Biophysical and structural mechanisms of resistance against pod borer complex in pgeonpea - A review

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Abstract

Host plant resistance is an important tool for minimizing the losses in pigeonpea due to pod borer, Helicoverpa armigera *(Hubner), spotted pod borer,* Maruca vitrata *(Geyer) and pod fly,* Melanagromyza obtusa *(Malloch) which are the most threatening hidden pests of pigeonpea crop. Resistant cultivars has a remarkable potential for use in integrated pest management programme. The biophysical, morphological and structural attributes of plants plays an important role in plant defense mechanisms. The glandular (type A and type B) and non-glandular (type A) trichomes on pods of top and middle canopy of the plant and pod wall thickness were associated with resistance to* H. armigera, M. vitrata *and* M. obtusa *whereas, the non-glandular lengthy (type C) trichomes and pod length were associated with susceptibility to the said insects. The expression of resistance to* H. armigera, M. vitrata*, and* M. obtusa *was associated with the high amount of fat, phenol and tannin content. Whereas, the higher amount of crude protein and total soluble sugar content were responsible for higher pod infestation.*

Keywords: Biophysical, Structural Mechanisms, Resistance, Pod Borer Complex, Pigeonpea.

Introduction

In the semi-arid tropics, pigeonpea [*Cajanus cajan* (L.) Millspaugh] is one of the major grain legumes (Nene *et al.,* 1990) and it is grown in 50 countries in Asia, Africa and the Caribbean as a lifeline requirements such as food fodder, fuel wood, hedges, windbreaks, rearing lac insects, soil conservation, green manuring and roofing etc. (Sharma *et al.,* 2003). Because of heavy infestation by insect pests, the productivity of this crop has remained stagnant over the past decades. More than 200 species of insects have been reported which feed on this crop worldwide and cause heavy annual losses (Reed and Lateef, 1990). Among them, the pod borer complex *viz*., gram pod borer, *Helicoverpa armigera* (Hubner), spotted pod borer, *Maruca vitrata* (Geyer) and pod fly, *Melanagromyza obtusa* (Malloch) are of prime importance throughout the world which feeds on reproductive parts of the plant (Taylor, 1967; Shanower *et al.,* 1999; Sharma, 2001;). Annual losses due to these pod borers complex damage have been reported to be US $ 400 million by *H. armigera*, US $ 30 million by *M. vitrata* and US $ 256 million by *M. obtuse* (ICRISAT, 2007; ICRISAT, 1992a; ICRISAT, 1992b).

Insect pest damage is often considerably affected by the chemical composition and morphological features of the plants. Identification and utilization of cultivars resistant/ tolerant to pod borer complex can have remarkable advantages, particularly for relatively low value pigeonpea crop (Sharma *et al.,* 2003). These resistant or less susceptible cultivars can be used in developing resistance breeding programs which would provide environmentally sound tool for sustainable pest management (Sharma, 2005). However, more than 14,000 cultivated genotypes of pigeonpea tested against *H. armigera* and *M. obtuse* resistance showed low to moderate level of resistance (Reed and Lateef, 1990; Singh and Singh, 1990). High level of resistance to *H. armigera*, *M. vitrata* and *M. obtusa* in some pigeonpea lines have been reported by several workers (Lateef and Pimbert, 1990; Sharma *et al.,* 2001; Green *et al.,* 2006; Sunitha *et al.,* 2008).

Several morphological or structural traits of plants such as trichome density and trichome length on leaves and pods and pod wall thickness have been reported to be associated with resistance to pod borers (Lateef and Reed, 1981; Jeffree, 1986; David and Easwaramoorthy, 1988;

