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Ashok Kumar Sau

Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India

Rajesh

Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India

Mukesh K Dhillon

Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India

Corresponding Author Ashok Kumar Sau Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India

Aspects of host plant resistance with reference to Sesamia inferens (Walker): A review

Ashok Kumar Sau, Rajesh and Mukesh K Dhillon

Abstract

The loss of productivity due to insect pest infestations in agricultural crop production is a major concern. Farmers use the chemical method for quick relief from insect infestation, but it has several drawbacks, such as insecticide resistance development, resurgence of insect pests, pesticide residue issues, adverse effects on non-target organisms, and environmental pollution. Cereals and millets are vulnerable to a variety of biotic and abiotic stresses. The polyphagous pink stem borer, *Sesamia inferens* (Walker) (Lepidoptera: Noctuidae) which is gaining national importance, is limiting cereal and millet cultivation. Because its larvae and pupae are hidden within the stem, no management approaches have been proven to be helpful in controlling the threat. Host plant resistance (HPR) to insect pests is an environmentally acceptable and cost-effective form of pest control that is compatible with all insect pest control strategies. Recognizing the mechanism and basis of plant resistance, understanding pest biology and nature of damage, and finding the source of resistance is the prerequisite for generating insect-resistant varieties. Since the *S. inferens* is a major pest of maize this review paper is mainly deals with the elements of host plant resistance against *S. inferens* in maize.

Keywords: host plant resistance, Sesamia inferens, biology, maize, biochemical basis

Introduction

Host plant resistance refers to heritable qualities of a cultivar to counteract the activities of insects so as to cause minimum reduction in yield as compared to other cultivars under similar conditions ^[1]. It allows a plant to prevent insect pests from selecting a host plant for settling, oviposition, and feeding, and even if they do, it interferes with insect pests' biology by affecting their growth and development and reducing their survival, or else plant have the ability to tolerate or recover from insect injury. As a result, insect pests are unable to develop successfully on the resistant plants ^[2]. Mechanisms of resistance are classified in to three categories viz., antixenosis/non-preference, antibiosis and tolerance/recovery. Antixenosis mechanism of resistance influence larval orientation, settling and feeding response due to presence of chemical and/or morphological factors ^[3]. Antibiosis mechanism of resistance affects biology of the insect, and the most commonly observed adverse effects are in terms of nutritional physiology including consumption, assimilation, utilization and subsequent allocation of food resources for reproduction. Since plant resistance is the result of interaction between the plant and the insect, four resistance characteristics viz., heritable, relative, measurable and variable are important to compare the performance of particular genotype for resistance to target insect ^[4].

Among the cereals, maize is one among the most important crops of the world which together with rice and wheat, provides at least 30% of the food calories to more than 4.5 billion people in 94 developing countries of the world. It is also a key ingredient of the animal feed and is used extensively in industrial products, including the biofuels production. Maize is having an important role in the livelihood's security of millions of poor farmers and an important source of food and nutritional security for the millions of people in the developing world. Of the total, 75% is being used as poultry feed and human food, however, 25% is used for animal feed and industrial purposes ^[5]. It is an important component of feed for the meat industry, in the poultry industry on average broiler rations contain 60–65% maize only ^[6]. The production of maize in India is 27.23 million tonnes in 9.18 million hectares with productivity of 2965 Kg/hectare ^[7] which is much lesser than it yields potential, and limited by biotic and abiotic stresses. Among the insect pests attacking the maize crop, the lepidopteran stem borers infest the crop right from seedling to maturity stage, and are considered as major constraints of yield loss ^[8, 9]. Seventeen species belonging to two taxonomic families i.e., Crambidae and

Noctuidae have been found to attack maize in various parts of Asia. Out of which, *Sesamia inferens* (Walker) (Lepidoptera: Noctuidae) is of great importance causes considerable yield losses to maize ^[10]. In India, the maize production is highly influenced by the attack of *S. inferens*. This review major focus on the aspects of the biology, nature of damage, mechanisms, bases of resistance and identification of sources of resistant genotypes from the germplasm in maize.

