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The role of leaf surface wetness in larval behaviour of the sorghum shoot fly, *Atherigona soccata*

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Abstract

The susceptibility of sorghum to the shoot fly *Atherigona soccata* Rondani, (Diptera Muscidae) is affected by seedling age and is highest when seedlings are 8–12 days old This corresponds with high moisture accumulation on the central leaf which is the path of newly hatched larva as it moves downwards from the oviposition site, towards the growing apex Studies showed that leaf surface wetness (LSW) of the central shoot leaf was higher in 10-day old seedlings than in seedlings of other ages Similarly, LSW was much higher in the susceptible sorghum genotype CSH 1 than in the resistant genotype IS 2146 Larvae moved faster towards the growing point and produced deadhearts much earlier in CSH 1 than in IS 2146 They also moved faster in 10-day old seedlings than in seedlings of other ages It was also shown that the leaf surface wetness of the central shoot leaf is a more reliable parameter of resistance than the glossy leaf trait or trichome density

Introduction

Several species of the genus *Atherigona* (Diptera Muscidae) (primarily *A succata* Rondani) are serious insect pests of sorghum in Africa and India (Young & Teetes, 1977) Traditional methods of control are early planting and seed-furrow treatment with granular insecticides, the latter being practised more in India than in Africa The existence of resistance in sorghum to the shoot fly was first reported by Ponnaiya (1951) Several sorghum lines with resistance to the shoot fly have since been reported (Rao & Rao, 1956, Blum, 1967, Singh *et al*, 1968, Young, 1972, Jotwani, 1978, ICRISAT, 1978) although the levels of resistance are not sufficient to prevent considerable loss in crop stand when infestation levels are high

Resistance to sorghum shoot fly has been attributed to non-preference for oviposition (Blum, 1967) which may be due to the presence of trichomes on the leaf surface (ICRISAT, 1978) and an associated glossy trait (Maiti & Bidinger, 1979) Similarly, the presence of lignin and silica deposits may contribute towards the mechanical resistance of seedlings to penetration by the larvae (Blum, 1968) Raina (1985) has also postulated that biochemical deficiencies or the presence of chemical factors in resistant cultivars may adversely affect the development and survival of larvae

The white, elongate eggs are laid singly on the undersurface of leaves. On hatching, larvae initially move along the leaf lamina, then downwards along the central shoot towards the growing point. Studies have shown that the time of hatching coincides with the presence of moisture on the leaf (Raina, 1981) and that shoot fly abundance is affected by temperature and relative humidity (Taneja *et al.*, 1986).

In preliminary observations, we found that newly hatched shoot fly larvae survived for less than 30 min in dry petri dishes or filter paper but lived for over 24 h on slightly wet surfaces (ICRISAT, 1988). On further examination, it was found that, as distinct from other leaves, the central shoot leaves of seedlings retained some surface moisture which in some cases appeared as water droplets on the leaf surface. This moisture is different from dew accumulation on expanded leaves or rain water within the whorl, which can easily be dislodged by gentle tapping. This finding led to studies on the relationship between wetness of the central shoot leaf and larval movement towards the growing point. Moisture accumulation in the whorl leaves is attributed to condensation of moisture in the surroundings of the leaves and its deposition on the leaf surface, and to actual development of positive water potential in the leaf tissue resulting in water being exuded from the leaf (Slavik, 1974).

Shoot fly larva behaviour was monitored from egg hatch until its arrival at the growing point. Leaf surface wetness and trichome density were measured and the speed of larval movement and deadheart formation were monitored. We also correlated our results with existing information on the glossy leaf trait and damage to shoot fly resistant sorghums.

Materials and methods

Field experiments were conducted using plants in small plots (1 × 1 m) with a plant spacing of 15 × 10 cm. Potted plants were grown in 10 cm diameter plastic pots. Recommended agronomic practices were carried out where applicable.

