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Plant defenses against herbivorous insects: A Review

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Abstract
There are complex and dynamic interactions, mainly related to food, between plants and insects since hundreds of millions of years ago. Plants have evolved several intricate kinds of defense systems to defend themselves from the herbivores for its survival. Plants lack nervous system like those of animals, but they can readily sense and respond to the insect attack through various signaling 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 thigmonasty, waxy layers on plants, trichomes, tissue toughness etc. 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. Another strategy of defense without actually having any resistance factor is plant tolerance. In this review, an overview of these defense systems is provided.

Keywords: defence, plants, hervibore, insects and food

Introduction
Plants and insects have co-existed for several hundred million years as plants offer food and enormous variety of new habitats and niches for insects. Phytophagous insects have been adapting to exploit their host plants; however the plants have also evolved defensive systems to counteract the herbivore attack (Bruce 2015) [8]. Evidence for arthropod herbivory dates back at least 400 million years (Schmelz 2015) [54]. For example, the characteristic spiny system of the earliest land plants (Devonian period) were considered as defense against insect attack (Dhaliwal 2006) [13]. Humans depend almost exclusively on plants for food, since plants are the direct source of food. Moreover, plants provide many important non-food products including wood, dyes, textiles, medicines, cosmetics, soaps, rubber, plastics, inks, and industrial chemicals. Understanding how plants defend themselves from herbivores is essential in order to protect our food supply and develop resistant plant species (Freeman and Beattie 2008) [17].

How plant recognizes insect herbivore?
Pattern recognition is a fundamental process in the immune responses of both plants and animals. Plants possess surveillance systems that are able to detect highly specific herbivore-associated cues as well as general patterns of cellular damage, thus allowing them to mount defenses (Bruce 2015) [8]. This feature is needed to avoid wasting expensive defense resources. Plants can evaluate different kinds of feeding that lead to different quantity and quality of damage on plant tissue. Leaf defoliators cause damage by chewing, snipping or tearing. Leaf miners feed between the epidermal cell layers, while rasping and sucking herbivores suck the liquid content from lateral cells. Phloem-suckers insert stylet between the cells and into the phloem (Fürstenberg-Hägg *et al* 2013) [18]. Vibrations caused by *Pieris rapae* larvae while feeding on *Arabidopsis thaliana* induced higher levels of glucosinolate and anthocyanin defenses than the non infested plants (Appel and Cocroft 2014) [2].
Herbivore associated elicitors (HAE) in the saliva of insects help the plant to distinguish between general wounding and insect feeding. HAEs can be of diverse structure like enzymes, modified forms of lipids, sulphur containing amino acids, peptides released from digested plant protein (Bonaventure *et al* 2011) [6]. The first fully characterized HAE was the hydroxyl

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Fatty acid conjugate (FAC) volicitin in *Spodoptera exigua* oral secretions (Schuman and Baldwin 2016) [56]. In response to the HAE, plants may release volatile organic compounds (VOCs) which may repel harmful insects or attract beneficial predators that prey on the herbivorous insects (Freeman and Beattie 2008) [17]. For example: Oral secretion of *Schistocerca gregaria* elicits a rapid accumulation of various oxylipins, including 12-oxo-phytodienoic acid (OPDA) in Arabidopsis which play an important role in the activation of herbivory-induced responses.

The defense mechanism of plants can also be initiated after the identification of chemical elicitors or regulators from insect egg ovipositional fluid (Xin *et al* 2016) [69]. Eggs represent a future threat for the plant and the anticipation of damage by a preactivation of defenses could provide an advantage to the host. In *Pisum sativum* pods, growth of undifferentiated cells is triggered upon oviposition by the pea weevil, which elevates the egg from the surface, increasing the risk of desiccation, predation, or falling off the pod (Little *et al* 2007) [39].

