

The dynamics of leaf surface wetness of sorghum seedlings in relation to resistance to the shoot fly, *Atherigona soccata*

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Abstract

In quantitative measurements of leaf surface wetness (LSW) of the central whorl leaf of sorghum seedlings in August (rainy season) and November (post-rainy season), the highest amount (6.29 mg of water) was recorded in August in the shoot fly *Atherigona soccata* (Diptera: Muscidae), susceptible sorghum genotype CSH 1, while the lowest (0.07 mg) was recorded in November in the resistant genotype IS 18551. Studies on diurnal fluctuation revealed that LSW was lowest at sunset, was highest between 02.00 and 04.00 h (closely corresponding with hatching of shoot fly eggs) and dropped before sunrise. This fluctuation was associated with the evaporation of water from the plant during the night. More LSW accumulation occurred during the main crop season (June–October) than in the post-rainy season (November–April). Annual fluctuation of LSW followed trends similar to the population dynamics of shoot fly and crop infestation and were correlated with rainfall, temperature and relative humidity. Measurements of leaf temperature and the vapour pressure gradient between the leaf and the air indicated that leaf surface water originates from the plant. This was further supported by the different amounts of LSW on susceptible and resistant cultivars with similar microclimatic conditions.

Introduction

The sorghum shoot fly *Atherigona soccata* Rondani (Diptera: Muscidae) attacks sorghum in the first 4–5 weeks after seedling emergence, causing death of the central shoot. This damage is referred to as deadheart of seedlings. Fly populations start increasing in July, a few weeks after the arrival of monsoon rains and peak infestations with severe damage to young sorghum seedlings occur in August (Taneja *et al.*, 1986). A second peak occurs in October/November. Rainfall, hu-

midity and temperatures were found to influence shoot fly populations.

Plant resistance is important in pest management in dryland crops and a high degree of resistance is particularly desirable for shoot fly control (Rana *et al.*, 1985). Resistance to shoot fly has been attributed to non-preference for oviposition and may be due to the presence of trichomes on the leaf surface (ICRISAT, 1978) and/or glossy leaf trait (Maiti & Bidinger, 1979). Other resistance mechanisms which affect larval development have been associated with the pres-

ence of lignin and silica deposits (Blum, 1968). The importance of dew or moisture on the leaves in relation to larval survival has also been reported (Blum, 1963; Raina, 1981). In recent studies, Nwanze *et al.* (1990) associated resistance with the accumulation of moisture on the unexpanded central whorl leaf of sorghum seedlings. The central leaf is the path of newly hatched larva as it moves downwards from the oviposition site towards the growing point. We showed that (a) leaf surface wetness (LSW) was greater in 10-day old seedlings than in seedlings of other ages, that (b) LSW was greater in susceptible genotypes than in resistant ones and that (c) larvae moved faster towards the growing point and produced deadhearts much earlier in susceptible than in resistant genotypes.

The conclusions from our earlier studies (Nwanze *et al.*, 1990) raised several questions which are related to (a) the dynamics of LSW production, (b) leaf surface structure and (c) soil and plant water relations. In this paper we are addressing the first question while the other two questions will be addressed elsewhere. We needed to know how LSW is affected by seasonal weather variations and how this relates to shoot fly population and crop damage. To improve our understanding of how LSW is formed, we related diurnal fluctuations in LSW to the plant microclimate. We report a series of experiments which were conducted in 1989/90 to address these issues. In order to use LSW as a practical tool in resistance screening, we compared quantitative and visual estimates of LSW in different genotypes and also compared these in potted seedlings and seedlings from field plots.

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. Field experiments and potted plants received daily irrigation throughout the year except on rainy days

when field plots were not irrigated for 2–3 days after the rain had ceased.

