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Insect-plant biochemical interactions for plant defense against spotted stem borer, *Chilo partellus*: A research summation

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Abstract
Maize is one of the most important cereal crop which has been reported to be attacked by 139 different insect pests in different phenological stages. Host plant resistance, which is economically viable and ecologically sound can be effectively utilized for managing various insect pests. Various morphological and biochemical characters governing the host plant resistance include a number of trichomes, trichome density, surface wax, leaf toughness and amino acids, proteins and various lipophillic compounds. Thus depending on the capacity to fulfill the nutritional requirement of an insect, a host can be resistant or susceptible. At times, the genotypes identified as resistant/tolerant to *C. partellus* under one agro-ecological region have been found to be susceptible at another region, might be because of genotype x environment interactions. Several biochemical factors, protein and lipids are the major determinants for quality of a host. The nutritional value of protein is determined by its amino acid contents. Apart from protein synthesis, high levels of free amino acids are reported to have some additional functions in neural transmission, detoxification, and synthesis of phospholipids, energy production, and morphogenetic processes that have important biological roles in insects' growth and development. Fatty acids are compounds of basic significance associated with biology of insects including storage of metabolic energy, cell and bio-membrane structure, and in regulatory physiology of insects. The requirement of amino acids and lipophillic compounds for insects can be studied in different agroecologies and this could have implications in developing resistant/tolerant varieties against a particular insect.

Keywords: Maize, amino acids, lipophillic compounds, host plant resistance

Introduction
Maize (*Zea mays* L.) is considered as one of the most important cereal crops after rice and wheat, which plays a vital role in the food economy of the world [99]. Maize is a multipurpose crop, providing food and fuel for human beings, feed for animals, poultry and livestock [75]. It is grown on 8.3 million ha with a production of 21 Mt [36]. Various constraints limit the production of maize, among them insect pests are considered as major yield reducing factors [65]. A total of 139 insect pests have been recorded attacking maize at different phenological stages of plant growth [28]. Among the insect pests attacking maize; spotted stem borer, *C. partellus* (Swinhoe) (Lepidoptera: Crambidae) attain the status of key pest causing 18 to 25% yield loss in Asia [26]. In India, 26.7 to 80.4% crop losses have been recorded across different agro-climatic regions [69, 76]. *C. partellus* is not only the major pest of cereals in Asian countries, it has also attained the status of serious pest worldwide under maize and sorghum cropping systems [6, 92, 91]. Nevertheless, it has also been noted as a pest of pearl millet [43], sugarcane [7] and rice [59]. Due to internal nature of damage, this pest is very difficult to control by conventional insecticides and biological control agents. Thus, there is a need to develop alternative management strategies through production of elite resistant/tolerant variety. The use of insect resistant cultivar has been designated as an essential component of IPM which offers an economically stable and ecologically viable mean to minimize the damage caused by the spotted stem borer.

Importance of host plant resistance to insects
Resistance to stem borer damage is expressed in terms of antixenosis, antibiosis and tolerance. Resistance to *Chilo partellus* is generally governed by additive gene action [86]. Furthermore the resistance expressed by a particular genotype is governed by various environmental

factors, so potential genotypes are usually evaluated by exposing them to different environments before desirable ones are selected. Genotype × environment interaction is one of the important attributes associated with the differential performance of genotypes tested at different locations [12]. Both genetic and environmental effects are reported to be the contributing factor for expression of phenotypic variation [5]. At times, the genotypes identified as resistant/tolerant to *C. partellus* under one agro-ecological region have been found to be susceptible at another region, might be because of genotype x environment interactions; however, existence of genetically different populations of *C. partellus* in different agro-climatic zones of India also can not be ignored. The differential response of a genotype for a particular trait across diverse ecologies is defined as the genotype (G) × environment (E) interaction. The G × E interaction impose difficulty in selecting the best performing and most stable genotypes. Thus it is important to consider G × E interaction in plant breeding programs because it is one of the major constraints in selection of a particular genotype in any given environment.