Plant species[b]	HAEs	Insect species[a]
Nicotiana tabacum (tobacco)	Glucose oxidase (GOX)	*Helicoverpa zea*
Nicotiana attenuata (coyote tobacco)		*Spodoptera exigua*
Medicago truncatula		*Helicoverpa armigera*
Solanum lycopersicum (tomato)		Other *Lepidoptera* and *Hymenoptera*
Phaseolus lunatus (lima beans)	β-Glucosidase	*Pieris brassicae*
Zea mays (maize)		
Brassica oleracea (cabbage)		
Zea mays	N-Acyl-amino acids (FACs)	*Spodoptera exigua*
Glycine max (soybean)		*Manduca sexta*
Solanum melongena (eggplant)		*Teleogryllus taiwanemma*
Nicotiana attenuata		*Drosophila melanogaster*
Solanum nigrum		Several *Lepidoptera*
Zea mays	Caeliferins	*Schistocerca americana*
Arabidopsis thaliana		
Vigna unguiculata (cowpea)	Inceptin	Produced by degradation of a plant ATP synthase during folivory by *Spodoptera frugiperda*
Some Fabaceae		
Solanum lycopersicum	Oligouronides	Produced by degradation of plant cell walls during insect folivory

Examples of HAEs that induce specific responses in plants during insect folivory (Bonaventure *et al* 2011) [6]

Signaling in plants
After recognition of insect herbivore, the detected signals are transduced through a network of multiple signaling transduction pathways, which eventually leads to changes in gene expression and ultimately the production of defense chemicals (Chen 2008; Duan *et al* 2014) [11, 14].

Plants continuously interact with the external world through plasma membrane. The first intercellular signal in plants is the stimulus-induced change in plasma membrane potential (Vm) which is followed by a fast electric signal through the entire plant. Immediately after this signal, the cytosolic free Ca^{2+} concentration have been found to be increased at the site of herbivory which is usually much lower in healthy cells. The increased level of Ca^{2+} is recognized by some Ca^{2+}-sensors or calcium-binding proteins, which can activate many calcium dependent protein kinases. These kinases regulate the function of many stress responsive genes, resulted in the phenotypic response of stress tolerance (Tuteja and Mahajan 2007) [62].

Protein kinases like Mitogen-activated protein kinase (MAPK) are important pathways that regulate cellular responses to both external and endogenous stimuli in plants. Within minutes of feeding damage, elevated MAPK activity can be detected proximate to the feeding site and in remote locations within the damaged leaf. MAPK activation occurs both up- and downstream of calcium signaling, which is also

associated with herbivory but not with mechanical damage (Schuman and Baldwin 2016) [56].

Several components have been identified that are involved in the systemic induction of defense responses like systemin peptides, oligogalacturonides (OGAs) and jasmonates. The kinase signaling induces synthesis of jasmonic acid which plays important role in systemic signaling. Jasmonates (JA) is transported within the plant and induces the transcription of defense-response genes, both in wounded and unwounded tissues. It can trigger various defense responses (Fürstenberg-Hägg *et al* 2013) [18]. When sorghum (*Sorghum bicolor*) is attacked by a phloem-feeding greenbug aphid (*Schizaphis graminum*), many jasmonic acid (JA)-regulated genes were activated that were effective in plant defense (Zhu-Salzman *et al* 2004) [70]. JA is synthesized within minutes of the perception of a threat and exerts transcriptional control over thousands of genes to affect resistance to herbivory. It also induces the re-budgeting of resources from tissue expansion to the production of defense compounds (Havko *et al* 2016) [23].

Defense responses
Plant defense responses include direct and indirect defense responses.

1. **Direct defenses:** All plant traits that affect susceptibility of host plants by themselves. Direct plant defense against

herbivorous insects comprise plant traits that negatively affect insect preference (host plant selection, oviposition, feeding behavior) or performance (growth rate, development, reproductive success) resulting in increased plant fitness in a hostile environment (Howe and Schaller 2008) [28].

