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An overview of physiological role of phytochemicals in insect pests-implications for pest management

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Abstract

The insect-plant interactions entail several intricate processes involving ecological, physiological, biochemical and behavioural aspects wherein the secondary metabolites play a pivotal role. Flavonoids especially pectolinarigenin in isolated from *Clerodendrum plomidis* exhibited strong ovicidal activity against *Earias vittella*. Mono terpenes like pulegone from *Mentha pulegium* and resins from conifers have toxic as well as insect feeding deterrence against bark beetles. Digestive enzyme inhibitors are proteins that block the normal digestion and absorption of nutrients by vertebrate and invertebrate herbivores. Oviposition deterrent effect has been exhibited by Pierirapae when fed upon cardenolides from *Erysimum cheiranthoides* rapae, and the active compounds were identified as strophanthidin glycosides.

Keywords: physiological role, phytochemicals, pests-implications, pest management

Introduction

Plants, over their life time, always have resisted attackers by production and exudation of constituents, playing a key role in their defense mechanisms. Most healthy plants produce a broad range of chemical barriers (Harborne, 1973) [22]. These Phytochemicals can be subdivided into two major groups viz., primary and secondary metabolites. The substances that are produced by the plant cells that are directly involved in its growth, development and reproduction (sugars, proteins, amino acids, and nucleicacids) are 'primary metabolites' while components that are not directly involved in growth or reproduction but are often involved with plant defense are categorized as 'secondary metabolites'. The secondary metabolites that contribute for plant defense can be broadly classified as alkaloids, nitrogen compounds (cyanide and cyanogenic glycosides), glucosinolates, cardenolides, iridoid glycosides, lectins, tannins and lignins, phenolics and phenyl propanoids, and terpenoids and steroids (Harborne, 1973) [22].

The insect-plant interactions entail several intricate processes involving ecological, physiological, biochemical and behavioural aspects wherein the secondary metabolites play a pivotal role. A systematic evaluation of the kinds of plants fed upon by larvae leads to the conclusion that secondary plant metabolites play a leading role in determining patterns of utilization for all phytophagous insects (Harvelland Tollrian, 1999) [23]. Insects select plants for both food and as sites for oviposition with the help of a range of chemoreceptors (gustatory and olfactory chemoreceptive systems) located mainly on their antennae and mouthparts. These chemoreceptors enable them to discriminate a wide range of chemical compounds even at very low concentrations and help to encode this information by the decoding command centers localized in the central nervous system (Dethier, 1960) [11]. Plant constituents in sufficient concentration are unpalatable to an insect and exert an undesirable physiological effect in them. Such a plant is protected from the attacks of phytophagous insects; therefore, plant secondary compounds have received much attention as proximate and ultimate determinants of host-plant range in phytophagous insects.

Each of the group of phyto constituents affects one or the other physiology of the invading insects and possesses a number of biological properties of repellence, feeding deterrence, growth disruption, mating disruption etc.

They may have an individual effectors work in synergy. Therefore by investigating the phytochemicals in the given botanical, we can think of the suitable physiological process that could be targeted. This review summarizes different physiological changes that are brought about in the insects by phytochemicals and probably form a basis for their deployment in crop-plant protection programs.

Physiological Alterations Mediated By Phytochemicals

There are various approaches of pest management based on the physiological alterations brought about in the insects by several group of phytochemicals and can be broadly categorized as follows,

- Feeding inhibitors/Antifeedants
- Enzyme and metabolite inhibitors
- Growth inhibitors
- Oviposition deterrents and Ovicides

a) Feeding Inhibitors

In order to attain its ideal growth, developmental and reproductive performance, insect must obtain adequate amounts of necessary nutrients in a relative balance and hence depends on the consumption and utilization of food. This involves altering the nutritional composition of the food it has consumed by inter-conversions, syntheses, selective concentration and excretion and reliance on micro-organisms that help in detoxification. The amount, rate, as well as, the quality of food consumed by the larvae largely influences its performances like growth rate, developmental time, final body weight, adult performance, fecundity, dispersal ability, and probability of survival. It is observed that any variation in the availability and abundance of food prevent insects from attaining their physiological potential i.e., ideal/optimal values for growth rate, reproductive rate, flight behavior and other physiological and behavioral processes (Slansky & Scriber, 1985).

Feeding inhibitors also called 'antifeedants' or 'feeding deterrents' (Dethier *et al.*, 1960)^[11], are generally considered to play an important role in insect feeding (Isman, 2002). In insects, olfaction plays a key role in location of the food. When they encounter plants for food, chemical information obtained from the plant is decisive in either accepting or

rejecting it as food plant (Koul, 2004). A group of chemoreceptors near the tip of the labrum are particularly important in monitoring the presence of feeding deterrents involving a complex mechanism as well as for food intake. Certain chemicals may affect only some steps in feeding sequence. In the larvae of *Bombyx mori* flavonoids like iso quercitrin and morin were reported to induce biting but do not lead to ingestion (Bernays, 1985). Insects that feed on specific plant taxa require the presence of characteristic compound while some species that have restricted host range have chemosensory neurons in the mouthpart sensilla, which respond specifically to the indicator chemicals. Lepidopteran larvae possess sensory neurons that are specific to different types of chemicals such as water, sugars, salts and deterrents (Schoohoven, L., 1973). Information from all the sensory inputs is integrated in the central nervous system, which gives the appropriate motor output.

