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Mechanisms of Stem Borer Resistance in Sorghum

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S.L. Taneja[1] and S. Woodhead[2]

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Abstract

*A number of sorghum genotypes resistant to the spotted stem borer (*Chilo partellus *Swinhoe) have been identified using natural and artificial infestations at ICRISAT Resistance is attributed to ovipositional nonpreference and antibiosis mechanisms The major plant characters identified include early panicle initiation and rapid internode elongation In resistant genotypes, these factors were reflected in the success of first instar larval establishment in the leaf whorl, interval between hatching and larvae boring in the stem, larval mass, and survival rate Success of the first instar larvae to establish in the whorl is also influenced by physical and chemical plant characteristics A chemical factor in the surface wax of some sorghum genotypes is associated with larval disorientation*

Résumé

***Mécanismes de la résistance aux foreurs des tiges chez le sorgho :** Un certain nombre de génotypes du sorgho ayant une résistance au borer ponctué du sorgho (*Chilo partellus*) ont été identifiés à l'ICRISAT grâce à des infestations naturelles et artificielles Cette résistance est attribuée à une non préférence des femelles pour la ponte et à des mécanismes d'antibiose Les principaux caractères impliqués sont l'initiation précoce des panicules et une élongation rapide des entre-noeuds Chez les génotypes résistants ces facteurs ont influencé l'installation des larves de premier stade dans le cornet foliaire, l'intervalle de temps entre l'éclosion des oeufs et le moment où les larves pénètrent la tige, la quantité de larves mineuses et leur taux de survie L'installation des larves de premier stade dans le cornet foliaire est également influencée par des caractéristiques physiques et chimiques de la plante Un constituant chimique de la cire de surface de certains génotypes est responsable pour la désorientation des larves*

Introduction

Development of sorghum cultivars resistant to the spotted stem borer, *Chilo partellus* Swinhoe is one [of t]he major research activities at ICRISAT A [num]ber of sorghum genotypes resistant to *C partellus* have been identified (Taneja and Leuschner 1985) Knowledge of these mechanisms of resistance is essential to fully understand and utilize resistant genotypes in the management of this pest

All three types of resistance mechanisms (nonpreference, antibiosis, and tolerance) defined by Painter (1951) have been observed in sorghum genotypes resistant to *C partellus* (Jotwani et al 1971, 1978, Jotwani 1978, Lal and Pant 1980, and Dabrowski and Kidiavai 1983) Experiments have been

1 Entomologist, Sorghum Group, Cereals Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Patancheru, Andhra Pradesh 502 324 India

2 Section Head, Insect Crop Relations, Pest and Vector Management Department Tropical Development and Research Institute (TDRI) College House Wrights Lane, London W8 5SJ UK

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conducted at ICRISAT Center under artificial infestation and at Hisar under natural infestation to differentiate resistance mechanisms and associated factors in a set of 20 genotypes, which have shown various levels of resistance/susceptibility to *C. partellus*. Experimental methods have been previously reported (Taneja and Leuschner 1985).

Ovipositional Nonpreference

This trial was conducted at Hisar during the rainy seasons of 1986 and 1987 under natural infestations. Egg laying observations were made at 3,4, and 5 weeks after crop emergence.

Total numbers of egg masses were significantly higher on the susceptible genotypes (ICSV 1 and CSH 1) than most of the resistant ones (Table 1). The lowest number of eggs (2-3 egg masses per 50 plants) were recorded on genotypes IS nos. 2309, 5538, 18551, 18573, 18580 in 1986, and on IS nos. 7224 and 8811 (14-26 egg masses per 50 plants) in 1987. Ovipositional nonpreference, as a mechanism of *C. partellus* resistance in sorghum has also been reported on some resistant genotypes by Lal and Pant (1980), and Dabrowski and Kidiavai (1983).

Table 1. Oviposition of spotted stem borer *Chilo partellus* on 20 sorghum genotypes under natural infestation, Hisar, rainy seasons 1986 and 1987.