Plant physical condition is influenced by different environmental conditions in diverse agroclimatic conditions which ultimately influence the spatial and temporal pest dynamics leading to differential yield losses. The ability of a plant to provide holistic nutrition to the insects determines the quality of a host. Thus a plant can be either resistant or susceptible based on its inherent ability to impart nutrition to the insect which is also influenced by environmental factors. Different agroecological regions act as modifier of the nutritional quality of the host thus regulate the insect-plant interaction which ultimately regulate the differential insect reaction (resistance or susceptibility) in insects towards different plant genotypes in diverse agroecological conditions. *C. partellus*, attained the status of key pest of maize, because of its adequate nutritional balance out of which different amino acids play a crucial role in determining the nutritional quality of maize. Resistance, a relative character which is determined by the amino acid composition of the plant has been reported to vary in different agroclimatic conditions [71], thus making the maize- stem borer interaction variable in different agroecological conditions.

Sources of spotted stem borer resistance

Host plant resistance is one of the most economical and environmental friendly methods and recognized as a long-term control measure against insect pests [60]. It is one of the effective means of minimizing losses due to insect pests. However, most of the maize varieties and hybrids released for cultivation are susceptible to *C. partellus* [54]. Screening of maize germplasm for resistance to spotted stem borer, *C. partellus* has been reported to impart low to moderate levels of resistance to this pest [20, 72, 84, 47], and several new sources with high levels of stem borer resistance have also been reported and supplemented to the existing resistance sources [27].

Mechanisms of resistance to spotted stem borer

In resistant varieties of maize, all the three mechanisms of resistance, *viz*., non-preference, antibiosis and tolerance have been reported to be functional [82, 83, 57]. In Asia, various experiments have been carried out to elucidate the mechanism of resistance/ susceptibility in the two maize genotypes, Antigua Group 1 (Resistant) and Basi Local (Susceptible), against *C. Partellus* [54]. The most notable sources of resistance to *C. partellus* are Antigua Group 1, Population 590, and Population 390 of CIMMYT. Little information is available on sources of resistance to second generation *C. partellus.* Kumar [55] studied the larval establishment and damage by *C. partellus* on plants at anthesis. Severe yield losses can occur at anthesis because *C. partellus* attacks maize directly in the growing ear. Kumar [56] reported a few sources of resistance to second-generation *C. partellus*. The third aspect, tolerance has not been studied adequately well in maize resistance to *C. partellus* although this is the most desirable type of resistance in plants. With tolerance as a mechanism of resistance to insects, the insects are relieved of the strong selection pressure evident in the case of strong antibiosis in plants to insects [3, 54-56].

Basis of resistance to spotted stem borer

Plant characteristics including both morphological and biochemical are responsible in determining the host plant quality [93, 8, 67, 70, 1]. Trichomes on the upper leaf surfaces of resistant genotypes were found related to oviposition non-preference by *C. partellus* [35, 2]. Plant chemicals influence the resistance/susceptibility of the plants either by determining the orientation, feeding and oviposition behaviour of the insects, or by determining the metabolism of insects serving as toxins interfering with the metabolic processes of insects [58, 54, 55, 56]. Plant resistance to insects is complex and depends on interaction of constituent characters, leading to expression of resistance to insect pests [29].

Morphological and anatomical characters imparting resistance to maize stem borer

Several morphological and anatomical plant characters have been reported to be responsible for resistance to insect pests in maize [34, 58, 57, 73, 74, 27]. The role of trichomes in inhibiting oviposition by *C. partellus* has also been experimentally demonstrated earlier [58, 95, 64]. Trichome densities, surface waxes and leaf toughness are considered to have negative effect on the oviposition and development of *C. partellus* [68, 81].

Biochemical factors

Biochemical mechanism of insect defense in crop plants is key to insect-plant interactions, and mainly governed by constitutive and/or induced plant metabolic compounds. The amino acids, phospholipids, fatty acids, steroids, and ascorbic acid have been found to serve as phagostimulants for various insect species [24]. Numerous biochemical factors in maize have also been reported to be associated with resistance/susceptibility to insect pests [49, 50, 57, 73, 74, 86]. Biochemical factors such as phenols and sugars also play an important role in plant defense mechanism to *C. Partellus* [75]. Lignin and other phenolics can strengthen cell walls against digestion and therefore can be anti-nutritional for spotted stem borer [14]. Fiber composed of cellulose, hemicellulose and lignin are the primary plant cell wall components and shows resistance to stem borers [80]. Different concentrations of nitrogen, phosphorus, potassium, iron and silicon in stem tissues are responsible for resistance and susceptibility to *C. partellus* in maize in CM 137 and HY 464 [48]. Distinctly low leaf chlorophyll, carotenoid, nitrogen, crude protein and moisture content were noticed in resistant varieties as compared to susceptible ones [74].