Egg laying pattern of Sesamia inferens

Adult female S. inferens chose the inner side mostly of the first and second leaf sheath for oviposition. The studies on egg laying pattern revealed that the number of eggs laid by S. inferens were significantly higher in the first leaf sheath (59%) followed by second leaf sheath (27%) and least number on basal leaf sheath (14%) of maize plants [11, 12]. Conversely, the third leaf sheath (80%) of paddy was preferred over second leaf sheath (13%) for egg laying by S. inferens females^[13]. In study the maximum number of plants used by a single female for egg laying were four out of ten plants offered. The total oviposition period was recorded up to 7 days, and maximum number of eggs was obtained on second day of adult emergence ^[12]. The choice of host by insect for egg laying is indication of antixenosis factor present in that plant ^[14]. The thermal constants for egg, larval and pupal stages were recorded as 64-, 535- and 164-Degree Days while, the lower developmental threshold was found to be 13, 8 and 11°C, respectively [15].

Biology of Sesamia inferens on different hosts

Pink stem borer appears at the end of March and continually present till November in the maize crop, with peak in spring ^[16]. A female of S. inferens lays 150-400 eggs between the leaf sheath and the stem of maize plant with 87% of hatchability ^[17] the total number of eggs laid were recorded from 30 to 191 on selected maize germplasm by Divekar et al., (2019)^[18]. The colour of eggs is creamy-white and around 0.7 mm in diameter, with fine ridges in longitudinal line from the upper pole^[19]. The eggs start to hatch within 7 days and the larva passes through eight instars and complete the larval development within 68 days on wheat ^[20]. Similarly, Rajendra (1976)^[21] reported that the egg period of *S. inferens* lasts for 8-9 days in February month and larvae pass through eight instars. However, Joshi (2005) [13] reported that S. inferens passes through 6-8 instars and complete the larval development within 53-74 days on rice while according to Viswajyothi et al., (2019)^[22] there were six larval instars and the larval development was completed in 29.95±0.16 days on maize. Pupal period is 9-11 days and adults live for five to seven days ^[21] and there are ~5 overlapping generations in a year [16]. Total life span of S. inferens females and males were found to vary from 63-72 days and 45-58 days, respectively ^[23]. Joshi et al. (2009) ^[17] reported that on Ragi, the duration of the life-cycle of S. inferens were averaged 46 days in summer and 71 days in winter season and completed four generations in a year.

Seasonal abundance of Sesamia inferens

The pink stem borer hibernates in rice stubbles in winter from November to March and adults emerge in mid-April and lay eggs ^[24]. The highest larval population of *S. inferens* was found during last week of February on maize crop and peak activity of adult moths was found during 2nd week of March in Chandigarh ^[25]. *S. inferens* was first appeared in third week of

August (10% dead-heart) and reached to its peak infestation level (60% dead-heart) during the third week of September on maize ^[26]. In India, it has been reported as economically important pest of cereal crops in Andhra Pradesh, Tamil Nadu, Karnataka, Maharashtra, Madhya Pradesh, Orissa, West Bengal, Assam, Bihar, Uttar Pradesh, Delhi and Punjab ^[27].

Cold tolerance in Sesamia inferens

Low winter temperature is main environmental constraint for survival of many insect species, but *S. inferens* has mechanism to survive cold winters. The maximum tolerance recorded in *S. inferens* larvae was found in January collected larvae. Before March water content of larvae was found to stabilize at low level of 63.5 percent, but after that it rose significantly to 75.2 percent. Low molecular weight sugars and polyols (glycerol, trehalose, fructose, glucose, *myo*-inositol) associated with freeze tolerance activity were increased from low levels to their peaks in January, after that declined ^[28]. The adaptation mechanisms will help *S. inferens* to survive in the winter and from March onward it starts to infest the different field crops.