Seedling susceptibility. In order to obtain seedlings at a range of crop age from 1–21 days old, three sorghum genotypes, IS 2146 (resistant), IS 1054 (local commercial variety) and CSH 1 (susceptible) were sown in July 1987 in separate plots at daily intervals for 21 days. Plants were thinned to one plant per hill on the fourth day after emergence (DAE) except for the 1–4 day old seedlings which had to be thinned earlier. To avoid contamination from natural infestation, seedings were examined daily and shoot fly eggs were removed. At 21 DAE, the plants were covered with a 3.5 × 2 × 1 m fine wire-mesh cage and gravid female flies from field-collections were introduced overnight at a density of one fly per four plants. Egg numbers were recorded on the next day and deadhearts five days after infestation. This experiment was repeated in August and September and data obtained were combined.

Leaf surface wetness (LSW). Leaf surface wetness was assessed for different cultivars and at different ages of sorghum seedlings. Using the same genotypes, 210 seedlings per genotype were grown in pots outside the glasshouse at a rate of five seedlings per pot. At emergence, the seedlings were split into groups to obtain a range of crop ages of 1–21 days. For each genotype one group of seedlings of the same age was examined every day, between 06.30 and 08.30 h, for the degree of leaf surface wetness (LSW). This was done by first excising the un-expanded central shoot leaf and then examining it when spread out under a binocular microscope. LSW was assessed using a visual score scale of 1–5, where 1 = no apparent moisture to a very thin film of moisture on the leaf lamina and 5 = leaf lamina densely covered with water droplets.

Egg hatch and larval movement. Ten-day old potted seedlings of CSH 1 and IS 2146 were exposed overnight to oviposition by field-collected gravid female flies. After oviposition, a batch of five plants of each genotype that were infested with only one egg per plant were selected for observation. Starting from 36 h after infestation (usually at 20.00 h), the eggs were closely monitored, using a magnifying hand lens until they hatched Thereafter, the movement of individual larvae along the leaf lamina were monitored until their arrival at the leaf funnel This procedure was repeated six times for a total of 30 larvae for each sorghum genotype

Another experiment was conducted to measure the speed of larval movement from the leaf funnel to the growing point Three age groups 5, 10, and 14-day old seedlings of CSH 1 and IS 2146 were raised in pots at the rate of five plants per pot in sufficient numbers They were exposed to shoot fly oviposition as described earlier However, in order to ensure uniformity in hatching, seedlings were exposed to oviposition for only one hour between 05 00 and 06 00 h To measure the speed of larval movement from the leaf funnel down to the growing apex, the larval position within the stem was determined by destructive sampling To achieve this, beginning 30 min after egg hatch, the stems (i e from the base of the leaf funnel to the root crown) of ten randomly selected seedlings of each cultivar were cut into lengths of 0 5 cm and each individual piece was then placed in a marked groove of a plastic strip containing 40% alcohol Sampling was repeated at intervals of 30 min for a period of 8–10 h The stem pieces were later examined for the presence of shoot fly larvae This procedure was repeated for each age group

Evaluation of resistant sources Forty two sorghum germplasm lines have been listed as less susceptible to shoot fly at ICRISAT Center (Taneja & Leuschner, 1985) These lines were re-evaluated for their resistance and observations of LSW, egg laying and deadhearts were recorded Genotypes IS 1054 and CSH 1 were included in this trial as checks

All data were subjected to an analysis of variance A correlation analysis was also run to compare the relative importance of LSW, trichome density and the glossy leaf trait in shoot fly damage Data on trichome density and glossy leaf trait were obtained from existing data files

Results

Seedling susceptibility Generally, in all three genotypes, 8–12 day-old seedlings were preferred for oviposition and suffered more shoot fly damage than young (1–5 days old) and old (14–21 days old) seedlings (Fig 1b and c) However, there were distinct differences between genotypes in the number of eggs laid, with genotype CSH 1 receiving the highest number of eggs per plant Genotype IS 2146 was least preferred for oviposition and exhibited the lowest variation in ovipositional preference in relation to seedling age (Fig 1b)

Shoot fly damage to seedlings, observed as deadhearts, also occurred at all seedling ages although it was very low (<20%) during oviposition on 1–3 day-old seedlings of IS 1054 and IS 2146 (Fig 1c) As in the case of egg laying, 8–12 day-old plants were most susceptible At