Direct defense mechanisms are described below
Plant secondary metabolites
Apart from the primary metabolites used for growth, development and reproduction, plants also synthesize a broad range of secondary metabolites, also known as bioactive specialized compounds, which are toxic to herbivores and act as defense compounds (Wittstock and Gershenzon 2002) [67]. These are targeted especially against biological systems unique to herbivores, such as the nervous, digestive and endocrine organs, and are produced both constitutively and upon induction. Plant secondary metabolites can be divided into three chemically distinct groups viz: Terpenes, phenolics, N and S containing compounds (Khan and Mohammad 2011) [34].

a. Terpenes: These compounds are derived from five-carbon isoprene units. On the basis of C_5 units, we can classify the terpenoids as C_5 (hemiterpenes), C_{10} (monoterpenes), C_{15} (sesquiterpenes), C_{20} (diterpenes), C_{25} (sesterpenes), C_{30} (triterpenes), C_{40} (tetraterpenes), $>C_{40}$ (polyterpenes) (Singh and Sharma 2015) [58]. The insecticidal activity of the terpenes is either due to their action as antifeedants, toxins or as modifiers of insect development. Some important terpenoid deterrents and toxins are gossypol, polygodial, glaucolide-A, pyrethroids and cucurbitacins. Desert plants consist of a number of terpenoids and sesquiterpenoids that are found to be good insect deterrents (Bennett and Wallsgrove 1994) [5]. Azadirechtin (triterpene) is one of the most potent feeding deterrent to many insects, exerts various toxic effects and inhibits egg maturation (Rosenthal and Berenbaum 1991) [50].

b. Phenolics: Phenolic are aromatic ring bearing compounds with one (phenol) or more (polyphenol) hydroxyl substituents. Some important phenolic defense compounds are coumarin, furano-coumarins, ligin, flavonoids, isoflavonoids and tannins. Isoflavonoids isolated from wild relatives of chickpea, *Cicer arietinum*, deter larval feeding by *Helicocoverpa armigera*. Salicylates in Salix leaves reduces feeding and growth of polyphagous larvae of *Operophtera brumata* (Lattanzio *et al.* 2006) [36].

c. N and S containing compounds: Sulfur compounds include glutathione, glucosinolates, phytoalexins, thionins, defensins and allinin. Nitrogen compounds include alkaloids, cyanogenic glucosides, and non-protein amino acids. Glucosinolates are sulfur- and nitrogen-containing plant secondary metabolites common in the Brassicaceae, the increasing levels of which resulted in a decrease of damage by generalist herbivores (Redovnikovic 2008) [48]. High concentrations of sinalbin (glucosinolate) found in young cotyledons is repellent to the flea beetle, *Phyllotreta cruciferae* (Hopkins *et al* 2009) [27].

d. Anti nutritional/ digestive proteins: 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:

1. **Alpha amylase inhibitor:** These inhibit α-amylase, enzyme that plays a role in digestion of starch and glycogen in insects (Sales *et al* 2012) [52]. α-amylase inhibitor from cowpea seeds, *Vigna unguiculata*, inhibited α-amylase from *Callosobruchus maculates* larvae by 50%. Triticale-α amylase inhibitor has a strong inhibitory activity on *Eurygaster integriceps* gut α-amylase (Mehrabadi *et al* 2010) [40].

2. **Chitinase:** Chitin is the major component of the insect cuticle and peritrophic membrane and chitinases is used as a pest management tool to degrade peritrophic membrane of insect alimentary canal (Chandrasekaran 2014) [10]. Development of Colorado potato beetle is inhibited by poplar chitinase in transgenic tomato (Sharma *et al* 2011) [57].