Nature of damage of Sesamia inferens

At the time of hatching, pink stem borer larvae remain inside or behind the leaf sheath and feed on the epidermal layer of the leaf sheath in groups. The first feeding site for larvae is the bottom most leaf sheath. Because of feeding, watersoaked lesions are formed on the infested leaf sheath in the initial stages of feeding which are visible from outside. Thereafter by boring through the sheath, the larvae reach to the central growing point of plant. Subsequently, it feed on leaves in the whorl in folded condition which results in formation of oblong (elongated or oval) shot holes of 2-3 mm size in parallel rows when leaf become unfolded. As plant grows, these holes extend and become slits and streaks. In extreme cases, tunneling on mid rib is also evident on the leaf blades and plants show ragged like appearance. Infestation in the growing point of the shoot result in drying up of central leaf, formation of dead heart at seedling stage in cereals and white ears at ear head stage in wheat as well as rice. Maximum amount of damage on stem are between first to fifth internodes. Exit holes (2-5 holes per plant) may be found on the stem. The stem tunnels may be horizontal (sometimes extended to other internodes) S-shaped or circular or vertical. Dark circular ring like cuts on lower internodes may be seen externally in the stem and excreta also present on stems outer surface near the bore hole ^[29]. Single larva may cause damage to more than one plant, as larva could leave the old tunnels and prepare fresh ones. In artificial infestation of maize crop with S. inferens, the highest mean Leaf Injury Rating (LIR) were recorded when larvae were released at 2 leaf stage (7 DAG). The LIR increase with increasing in larval density irrespective of the age of crop. It shows that maize crop at 2 leaf stage is most critical stage for S. inferens infestation irrespective of the larval density per plant ^[30].

Extent of damage done by Sesamia inferens

Stem borers are categorized as the most damaging group of insect pests in maize production and estimated to cause an average annual loss of ~18%. Among them *S. inferens* is key pest of Rabi maize causing major damage in peninsular India and is present throughout the year. It also causes extensive damage in the northern states in Rabi maize ^[31]. Pink stem

borer may cause up to 78.9% damage in maize crop during winter ^[32] with estimated annual loss of Rs. 110 million in India ^[14]. It is a polyphagous pest and feed on variety of cereals *viz.*, sorghum, pearl millet, finger millet, wheat, rice, oats, barley and sugarcane. Ragi is being increasingly attacked by *S. inferens*. Pink stem borer is emerging pest of wheat crop in India because of change in cultivation and tillage pattern ^[33]. The yield loss due to *S. inferens* vary from 25.7 to 78.9% in maize and more than 11% in wheat ^[34, 35].

Assessment of damage done by Sesamia inferens

Foliar lesions, dead heart and stem tunnelling are the main damaging parameters used for the damage assessment of stalk borers like C. partellus and S. inferens. Yield loss caused by the stalk stem borers is mainly because of stem tunnelling of the maize plants ^[36]. Foliage damage, number of entry or exit holes, number of egg masses, percentage of stem length tunneled and stalk breakage due to attack of stem borer are some of the very important parameters which distinguish between resistant and susceptible genotypes or varieties. Moreover, resistance/susceptibility index is calculated by relative ratios of all the parameters for every genotype. Some important parameters like leaf damage, dead heart and stalk damage are generally considered in breeding programme of maize to develop resistant genotype. Based on the nature and extent of damage, a rating scale of 1 (healthy plant) to 9 (dead heart) is used in the screening of maize genotypes for resistance to S. inferens. It categorizes the maize plants in three distinct groups, namely least susceptible (1-3 score), moderately susceptible (4-6) and highly susceptible (7-9)^[37].