1986		1987	
Genotype	Egg mass on 50 plants	Genotype	Egg mass on 50 plants
IS 1044	7	IS 2205	32
IS 2123	10	IS 2376	53
IS 2205	9	IS 4546	46
IS 2269	6	IS 5075	46
IS 2309	3	IS 5469	79
IS 4776	9	IS 5470	42
IS 5469	10	IS 5480	44
IS 5538	2	IS 5566	33
IS 5585	4	IS 5571	44
IS 12308	17	IS 7224	26
IS 13100	10	IS 8811	14
IS 13674	5	IS 17742	38
IS 18333	13	IS 17745	62
IS 18551	3	IS 17948	55
IS 18573	3	IS 18578	55
IS 18577	7	IS 18584	35
IS 18579	6	IS 18585	52
IS 18580	2	IS 18677	33
ICSV 1	25	ICSV 1	104
CSH 1	41	CSH 1	110
SE	±4.4		±14.4
CV (%)	33		25

Establishment of Young Larvae in the Whorl

The success of newly hatched larvae of *C. partellus* in attaining the feeding site (plant whorl) varies with cultivar, and some resistant genotypes show a marked reduction in the proportion of larvae that establish on the plant. Various factors appear to be responsible for this tendency, including environmental effects (Bernays et al. 1983), and the physical and chemical characteristics of the plant (Woodhead and Taneja 1987).

Detailed observations in the field at ICRISAT Center showed that the climb to the whorl after hatchig was hazardous and, particularly on resistant genotypes, many larvae never reached their feeding site. Hatching normally occurs shortly afte when conditions are most favorable for success; there is usually little wind, and the temperature is low. In order to survive, larvae must reach the whorl expediently, avoiding desiccation as the temperature rises, or being blown off the plant as wind speed increases during the day. Also, the longer the time larvae spend crawling up the plant, the more susceptible they are to possible predators. Several physical characteristics of the resistant genotypes have been shown to affect the success of the larvae to reach the whorl, including a disorienting effect that has been attributed to the chemical composition of the surface wax of some cultivars (Woodhead 1987).

Physical Characteristics

Orientation of Leaf to Stem

Upward movement of *Chilo* larvae has been sho to result from positive phototaxis (Bernays et . 1983, 1985). As the larvae climb the culm they avoid the shadow cast by the leaves, thus follow a spiralling path around the culm. Susceptible genoypes have floppy leaves making an angle greater than 45° between the leaf and the culm, whereas resistant sorghum cultivars have very erect leaves which cast little shadow. On these genotypes, larvae continue upwards onto the leaves, rather than avoiding them. Once on the leaves they eventually crawl to the edge, and, on resistant genotypes the orientation of the edge trichomes is such that the larvae tend to move towards the leaf tip and from there disperse. Even on susceptible genotypes, some larvae will wander onto the leaves, fewer disperse after becoming reoriented at the leaf edge. Thus erectness of leaves and orientation of the leaf trichomes are physical factors that affect resistance to establishment. Cultivars with narrow, erect leaves have long been recognised by sorghum breeders as also resistant to shootfly (*Atherigona soccata*) (Blum 1972). This characteristic is usually associated with glossiness, and is only expressed clearly in young plants about 15-20 days after emergence (DAE). In trials at ICRISAT Center and Hisar in 1982-84, when 20 genotypes were screened for resistance under artificial and natural infestations, and assessed for physical and chemical resistance characteristics, the only physical character common to all resistant genotypes was this trait of erect, narrow leaves (Woodhead and Taneja 1987).