Quantitative measurement of LSW. LSW was quantified by first weighing a strip (3 × 1 cm) of absorbent filter paper (Whatman no. 4), then excising the unexpanded central shoot leaf, spreading it out, then blotting the moisture from the leaf and re-weighing the filter paper immediately on a Mettler balance (model AE 160). The difference in weight was equal to the amount of water removed from the leaf surface. This study was conducted with five sorghum genotypes, IS 18551 and IS 1057 (shoot fly resistant), IS 1054 (moderately resistant), IS 1046 and CSH 1 (susceptible) using four age groups (5, 10, 14 and 21 day-old seedlings). There were two sets of experiments: (a) to quantify the differences in LSW between cultivars, LSW was measured in a set of 10 seedlings of each genotype in the same age group on the same day. This was repeated for the four age groups. (b) to quantify the differences in LSW between ages within a cultivar, LSW was measured in a set of 10 seedlings of each age group of a particular genotype on the same day. This was repeated for the five genotypes. Measurements were carried out between 04.00 and 06.00 h and the experiments were conducted twice: in August and in November, 1989.

Visual vs. quantitative measurements. Previously (Nwanze *et al.*, 1990) assessed LSW 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. In the majority of the studies reported here we were interested in comparative estimates rather than the absolute values of LSW over time. The quantitative measurement of LSW is tedious and time consuming, especially when several genotypes and seedling age groups are involved. We therefore compared the values obtained using both the visual scoring system (which is less tedious and less time consuming) and the absorbent filter paper technique. Two sets of ten 10-day old seedlings each of CSH 1 and IS 18551 were used. This experiment was conducted twice

in November 1989. Visual estimates were done according to Nwanze *et al.* (1990) and quantitative measurements as described above. Observations were recorded at 2 hourly intervals between 18.00 h on day 1 and 06.00 on day 2.

Potted plant vs. field plot experiments. Many of our studies involved observations at 2 hourly intervals over 24 h periods, so we wanted a convenient location using potted plants as an alternative to field plots. We compared LSW in potted plants grown beside greenhouse facilities with plants from field plots. LSW was assessed using the visual score method in two sets of ten 10-day old seedlings each of CSH 1 and IS 18551. Observations were recorded at 2 hourly intervals between 18.00 h on day 1 and 16.00 h on day 2. This experiment was conducted three times in August and September 1989.

Diurnal fluctuation of LSW. Using potted 10-day old seedlings of CSH 1 and IS 18551 and the visual scoring system, we monitored LSW at 2 hourly intervals over 24 h periods (18.00 h–16.00 h). This study was conducted at fortnightly intervals from October 1989 to September 1990.

During each fortnightly observation, several micro-climatic variables were measured. Plant temperature was measured with copper/constantan thermocouples (wire diameter 0.2 mm) inserted in the central leaf whorl of two seedlings of each cultivar. Net radiation at approximately 25 cm above the plant canopy was measured with a Funk type net radiometer (Swisteco, Type S1). Wind speed was measured at 0.5 m above the plant canopy with a sensitive cup anemometer (Met one, 014A) and air temperature and humidity were measured at the same height with two ventilated psychrometers. The temperature sensors in the psychrometers were copper/constantan thermocouples (wire diameter 0.5 mm). Signals from all the instruments were recorded with a data logger (Campbell CX21) programmed to give mean values every 15 min. The thermocouples were configured to give absolute temperature using the reference junction compensation system of the data logger. All thermocouples were

compared with each other and agreement was better than $\pm 0.25^\circ\text{C}$. The manufacturer's calibrations were used for the anemometer and net radiometer.

Annual fluctuations of LSW and shoot fly population. We monitored the seasonal variation in LSW between 1989 and 1990. Three sorghum cultivars (CSH 1, IS 1054 and IS 18551) were sown at weekly intervals in small plots from June 1989 to April 1990. (ICRISAT maintains a close season from 15 April to 15 June when no crops are usually grown as a plant protection measure against carry-over populations of pests). Using the visual score method, LSW was recorded weekly at 08.00 h on 10 randomly selected seedlings of each cultivar at 10 days after seedling emergence (DAE). Egg counts were taken at 14 DAE and deadhearts at 21 DAE on all remaining plants.