Shanower *et al.,* 1996; Shanower *et al.,* 1997; Halder *et al.,* 2006). According to David and Easwaramoorthy (1988) and Duffey (1986) trichomes act as an insect resistance mechanism as a physical barrier limiting an insect's contact with the plant, by producing toxic compounds which poison the insect through contact, ingestion/ inhalation and by producing gummy, sticky or polymerized chemical exudates which impede the insects. However, the pod wall toughness had not played any appreciable role on cowpea resistance to the *M. testulalis* larvae (Oghiakhe *et al.,* 1992). Similarly, trichome orientation and their types, density and length influences the plant defense mechanism against insect-pests (Bernays *et al.,* 2000; Valverde *et al.,* 2001; Aruna *et al.,* 2005; Sharma *et al.,* 2009). The role of trichomes as a plant defense mechanism against insects has been well documented in tomato (Simmons *et al.,* 2004; Simmons and Geoff, 2004), soybean (Lam and Pedigo, 2001) and *Arabidopsis* (Karkkainen and Agren, 2002). Hypothesized have been mentioned that glandular trichomes act as physical barrier resulting mortality of arthropod pests (Muigai *et al.,* 2002) due to some toxic compounds produced by the trichomes (Kennedy, 2003).

Likewise, the morphological traits, role of chemical traits such as higher amount of total phenols, fat content, tannin content and lower amount of crude protein, total soluble sugar, reducing and non-reducing sugars and total amino acids as an insect defense mechanism has been well documented against pod borer complex (Sharma *et al.,* 2009; Moudgal *et al.,* 2008; Pandey *et al.,* 2011). The chemical compounds in trichome exudates and pod wall surfaces also influences the host plant selection and colonization by pod borer complex (Bernays and Chapman, 1994; Hartlieb and Rembold, 1996; Green *et al.,* 2002, 2003). The importance of antixenosis mechanism of resistance against *H. armigera* and *M. vitrata* in pigeonpea has been discussed well by several workers (Kumari *et al.,* 2006; Sunitha *et al.,* 2008; Sharma *et al.,* 2009). Anti-nutritional factors such as phenols, tannins, protein inhibitors, oligosaccharides and phytic acids have also been reported to influence the host plant suitability (Singh, 1988). The study of above components associated with resistance against pod borer complex in detail can be helpful for making sound management practices and will justify the role of biophysical and structural traits in relation to expression of resistance against pigeonpea pod borer complex.

Role of morphological components against pod borer complex:

Plant type

Types of plant growth (determinate and indeterminate) affect genotypic susceptibility to the borer complex. According to Kushwaha and Malik (1987) and Reddy *et al*. (2001) determinate and indeterminate genotypes of pigeonpea were found susceptible to lepidopterous pod borers and *M. obtusa*. Saxena *et al*. (2002) revealed that *M. vitrata* damage in determinate accessions (66-75%) was higher than that of non-determinate accessions (41-50%). Mohapatra and Srivastava (2003) found determinant varieties susceptible to *M. vitrata* infesting pigeonpea. Moudgal *et al*. (2008) reported the resistance to pod fly is not linked with plant growth type in pigeonpea.

Trichome density and their types/ orientation

Morphological traits/ structures of the plant are the frontline barriers and provide resistance against insect-pests. This defense against insect-pests occurs though the presence of trichomes on plant surfaces (Bernays and Chapman, 1994; Sharma *et al.,* 2009; He *et al.,* 2011). Trichome density, their length, orientation, and types provides direct defense against insect-pests by affecting the physiology of herbivores (Jeffree, 1986; David and Easwaramoorthy, 1988; Peter, 1995) in many crops. Trichome exudates on the pod surface is also affects the ovipositional behavior of insects (Bernays *et al.,* 2000). Density of non-glandular trichomes in pigeonpea wild species prevents the larvae from feeding on the pods and limits the establishment of the borer (Peter and Shanower, 1998). *H. armigera* females not deposit their eggs on pods of some wild relatives of pigeonpea such as *C. scarabaeoides* and *C. acutifolius* with non-glandular trichomes, whereas, species with glandular trichomes are susceptible to *H. armigera* larvae (Sujana *et al.,* 2008).