Detachment of Leaf Sheath from Culm

Adults of *C. partellus* frequently lay their eggs on the underside of basal leaves of young sorghum plants from where the newly hatched larvae make their way to the culm. These lower leaves can become detached from the culm, a characteristic more noticeable in some genotypes than in others. Where detachment occurs, larvae have been observed to go behind the sheath, settle, and attempt to feed there. Although this is the favored feeding site for young larvae of *Sesamia* sp, most of which tunnel into the stem shortly after hatching, there is no evidence that young *Chilo* larvae can feed successfully on the tough culm, and insects that attempt to feed here rarely survive (Woodhead and Padgham,). Thus the tendency for detachment of the sheath from the culm can be an effective resistance mechanism to *Chilo* establishment.

Leaf Bases and Ligular Hairs

Detailed observations also showed that on approaching the base of a leaf, particularly on an erect-leafed genotype, there was a tendency for larvae to investigate the basal area of the leaves. On some genotypes the edges of the leaf base are tightly curled such that a small 'pocket' is formed that larvae can enter. Some larvae were observed to remain in these pockets for several hours. It has been postulated that host odor, humidity, and leaf color associated with this pocket are similar to those of the plant whorl, explaining the tendency of larvae to remain there. Larvae are also attracted to the leaf axil and frequently remain there for some time. Some genotypes have pronounced ligular hairs and it appears that larvae may become trapped in these hairs.

These types of mechanisms of resistance appear to be effective because they delay the larvae in an atmosphere of host odor and dark, simulating conditions in the whorl. Bernays et al. (1985) reported that the positive phototactic response, essential to maintain the directional climb to the feeding site, is labile and rapidly lost on entry to the whorl. It is a similar effect to that reported for the silkworm *Bombyx mori* on mulberry, in which loss of phototactic response serves to keep the larvae on their host (Shimizu and Kato 1978). Sorghum genotypes on which this type of behavior is observed have lower rates of climbing success and lower final establishment rates, although climbing success has less impact in terms of crop loss to stem borer than leaf orientation.

Internode Length

Plant height affects larval success rates in that the further they climb, the more liklihood of desiccation or attack by predators, and the greater the exposure to unfavorable environmental conditions. This characteristic only operates as a resistance mechanism in plants where the internodal distances are large, and is particularly noticeable in native sorghums that are often tall and thin-stemmed in contrast to the short, high-yielding hybrids.

Surface Wax Effects

Sorghum plants develop a white bloom of epicuticular wax (Freeman 1970), which is variable in extent, and genotype dependent (Ayyangar and Ponnaiya 1941). It is clearly visible to the naked eye in some genotypes (e.g., CSH 1 and IS 1151) and in mature plants it forms a thick layer on the culm. It has been shown that when this wax layer is conspicuous, it affects climbing by *Chilo* larvae (Bernays et al. 1983). Larvae accumulate wax around their prolegs as they move over the plant surface which impedes their progress. Larvae have been found to climb almost twice as fast on stems of IS 1151 from which the wax had been removed, compared with stems prior to removal of wax. Thus surface wax can have a gross effect on larval success rates, although under wet conditions the superficial wax is often washed off plants in the field. In general, larvae climb more slowly and have a lower success rate on wet plants, an added factor which complicates interpretation of the importance of a thick wax layer in resistance.

In addition to the gross effects of thick surface waxes on larval movement, it has been shown that on some resistant genotypes there is a disorienting effect which has been attributed to the chemical composition of the epicuticular wax (Woodhead 1987). It was first observed on young plants of IS 2205 during field studies at ICRISAT Center. After egg hatch, larval progress towards the whorl was monitored. Although the primary stimulus was positive phototaxis on all genotypes studied, on IS 2205 a behavior pattern was observed which was characterized by hesitation, circling, and stopping completely for periods of up to several minutes. All these activities were accompanied by raising and side-to-side motion of the head and upper abdomen in a searching movement. Apparently, insects were not biting as they crawled over the plant surface, but were receiving cues from it which reinforced their upward movement on susceptible genotypes, and disoriented them on resistant ones. Examination of the surface of resistant and susceptible genotypes by scanning electron microscopy revealed differences in epicuticular wax morphology, which were known to indicate differences in chemical composition (Baker 1982). Detailed analysis of surface wax extracts showed a similar composition for all genotypes with the exception of a consistent concentration difference in a compound that co-eluted with the 32 carbon n-alkane. This compound was present in very low amounts in the wax of IS 2205, whereas in IS 1151 and CSH 1 waxes, the concentration was more than double. It appears that larvae of *Chilo* identify their host plant by chemical cues received as they crawl over the plant surface. If any of the cues is missing, or not sufficiently strong, the insect is disoriented, the upward climb is interrupted, and fewer larvae are successful in reaching the whorl and establishing on the plant.