Adult populations of shoot fly are monitored on a routine basis at the ICRISAT farm using fish-meal traps (Taneja *et al.*, 1986). Five fish-meal traps are randomly distributed on the farm and one of these is located 20 m from our experimental plots. Fly populations were obtained from this trap on every third day.

Daily mean values of rainfall, air temperature, relative humidity and wind speed were also obtained from the ICRISAT meteorological observatory.

Statistical analysis

Data were subjected to analysis of variance or student's t-test.

Results

Quantitative measurement of LSW. LSW was higher in all cultivars and all age groups in August than in November (Tables 1 and 2). In August it was highest in 10-day old seedlings but in November, it was highest in 14-day old seedlings. The highest LSW (6.29 mg) was recorded in August in 10-day old seedlings of susceptible CSH 1

Table 1. Quantitative measurement (mg) of leaf surface wetness (LSW) of five sorghum genotypes in seedlings of different ages (August 1989)

Cultivar	Type	5 DAE	10 DAE	14 DAE	21 DAE	Mean	SE \pm
IS 1057	R	2.56	2.70	1.70	1.17	2.03	0.17
IS 18551	R	2.04	2.33	1.73	1.58	1.92	0.13
IS 1054	MR	1.82	2.10	1.52	1.36	1.70	0.09
IS 1046	S	2.19	4.25	3.23	1.64	2.83	0.24
CSH 1	S	3.63	6.29	3.96	2.55	4.10	0.32
Mean		2.45	3.53	2.43	1.66	-	-
SE \pm		0.17	0.28	0.31	0.14	-	-

1/ S = Shoot fly susceptible, R = resistant and MR = moderately resistant

2/ DAE = days after emergence

(Table 1) while the lowest (0.07 mg) was recorded on 5-day old seedlings of resistant IS 18551 in November (Table 2). There were significant differences in LSW between resistant and susceptible genotypes but differences within each group were not significant. Similarly, for each cultivar, there were significant differences in LSW at different seedling ages. These differences were higher and more significant in August than in November.

Visual vs. quantitative measurements. We obtained similar trends in LSW for visual estimates and quantitative measurements using absorbent filter paper (Fig. 1). For both methods, the lowest LSW occurred at 18.00 h (1.0 visual score and 0.3 mg for CSH 1) and the highest (2.7 visual score and 2.2 mg for CSH 1) was obtained at 02.00 h.

Potted plants vs. field plot experiments. There were no significant differences in LSW between seedlings grown in pots and those in field plots (Fig. 2). At peak LSW in CSH 1, we recorded visual scores of 4.2 and 4.4 respectively from potted seedlings and field plots. Similar high correspondence was observed on all occasions. LSW for IS 18551 remained consistently low (<2) in seedlings from both methods.

Diurnal fluctuation of LSW. In CSH 1, LSW was lowest at sunset, rose through the night and then dropped a few hours before sunrise (Fig. 3). This confirms the results of the first experiment in which LSW was measured by the filter paper method in August and November only (Tables 1 and 2). Peak LSW occurred at 02.00 h during the rainy season but at 04.00 h during the post-rainy

Table 2. Quantitative measurement (mg) of leaf surface wetness (LSW) of five sorghum genotypes in seedlings of different ages (November 1989)

Cultivar	Type	5 DAE	10 DAE	14 DAE	21 DAE	Mean	SE \pm
IS 1057	R	0.30	0.42	0.67	0.53	0.48	0.06
IS 18551	R	0.07	0.11	0.16	0.14	0.12	0.02
IS 1054	MR	0.33	0.32	0.48	0.32	0.36	0.05
IS 1046	S	1.27	2.09	3.31	2.65	2.33	0.23
CSH 1	S	2.85	2.99	3.70	3.01	3.14	0.27
Mean		0.96	1.19	1.66	1.33	-	-
SE \pm		0.19	0.25	0.46	0.48	-	-

