al.*, 2001).

2.1.3.1. α-amylase inhibitors

The lectin-like α-amylase inhibitors (α-AI) are found in cereal seeds, such as *Triticum* spp.(wheat) and *Hordeum vulgare* (barley), and in monocots, such as *S. bicolor* and *Z. mays*. The activities of these inhibitors are directed against α-amylases from animals (including insects) and microorganisms, used for starch breakdown, and seldom affect the plant amylases (Falco *et al.*, 2001). Wheat α-AIs can inhibit *Tenebrio obscurus* (mealworm), *Tribolium* spp. (flour beetles), *Sitophilus* spp. (wheat weevils) and *Oryzaephilus* spp. (grain beetles) among other stored-grains insect pests, and provide complete protection in transgenic peas towards *Bruchus pisorum* (pea weevil) (Morton *et al.*, 2000). A-AI-1 from *P. vulgaris* was tested against 30 agricultural pests, such as insects, mites, gastropods, annelid worms, nematodes, and fungal phytopathogens. It was shown to be a very efficient and selective inhibitor against Coleoptera, Diptera and Hymenoptera, as well as against annelid worms, but not towards Lepidoptera or Hemiptera (Kluh *et al.*, 2005). Furthermore, transgenic *P. sativum* harboring the cDNA encoding the α-AI of *P. vulgaris* showed protection against various insect herbivores (Schroeder *et al.*,1995).

2.1.3.2. chitinases

Chitin is the major component of the insect cuticle and peritrophic membrane and chitinases are used as a pest management tool to degrade peritrophic membrane of insect alimentary canal (Chandrasekaran 2014).Chitinases have therefore been proposed to have a role in defense against insect pests (Jouanin *et al.*, 1992). For example, it was reported that development of Colorado potato beetle is inhibited by poplar chitinase in transgenic tomato (Sharma *et al* 2011).Indeed, several transgenic plants over expressing chitinases have proved to be resistant against insect herbivores. For instance, transgenic *S. lycopersicum* is resistant to *Leptinotarsa decemlineata* (Colorado potato beetle) (Lawrence and Novak, 2006), transgenic *N. tabacum* repels *M. sexta* (Ding *et al.*, 1998), and *Lacanobia oleracea* (tomato moth) is repelled by transgenic *S. tuberosum* (Gatehouse *etal.*, 1997).

2.1.3.3. lectins

One particular class of entomotoxic proteins present in many plant species is the group of carbohydrate binding proteins or lectins (Vandenborre 2011). Lectins come into contact with the glycoproteins lining the intestinal area of insect inhibiting the absorption of nutrients ((Vandenborre *et al.*, 2011). First lectin to which anti-insect properties were ascribed on the basis of its deleterious effect on the larvae of bruchid beetle *Callosobruchus*((Edelman *et al.*, 1972). One of the most important properties of lectins is their survival in the digestive system of herbivores that gives them a strong insecticidal potential (Vandenborre *et al.*, 2011). They act as antin-utritive and/or toxic substances by binding to membrane glycosyl groups lining the digestive tract, leading to an array of harmful systemic reactions (Chakraborti *et al.*, 2009; Vandenborre *et al.*, 2011). Lectins have been found to be promising against Homopteran, (Chakraborti *et al.*, 2009)Lepidopteran and Coleopteran insects(Macedo *et al.*, 2007). For instance, lectin from Phaseolus vulgaris was found to have a lethal effect on the bruchid grubs (Liener, 1991). Similarly, the soybean lectins (*Phaseolus vulgaris agglutinin* and arcelin) have been shown to inhibit larval growth of a leaf-defoliating insect, Manduca sexta (*C. maculatus*) (Gatehouse and Gatehouse1998) and bean weevil(*Zabrotes subfasciatus)* (Osborn *et al.*, 1988*)*. Furthermore, wheat germ agglutinin (WGA) from corn inhibits Southern corn rootworm (*Diabrotica undecimpunctata howardi*) larval growth by at least 40% (Czapla and Lang, 1990).

2.1.3.4. polyphenol oxidases

Polyphenol oxidases (PPOs) are important enzymes in plants that regulate feeding, growth, and development of insect pests, and play a leading role in plant defense against the biotic and abiotic stresses (He*et al.*, 2011).They are among the major enzyme families inducedby wounding due to herbivory (Thaler *et al.*, 1996). Polyphenol oxidases catalysethe oxidation of ortho-oriented dihydroxy phenolic compounds, thereby generating quinones, which are highly reactive moleculesthat can either spontaneously polymerise or damage proteins,amino acids and nucleic acids via an alkylation reaction(Constabel and Barbehenn, 2008).