The mode-of-action of most antifeedants is directed at the taste cells. A gustatory sensillum in an insect contains receptors selective for deterrents and others for stimulants (such as sugars and amino acids). Most of the antifeedants act likely by stimulating a deterrent receptor, which further sends a signal to the feeding center in the insect's central nervous system while some antifeedants are believed to block or interfere with the perception of feeding stimulants, while others may cause erratic bursts of electrical impulses in the nervous system preventing the insect from acquiring appropriate taste information on which it may choose an appropriate feeding behavior (Isman, 2002). Physical attributes like toughness, shape, surface pubescence etc. also influence the ability of an insect to consume and digest its food.

Antifeedants can be found amongst all the major classes of secondary metabolites— terpenoids, alkaloids, and phenolics (Harborne, 1973)^[22]. Isman (2002) has provided a list of insect antifeedants belonging to various classes of secondary metabolites isolated from various terrestrial plants (Table1). Terpenoids are the largest and most diverse class of phyto constituents that exhibit enormous chemical variety and complexity with respect to structure as well as their biological activities (Gershenson and Croteau, 1991).

Table 1: Insect antifeedants isolated from terrestrial plants (Isman, 2002)

Sl. No.	Chemical type	Compound	Plantsource
1	Monoterpene	Thymol	<i>Thymus vulgaris</i> (Lamiaceae)
2	Sesquiterpene lactone (germacanolidetype)	Glaucolide A	<i>Vernonia species</i> (Asteraceae)
3	Sesquiterpene (drimane type)	Polygodial	<i>Polygonum hydropiper</i> (Polygonaceae)
4	Diterpene (abietane type)	Abieticacid	<i>Pinus species</i> (Pinaceae)
5	Diterpene (clerodanetype)	AjugarinI	<i>Ajugaremot</i> (Lamiaceae)
6	Triterpene(limonoid type)	Azadirachtin	<i>Azadirachta indica</i> (Meliaceae)
7	Triterpene(cardenolidetype)	Digitoxin	<i>Digitalis purpurea</i> (Scrophulariaceae)
8	Triterpene(ergostanetype)	WithanolideE	<i>Withania somnifera</i> (Solanaceae)
9	Triterpene(spirostanetype)	Aginosid	<i>Allium porrum</i> (Liliaceae)
10	Alkaloid (indoletype)	Strychnine	<i>Strychno snuxvomica</i> (Loganiaceae)
11	Alkaloid (steroidal glycoside)	Tomatine	<i>Lycopersicone sculentum</i> (Solanaceae)
12	Phenolic (furanocouarin)	Xanthotoxin	<i>Pastinaca sativa</i> (Apiaceae)
13	Phenolic (lignan)	Podophllo toxin	<i>Podohyllum peltatum</i> (Berberidaceae)
14	Phenolic (benzoate ester)	methyl salicylate	<i>Gaultheria procumbens</i> (Ericaceae)

The mono terpenoid esters like pyrethroids from the leaves and flowers of *Chrysanthemum* species are best known insect toxins (Casida, 1973)^[8]. The toxic effect of mono terpenes from *Pseudotsuga menziesii* against western spruce budworm *Christoneura occidentalis* affecting the larval growth and

survival have been well documented by Cates *et al.*, (1987). Mono terpenes like pulegone from *Mentha pulegium* and resins from conifers have toxic as well as insect feeding deterrence against bark beetles (Rosenthal, 1991). Several types of diterpenes including the clerodanes from *Teucrium*