Amino acids for insect nutrition and associated with insect resistance

Apart from protein synthesis, high levels of free amino acids are reported to have some additional functions in neural transmission, detoxification, and synthesis of phospholipids, energy production, and morphogenetic processes that have important biological roles in insects' growth and development. 22 standard amino acids were reported till date, out of which selenocysteine and pyrrolysine are incorporated into proteins by distinctive biosynthetic mechanisms, whereas remaining 20 are directly encoded by the universal genetic code. By using Rose's deletion method the amino acid requirement for insects for 20 different amino acids were detected. Some insects have identical requirement for amino acids, whereas some differ significantly in their requirement for life processes. *Delia antique* (Meigen), *Pectinophora gossypiella* (Saunders), and *Trogoderma granarium* Everts have similar amino acid requirements [46]. This has resulted that the L-forms of Arginine, Histidine, Isoleucine, Leucine, Lysine, Methionine, Phenylalanine, Threonine, Tryptophan and Valine are essential, while the L-forms of Alanine, Aspartic Acid, Cysteine, Cystine, Glutamic Acid, Glutamine, Glycine, Proline, Serine and Tyrosine are reported to be non-essential for majority of the insects studied [79, 17]. The essentiality and non-essentiality of a particular amino acid also differs from organism to organism. Non-essential amino acids found for rat (Proline, Serine, Cystine, and Glycine) were observed to be essential for some insects [42, 45, 46, 25, 88, 41]. Essential amino acids are reported to contribute to synthesis of protein having a carbon skeleton and cannot be synthesized *de novo* by the insects [23], whereas non-essential amino acids play a distinct role in insect defense which are synthesized by insect itself and the amino acids, that affect insect development are dose and species-dependent [45, 40, 94, 37, 4, 52, 16, 100, 19]. Insects are unable to complete it's particular life process if it is deprive of any essential nutrient [40, 100]. Moreover the amino acid deficiency in larval stages also affects the performance of an adult. Cangussu and Zucoloto [16] reported that protein deficiency during the immature phase was cause of reduce adult emergence, adult female size, and oocyte maturation and also increase the duration of the larval phase of *Ceratitis capitata.* High concentrations of glycine and serine were observed to be extremely toxic and had an inhibitory effect on the growth of *D. melanogaster* [45].

The leaf-eating by insects depends on their ability to acquire essential amino acids from dietary protein for their optimal growth. Amino acids being the major source of nitrogen their content in sap act as limiting factor in determining the survival of sap feeding insects. Amino acids, aspartic acid and glutamic acid are reported to cause toxicity to aphids and whiteflies when provided at higher concentration in artificial diet. The low amino acid content of plant tissue, poses a major nutritional challenge to phytophagous insects. Protein as both the major macronutrient and the most commonly limiting nutrient for insect growth is essential for life processes of insects [61]. The essentiality of amino acids is indicated as insect diets containing nutritionally unbalanced amino acids affect herbivory and may also influence host plant utilization pattern among various insect herbivores [63, 51, 44, 11]. For aphid, *Myzus persicae* sucrose and amino acid content were observed to play important role in probing response and feeding rate [62]. Moreover less aspargine content in rice variety impart resistance to brown plant hopper, as this particular amino acid content is less in Mudgo variety of rice, it is said to be resistant [90]. Brown plant hopper population is stimulated to feed on rice by the presence of two dicarboxylic amino acids such as aspartic acid and glutamic acid [89]. The free amino acid content of watermelon had a significant positive correlation with fruit fly infestation, whereas ascorbic acid contents had a significant negative correlation with percentage fruit infestation and larval density per fruit. Amino acids are major resistance factor for aphids as plants containing low level of amino acids impart resistance to aphids in soybean [21]. The soybean aphid *Aphis glycene* were reported to prefer plants having higher amino acid content. Concentrations of asparagine, aspartic acid, and glutamic acid have also been reported to be responsible for antibiosis against *Myzus persicae* (Sulzer) and white fly, *Bemisia tabaci* (Gennadius) [30]. A number of amino acids especially lysine has been reported to impart resistance to sorghum shoot fly [85]. Moreover resistant lines of oat and barley contain higher amount of glutamic acid and higher quantity of asparagine [98].