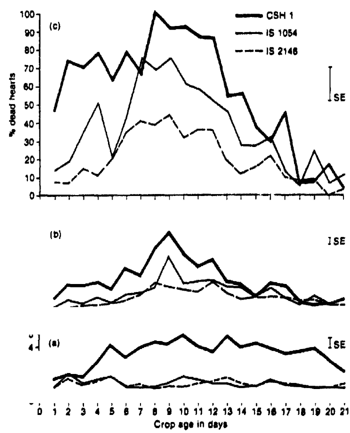

Fig 1 (a) Leaf surface wetness (LSW), (b) shoot fly oviposition and (c) damage (% deadhearts) on sorghum seedlings in relation to genotype (susceptible CSH 1, moderately resistant IS 1054 and resistant IS 2146) and crop age (Standard error (SE) bars for all cultivars combined)

this age, CSH 1 suffered between 85–100% damage and IS 2146 between 35–45%.

Leaf surface wetness (LSW). There were distinct differences in LSW between the susceptible genotype CSH 1 and resistant IS 2146 (Fig. 2). On CSH 1, LSW had a score of <2 in 1–4 day old seedlings but was highest (4.8) in 10-day old seedlings (Fig. 1a). At this age, the central shoot leaf was densely covered with water droplets (Fig. 2d). It again dropped to <3 in 21-day old seedlings. On IS 2146, LSW was very low (<2) at all stages of seedling growth and there was no visible moisture on the leaf (Fig. 2a).

Egg hatch and larval movement. Hatching usually occurred in the early hours of the morning, 36–48 h after oviposition. On CSH 1, this was

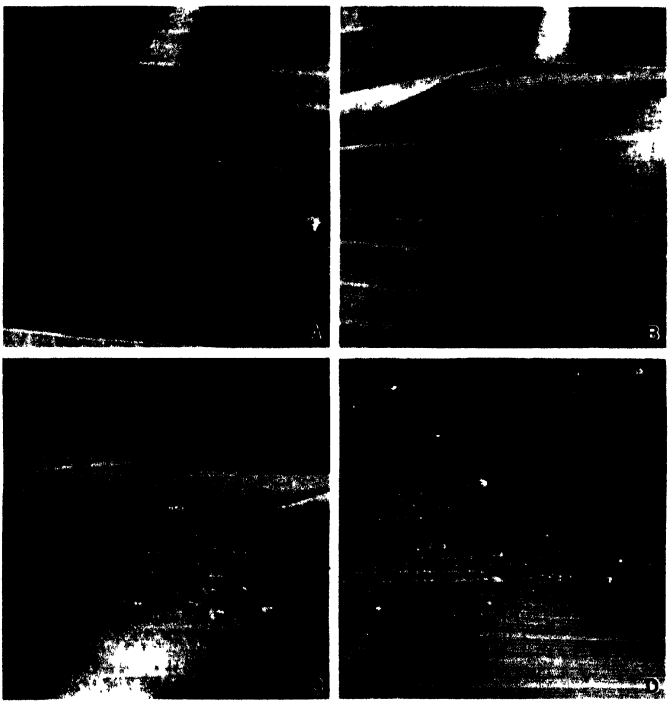

Fig. 2. Leaf surface wetness (LSW) of central shoot leaves of 10 day-old seedlings (A) IS 2146, glossy resistant (B) IS 1057, non-glossy resistant (C) IS 1046, glossy susceptible and (D) CSH 1, non-glossy susceptible.

between 22.00–03.00 h and on IS 2146, between 01.00–06.00 h. After hatching, larvae rarely moved along the abaxial surface of the leaf. Usually, within a minute or two on this surface, they moved onto the adaxial side and then continued towards the leaf axil. In all the cases observed, the larva then migrated upwards from the axil, and along the stem in a spiral fashion until it arrived at the funnel (Fig. 3). In contrast to Raina (1981) we did not observe that the larvae, after reaching the axil, immediately moved downwards between the leaf sheath and the central shoot. Irrespective of the leaf on which the egg was laid, there was an initial upward movement to the funnel from where it continued downwards along the central shoot. The time spent from egg hatching until arrival of the larvae at the funnel varied considerably between genotype CSH 1 and IS 2146. On CSH 1, it took only 11 min (range 5–20 min)