3. **Lectin:** One particular class of entomotoxic proteins present in many plant species is the group of carbohydrate binding proteins or lectins (Vandenborre 2011) [63]. Lectins come into contact with the glycoproteins lining the intestinal area of insect inhibiting the absorption of nutrients. First lectin to which anti-insect properties were ascribed on the basis of its deleterious effect on the larvae of bruchid beetle *Callosobruchus maculatus* (Peumans and Damme 1995) [45].

4. **Polyphenol Oxidases:** Polyphenol oxidases (PPOs) are ubiquitous copper-containing anti-nutritive enzymes which use molecular oxygen to oxidize common ortho-diphenolic compounds to highly reactive quinines. PPO-generated quinones further react with amino acids reducing their availability. It causes typical browning of plant extracts and damaged plant tissues. Overexpression of PPO genes in tomato and hybrid aspen (*Populus tremula × Populus alba*) resulted in increased insect resistance, and silencing of PPOs resulted in increased susceptibility to insect herbivory (Araji *et al* 2014) [3].

5. **Proteinase inhibitor:** Proteinase inhibitor act as anti-metabolic proteins, which interfere with the digestive process of insects. These inhibit proteases present in insect guts, causing a reduction in the availability of amino acids necessary for their growth and development. Pepstatin, a powerful and strong inhibitor of aspartyl proteases has been shown to inhibit proteolysis of the midgut enzymes of Colorado potato beetle, *Leptinotarsa decemlineata* (Habib and Fazili 2007) [22].

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*. 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) [55]. 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) [41].

e. Mecahnical features: Mechanical defenses lessen the impact herbivores have on plant's fitness. Plant mechanical defenses act negatively on herbivores, diminishing their larval and adult performance.

1. Thigmonasty: Thigmonastic movements in some plants occur in response to touch, shaking, thermal or electrical stimulus and are used as a defense in some plants. The leaves of the sensitive plant *Mimosa pudica*, also known as touch me-not plant, close up rapidly in response to such external stimuli. This response is not a growth movement but turgor movements caused by osmotic pressure of the pulvini cells at the base of leaves (Mondal and Parui 2013) [42]. This is then spread via both electrical and chemical means through the plant; only a single leaflet need be disturbed.

Thigmonasty in *Mimosa pudica*

This electrical impulse acts on a plant hormone which makes the water migrate from the cells of pulvinus to the intercellular. This water movement causes the pulvinus to lose its firmness making the leaf to fold. Similarly, all the pulvini lose firmness and become limp due to which all the leaves above them collapse and fold up. At a gap of 15 to 30 minutes after the leaves have folded, water usually diffuses back into same cells of pulvinus from which it left, and the leaf returns to its original position (Tabasum 2017) [60].

The rapid folding of the leaflets may serve to both scare away potential predators and give the appearance of a less voluminous meal. Alternatively, the leaf movements may be a mechanism to expose protective thorns (Braam 2004) [7]. It may also physically dislodge small herbivores, such as insects.

2. 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) [19]. 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) [30].
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) [66].

f. Morphological Features: Physical barrier are the first line of plant defense against insect pests. All plant parts offer some sort of resistance against herbivory. They range from tissue hardness to highly complex glandular trichomes and spines.

1. Waxes: Epicuticular waxes are the major components of a plant cuticle and play an important role in protecting aerial organs from damage caused by biotic and abiotic stresses. The slipperiness on plant surface is increased due to waxes, which reduces the grip of insect herbivores and prevent them from feeding or ovipositing on the leaf surfaces. Young leaves of *Eucalyptus globulus* possess wax layer on its surface making it slippery and reduces adherence herbivorous psyllids (Walters 2011) [64]. Waxy surface of triticale plant acts as an anti-feedant and deterred probing and feeding by grain aphid *Sitobion avenae*.