Trichome length had significant and negative association with the pod damage by *M. vitrata* in pigeonpea and the length of the trichomes act as a physical barrier to feeding by the spotted pod borer (Devi *et al.,* 2013). The role of trichomes in pigeonpea have been well documented by Peter *et al*. (1995) and Romeis *et al.* (1999), trichome length and density provides potential of host plant resistance mechanism in pigeonpea. Trichome minimizes the insect feeding habit and damage through repellent activity of exudates, avoid maximum contact with the surface of the plant, entrapment by means of physical and chemical actions, biotic and abiotic agents have maximum action time to the damaging stage of the insect resulting inhibiting the larval growth and reduce the oviposition efficiency (Devi *et al.,* 2013). Trichome density on leaves and trichome length on pods have significantly contributed to the resistance in ICPL 98003 and ICPL 98008 to *M. vitrata* (Sunitha *et al.,* 2008).

Moudgal *et al.* (2008) reported that the density of non-glandular trichomes was higher than the glandular trichomes across the tested genotypes and the pods of pod fly resistant genotypes (GP 75, GP 118, GP 233, and GP 253) had significantly more number of glandular and non-glandular trichomes than the susceptible genotypes (GP 25, GP 183, GP 242, and GP 248), and the commercial checks across plant types and maturity groups, suggesting that trichome density is associated with resistance to *M. obtusa* in pigeonpea. According to Jat *et al*. (2018), non-glandular pod trichomes (type A) was significantly and negatively correlated (-0.923** and -0.728*) with pod fly infestation in different sowing dates. Trichome density on upper and lower surfaces of the leaf (390 and 452/9 mm^2), and length (3.5 mm) and trichome density (442/9 mm^2) and length (5.9 mm) on pods of short duration pigeonpea genotypes were found positively correlated with the resistant genotype ICPL 98003 (Sunitha *et al.,* 2008).

Pod wall thickness

Pod wall thickness was also significant and negatively correlated (-0.834*, -0.705* and -0.745*) with pod fly infestation in different sowing dates (Jat *et al.,* 2018). Similarly, pod wall thickness was associated with resistance to *M. vitrata* and *H. armigera* in pigeonpea crop and the correlation was significant and negative (r = -0.909**, r = -0.739*, r = -0.801*) and (r = -0.870*, r = -0.840*, r = -0.843*) (Jat *et al.,* 2018, 2019). Thicker pod wall exhibited lesser preference for larvae than the genotypes evincing thinner pod wall and it can be regarded as a non-preferential attributes for *H. armigera* (Jagtap *et al.,* 2014). Similarly, Sunitha (2006), has been reported that pod wall thickness showed a highly significant and negative correlation with pod damage by *M. vitrata* in pigeonpea. The thickness of the pod wall associated with resistance to *M. vitrata* has earlier been studied as one of the insect resistant traits in cowpea (Sharma, 1998) and in mungbean (Halder *et al.,* 2006). Whereas, non-significant and negative correlation between pod wall thickness and per cent pod damage has been reported by Wubneh and Taggar (2016) in pigeonpea crop.

Chlorophyll content

Infestation of pod fly was significant and positively correlated (0.861* and 0.719*) with chlorophyll content of seed as well as pod wall in pigeonpea. However, the chlorophyll content of seed as well as pod wall did not show any significant association with *Maruca vitrata* pod damage in different sowing dates (Jat *et al.,* 2018). Correlation studies carried out by Mallikarjuna *et al.* (2009) stated that pod color had significant relationship with the *M. vitrata* larval incidence in dolichus bean. Tripathi and Purohit (1983) noted maximum pod borer damage on green color pods in pigeonpea as compared to pods having brown streaks. Varieties with green color pod wall were found more susceptible to the pod borer complex in pigeonpea. Whereas, according to Jagtap *et al.* (2014) genotypes having green and green with brown streaks color pods evinced lesser preference for *H. armigera* larval feeding than the genotypes having green pods with purple streaks. The significant and positive correlation between chlorophyll content of seed as well as pod wall and *H. armigera* has been observed by Jat *et al*. (2019). Similarly, Dua *et al.* (2005) also gave confirmation support of brown seed and green pod having streaks associated with resistance to *H. armigera* in pigeonpea.