Basis of resistance to pink stem borer

Morphological, allelochemical biochemical and characteristics of a plant determine its quality and host suitability to stem borer ^[38]. Plant morphological characters interfere with insect behavioral activities such as mating, oviposition, feeding and ingestion. To measure orientation and settling behavior of S. inferens, various choice tests have been developed and used for such studies. The no choice tests have been performed to determine level of antibiosis in various maize hybrids ^[39]. Apart from various morphological characteristics such as plant height, trichrome, pubescence hair, stem hardiness, leaf texture, glossiness and tassel ratio ^[40], biochemical characteristics *viz.*, tannin, phenol, flavonoids, chlorophyll, carotenoids, protein, sugar, starch have also been reported to be effective for imparting resistance to insect pests in maize [41, 42]. Biochemical characteristics of plant adversely affect the feeding behavior of insect by producing toxic substances which ultimately prevent metabolic processes ^[43]. The feeding potential of first instar larvae of European corn borer, Ostrinia nubialis (Hubner) on young seedlings of resistant maize genotypes was found reduced due to biochemical factor, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA). The concentration of DIMBOA in maize plant decreases with plant age ^[44]. Expression of resistance in host plant not only governed by single constitutive factor, but is the result of interaction between all the constitutive biochemical factors ^[45]. Phenol compounds could play an important role in resistance to stem borer S. nonagrioides. The amount of free *p*-coumaric acid was correlated with the resistance level in different maize genotypes. Higher amount of p-coumaric in the pith could contribute to general resistance to stem borer attack. Jointly with ferulic acid, the p-coumaric could provide

resistance mechanisms also through cell wall fortification and lignification ^[46].

The constitutive and induced plant metabolic compounds govern the insect-plant interaction, which ultimately leads to plant defense against insects ^[47]. Host plant quality can be determined by specific allelochemicals, nutrients and anatomical factors present in the host plant ^[48]. The sum of all the morphological, biochemical and anatomical plant features contribute to durable resistance against insect pests ^[49]. Antinutritional factors like lignin and phenolic compounds also play a major role in plant defense against herbivores ^[42]. The plant chemicals influence the resistance/susceptibility to insect pests in several ways: like, by determining the orientation, feeding and oviposition behaviour of the insects, by determining the metabolism of insects, which could be either helpful in normal metabolic processes resulting in insect's normal survival, development and egg production, or production of plant toxins interfering with survival, development and egg production. The induced plant defense chemicals adversely affect growth, development, feeding and survival of insect and overcome damage by the herbivores ^{[50,} 51]

Morphological factors responsible for resistance to pink stem borer

Six inbred lines with different levels of stem resistance against S. nonagrioides were compared in several trials. Potential structural resistance factors are the rind and pith puncture resistance (RPR and PPR), rind thickness, length of the meristematic area (LMA), and pith parenchyma interlumen thickness (PPIT). Susceptible inbred lines normally showing the higher values for the LMA, so PPIT and LMA was the most promising indicator of resistance in maize against pink stem borer ^[52]. In S. nonagrioides resistant inbreds of maize (CM151, CO125 and EP39) there is low damage in the stem due to antibiotic pith that also affected the weight and the larval survival of stem borer. So, pith antibiosis appeared to be one of the factors that confer resistance against stem borer ^[53]. The leaf sheath of maize plants appears to play a role in the successful development of neonates of S. nonagrioides. In the presence of phenolic carbohydrate complexes, fiber strength increases, which provides a tough physical barrier to restrict insect penetration and render nutrients within tissues less accessible ^[54]. Plants anti-nutritional defenses against insects reduces the nutrient value and limit food supplies to insects through physical barriers such as the cell wall fortification. Lignin and other phenolics can strengthen cell walls against digestion ^[55].