tomentosum, (Soundaryadevi *et al.*, 2003) ^[62], isoryanodane diterpenes from *Persea indica* (Braulio Fraga *et al.*, 1997) ^[6] are well known antifeedants against *Spodoptera litura* along with grayanoid terpenes from *Rhododendron molle* against *Leptinotarsa decemlineata* and *Spodoptera frugiperda* (Klocke *et al.*, 1991). Sesquiterpenes (15-carbon skeleton) with potent antifeedant action include the drimanes, and these sesquiterpene lactones are from Asteraceae. One particularly well-studied example is the drimane polygodial extracted from the foliage of *Polygonum hydropiper* (Luis Moreno-Osorio *et al.*, 2007; Adeyemi, 2010) and stem bark of *Drimys winteri* (Zapata *et al.*, 2009) ^[68] against lepidopteran larvae. The deterrent effect of polygodial and other drimane aldehydes may be as a result of blocking of the stimulatory effects of glucose and sucrose on chemosensory taste receptor cells found on the mouthparts (Jansen and de Groot, 1991) ^[28]. These sesquiterpene lactones from *Viguieratu cumanensis* (Clarisa Vaccarini, 2002) ^[9], *Centaurea maculosan* (Landau *et al.*, 1994) ^[33] belonging to asteraceae have also been reported to impart antifeedancy in general to the herbivores like *Spodoptera littoralis* and *Leptinotarsa decemlineata* (Azucena Gonza'lez-Colomaa, 2005) ^[5] and specialist herbivorous insects like *Strenodes straminea* (Landau *et al.*, 1994; Adekenov, 1995) ^[33]. Among the triterpenoids, well studied ones include limonoids from the neem (*Azadirachtaindica*) against Lepidopterans like *Helicoverpa armigera* (Murugan *et al.*, 2011; Koul *et al.*, 2004), *Cnaphalocrocis medinalis* (Guene'e) (Senthilnathan *et al.*, 2005) and Coleopterans like *Epilachna paenulata* Germ. (Maria Carpinella *et al.*, 2003) ^[35]. The antifeedant effects of limonoids from chinaberry trees (*Melia azedarach*) on *Agrotisipsilon* (Mekhlif, 2009) as well as azadirachtin too; sendanin, and limonin from Citrus species against several Hemipterans like *Aphis glycines* Matsumura (Kraiss & Cullen, 2008), Lepidopteran *Spodoptera litura* (Isman, 2002), and Coleopteran pests like *Harmonia axyridis* Pallas (Kraiss & Cullen, 2008) are also reported. Other antifeedant triterpenoids include steroidal saponins, cardenolides, and withanolides extracted from solanaceous plants belonging to the genera *Withania*, *Acnistus*, *Physalis*, *Jaborosal* and *Datura* (Isman, 2002; Adeyemi, 2010; Gebreyesus and Chapya, 1983) ^[18].

The best known example of simple phenolics being feeding barriers to insect herbivores include the coumarins from *Clausena anisata* (Rutaceae) against *Spodoptera exempta* (Gebreyesus and Chapya, 1983) ^[18] and neolignans represented by salicylates in *Salix* leaves that affect the feeding and growth of the polyphagous larvae of *Operophtera brumata* (Havill and Raffa, 2000). Alkaloids with well documented antifeedant effects on insects include certain indoles on *Agrotisipsilon*, (Jeyasanker, 2012) and the solanaceous glycoalkaloids on *Leptinotarsa decemlineata* Melville *et al.*, 1985) ^[37].

Enzyme and metabolite inhibitors

The production and secretion of digestive enzymes is related to the feeding pattern of insects as well as the time of moult, rising to a maximum when the insect starts to feed and declining when it stops for moulting. Enzyme production may be regulated by the chemicals in the food acting directly on the midgut epithelium. This is called secretagogue mechanism. Different enzymes are controlled so that only those appropriate to the food in the gut are produced. Enzyme regulation may also be under the neurosecretory system

involving the brain or humoral control, in response to the hormones released at the time of feeding. This may occur together with secretagogue regulation modulating the overall amounts of an enzyme produced under a given physiological condition.

The need to co-ordinate digestion with food intake arises from the need to conserve resources; hence enzyme production is closely related to feeding behavior and the movement of food through the alimentary canal. After ingestion, food is retained in the foregut and its subsequent transfer to the midgut is related to haemolymph osmotic pressure, which is further related to the feeding status of the insect. For instance, an insect with high haemolymph osmotic pressure following feeding retains food in the crop until the insect is better able to absorb the products of digestion.

Digestive enzyme inhibitors are proteins that block the normal digestion and absorption of nutrients by vertebrate and invertebrate herbivores. Many plants and seeds contain proteins that specifically inhibit pathogen and pest enzymes by forming complexes that block active sites or alter enzyme conformations, ultimately reducing enzyme function. These proteins are generally small and rich in the amino acid cysteine. They include defensins, amylase inhibitors, lectins, and proteinase inhibitors. Unlike simple chemicals such as terpenoids, phenolics, and alkaloids, proteins require a great deal of plant resources and energy to produce; consequently, many defensive proteins are only made in significant quantities after a pathogen or pest has attacked the plant.

In insects, a large part of the food ingested is macromolecular in the form of polysaccharides and proteins while lipids are present as glycerides, phospholipids and glycolipids. Usually, small molecules pass into the tissues and larger ones must be broken down into smaller components before absorption. Enzymes concerned with digestion are present in saliva and in the secretions of the midgut. Regardless of their feeding habits, most insects must digest proteins, carbohydrates and lipids hence have a similar array of enzymes in the midgut. Nevertheless, the enzymes produced do reflect the type of food eaten by them at different stages of life cycle. In addition, the microflora in the gut may facilitate digestion.

Proteases, a group of enzymes that hydrolyze peptide bonds and convert protein to amino acids, have a crucial role in food digestion by insects (Terra & Ferreira, 2005). It is observed that membrane-bound protease from the midgut epithelium of *Bombyx mori* is transported to the ectoperitrophic space as a particulate material to the peritrophic membrane, and thereafter released into the endoperitrophic space (Eguchi M., *et al.*, 1982). Several enzymes released; based on food materials, have critical roles in the process of digestion. The control of digestive enzyme synthesis and their subsequent secretion into the lumen is activated by the quantity and quality of food consumed. Any disruption in their activity disables insects to provide their nutrients for biological requirements. The effect of *Artemesiaannua* extract on the protease enzyme showed that it interferes with the rate of breakdown of the enzyme-substrate complex. Thus, the plant extracts inhibit the enzymes by decreasing the affinity of the enzyme to substrate (Morris, 1978) ^[38].