2. Tissue Hardness: Leaf toughness affects the penetration of plant tissues by mouthparts of piercing-sucking insects, and also increases mandibular wear in biting-chewing herbivores, thus preventing herbivore feeding. Sclerophylly refers to the hardened leaves, reduces the palatability and digestibility of the tissues, thereby, reducing the herbivore damage (War *et al* 2012) [65]. Successful stylet penetration of *Parabemisia myricae* (Hemiptera, Aleyrodidae) in its host plant leaves is decreased with increasÍng host tissue hardness and age. In addition, females prefer young leaves and survive better on - them as opposed to old, hard leaves (Fernandes 1994) [15]. Cell wall reinforcement for enhanced leaf toughness results from the deposition of chemicals such as lignin, cellulose, suberin and callose, small organic molecules (e.g. phenolics) and even inorganic silica particles which provides mechanical resistance to insect feeding and/or plant penetration (Keeping and Kvedaras 2008) [32].

3. Pubescence: The plant is often covered with epidermal outgrowths called trichomes. Trichome density negatively affects the insect feeding, ovipositional responses and the larval nutrition of insect pests in many species of plants (Levin 1973) [37]. In addition, dense trichomes affect the herbivory mechanically, and interfere with the movement of insects and other arthropods on the plant surface, thereby reducing their access to leaf epidermis. These can be straight, spiral, hooked, branched or unbranched and can be glandular or nonglandular. Glandular trichomes secrete secondary metabolites including flavonoids, terpenoids, and alkaloids that can be poisonous, repellent, or trap insects and other organisms, thus forming a combination of structural and chemical defense (War *et al* 2012) [65]. Younger leaves of several herbaceous species are known to be more pubescent than older leaves because herbivore feeding or mechanical damage to leaves leads to newly formed leaves with higher densities of trichomes (Tian *et al* 2012) [61]. The hook like trichomes of *Passiflora adenopoda* (Passifloraceae) provides a specific and effective defense against its major class of herbivore. The trichomes are capable of deterring a non specialist herbivore *Heliconius* spp. butterfly larvae (Cardoso 2008) [9]. The host hairs entrap and kill larva by starvation and loss of hemolymph caused by numerous puncture wounds in the larval integument.
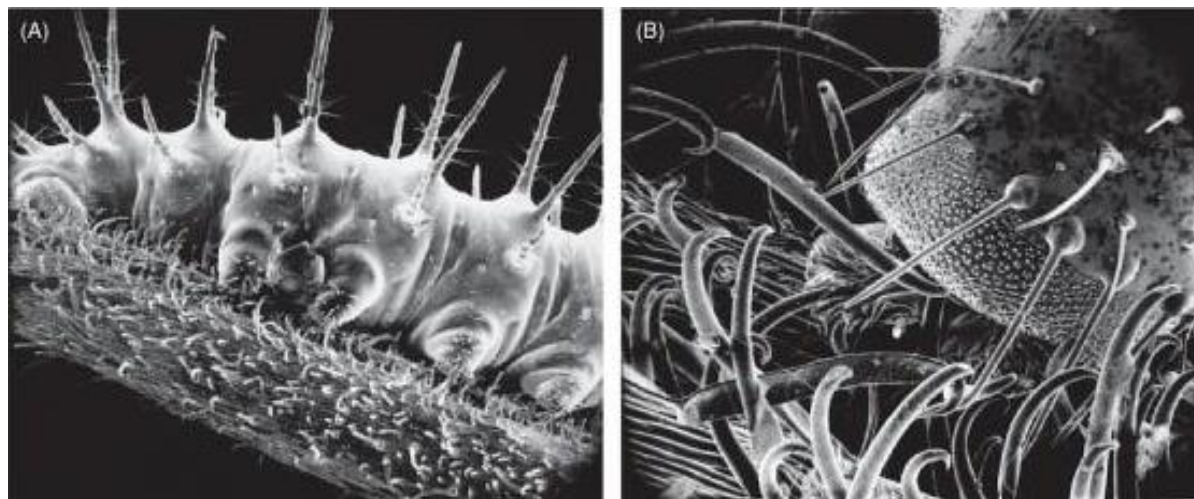
Hook like trichomes of *Passiflora adenopoda* tangling the prologs of *Heliconius* butterfly larva **(Gilbert 1971)** [20]