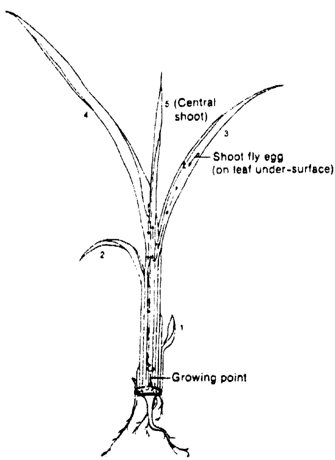

Fig. 3. Path of shoot fly larva from point of hatch to base of central shoot of a 10-day old seedling. 1–5 indicate respectively, first, second, third, fourth and fifth (unexpanded, central shoot) leaves.

while it took almost twice as long (20.2 min, range 8–30 min) on IS 2146.

Larvae continued to move downwards until 0.5–1.0 cm above the root crown at which point a cut was made around the central shoot. This eventually led to dessication of the central shoot, which is referred to as 'deadheart'. The speed of larval movement from the funnel to the growing apex also varied considerably between the genotypes and with crop age (Fig. 4). Larvae moved faster towards the growing point on susceptible CSH 1 than on resistant IS 2146, at all crop ages (5, 10, and 14 days). Larvae also moved relatively fast on 10-day old seedlings (Fig. 4b) but slow on 14-day old seedlings. On 5-day old seedlings of both CSH 1 and IS 2146 they arrived much earlier at the growing point (< 3 h) than on 10- or 14-day old seedlings due to shorter stem length.

Evaluation of resistant sources. LSW appeared generally low (< 2) in resistant genotypes but high (> 4) in susceptible genotypes (Table 1). The difference in LSW between resistant (eg. IS 18551) and moderately resistant (eg. IS 1054) genotypes was usually not perceptible which was reflected in seedling damage. The majority of shoot fly resistant genotypes expressed <45% deadhearts comparted to the susceptible checks IS 1046 and CSH 1 with respectively 76.5% and 95.7% deadhearts.

LSW was not directly found to be associated with the glossy leaf trait but rather with the degree of resistance. LSW can be low in both glossy and non-glossy resistant genotypes (Fig. 2) (eg. IS 2146, IS 18551 and IS 5511, Table 1) but high in glossy and non-glossy susceptible lines (eg. IS 1046 and IS 4224). But the majority of non-glossy genotypes were susceptible to shoot fly and showed a high LSW, except IS 1057, IS 5511, IS 1034 and IS 5072 (the latter two genotypes not shown in Table 1) which were resistant and had a low LSW. Trichome density was higher on the upper than on the lower leaf surface (Table 1) but this character did not show any direct relationship with shoot fly damage.

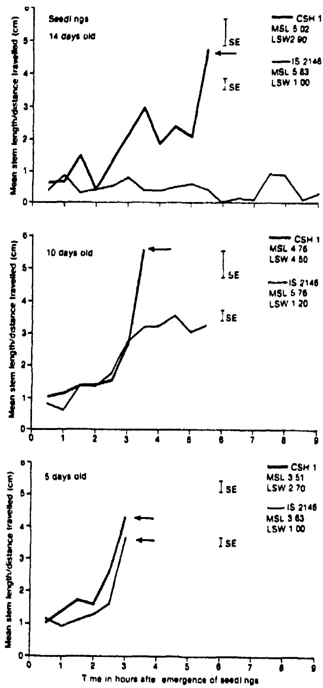

Fig 4 Shoot fly larval movement in sorghum seedling stem in relation to cultivar and crop age Arrows indicate larval arrival at growing apex MSL = mean stem length (cm), LSW = leaf surface wetness score, SE = standard error

Discussion

The susceptibility of sorghum to shoot fly damage is associated with seedling age and is highest when seedlings are 8–12 days old This period corresponds with the highest moisture accumulation on the central shoot leaf