Allelochemicals may also act as inhibitors binding to allosteric site that changes the conformation (i.e. tertiary structure or three-dimensional shape) of the enzyme so that the affinity of the substrate for the active site is reduced (Morris, 1978; Zibae and Bandani, 2010) ^[38, 69]. There are a number of plant protease inhibitors that bind to endo- and

ectopeptidases in insects and effectively inhibit growth, and likewise a number of plant α -amylase inhibitors. Inhibitors bind tightly to the enzyme's active site in a substrate-like manner, resulting in a stable complex unlike that of the weak complexes between enzyme-substrate and enzyme-product, which dissociate in a short span of time.

Ramos *et al.*, (2009) suggested that the toxic effect of the protease inhibitors induces the insect to eliminate its digestive enzymes in feces, complicating its digestion. In contrast, some insects, such as *Spodoptera littoralis* (Lepidopteran), can overcome the deleterious effects of protease inhibitors by synthesizing different proteases that are insensitive to particular inhibitors (Paulillo *et al.*, 2000; Brito *et al.*, 2001; De Leo *et al.*, 2001) [45]. Earlier studies on *Xantho galerucaluteola* Mull and *Eurygaster integriceps* Puton have shown similar reduction in protease and its substrate levels of haemolymph and midgut tissue due to the effect of *Artemisia annua* L. extracts (Shekari *et al.*, 2008, Zibae and Bandani, 2010) [59, 69]. Low protease activity in the midgut of insects feeding on azadirachtin treated food has been reported wherein azadirachtin reduced trypsin in the midgut of *Spodoptera litura* while the limonoids, salanin and nimbinen had no effects. Zhang and Chiu (1992) also reported low protease activity in *P. rapae* larvae feeding on too seeds an in treated food. Low protease, amylase, and invertase have been reported in *Periplaneta americana* by azadirachtin treated food. Azadirachtin prevents trypsin production in the midgut of *Manduca sexta*, and significantly affects digestive enzymes like protease, amylase and invertase in *S. litura* (Koul *et al.*, 1996). Studies by Senthil-Nathan *et al.*, (2006) and Zibae and Bandani (2010) [69] inferred that botanical insecticides may interfere with the production of certain types of proteases and disable them to digest ingested proteins. Zibae *et al.*, (2010) [69] investigated the sole and combined effect of *Artemisia annua* and *Lavandula stoechas* digestive enzyme activity in *Hyphantria acunea* Drury (Lepidoptera: Arctiidae) and reported that *A. annua* treatment decreased digestive enzyme activities in larvae in a dose-related manner.

Decreased levels of digestive enzymes with botanical extracts may also be attributed to imbalance in enzyme-substrate complex and inhibition of peristaltic movement of the gut (Hori, 1969), reduced phosphorous liberation for energy metabolism, and decreased rate of metabolism, decreased rate of transport of metabolites (Smirle *et al.*, 1996) [61]. Alexander V. Konarev *et al.* (2002) [30] has reported the presence of serine proteinase inhibitors (subtilisin and trypsin and/or chymotrypsin (T/C/SI) in *C. officinalis* L. (Asteraceae). Medhini *et al.*, (2012), have reported lowered protease activity in *S. litura* upon treatment with *Calendula* leaf extracts.

Protease inhibitors are typically produced in response to herbivore attack and inhibit digestive enzymes including trypsin and chymotrypsin. They occur widely in nature but have been well studied in legumes, solanaceous plants, and grasses. Trypsin inhibitors present in soybean were shown to be toxic to the larvae of flour beetle, *Tribolium confusum* (Lipke *et al.*, 1954) and *Callosobruchus maculatus* (Gatehouse and Boulter, 1983) [17] and *Manduca sexta* (Shulke and Murdock, 1983) [60]. Serine proteinase inhibitors have anti-nutritional effects against several lepidopteran insect species (Shulke and Murdock, 1983) [60]. Broadway and Duffey (1986a) [7] demonstrated the growth inhibitory effects of purified SBTI and potato inhibitor II (an inhibitor of both trypsin and chymotrypsin) on larvae of *Heliothis zea* and

Spodoptera exigua.

In most of the herbivore insects especially and in invertebrates in general, the digestion of leaf material is mediated by several symbiotic microorganisms that reside in the hindgut. Any compound that kills off a reasonable amount of these supporting bacteria could reduce the insect's digestive capabilities is another possibility for the reduced metabolism. When saponins are eaten by an insect, the hydrolytic conditions in the gut will activate the degradation of saponin from an inactive to an active form which could influence the microflora and/ or various digestion and absorption processes (Waterman, 1993) [64].