Lipophilic compounds for insect nutrition and associated with insect resistance

Fatty acids are compounds of basic significance associated with biology of insects. They play significant role in storage of metabolic energy, cell and bio-membrane structure, and in regulatory physiology of insects. The essentiality of lipid nutrients have been demonstrated by the deletion method, which measures the effect by eliminating one specific component from a chemically defined diet, substitution of an essential nutrient by analogues and the use of radio-labelled precursors to measure endogenous biosynthesis [24].The insects possessing symbionts in their body live on nutritionally poor or unbalanced diets throughout their life, e.g. phloem sap, vertebrate blood, and wood, and the symbionts (microorganisms) are believed to be a source of essential nutrients, primarily essential amino acids, vitamins, and lipids. Symbiotic bacteria in case of aphid impart it with various essential amino acids, lipids and sterols [32]. Nutritional factors are important determinants for plant utilization by the phloem feeding insects [32]. The nutritional barriers mainly constitute sugars and amino acids, which are regarded as the two most abundant classes of phloem-mobile nutrients [31], and there is a scanty information about the sterol nutrition in phloem-feeding insects. A minority of phloem-feeding insects, including some planthoppers have been reported to derive sterols from fungal symbionts [66], but in case of the great majority of phloem-feeders, bacterial symbionts cannot synthesize sterols *in vivo*. Therefore, most aphids, whitefly, psyllids, mealybugs and leafhoppers have been reported to meet their sterol requirements exclusively from phloem sap [9, 31]. The sterol profile of phloem sap can differ markedly from the sterol profile of bulk plant tissues [87, 10]. Aphids are reported to have limited capacity to convert phytosterols to cholesterol by dealkylation [15], but they differ in their capacity to utilize different phytosterols. In addition to sterols, most insects require polyunsaturated fatty acids, and many studies have shown that either linoleic or linolenic acids adequately fulfil this nutritional requirements [53]. The insects differ in their requirements for different fatty acids. Thelinoleic acid content is positively associated with adult emergence in *Homona coffearea*, when reared on meridic diet. Rock *et al*. [78] in their study concluded that a diet deprive of linseed oil will adversely affect the adult emergence of red-banded leaf roller *Argyrotaenia velutinana*, as the linseed oil contain linoleic acid and linolenic acid.

Deficiency of these two fatty acids caused emergence of adults with their wings partly or entirely lacking in scales. A butterfly species *Morpho peleides* contains a large amount of the polyunsaturated fatty acids linoleic and linolenic acids [97]. Essential fatty acid deficiency leads to scale wing syndrome in Lepidoptera and Hymenoptera. Various plant sources have been reported to contain several metabolite functional groups such as fatty acids, fatty alcohols, hydrocarbons, sterols and terpenoids, vitamin derivatives. Polyunsaturated fatty acids are considered as one of the most important dietary components of Lepidopteran insects [38, 39, 53]. The effect of wheat germ oil and various vegetable oils on scale condition and emergence of adults was positively correlated with the linoleic and linolenic acid content of the oils [78]. The ascorbic acid content is found to be positively associated with larval survival in codling moth, *Carpocapsa pomonella* [77]. Vanderzant [96] observed that linoleic acid was more active compound than linolenic acid in *Pectinophora gossypiella* in promoting the adult emergence. Linoleic acid deficiency symptoms were recorded both in *Schistocerca* and *Locusta* during final moult and wing formation [22, 23]. Similarly, adult emergence was observed to be less for *Anthonomus grandis* (Boheman) when reared on fat-free diets than on diets containing fat. This was due to the difficulty of the adults to emerge from the pupal cases [96]. Defatted wheat and alfalfa diet fortified with Linoleic acid were observed to reduce the wing syndrome (Crumpled wings) in *Mamestra brassica* Walker [13].

Conclusion

Study of various amino acids and lipophilic compounds in maize associated with resistance to various insect pests specially *C. partellus* could have implications for nutritional physiology, development and survival, and play important role in developing resistant varieties against *C. partellus* in maize. Furthermore, the metabolic pathways of diverse amino acids and lipophilic compounds can be elucidated and metabolic intermediates can be upregulated and downregulated as per nutritional requirements of the insects and resistant varieties can be developed. Molecular markers can also be developed for various biochemical constituents such as amino acids and lipophilic compounds to deploy in insect resistant breeding program.

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