4. Latex: Latex is a sticky emulsion which is a mixture of organic compounds produced by some plants and held under internal pressure in special cells called lacticifers. When injured, the canal system is severed and plants, such as Euphorbiaceae, Apocynaceae, Asclepiadaceae, and some Asteraceae, exude latex. The contents are exuded and may entrap or even poison the herbivore. Milkweed latices coagulate upon exposure to air and immobilize small insect larvae (Fernandes 1994) [15]. Latex may contain secondary metabolites, often in concentrations that are much higher than in leaves. Many of these compounds have toxic or antinutritive effects, whereas others increase the stickiness of the latex (Agrawal and Konno 2009) [1]. Such compounds are terpenoids, cardenolides, phenolics, alkaloids such as morphine in Papaver species, various proteins such as digestive cysteine proteases in *Carica papaya* and *Ficus* species, and proteinase inhibitors (Mithofer and Boland 2012) [41]. It is very effective against most generalist mining, boring, and chewing insect herbivores. The latex of *Calotropis procera* is reported as a source of promising insecticidal proteins against *Callosobruchus maculatus* (Ramos *et al* 2010) [47]. Many specialist insect herbivores are adapted to feed on plants that exude latex. This is often done either by destroying the lactifer routes in proximal area by vein-cutting and trenching or by developing physiological adaptations. For example, the larvae of the monarch butterfly feeding on Apocynaceae plants are adapted to cardenolides by a single amino acid mutation (Konno 2011) [35].

5. Resins: The resin-based defenses are well established in conifers. The resin is a mixture of monoterpenes, sesquiterpenes, and diterpene resin acids, accumulates in resin ducts and related secretory structures (Howe and Schaller 2008) [28]. Conifer resins repel bark beetle attack and are toxic to its egg, larval and adult stages (Rosenthal and Berenbaum 1991) [50]. Upon exposure to air, the highly volatile monoterpene fraction evaporates, leaving the insects trapped in the solidifying resin acids and the wound site. Although this complex resin-based defense system in conifers is preformed, it is further induced in response to wounding.

2. Indirect Defense Response
Indirect defenses include plant traits that by themselves do not affect the susceptibility of host plants, but can serve as attractants to natural enemies of the attacking insect (Chen 2008) [11]. The plants attract, nourish or house other organisms to reduce enemy pressure. This is done by producing volatiles, extra floral nectar, food bodies and nesting or refuge sites.

a) Volatiles: Leaves normally release small quantities of volatile chemicals, but when a herbivore attacked plant recognizes herbivore-associated elicitors, many more volatiles are released. The chemical identity of the volatile compounds varies with the plant species and with the herbivorous insect species. These volatiles attract both parasitic and predatory insects that are natural enemies of the insect herbivores (Pare and Tumlinson 1999). The HIPV's produced vary according to the plant and herbivore species, the developmental stage and condition of the plants and the herbivores. Parasitoids have to search for small well camouflaged herbivores that mostly inhabit the undersides of leaves. Therefore, the chances of parasitoids finding hosts by random searching are remote. Here volatiles play their role. Besides feeding, leaf injury caused by caterpillar movement and insect oviposition can also increase volatile emission.