Although larvae moved faster and caused more damage on 10-day old seedlings of the susceptible genotype CSH 1, deadheart symptoms appeared faster in 5-day old seedlings due to shorter stem length (Fig 4) Similarly, while larvae took the same time to reach the growing point and produce deadhearts in 5-day old seedlings of both CSH 1 and IS 2146, the time difference in older plants was quite significant In 14-day old seedlings of resistant IS 2146, larvae apparently were not able to reach the growing point by the end of our observation period of 9 h

There are no obvious explanations for the differences in hatching time on the various cultivars But it may be postulated that newly emerged larvae stand a better chance of survival on CSH 1, due to more favourable night time conditions, than later emerging larvae on IS 2146 Similarly, they are less exposed to desiccation and predation before reaching the protection of the funnel These factors enhance larval success, thereby contributing to the susceptibility of CSH 1

The importance of dew or moisture on the leaves for shoot fly resistance was reported by Blum (1963) and Raina (1981) The studies reported here indicate that, since larvae spend less than 30 min from egg hatch to arrival at the funnel and > 3 h from the funnel to the growing point, larval survival is affected more by the wetness of the central shoot than of the expanded leaves on which eggs are laid Admittedly, initial contact with moisture enhances larval movement and survival However, differences obtained in time spent on the expanded leaf between the genotypes CSH 1 and IS 2146 require further investigation

While Maiti & Bidinger (1980) submit that the glossy leaf character can be used as a measure of shoot fly resistance, they admit that some genotypes still fell into the more susceptible groups (e g IS 1046, Table 1) A waxy surface will permit an even spread of water on a surface but may not retain water in large droplets as a non-waxy surface does However, it is not just the amount of wax on a leaf surface that determines water retention but the physical arrangements of the wax platelets which determine the contact angle of water Hence a highly waxy leaf may in fact retain

Table 1 Summary of relationships between leaf characteristics of various sorghum genotypes and damage by the sorghum shoot fly *Atherigona soccata*

Genotype	Glossy trait[1]	Trichome density/mm		LSW[3]	No eggs/ 10 seedlings	% deadhearts
		US	LS[2]			
S 2146	G	142	54	1 2	7	38 6
S 18551	G	110	20	1 4	5	41 7
S 1046	G	0	0	4 4	12	76 5
S 1054	NG	77	0	2 3	6	41 0
S 1057	NG	112	10	1 8	5	34 4
S 5511	NG	49	37	1 0	6	40 7
S 4224	NG	66	4	4 3	14	66 4
CSH 1	NG	0	0	4 8	16	95 7
Mean (44 entries)		69	17	2 6	8	54 7
SE ±		18	13	0 5	0 2	28 3

G = glossy NG = non-glossy
US = upper surface LS = lower surface
LSW = leaf surface wetness

more water as droplets than a non-waxy leaf and vice-versa This may explain the results of Maiti and Bidinger and those reported in this studsy

Trichomes on the lower leaf surface may have more effect on the behaviour of adult flies during oviposition (since eggs are laid on the lower leaf surface) than on larval movement However, the trichomes on the upper surface may interfere with larval movement and survival since larvae immediately after hatching move onto the upper surface and then towards the leaf axil The results of the study reported here show however that shoot fly larvae spend very little time on the leaf on which the egg is laid compared to time taken to travel from the funnel to the growing point Maiti & Gibson (1983) also concluded that the correlation of deadheart with the density of trichomes was low and not significant Similarly, in the study reported here, correlations of leaf surface characteristics with deadheart were low and not significant for glossy trait and trichome density but highly significant (0 82) for LSW (Table 2) Although Maiti (1980) concluded that the presence of trichomes and the glossy trait have independent and apparently additive effects in reducing the incidence of deadhearts, he reported damage in the range of 61–84% which makes his conclusions questionable This is not the case

Table 2 Correlation matrix for sorghum seedling leaf characteristics and shoot fly damage (df = 43)

GLOSSY	1	1 0000				
TRI-US[a]	2	– 0 2677	1 0000			
TRI-LS[b]	3	– 0 2610	0 5329	1 0000		
LSWSC[c]	4	0 4330	– 0 4257	– 0 2547	1 000	
DH%[d]	5	0 4876	– 0 3891	– 0 1982	0 8209	1 0000
		1	2	3	4	5