Alpha-amylase inhibitors are proteins commonly found in legumes that bind to amylase enzymes and inhibit starch digestion. Mehrabadi *et al.*, (2011) have documented the amylase-inhibitory activities of the extracts of *Punica granatum* L. (Punicaceae), *Rheum officinale* B. (Polygonaceae), *Rhus coriaria* L. (Anacardiaceae), *Artemisia sieberi* B. (Compositae), *Peganum harmala* L. (Nitrariaceae), *Datura stramonium* L. (Solanaceae) and *Thymus vulgaris* L. (Lamiaceae) against stored grain pest *Callosobruchus maculatus* F. (Coleoptera: Bruchidae), *Rhyzopertha dominica* F. (Coleoptera: Bostrichidae), *Sitophilus granarius* L. (Coleoptera: Curculionidae), and *Trogoderma granarium* E. (Coleoptera : Dermestidae).

Secondary metabolites like tannins can bind a wide variety of compounds including carbohydrates that might attribute for the lowered sugar levels in the tissues. Phytoconstituents like triterpenoid saponins, flavonol glycosides and phenolic acids induce stress in the insects. Under such stress condition, there is reduced energy metabolism which in turn result in death of the insects (Etebari *et al.*, 2006) [15]. Similar results have been reported in *Agrotis ipsilon* by Abo-El-Ghar and Khalil, (1996) [1]. They have shown reduced amylase activity in the larvae fed with petroleum ether extract from *Ammi majus* L. and *Apium graveolens* L., acetone extract from *Melia azedarach* L. and water extract from *Catharanthus roseus* L. Similarly, Shekari *et al.* (2008) [59] and Zibae & Bandani (2010) [69] demonstrated the decreased α -amylase activity in the larval gut of the beetle *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae), elm leaf beetle and *Eurygaster integriceps* Puton (Hemiptera: Scutelleridae), respectively after treating them with plant extracts.

Lipases are water soluble enzymes while their substrates are not. The midgut cells of the insects produce several different esterases and lipases, which probably have specificity to different substrates. In caterpillars, galactosyldiglycerides, phosphatidylglycerols and phosphatidylcholines are hydrolysed to di- and mono- acylglycerides and free fatty acids. Lipases play a major role in storage and lipid mobilization. These enzymes are also the basic components in many physiological processes like reproduction, growth, and defense against pathogens. Most insects accumulate large amounts of lipid during larval period. The lipid store is then utilized to provide energy for the metamorphosis (Sakate and Pol, 2002) [51]. The lipid is stored in the fat body in the form of triglycerides (Price, 1975) [46] which may be released into the haemolymph for distribution to other tissues in the form of diacylglycerol by the action of triacylglycerol lipase (Hoffman and Downer, 1979; Gilbert *et al.*, 1965) [24, 19]. The lipases present in the fat bodies and other body tissues are considered as extra-digestive lipases as they are present outside the alimentary canal (Nandan *et al.*, 1973) [40]. Insect controls its fatty acid composition to meet the needs of

individual tissues and ontogenetic constraints (Howard and Styanley-Samuels, 1996) [26]. Senthil Nathan *et al.*, (2006) showed that treating *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Pyralidae), the rice leaf folder, with Btk, NSKE and VNLE (azadirachtin and neem components) sharply decreased the activity level of lipase in the midgut. Zibae *et al.*, (2008b) found inhibition of lipase activity in the midgut of *Chilo suppressalis* Walker (Lepidoptera: Pyralidae) when they add *A. annua* extract to enzyme samples *in vitro*. Zibae & Bandani (2010a) [69] found similar results when adults of *E. integriceps* fed on food containing *A. annua* extract.

Defensins are small cysteine-rich proteins that inhibit digestive proteins in herbivores. The precise mechanisms employed by plant defensins act upon molecular targets in the plasma membrane of pathogens. These defensins may inhibit pre-existing ion channels or form new membrane pores that disrupt cellular ion balance. Lectins are non-enzymatic proteins and glycoproteins that bind to carbohydrates and exhibit a wide range of functions including disruption of digestion in insects, disruption of protein synthesis and agglutination of blood cells invertebrates. The harmful effects of lectins on biological parameters of insects are larval weight decrease, mortality, feeding inhibition, delays in total developmental duration, adult emergence and fecundity on the first and second generation (Powell *et al.*, 1993; Habibi *et al.*, 1993) [21]. Various lectins from different sources have already been found to be toxic towards important members of insect orders, including Lepidoptera (Czapla & Lang, 1990), Coleoptera (Gatehouse *et al.*, 1984; Czapla & Lang, 1990) and Homoptera (Powell *et al.*, 1993).

Growth Inhibitors

Plants offer a rich source of novel compounds with insect growth regulatory (IGR) properties. The ample potential in using phytoecdysones as IGRs cannot be overlooked. It has been reported that there are more than 1,000 species of plants belonging to more than 200 families, 800 genera containing these bioactive substances (Varma and Dubey, 1998). Variations in the quantity and quality of a suitable food can have important effects on insect development. Usually, when food ingestion decreases, the duration of development is extended and the insect becomes smaller and lighter. The sufficiency of larval food is correlated in the quantity of nutrients stored for egg production; however more direct effects of nutrient levels occur in insects that feed as adults. It is assumed that the ultimate goal of a larva is to make its optimal genetic contribution to the next generation i.e., to achieve its maximal potential fitness and this is achieved by consuming and utilizing suitable food at particular rates that allow it to attain it has evolved, ideal growth performance and surviving long enough to produce a reproductively competitive adult.