Biochemical factors responsible for resistance to Sesamia inferens

Plants produce hundreds of thousands of unique low-mass natural products, known as secondary metabolites. Plants respond to herbivory through various biochemical mechanisms including limiting food supply, reducing nutrient value, reducing preference and inhibiting chemical pathways of the insect. Earlier studies have demonstrated that the plant attributes can affect herbivores, natural enemies of herbivores, and their interaction ^[56]. Plant secondary metabolites are different from primary metabolites in terms of their basic metabolic processes in plant as they are generally nonessential, but improve defense against microbial attack, herbivore feeding and control allelopathic interactions in plants ^[57]. These secondary metabolites are produced in plant tissue independent of the presence of the pest and development-specific manner. Production of toxic chemicals such as terpenoids, alkaloids, anthocyanins, phenols, and quinones were affecting the biology of insect. Plants contain significant quantities of various phenolic acids, as well as their glycosides and esters. Plant phenols constitute one of the most common and widespread group of defensive compounds, which play a very important role in plant resistance. These phenolic compounds are act by two defense concepts, the phenolic fortification of cell walls and the deterrent effect of fiber content. Main components that strengthen the cell wall as mechanical barrier are ferulic and p-coumaric acid [57]. Free phenols, mainly 4-coumaric and ferulic acid, were implicated as factors contributing to resistance of maize against maize weevil (Sitophilus sp), and recently, to pink stalk borer (S. nonagrioides). Furthermore, maize genotypes in which pith contain higher quantities of phenylpropanoids in cell wall was found resistant to S. nonagrioides. Presence of ubiquitous phenolic acids, especially ferulic acid, may contribute to insect resistance in maize. Free phenols, mainly p-coumaric (CA) and ferulic acid (FA), were implicated as factors contributing resistance to various insect pests including pink stalk borer, S. nonagrioides in maize [58]. The S. inferens feeding strongly induced defense responses resulted in the accumulation of higher content of phenolic acids-p-CA and FA in leaf tissues of resistant and moderately resistant genotypes possibly contributes to enhanced resistance in maize. Changes in FA content in stalk tissues of maize genotypes were induced due to wounding and regurgitation followed by S. inferens feeding ^[59]. Tannins have a strong deleterious effect and affect insect growth and development by binding to the proteins, reduce nutrient absorption efficiency and decrease the nutritive value of plants to herbivores. The increase in nitrogen content in maize seedlings significantly increase the larval survival, larval weight, and female fecundity, while silica content had opposite effect on these biological traits of S. calamistis Hampson ^[60]. Plant surveillance system detects attacks by specific signals and detected signals are then transduced through a network of signal transduction pathways, which eventually lead to the production of defense chemicals ^[61]. Salicylic acid is an important phytohormone involved in regulation of plant defense that generates a wide range of metabolic and physiological responses in plants involved in defense. Plants with high variability in defensive chemicals exhibit a better defense compared with those with moderate variability. The biosynthesis of these defense-related metabolites has a common root in the shikimic acid pathway ^[58]. Maize plants respond to the attack of S. nonagrioides through cell-wall fortification, activating genes involved in cell-wall organization, which finally is reflected in a higher concentration of some cell-wall components, especially in resistant genotypes. The amount of free phenolic compounds like p-coumaric acid was correlated with resistance to stem borer, S. nonagrioides in which p-coumaric together with ferulic acids could provide higher level of resistance through cell wall fortification and lignification. The amount of these compounds was correlated with the resistance level in the maize genotypes, with the resistant inbreds having the highest concentrations [46].

In plant defense against herbivores, reactive oxygen species (ROS) play a major role and act as secondary messenger for signaling various defense reaction pathways in plants ^[62]. Oxidative state of the host plants has been associated with

plant resistance to insects, which results in production of ROS are subsequently eliminated by antioxidative enzymes ^[63]. ROS promote beneficial oxidation to generate energy and kill microbial invaders and herbivore. But in excess, it can cause pigment co-oxidation, lipid peroxidation, membrane destruction, protein denaturation, and DNA mutation ^[64]. In order to prevent oxidation, plant itself develops important ROS scavenging mechanism^[65]. Antioxidative enzymes are the most important components in the scavenging system of ROS, and are involved in defense against herbivores. Induced resistance in host plants is regulated by various antioxidative defense enzyme such as peroxidases (PODs), polyphenol oxidases (PPO), phenylalanine ammonia lyase (PAL), superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase ^[66]. The enzymes that impair the nutrient uptake by insects include ascorbate peroxidases by oxidizing monoor dihydroxyphenols to o-quinones which in turn form covalent adducts with the nucleophilic groups of proteins. Qualitative or quantitative alteration in phenols and enhanced activity of antioxidative enzymes in response to herbivore attack is general phenomenon ^[67], and play major role in plant defense against stem borer [68].