PPOs appear frequently upon wounding, and are therefore suggested to play a defensive role. For instance, PPO activity has been associated with resistance to *L. decemlineata* (Castañera *et al.*, 1996), *Melanoplus* spp. (grasshoppers) (Alba-Meraz and Choe, 2002) and Lepidopteran larvae (Felton *et al* 1992a). Similarly, PPOs confer resistance to *spodopteralitura* (fab.), *h. armigera, bemisia tabaci* (gen.), *tetranychuscinnabarinus* (boisd.), *myzus persicae* (sulzer), *empoasca fabae* (harris), *aphis medicaginis* (koch), *s. exigua*, and *agelastica alni* (l.)(Usha and Jyothsna, 2010; He *et al.*, 2011).PPOs can also be combined with specific phenolic substrates in glandular trichomes to produce a kind of “super glue” to trap smaller insects (Falco *et al.*, 2001). Activity of PPOs has been associated with defence againsttherbivores such as Coleopterans (Castan˜era *et al.*,1996) andLepidopterans (Felton *et al.*, 1992a).

2.1.3.5. proteinase inhibitors

Proteinase inhibitors (PIs) cover one of the most abundant defensive classes of proteins in plants. Higher concentration of PIs occurs in storage organs such as seeds and tubers, and 1 to 10% of their total proteins comprise of PIs, which inhibit different types of enzymes and play an important role in plant defense against insect herbivory(Lawrence and Koundal, 2002;Dunse *et al.*, 2010). Insect proteinases are four in types and used to digest proteins but plant proteinase Inhibitors bind to these enzymes in insect gut and inhibit their activity, thereby reduce protein digestion, resulting in the shortage of amino acids, and slow development and/or starvation of the insects (Azzouz *et al.*, 2005). The most common are the serine proteases, which are found in Coleoptera, Lepidoptera and Orthoptera, which all have neutral or alkaline pH in their midgut lumen content. This class is further divided into the subclasses of trypsin-like, chymotrypsin-like, and elastase-like proteases. The cysteine and aspartic acid proteases have been identified in families with more acidic gut content, such as Coleoptera, Diptera and Hemiptera. The last and by far the smallest class contain the metalloproteinases (Rodrigues *et al.*, 2011).

Phloem-feeding herbivores do not have digestive proteinases and are instead dependent on free amino acids absorbed from the phloem sap as a source of nitrogen nutrients. Plants have inhibitors for all four classes of proteinases, which can delay larval development without directly causing mortality (Wolfson and Murdock,1995). They are supposed to inhibit the proteolytic activity of midgut enzymes and thereby decrease the availability of amino acids. This in turn leads to lessening of the synthesis needed for growth, development and reproduction (Broadway and Duffey, 1986).

2.2. PLANT INDIRECT DEFENSE MECHANISMS

The term indirect defense is used when plants attract, nourish or house other organisms to reduce enemy pressure (Dicke and Sabelis, 1988). This is done by producing volatiles, extrafloral nectar, food bodies and nesting or refuge sites. Thus, indirect defence refers to plant characters that enhance attraction or arrestment of natural enemies of the herbivore, such as predators and parasitoids (Sabelis *et al.*, 2001).It plays a pivotal role in protecting plants against herbivore attack. (Dudareva *et al.*, 2006; Tibebu, 2018; Abdul *et al.*, 2012). Indirect defenses can be constitutive or induced as a result of combined action of mechanical damage and elicitors from the attacking herbivore Abdul *et al.*, 2012. Production of volatiles and the secretion of extra floral nectar mediate interactions of plants with natural enemies of the insect pests (i.e., parasitoids or predators), which actively reduce the numbers of feeding herbivores ((Dudareva *et al.*, 2006; Maffei, 2010). Induced indirect defenses have received increasing attention recently and have been studied on the genetic, biochemical, physiological, and ecological levels (Dudareva *et al.*, 2006; Arimura *et al.*, 2009; Maffei, 2010).