Most of the herbivorous insects have developed synchronized growth and development patterns with the physiological status of their host plants. A number of plant growth regulators influence growth and development of the associated insects (Fischer *et al.*, 1987) [16]. The contents of proteins, carbohydrates and lipids in an animal's body are disturbed greatly due to this. The fluctuations in the enzyme systems and action of growth hormones result in the abnormal growth and developmental patterns due to disturbances in the metabolism and metamorphosis (Rabinder Kaur and Rup, 2003) [47].

Haydak (1953) showed that when the dietary protein of

several cockroaches is restricted, they slow down growth, but prolonged longevity. Many adult female insects need protein to mature their ovaries and eggs while it is crucial for successfully secrete juvenile hormone (JH) that is required for ovary and egg development. Male insect usually do not require protein to mature their sperm when they become adults. In general, optimal nutritional requirements change with age, sex, and physiological stress (Nation, 2001) [42]. Mordue (Luntz) & Nisbet (2000) have documented the growth regulatory effects of azadirachtin mostly concerned with its interference in the neuroendocrine system of the insects. Several plants have growth inhibitory activities against *Spodoptera litura* and *Helicoverpa armigera* (Baskar *et al.*, 2009).

The chemistry and mechanism of toxic action of these plant products to insects mainly focuses on insect growth hormones like juvenile hormone and ecdysones. If insects undergoing metamorphosis are treated with juvenile hormone (JH), they moult into intermediates, which are half immature and half adult, which die without gaining reproductive competence. The main hormones involved in growth regulation in insects are ecdysone and 20-hydroxy-ecdysone (moulting hormones) and juvenile hormone (JH). They are respectively produced in the prothoracic glands and corpora allata, through stimulation of hormones secreted in the brain (Wigglesworth 1972) [65]. Apart from the moulting process, many other different physiological functions in insects are controlled by neuro hormonal action. These include protein synthesis, reproduction, diapause and behavior; all could be therefore affected indirectly by the plant extracts/allele chemicals. Direct toxic effects observed on different tissues (Hori *et al.*, 1984; Schluter *et al.*, 1985; Nasiruddin & Mordue (Luntz), 1993) [25, 54] add complexity to the variety of physiological events that these allele chemicals could affect.

When the active plant compounds enter into the body of the larvae, the activity of ecdysone is suppressed and the larva fails to moult, remaining in the larval stage and ultimately dying (Koul and Isman, 1991). Morphological deformities at larval, pupal and adult stages are observed due to the toxic effects of extracts on growth and development processes. Since morphogenetic hormones regulate these processes, it can be suggested that allelochemicals in the extracts interfere with the hormones of the insect. Observations about the extended larval and pupal periods in some Lepidopteran pests upon treatment with *Chrystella parasitica* (L.) extracts (Balasubramanian *et al.*, 2008) have been reported. Insects demonstrate reduction in the consumption rate clubbed with retarded growth rate as an adaptive response serving to reduce their intake of the toxins, intending mainly not overload the capacity of their detoxification and excretory systems. If consumption and growth rate is slowed below its ideal value, fitness may be reduced due to an extended period of vulnerability to predators and may also upset the synchrony of the life cycle with changes in the abiotic environment, appearance of mates, host plants etc. According to Martinez and van Emden (2001), *S. littoralis* third instar larvae when exposed to different concentrations of azadirachtin took longer time to reach the pre-pupa in comparison with the control larvae. Similar results relating to the whole larval stage of *S. frugiperda* and *S. litura* were obtained by Behera and Satapathy (1997). Essential oil of *Vitex trifolia* and *Vitex aganus-castus* inhibited the growth of fifth instar larvae of *Spilosoma obliqua*. This treatment caused extended larval and pupal period (Tandon *et al.*, 2008). Prolonged larval and

pupal duration was observed when larvae of rice leaf folder were treated with pure triterpenes isolated from the plant *Dysoxylum alabaricum* Bedd., (Nathan *et al.*, 2009). This is due to the reduction in consumption by larvae. Prolonged larval period increased the larval mortality rate on *S. exigua* on *Cnaphalo crocismedinalis* (Senthil Nathan *et al.*, 2006) and on *S. frugiperda* (Torres *et al.*, 2003). Mala and Muthalagi (2008) reported that the larval duration was increased when the fifth instar larvae were fed with 0.8% neem oil extract treated leaves. Similar observation was reported by the use of extract of *Myrtillocactus geometrizans* on fall army worm, *S. frugiperda* (Torres *et al.*, 2003) and *Yucca periculosa* (Cespedes *et al.*, 2005).