1/ S = Shoot fly susceptible, R = resistant and MR = moderately resistant

2/ DAE = days after emergence

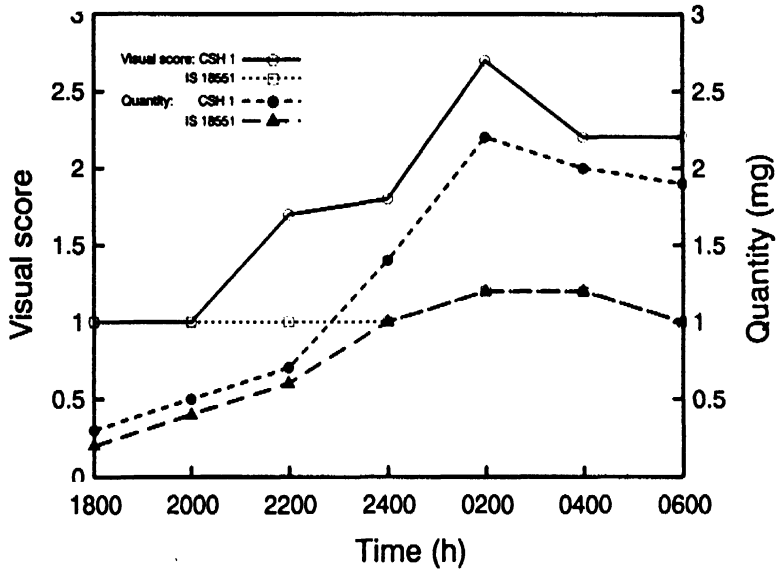


Fig. 1. Visual and quantitative measurements of leaf surface wetness of 10-day old sorghum seedlings of shoot fly susceptible CSH 1 and resistant IS 18551 at 2-hourly intervals. November, 1989.

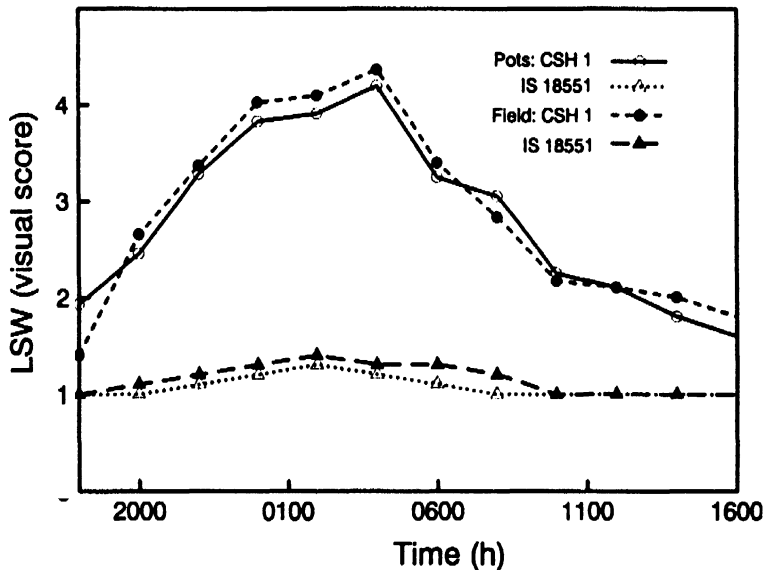


Fig. 2. Comparison of leaf surface wetness (LSW) in potted plants and field plots of 10-day old sorghum seedlings of shoot fly susceptible CSH 1 and resistant IS 18551 measured at 2-hourly intervals. August/September, 1989.

season. The highest visual score values were recorded in the months of August (4.8) and September (4.9). There was very little surface water

in IS 18551 and diurnal fluctuation was negligible. The score for LSW was always < 2.