The natural enemies of herbivores use plant odours for locating prey has been suggested several times (Vinson,1976), and Dicke and Sabelis (1988) outlined a framework for the mode of action and the evolution of indirect defence strategies, mediated by so-called info chemicals, which forms the basis for our current view of the phenomenon. Since then, induced indirect defences have been reported for many plant species under laboratory conditions, including Arabidopsis (van Poecke *et al.*, 2001), cotton (De Moraes *et al.*, 1998), tomato (Kant *et al.*, 2004) and maize (Schnee *et al.*, 2006). In 1999, Thaler showed that indirect defences can act in the field while, in 2001, Kessler and Baldwin showed that plant volatiles can establish indirect defences under natural conditions. They supplemented *Nicotiana attenuata* plants with synthetic volatiles and some of these increased the natural predation of herbivore eggs and repelled adult moths. In a later study with transgenic plants that were silenced for genes involved in volatile production, the same group showed that indirect defences can actually promote a plant’s fitness under natural conditions (Schuman *et al.*, 2012). Moreover, it was found that hyperparasitoids also respond to herbivore-induced plant volatiles; volatiles released by plants infested with parasitized caterpillars attracted more hyperparasitoids than volatiles emitted by plants infested with healthy caterpillars (Poelman *et al.*, 2012). Indirect defence is known to occur below ground as well. A well-known example is the release of the volatile b-caryophyllene by maize roots into the soil when attacked by larvae of the beetle Diabrotica virgifera virgifera; this compound was shown to function as an attractant for entomopathogenic nematodes that attack the beetle larvae (Rasmann *et al.*, 2005). Finally, restoring this function in maize varieties deficient in the release of bcaryophyllene from roots also increased attraction of the nematodes (Degenhardt *et al.*, 2009).

Volatiles are not the only means by which plants can increase the abundance of natural enemies in their vicinity. Natural enemies can be arrested by providing them with food, e.g. extrafloral nectar (Pemberton and Lee, 1996) or food bodies (Fischer *et al.*, 2002). Also, dead insects entrapped on sticky plants were shown to attract predatory insects such that overall herbivore damage decreased and fruit production increased (Krimmel andPearse, 2013). Finally, an alternative means by which plants establish indirect defence is to provide shelter (domatia) such as cavities or tufts of hair, for small natural enemies, which these can use to moult and/or to protect their eggs (Walter, 1996).

2.3. ROLE OF PLANT HORMONES IN INDUCED RESISTANCE IN PLANTS.

Plant defense against herbivore attack involves many signal transduction pathways that are mediated by a network of PLANT hormones. Plant hormones play a critical role in regulating plant growth, development, and defense mechanisms (Verhage *et al.*, 2010). A number of plant hormones have been implicated in intra- and inter-plant communication in plants damaged by herbivores. Most of the plant defense responses against insects are activated by signal transduction pathways mediated by JA, SA, and ethylene (Gill *et al.*, 2010). Specific sets of defense related genes are activated by these pathways upon wounding or by insect feeding.

2.4. REALLOCATION OF RESOURCES IN PLANTS

Plants accumulate and redistribute nutrients throughout their life cycle. Upon insect attack, they can be reallocated by the plant. Nitrogen is exported away from roots of *Centaurea maculosa* attacked by an insect, *Agapeta zoegana*. It has been reported that infested plants shifted Nitrogen flow to shoots, translocating almost twice as much N to the shoot even as root grazing reduced total N uptake by 30–50% (Schultz *et al* 2013). Another example is the allocation of sugars from infested green parts into the non-affected roots, as has been shown for *Manduca sexta*–infested *Nicotiana attenuata* plants. Thus, at the necessary time,all rescued material can easily be remobilized and used for building new above ground organs (Mithofer and Boland 2012).

3. CONCLUSION

Plants have been interacting with insects for several hundred million years, leading to complex defense approaches against various insect feeding strategies. In response to attack, plants have evolved a range of defenses to reduce the threat of injury and loss of productivity.The plant defense activated upon herbivory is a complex network of different pathways composed of direct and indirect defenses. Plants respond to herbivory through various morphological, biochemicals, and molecular mechanisms to counter the effects of herbivore attack. Defense mechanisms may be present constitutively or induced after damage by the insect herbivores. However, induced response in plants is one of the important components of pest control in agriculture, and has been exploited for regulation of insect herbivore population. Although induced responses have some metabolic costs, they are very important when aimed at alleviating the stress of immediate concern, as most of these chemicals are produced in response to herbivore attack.The cost on investing in defense can be quantified in reduced growth, lower photosynthetic production, and reduced plant fitness. Plant defenses reduce the ability of herbivores to obtain nutrients from plant tissue. Plants with diminished defense capability may suffer greater herbivore damage and exhibit lower overall fitness under conditions of herbivore stress than well-defended plants.

Plants lack nervous system like those of animals, but they can readily sense and respond to the insect attack through various signalling pathways in its system which further activates the direct and indirect defenses. Direct defenses include the production of toxins, digestibility reduction of insect, reallocation of resources in plants and morphological defense like waxy layers on plants, trichomes, tissue toughness etc. Moreover, direct defense compounds such as alkaloids, benzoxazinoids, glucosinolates, and terpenoids or protease inhibitors directly influence the insect performance and feeding behaviour whereas indirect defenses enhance the probability of attracting the natural enemies of herbivores by production of volatiles, the secretion of extra floral nectar, providing nesting spaces to the former. Generally plant defense mechanisms are very important and shall be exploited for insect pest management in plant protection and can be one of the components of integrated pest management.

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