The parasitoid braconid wasp, *Cotesia marginiventris* is attracted to maize seedlings that are attacked by the beet armyworm, *Spodoptera exigua* (Kessler and Heil 2011) [33]. The release of volatiles also provides an indirect defense against underground herbivory. Maize roots release (E)-β-caryophyllene in response to attack by larvae of *Diabrotica virgifera* (western corn rootworm), attracting *Heterorhabditis megidis* nematodes that feed on the beetle larvae (Howe and Jander 2008) [29].

b) Extrafloral nectaries: Nectar-secreting organs located on any above-ground plant part which are not involved in pollination are called extra floral nectaries (EFNs). These are widespread in plants, having been reported in more than 100 families. These function in plant defense against herbivory via the recruitment of predatory or parasitoid insects (Gish *et al* 2016) [21]. These structures are high on metabolic cost and are best seen in young and developing leaves, secreting copious amount of sugars and attracting numerous ants. Besides ants, these nectaries attract other arthropods including Araneae (jumping spiders), Diptera (tachinid flies), Coleoptera and Hymenoptera (ichneumonid, braconid and chalcidoid wasps) which can reduce the number of herbivores (Arimura *et al* 2005) [4].

Euphorbiaceae is the largest family with extrafloral nectaries which are always visible structures, attracting ants. Five major types are button-shaped, cup-shaped, stalk-shaped, pit-shaped, and pore-shaped. (Ling 2004) [38].
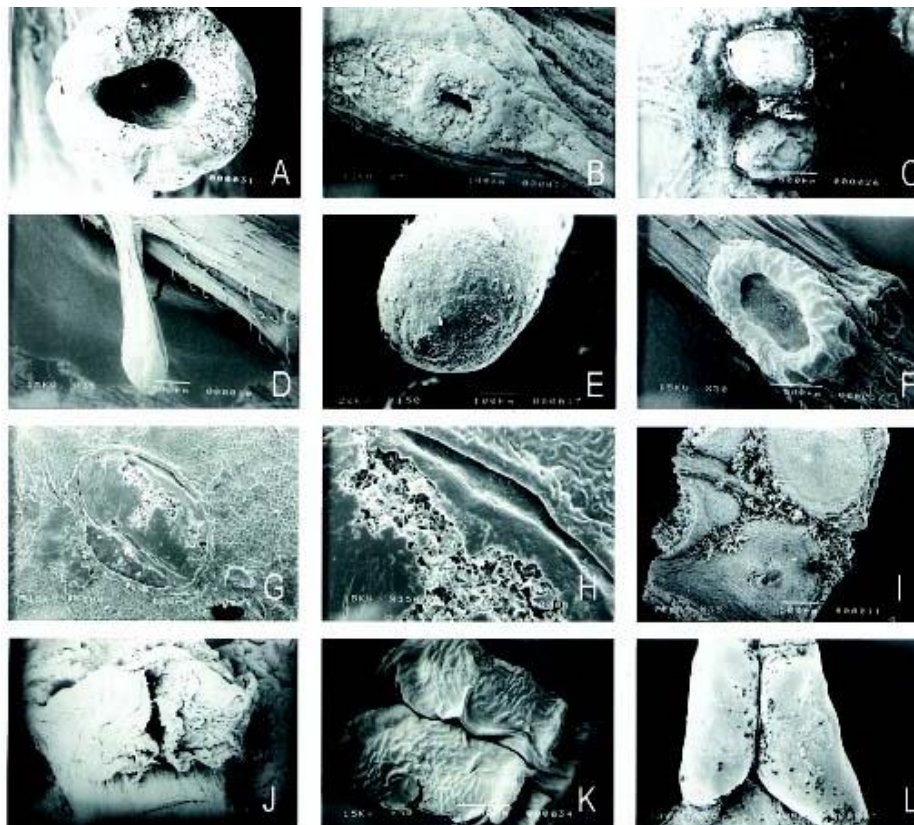
SEM micrographs of extrafloral nectaries. A, *Archidendron clypearia*; B, *Acacia confuse*; C, *Aleurites moluccana*; D & E, *Cassia surattensis*; F, *Leucaena leucocephala*; G & H, *Macaranga tanarius*; I,*Mallotus paniculatus*; J, *Ricinus communis*; K, *Sapium discolor*; L, *Sapium sebiferum* (Ling 2004) [38]