The insect growth regulators (IGRs) are generally selective in their toxicity, slow in their killing action, and safe to both the environment and the natural enemies of insect pests. JH and JH analogues (JHA) have been found in various plants that interfere with the control of several species of insects. Phytojuvenoids such as juvabione, farnesol, juvocimene I and II, sesamin and sesamol, thujic acid, sterculic acid, tagetone, ostruthin, echinolone, baku-chiol, juvadecone have been isolated from plants (Varma and Dubey, 1998). JHAs are more effective at the beginning stage of metamorphosis and embryogenesis in insects, such as freshly ecdysed last larval instars, freshly ecdysed pupal instars, and deposited eggs. Thus, embryogenesis is disrupted when young eggs are treated with JHAs. Application to early last instar larvae would result in the development of supernumerary instars, whereas treatment at the later stage would result in abnormal pupation and development of larval-pupal mosaics or intermediates (Koak and K  l  ner, 1997).

Anti-juvenile hormones such as precocenes isolated from *Ageratum haustonianum* (Bowers *et al.*, 1976) show anti allatotrophic activity (prevent JH synthesis) and accelerated the development of insects, producing dwarf sterile animals, which were unable to survive. Analogues of precocone, b-sarone which is a constituent of the rhizome of sweet flag (*Acorus calamus*) showed antigonadal activity in insects. The vapours of the oils have exhibited complete inhibition of ovarian development when given to a number of stored grain insects (Mathur and Saxena, 1975; Koul *et al.*, 1977a; Schmidt and Strelke, 1994) [32, 55].

In comparison to many other secondary metabolites, flavonoids are apparently not very toxic and have a low physiological activity in most insects. Isoflavonoids like maackiain and Judaic in decreased the weight gain of early stadia larvae of *Helicoverpa armigera*. Renwick *et al.* (1987) found that flavones glycoside, isovitexin-6''-D-β-glucopyranoside (XXI), retarded the growth of Native American butterfly, *Pieris napi oleracea*. Similarly, Hypercalin A, a phenolic from *Hypericum calycinum* flowers was deterrent and toxic to *Utetheisa ornatatrix* larvae (Gronquist *et al.*, 2001).

Oviposition Deterrents and Ovicides

The lipid components normally found on the surfaces of the aerial parts of the plant contribute for the plant defense mechanisms. Texture of the leaf is influenced by these epicuticular lipid components hence indirectly they play a role in insect attachment and, locomotion also. Then on polar extracts of plants parts i.e., lipid materials may mask the polar stimulants present in the leaf, thus preventing the insect's tarsal receptors from making the necessary contact with the substratum (Koon and Njoya, 2004; Dethier *et al.*, 1960) [31].

[11]. Among the phytophagous insects, host selection by ovipositing adults is crucial for the survival and development of their offspring. The oviposition stimulants and deterrents may often co-exist in plants and chemoreceptors sensitive to either stimulants or deterrents may play a key role in determining the final decision by an insect (Renwick and Radke, 1990) [50]. Specialist herbivores would lay their eggs only on the presence of characteristic stimulants, whereas generalists would oviposit based on the absence of deterrents (Renwick, 1983). In some insects for example gravid cabbage butterflies polar as well as nonpolar extracts of non-host crucifers were deterrent (Renwick and Chew, 1994) [48]. Ayyangar and Rao (1989) [4], Srinivasan and Sundarababu (1999) [63] have reported that the methanol and hexane extracts of neem seed kernel are not only larval repellents but also oviposition deterrents to the adults of *Spodoptera litura* and *Leucinodes orbanalis* respectively. Oviposition deterrence by neem under no-choice and choice conditions have been reported in *Cnaphalo crocismedinalis* (Saxena *et al.*, 1981), *Earias vittella* (Sohtra and Patel, 1992; Gajmer *et al.*, 2001) and *Crocidolomia pavonana* (Fagoonee, 1981). The main chemical components of oviposition deterrents that were observed in the larval frassor on the egg masses of *Ostrinia* species are myristic, palmitic, palmitoleic, stearic, oleic, linoleic and linolenic acids (Li and Ishikawa 2004). Oviposition deterrent effect has been exhibited by *Pieris rapae* when fed upon cardenolides from *Erysimum cheiranthoides* (Sachdev-Gupta *et al.*, 1993).

Cardenolides mediated is criminatory behavior of ovipositing butterflies. Recent studies by Oyeyele and Zalucki, (1990) [67] and Zalucki *et al.*, (1990) [67] have shown a relationship between cardenolide content of milkweeds and oviposition by them on arch butterfly, *Danaus plexippus* where in the females oviposited in plants that had significantly lower cardenolide levels compared to the ones with higher levels and control plants. Similar oviposition deterrent activity by cardenolides of crucifer, *E. cheiranthoides* was studied in cabbage butterfly, *P. rapae*, (Dimock and Renwick, 1991) [12] and the active compounds were identified as strophanthidin glycosides (Sachdev-Gupta *et al.*, 1990) [50].