Plant Growth Characteristics

Plant growth was monitored through destructive samplings at 2-day intervals up to panicle initiation stage, and at weekly intervals thereafter, recording plant height, number of leaves, panicle initiation, number of internodes, shoot length, and panicle length. The most significant parameters in resistant genotypes were found to be the time taken for panicle initiation, and shoot length (Table 2). Although it took more time for panicle initiation during the rainy season, similar trends were observed in most of the genotypes. Genotypes with early panicle initiation escape deadheart formation due to inability of larvae to reach the growing point which would already have pushed up above larval entry point. Thus although larvae may feed in the stem and cause tunneling, this activity alone may not cause deadhearts, the critical damage which is associated with grain yield loss. Genotype IS 12308 had very early

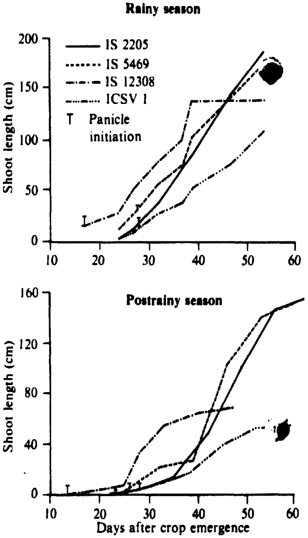

Figure 1. Shoot length and panicle initiation of four sorghum genotypes in relation to age of the crop, ICRISAT Center, rainy and postrainy seasons 1984/85.

panicle initiation (12 days in postrainy and 17 days in rainy seasons). Although, the final shoot length in this genotype has been similar to the susceptible genotype ICSV 1 (Fig.1), it is still resistant to deadheart formation because of the shorter time taken to panicle initiation.

Shoot length, i.e., faster internode elongation, has been observed as a significant growth characteristic in stem borer resistance. This characteristic also pushes the growing point upward, hampering the ability of larvae to reach it, and thus preventing deadheart formation. In the present study, a number of resistant genotypes with similar panicle initiation time escaped deadheart formation due to faster internode elongation. For example, two resistant genotypes, IS 2205 and IS 5469, having panicle initiation similar to susceptible ICSV 1, had greater shoot length during its growth period in both seasons (Fig.1).

Insect Biological Parameters

In a study on the effect of sorghum genotypes on insect biology, using blackhead stage eggs to infest plants 15-20 DAE, it was found that among the parameters measured, the most significant ones were first-instar larval establishment, time interval between larval hatching and boring into the stem, larval mass, and survival rate. A lesser proportion of larvae became established in the whorl in some of the resistant genotypes (Table 2), for example, in genotypes IS 12308 (25%), IS 13100 (39%), IS 2269 (40%), compared with ICSV 1 (51%) and IS 18573 (77%). Chapman et al. (1983) and Bernays et al. (1983) observed marked differences in the establishment of first-instar larvae among resistant and susceptible cultivars.

In some resistant genotypes, it took more time for the larvae to arrive at the base of the stem for boring.

Table 2. Factors associated with stem borer resistance in sorghum, ICRISAT Center.