Sources of resistance to Sesamia inferens

For a good host plant resistance program, it is necessary to establish an efficient and reliable screening technique of the maize genotypes that ensures the desired level of insect pressure uniformly on all plants, at the most susceptible stage of the crop. These necessities can be fulfilled either by selection of a location where the insect pest occurs regularly (hot spot) or by testing the germplasm materials under the artificial infestation with insectary reared insects. The most critical damage which causes the maximum grain yield reduction is formation of dead-heart. This symptom can be achieved only if we are infesting the relatively young plants. In this programme efficient planning is necessary to produce sufficient numbers of insects which can infest the test material at the proper growth stage and uniformly to all plants ^[69].

In the screening programme of ten genotypes of maize against S. inferens, the leaf injury varied from 5.03 to 7.9 in which genotype Madhuri and BML 7 recorded as lowest leaf injury while Basi Local and HQPM-1 as highest leaf injury. Basi Local shows the highest dead-heart (39%) in plants ^[70]. Another research on screening of 15 maize genotypes were carried out for their reaction to stem borers, the hybrids Super 900M and Bioseed 9681 was found resistant to S. inferens, whereas, NK 6240, NK 30 and Arjun were highly susceptible in terms of leaf damage score and per cent infestation ^[71]. Nagarjuna, et al. (2015)^[72] conducted research on screening of nine hybrids of maize for resistance to S. inferens in which hybrid CP-828 and NAH 2049 showed minimum damage while Allrounder and Bioseed-9544 showed maximum damage. Screening of ten maize genotypes based on the deadhearts and leaf injury rating, with artificial infestation of S. inferens under field conditions, it was found that maize genotype Madhuri is highly resistant, BML 7 and HKI 163 moderately resistant, and the remaining genotypes viz., HQPM 1, MP 717, BML 6, BH 40625 and BH 1576 are highly susceptible ^[73]. In another research on screening of 22 hybrids of maize against S. inferens, based on number of pin hole, leaf injury rating, dead-heart and grain yield, Hishell was found most tolerant, while IAHM-2013-09 and IAHM-2013-26 tolerant ^[26] while the genotypes BU1, BU2, BU3 and BU5 were found to be relatively resistant to borers attack in

another study ^[74]. The maize genotypes CPM 1, CPM 2, CPM 4, CPM 8, CPM 15 and CPM 18 were found resistant to C. partellus ^[5] and have antibiosis mechanism of resistance against this pest ^[42]. Among the 56 inbred lines screened, eight lines, viz., BGS-86, CM111, CML141, CML33#-4, DML-1432, EC619101, HEY Pool-2011-30-4-1-2-2-1 and HEY Pool-2011-41-2- 1-1-1-1 were found resistant to S. inferens^[75]. This difference in resistance may be due to their morphological, biochemical characters and genetic variations. The S. nonagrioides attack significantly increased the DIMBOA content in leaf tissues of maize inbred lines, A-619 and W-117 as compared with healthy seedlings which shows resistance to this pest [76]. The three mechanisms of defense to the pink stem borer (S. nonagrioides) attack (antixenosis, antibiosis, and tolerance) were found among inbred lines and hybrids of maize and multi-trait selection scheme using damage traits and yield could improve the defense level against this pest ^[77].

Conclusion

Several management strategies including crop rotation, field sanitation, biological control agents and synthetic pesticides have been recommended for S. inferens but none of these have been found effective for successfully control of this pest particularly when the larvae enter inside the stalks. Under such situations, HPR could be one of the most effective mean of minimizing losses due to this pest. For a good HPR program, it is necessary to establish an efficient and reliable screening technique of the genotypes that ensures the desired level of insect pressure uniformly on all plants, at the most susceptible stage of the crop. Many wild relatives and native cultivars of plants have important genetic variants that have yet to be utilized for agricultural enhancement. There are so many genotypes of maize reported to be resistant to this pest by different worker by following different screening techniques. This synthesized information is useful for future breeding programs aiming at resistance to S. inferens infestation for effective and sustainable management. Further, substantial yield losses and insecticidal applications can be minimized resulting in an eco-friendly environmental footprint.

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