Pod length/ number of seeds per pod

Generally a significant positive correlation between pod length and pod borer infestation in pigeonpea is happened. But the hypothesis is favored and unfavored by the research findings. Jagtap *et al.* (2014) reported that the genotypes having shorter pod length were preferred lesser by larvae than genotypes having longer pods. Shorter peduncle length and petiole length were also least preferred by larvae than genotypes having longer peduncle length and petiole length. Similarly, Thakur *et al. (*1989), Veda *et al.* (1975) and ICRISAT (1983) observed positive relationship between pod length and pod borer, *M. vitrata* and pod fly infestation. According to Sunita *et al.* (2013) the pod length of pigeonpea genotypes showed a non-significant negative correlation with pod damage due to *M. vitrata* and the genotypes with long pods recorded less pod damage. However, Gumber *et al*. (2000), Kapil *et al.* (2010) and Moudgal *et al.* (2008) reported that there is no association between pod length and *M. vitrata* and pod fly damage. Influence of seed characters on the incidence of pod borers in pigeonpea has been reported and positive correlation between seed width and incidence of pod borers (0.01 to 0.492) has been observed except for *M. vitrata* (-0.080) (Sahoo and Senapati, 2000).). On the contrary, seed length had a negative effect on the incidence of most borer species except *H. armigera* (0.069).

Biochemical constituents in the host plant (such as sugars, proteins, fats, sterols, and essential amino acids, and vitamins) influence host plant suitability to insect pests (Painter, 1958). Total soluble sugars in pigeonpea pod wall influence pod damage by *H. armigera*. Protein content of the pod wall is associated with susceptibility, while total sugars are associated with resistance to *M. obtusa* in pigeonpea. Amylase and protease inhibitors in pigeonpea and its wild relatives have been shown to have an adverse effect on growth and development of *H. armigera* (Parde *et al.,* 2012). Chemical compounds in trichome exudates and on pod wall surface also influence the host plant selection and colonization by *H. armigera* (Hartlieb and Rembold 1996; Green *et al.,* 2002, 2003). Pigeonpea plant also contains anti-nutritional factors such as proteinase inhibitors, oligosaccharides, phenols, tannins and phytic acid (Singh, 1988), which may influence the host plant suitability to *H. armigera*. According to Jat *et al*. (2019), the expression of resistance to *H. armigera* was also associated with the high amount of fat, phenol and tannin content. Crude protein and total soluble sugar content were responsible for higher pod infestation. Similarly, expression of resistance to *M. vitrata* was also associated with the low amounts of crude protein and total soluble sugar and higher amount of fat content, phenol content and tannin content of seed as well as pod wall (Jat *et al.,* 2018). Maximum infestation of pod fly was observed when pigeonpea crop having higher amount of crude protein content in seed as well as pod wall in even pigeonpea crop sown at different intervals. Whereas, the fat content and condensed tannins of pod wall was significantly negatively correlated (-0.750*) and (-0.763*). However, total phenol content of seed as well as pod wall did not show any significant relationship with pod fly infestation (Jat *et al.,* 2018).