The temperature of the central whorl leaf was

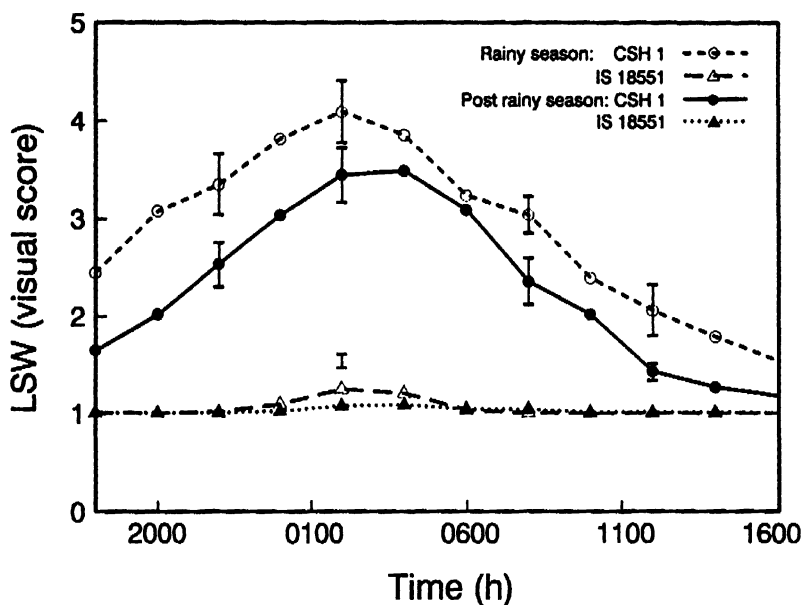


Fig. 3. Diurnal fluctuation of leaf surface wetness (LSW) of 10-day old sorghum seedlings of shoot fly susceptible CSH 1 and resistant IS 18551 measured at 2-hourly intervals between October 1989 and September 1990. Rainy season = June–October, post-rainy season = November–April.

generally less than air temperature at night. Comparing mean values for July and August (to represent the early-rainy season) with means for November and December (to represent the post-rainy season), the difference between leaf and air temperature ($T_l - T_a$) at night was more negative in the post-rainy season (Fig. 4a and b). This is largely explained by net radiation which was also more negative at night in the post-rainy season (Fig. 4c and d). In addition, faster wind speeds in July–August (Fig. 6b) would lead to a less negative value for $T_l - T_a$. There were no significant differences between cultivars in $T_l - T_a$ for either season.

The potential for the exchange of water vapour between the leaf and the air is given by the vapour pressure gradient (VPG). VPG is defined here as $e_s(T_l) - e_a$ where $e_s(T_l)$ is the saturated vapour pressure at leaf temperature and e_a is the vapour pressure of the air (Fig. 4e and f). Comparing the rainy and post-rainy seasons, the diurnal range of VPG is less in the rainy season when values are always significantly greater than zero (Fig. 4e). In the post-rainy season, minimum values for VPG

are close to zero, but usually slightly positive, from 02.00 h to 06.00 h (Fig. 4f). The rate of decrease of LSW between 02.00 h and 06.00 h is much greater in the rainy season than in the post-rainy season (Fig. 4g and h).

Annual fluctuation of LSW and shoot fly population. LSW was highest during the main crop season (June–October) with major peaks from late July to mid-September when maximum visual scores ranged from 4 to 5 in susceptible CSH 1 (Fig. 5a). Another major peak occurred from late December to early January. Other minor peaks occurred during the year but the smallest values for LSW were recorded from late October to early December and subsequently in late February and March. Compared to CSH 1, LSW was significantly lower in other cultivars. No observations were recorded during the close season from mid-April to mid-June.