Genotype	Borer dead-hearts	Days for panicle initiation	Shoot length (cm) 28 DAE[1]	Larvae recovered in whorl (%) DAI[2]	Larvae recovered in stem 10 DAI	Larval mass (mg larva^{-1}) 21 DAI	Total insects recovered (%) 28 DAI
IS 1044	44	53	15	54	9	92	28
IS 2123	27	33	21	54	7	93	15
IS 2205	51	39	13	57	16	103	9
IS 2269	-	33	11	40	17	127	22
IS 2309	40	30	14	53	35	85	8
IS 4776	41	40	9	44	10	109	20
IS 5469	22	33	26	57	11	98	25
IS 5538	-	56	6	56	12	99	22
IS 5585	51	33	19	41	9		15
IS 12308	43	17	50	25	31	89	21
IS 13100	45	25	46	39	7	88	18
IS 13674	55	28	24	64	24	101	26
IS 18333	65	53	10	58	21	85	10
IS 18551	48	38	12	62	10	109	23
IS [illegible]	49	56	6	77	10	140	20
IS [illegible]	58	51	8	41	21	84	21
IS 18579	49	40	8	42	13	92	15
IS 18580	55	40	11	57	12	99	19
ICSV 1	76	33	10	51	17	115	20
CSH 1	63	28	9	42	13	94	24
Mean				51	15	99	19
SE				±6.5	±4.3	±6.5	±4.5
CV(%)				18	45	9	33

1. DAE = days after crop emergence.
2. DAI = days after infestation.

This may be due to nutritional content of particular genotypes which may prolong the larval period. In genotypes IS 1044, IS 2123, IS 5585, and IS 13100, less than 10% of the larvae were observed at the base of the plant 10 days after the infestation, compared with 21% on IS 18333 and 35% on IS 2309 (Table 2). Prolongation of larval period on resistant genotypes was also reported by Jotwani et al. (1978).

Larval mass was significantly lower (<90 mg $larva^{-1}$) in six genotypes (IS 2309, IS 5585, IS 12308, IS 13100, IS 18333, and IS 18577) compared with IS 18573 (140 mg $larva^{-1}$), and ICSV 1 (115 mg $larva^{-1}$).

Survival rate, measured by the total insect recovery, was significantly lower in IS 2205, IS 2309, and IS 18333 (8-10%) compared with 28% in IS 1044 and 24% in CSH 1. Low survival rate of *C. partellus* on resistant genotypes of sorghum have also been observed by Lal and Sukhani (1979).

Parameters studied indicate antibiosis mechanisms involved in borer resistance, which have also been observed by many workers (Jotwani et al. 1971, 1978, Lal and Sukhani 1979, and Dabrowski and Kidwai 1983). The present study also indicates that different combinations of factors are involved in confirming stem borer resistance in various genotypes. This information is vital for borer resistance breeding programs.

Tolerance

Jotwani (1978) reported significantly lower yield loss to stem borers in breeding selections such as 124, 175, 177, 446, 447, 731, 780, 827, and 829, than in CSH 1, and attributed this to tolerance mechanism. In spite of severe leaf injury and stem tunneling in these selections, the final plant stand was very good and most of the plants had normal panicles. Similar results were obtained in genotype IS 2205 by Dabrowski and Kidiavai (1983).

Conclusion

Ovipositional nonpreference, antibiosis, and tolerance type of mechanisms exist for stem borer resistance in sorghum. The major plant characteristics associated with resistance are early panicle initiation, and faster internode elongation. Reduced larval establishment in the leaf whorl, longer time interval between larval hatching and boring into the stem, lower larval mass and survival rate have been observed in resistant genotypes. Several physical (leaf orientation, leaf sheath detachment, leaf bl and ligular hairs, and internode length), and chemical characteristics of the resistant genotypes have been shown to affect the success of the larvae to reach the whorl, including a disorienting effect. Different combinations of factors are involved in conferring resistance in a particular sorghum genotype. This infomation is vital for borer resistance breeding programs, where resistant sources with diverse mechanisms may effectively be used either in a pedigree or population breeding approach.

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