Trichome – upper surface
Trichome – lower surface
Leaf surface wetness score
Percent deadhearts

with LSW. All genotypes with an LSW <2 are resistant (<45% deadheart) irrespective of glossiness or trichome density (Table 2). For example, IS 1046, although glossy but without trichomes, has a high LSW (4.4) and a shoot fly damage of 76.5%. On the other hand, IS 1057 which is nonglossy and with trichomes, has a low LSW (1.8) and a shoot fly damage of 34.4%. These results strongly indicate that low leaf surface wetness of the central shoot leaves of sorghum seedlings is an important factor in resistance to shoot fly.

This conclusion has several implications and brings on several questions: What are the factors and processes involved in leaf surface moisture accumulation and retention? What is the role of the stomata, trichomes, surface wax and the glossy trait in relation to LSW? Can leaf surface wetness be manipulated in field sorghum, such as under irrigated cultivation by imposing soil water stress? What moisture stress threshold is required? The answers to these questions will require interdisciplinary studies between entomologists, crop physiologists and microclimatologists. Current research at ICRISAT Center is addressing some of these questions.

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Résumé

L'influence de la humidité de la surface foliaire sur le comportement de la mouche des pousses du sorgho

La sensibilité du sorgho à la mouche des pousses du sorgho, *Atherigona soccata* Rondani, est liée à l'âge de la plantule. Elle est plus forte lorsque la plantule est âgée de 8 à 12 jours et la sensibilité est maximale à 10 jours. A ce stade de croissance on observe une forte accumulation d'humidité sur la feuille centrale de la tige. Les jeunes larves traversent cette zone humide lorsqu'elles descendent vers la zone de croissance à partir des pontes déposées sur la face ventrale des feuilles déroulées.

Des études ont été menées à l'ICRISAT (Inde) sur la relation entre l'humidité de la feuille centrale de la tige des plantules du sorgho et les dégâts provoqués par la mouche des pousses. L'humidité de la surface des feuilles (HSF) a été estimée grâce à une échelle visuelle graduée 1 à 5 où, 1 = pas d'humidité apparente et 5 = surface de la feuille recouverte de gouttes d'eau. La HSF est plus élevée sur des pousses de sorgho âgées de 10 j que sur les pousses appartenant à d'autres classes d'âge. Les valeurs observées sont également plus fortes pour les variétés non résistantes à ce ravageur (CSH 1, 4.8) que pour les variétés résistantes (IS 2146, (2). La vitesse du déplacement larvaire entre le cornet et la zone de la croissance varie en fonction de l'âge de la plante et des cultivars. Les larves migrent plus rapidement vers la zone de croissance et provoquent la mort du coeur du sorgho plus tôt dans la variété CSH 1 que dans IS 2146. Les larves se déplacent plus rapidement dans les pousses âgées de 10 j que dans les pousses appartenant à d'autres classes d'âge.

Des études ont également démontré que la HSF n'est pas directement liée au caractère feuille lisse où à la densité des trichomes. La HSF est faible pour les génotypes résistants présentent où non le caractère feuille lisse. Par contre la HSF est élevée pour les génotypes non résistants présentant le caractère feuille lisse ou non. Aucune relation directe entre la densité des trichomes et les dégâts provoqués par la mouche des pousses n'a pu être mise en évidence. L'analyse des correlations établie pour les caractères de surface des feuilles avec la mort du cœur des sorghos indique que les correlations sont faibles et non-significatives pour le caractère feuille lisse (0.49) et la densité des trichomes (0.39 et 0.2). Par contre les correlations sont fortes et significatives pour la HSF (0.82).

On conclue que la HSF de la feuille centrale de la tige est un facteur important dans le déterminisme de la résistance du sorgho vis à vis de la

mouche des pousses. Les relations entre les processus physiologiques de la plante et les facteurs impliquées dans l'accumulation d'eau sur la surface des feuilles font actuellement l'objet d'études détaillées

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