EFN consists mainly of monosaccharides and disaccharides, amino acids, carbohydrates, lipids, proteins. The production of EFN is increased by herbivory and decreased in the absence of herbivory. Examples of plant bearing EFN are cotton (*Gossypium* spp.); fruit trees in the genus *Prunus*, such as cherry, plum, almond, and peach; legumes such as bean (*Phaseolus vulgaris*), lima bean (*Phaseolus lunatus*) and cowpea (*Vigna unguiculata*); *Cucurbita* spp., such as pumpkin and zucchini; or cassava (*Manihot esculenta*) (Heil 2015) [26]. EFN secretion by field-grown *Macaranga tanarius* was reported to be increased after herbivory, artificial leaf damage and exogenous jasmonic acid (JA) application (Heil *et al* 2001) [25].

Ants are by far the most frequent visitors of these glands because of their predatory and aggressive behavior toward the herbivores reducing significantly the damage caused to the plant by the latter. The ants of subfamilies Formicinae and Myrmicinae are associated with the EFNs of plants *Qualea grandiflora*, *Caryocar brasiliense* and *Ouratea hexasperma* (Oliveira and Marcio 1998) [43].

c) Nesting spaces: Plants provide nesting space for ants, and ants defend plants against herbivores. Myrmecophyte plants offer ants pre-formed nesting sites, or "domatia," in hollow stems (e.g., *Cecropia*, *Leonardoxa*, *Macaranga*), thorns (*Acacia*), petioles (*Piper*), or leaf pouches (e.g., *Hirtella*, *Maieta*, *Scaphopetalum*, *Tococa*). The tree *Cordia alliodora* can decrease herbivory by promoting *Azteca pittieri* ant-colony growth, by sustaining space and food investment in ants, as long as the tree continues to grow. Another species of the same genus of ants colonies, *Azteca chartifex*, mostly selected *Goupia glabra* (Goupiaceae) trees to build their nests and plant signals induced workers to recruit nestmates, which patrol the leaves, likely providing the plant with a biotic defense (Dejean *et al* 2008) [12]

d) Tolerance: Plant defenses against herbivores are generally not complete so plants also tend to evolve some tolerance to herbivory. Tolerance is the ability of plants which are lacking resistance characters, to mitigate the negative effects caused by herbivory. Quantitative genetics studies have demonstrated that tolerance to herbivory is a heritable trait, subject to the action of natural selection, and it is therefore likely to evolve as an adaptive defense to herbivory (Fornoni 2010) [16].

Many intrinsic plant factors, such as growth rate, change in inner hormone, storage capacity, photosynthetic rates, nutrient allocation and uptake, activation of dormant meristems, changes in plant phenology and plant architecture can affect the extent to which plants can tolerate damage (Rosenthal and Kotanen 1994; Jian-Ming 2005) [51, 31]. The extrinsic factors such as plant's abiotic and biotic environment can also affect tolerance to herbivory. Plants are more tolerant when they receive early season herbivory and are in environments free from competition with high light, nutrients and water availability (Strauss and Agrawal 1999) [59].

The advantages of tolerance are that it is a plant response and does not by itself affect insect behavior, reproduction, growth, or development. Hence it does not exert selection pressure on the insect population for new biotypes. It has none of the deleterious effects on natural enemies. Moreover it does not decrease their prey populations (Rees *et al* 1994) [49].

Conclusion
Plants, being the main food source for a wide array of living organisms including insects, are attacked by them. Despite of being unable to move and lacking an immune system like animals, plants have developed diverse mechanisms of

morphological and chemical defenses against the herbivorous insects. There are vast scopes to clarify and unravel the new mechanisms and systems in plant defense. An understanding of these defense systems in plants can be utilized for interpreting the complex and dynamic plant-insect interactions and for exploiting it in pest management in crops. Improved crop cultivars with enhanced resistance can be developed, which can act as one of components of the integrated pest management, reducing the need to rely upon chemicals and making agriculture more environment friendly.

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