Oviposition deterrents for one insect may affect the behavior of associated insects in different ways. It was found that a fraction containing cardenolides from *E. cheiranthoides* that would deter *P. rapae* oviposition were actually stimulatory to *Plutella axylostella* (Renwick and Radke 1990) [50]. More studies are needed to better understand the hosts' election mechanisms of phytophagous insects and in particular to evaluate the involvement of deterrents in insect-plant interactions. In nature host recognition by phytophagous insects involves multiple sensory modalities, involving visual, olfactory and gustatory cues. It is observed that the volatile fatty acids, detected by the antennae of females in *Ostrinia furnacalis* (LeiGuo, 2009); in *Helicoverpa armigera* (Xu *et al.*, 2006) [66], deterred females from oviposition. Similarly, the contact chemoreceptors, located on the fore tarsi in some of the female insects, are responsible for detection of both host and non-host allelochemicals at oviposition site (Roessingh *et al.*, 1991; Nishida, 1995) [49, 43].

Ovulation and oviposition in insects are interrelated complex behavioural events involving neurosecretory processes. Subsequent to oogenesis at the ovarioles, the egg passes through the innervated lateral and common oviducts and reaches the egg-laying chamber located between the valves at the base of the ovipositor from where it is expelled out of the

body. The phytoconstituents like monoterpenoids known to be mostly accumulated in the epidermal glands and glandular trichomes of leaves of Compositae members act as neurotoxins and can specifically bind to the sodium channel proteins of the nerve membrane thereby inducing uncoordinated movement and sometimes paralysis in insects (Scharf, 2003) [53]. The phytoconstituents would probably interfere with neurosecretory system of the insect and the failure of its functionality cause retention of the eggs in the lateral oviducts leading to reduction in the number of eggs lay. The ability of monoterpenoids and saponins to reduce oviposition has been extensively studied. Poor hatchability of the oviposited eggs and reduced life span of adults could be due to the residual effect of these phytoconstituents as observed in pests treated with extracts of botanicals.

Phytochemicals might affect the egg hatchability by interfering with different stages of embryogenesis. Poor hatchability could be either a result of under development or cessation of the embryonic development. This may be explained as due to the inhibiting influence of the phytoconstituents like monoterpenoids in the extracts act against insects as toxins especially on the vital enzymes, which are involved in the embryonic development (Keane and Ryan, 1999; Enan, 2001) [29, 14]. Changes in the permeability of the vitelline membrane and/or chorion during embryogenesis may facilitate the diffusion of vapours into the eggs so that vital physiological and biochemical processes are affected (Gurusubramanian and Krishna, 1996) [20]. The failure to hatch could also be due to the effects of the anti-juvenile hormone activity of the extracts as observed in *S. litura* eggs upon treatment with juvenoids (Abo-el-Ghar, *et al.*, 1996) [1] or incomplete blastokinesis in the embryo and abnormal breakage of extra embryonic membranes as reported by Enslee and Riddiford (1997) or due to the toxicity of the inherent constituents of the extracts (Rajapakse & Senanayake, 1997; Riedl *et al.*, 1995). Phytolipids also block the supply of oxygen to the developing embryo. The duration of respiratory depression and the dosage of oil/phytochemical in contact with the egg decide the extent of effect, either, incomplete development or mortality. In addition to this, the rate of diffusion, penetration, distribution distinctiveness of the phytoconstituents inside the eggs after application and the effect of external environmental factors such as temperature and/or humidity might also play an important role upon embryonic development (Papachristos and Stamopoulos, 2004) [44].

Monoterpenoids from *Eucalyptus globulus* leaf oils showed ovicidal effect on *Pediculus humanus* (Young *et al.*, 2004) while those from *Bifora radians*, *Arcticum lappa*, *Humulus lupulus* against *Paralobesiaviteana* (Ayhan *et al.*, 2011). Flavonoids especially pectolinarigenin isolated from *Clerodendrum plomidis* exhibited strong ovicidal activity against *Earias vittella* (Chellai Muthu *et al.*, 2013). Similarly ovicidal activity from flavonoid compounds isolated from *Poncirus trifoliata* (Rajkumar & Jebanesan, 2008), *Ricinus communis* (Upasani *et al.*, 2003), *Calotropis gigantea* (Kumar *et al.*, 2012), *Syzygium lineare* (Jeyasanker *et al.*, 2013) are well reported in literature. Coumarins have a varied range of effects on the herbivores. A simple coumarin bergamot in has ovicidal effect against *Leptinotarsa decemlineata* (Carrasco *et al.*, 1981), *Drosophila melanogaster* (Kogan *et al.*, 1983). Furano coumarins also exhibit deterrent and toxic to arrange of insects like *Battus philenor*, *Depressaria pastinacella*, *Eurytides marcellus* and *Heliothis zea* (Berenbaum and Neal,

1985).

Future Perspective

The usage of these phytochemicals facilitate development and exploitation of naturally occurring plant defense mechanisms, thereby reducing the over usage of synthetic pesticides. If the exact mode of action of each of the phytochemical can be ascertained, it would be more appropriate to interfere at any particular physiological process of the pest and tamper its activity thereby making it ineffective.

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