Other phenolic compounds

The role of feeding stimulants to the larvae of *H. armigera* have been discussed by several workers. Secondary compounds affect the food selection behavior by *H. armigera* in many cultivated legume crops (Simmonds and Stevenson, 2001) and they act as a feeding stimulants or feeding deterrents. These compounds on the surface of pods of *C. cajan* may also modulate the feeding of larvae of *H. armigera*. Shanower *et al*. (1997) reported that acetone extracts from the pod surface of a variety of *C. cajan* (ICPL 87) susceptible to pod-borers stimulated the feeding of third-instar *H. armigera*. The feeding stimulant property of hexane, methanol, and water extracts of *C. cajan* (ICPL 87) pods against fifth instar larvae of *H. armigera* was also reported by Green *et al*. (2002) with the methanol extract being most stimulatory. Four phenolic compounds (isoquercitrin, quercetin, and quercetin-3-methyl ether, by comparing UV spectra and HPLC retention times with authentic standards and fourth compound was isolated by semi preparative HPLC and determined to be 3-hydroxy-4-prenyl-5 methoxystilbene-2-carboxylic acid (stilbene) by NMR spectroscopy and mass spectrometry) of pod surface of *C. cajan* were identified (Green *et al.,* 2003) against fifth instar of *H. armigera* in methanol extract and observed that quercetin, isoquercitrin, and quercetin-3-methyl did not affect the selection-behavior of fifth instar *H. armigera.* However, larvae were deterred from feeding on glass-fiber disks impregnated with the stilbene. Furthermore, larvae exposed to quercetin-3-methyl ether consumed significant amounts of both disks. In a binary-choice bioassay, a combination of quercetin-3-methyl ether and the stilbene on one disk and pure quercetin-3-methyl ether on the other disk resulted in increased consumption of both glass-fiber disks by larvae. In contrast, consumption was reduced if the combination was presented to larvae on one disk with purified stilbene on the other disk. Phenolic compound quercetin is the most widespread in plant kingdom and reported in many higher plants with frequently occurred in glycosylated forms such as isoquercitrin and rutin (Harborne *et al.,* 1999). Besides, this stilbene previously have been reported from the leaf surface of *C. cajan* that had been challenged with the fungus, *Botrytis cinerea* (Cooksey *et al.,* 1982). However, quercetin and derivatives of quercetin do not affect the feeding behavior of Lepidoptera larvae (Lindroth and Peterson, 1988; Faini *et al.,* 1997).

Deterrent and growth inhibitory property of concentrations of isoflavonoids against *H. armigera* have been reported in chickpea by Simmonds and Stevenson (2001). Concentrations of quercetin glycocides and phenyl propanoids in developing cultivars of groundnut having deterrent action have been reported against larvae of *Spodoptera litura* (Stevenson, 1993). Some other phenolic compounds, such as schaftoside (an apigenin-C-glycoside) also deter feeding and growth of brown plant hopper, *Nilaparvata lugens* and plant hoppers (Grayer *et al.,* 1994; Stevenson *et al.,* 1996). Rutin (quercetin-3-O-rhamnosyl [1→6] glucoside) similarly deters feeding by *Heliothis zea* (Boddie) and *H. armigera* at concentrations in excess of 10−3 M (Blaney and Simmonds, 1983).

Conclusions

For cultivation of short duration pigeonpea varieties, morphological traits, and biochemical components are quite important components of resistance against pod borer complex. Types of trichome, their orientation, density, and length influence the host plant resistance/ susceptibility to insect pests (Jeffree, 1986; David and Easwaramoorthy, 1988; Peter *et al.,* 1995; Valverde *et al.,* 2001; Gurr and McGrath, 2001). However, according to Chu *et al*. (2000), trichomes at times also impart susceptibility to whitefly, *Bemisia tabaci* (Gen.) in cotton. Among the types of trichomes, glandular trichomes and their exudates act as an important resistance mechanism to insects owing to the compounds exuded by them (Ranger and Hower, 2001; Frelichowski and Juvik, 2001). The hypothesis given by Hartlieb and Rembold (1996) stated that glandular secretions from trichomes in pigeonpea act as attractants to the adults of *H. armigera.*

Additionally, biochemical components present in the tissues of the host plant exert a profound influence on biology of insect pests (Beck, 1965; Smith, 1989; Sharma, 2009). In wild relatives of the pigeonpea, the total soluble sugars were less as compared to the pods of cultivated pigeonpea with higher sugar content, and this may be one of the factors leading to greater feeding by *H. armigera* larvae on the pods of cultivated pigeonpea compared to that on the accessions of wild pigeonpea (Sharma *et al.,* 2009). MacFoy *et al.* (1983) recorded high concentrations of sugars and amino acids in the cowpea cultivar Vita-1, which is susceptible to spotted pod borer, *Maruca testulalis* (Geyer). Low amounts of phenols in the pods and flowers of pigeonpea cultivars might be another reason for their high susceptibility to *H. armigera* and *M. testulalis* (Ganapathy, 1996). According to Smith (1989), condensed tannins in plants act as insect growth inhibitors owing to their presumed binding to the proteins.

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