Several generations of shoot flies occurred during the year (Fig. 5b). The population density slowly built up with the onset of rains in June and gradually increased in late July with a major peak

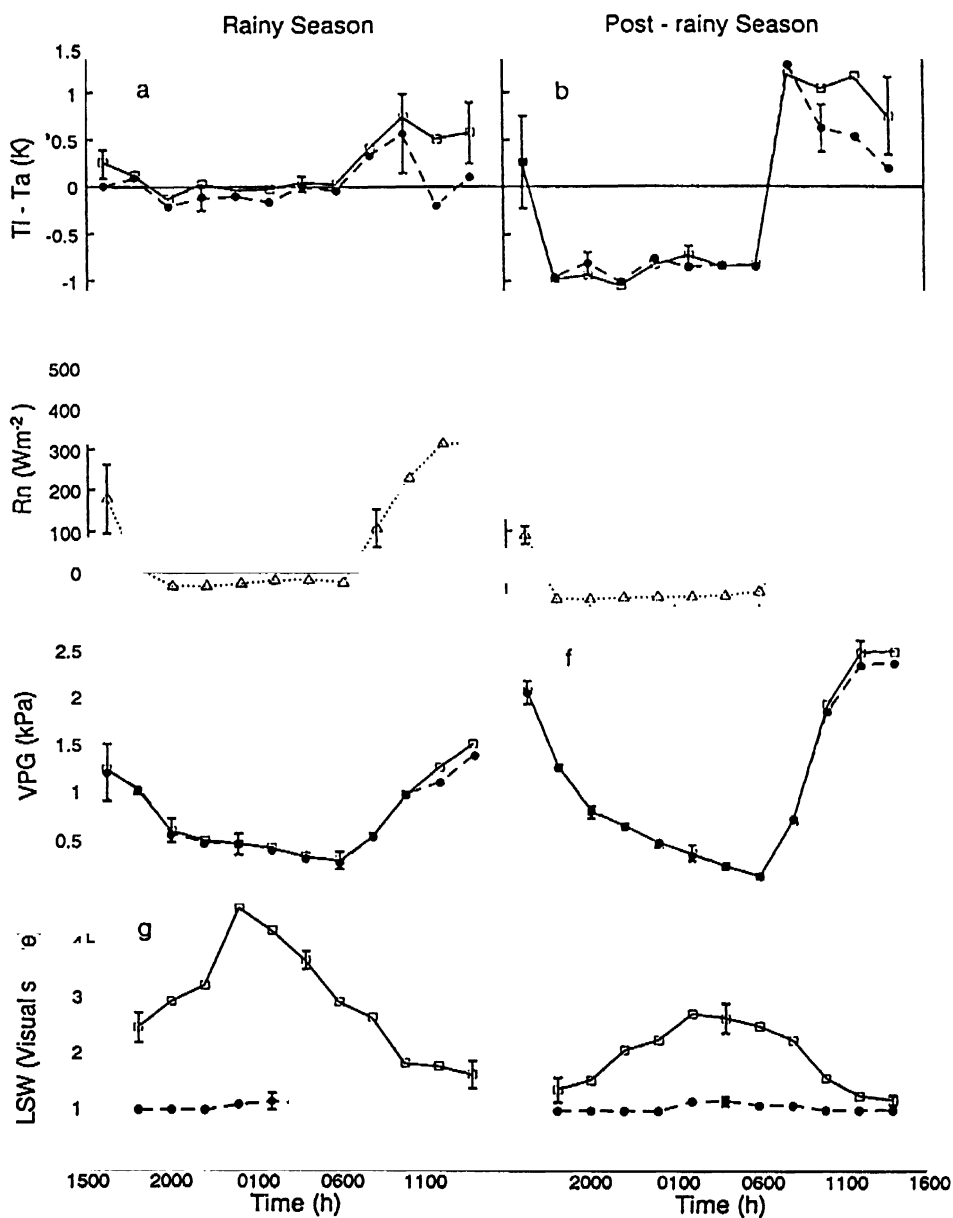


Fig. 4. Relationships between diurnal fluctuations in (a and b) leaf and air temperature difference ($T_l - T_a$), (c and d) net radiation (R_n), (e and f) vapour pressure deficit (VPG), and (g and h) leaf surface wetness (LSW) of 10-day old sorghum seedlings of shoot fly susceptible CSH 1 (□—□) and resistant IS 18551 (●—●) between October 1989 and September 1990. Rainy season = June–October, post-rainy season = November–April.

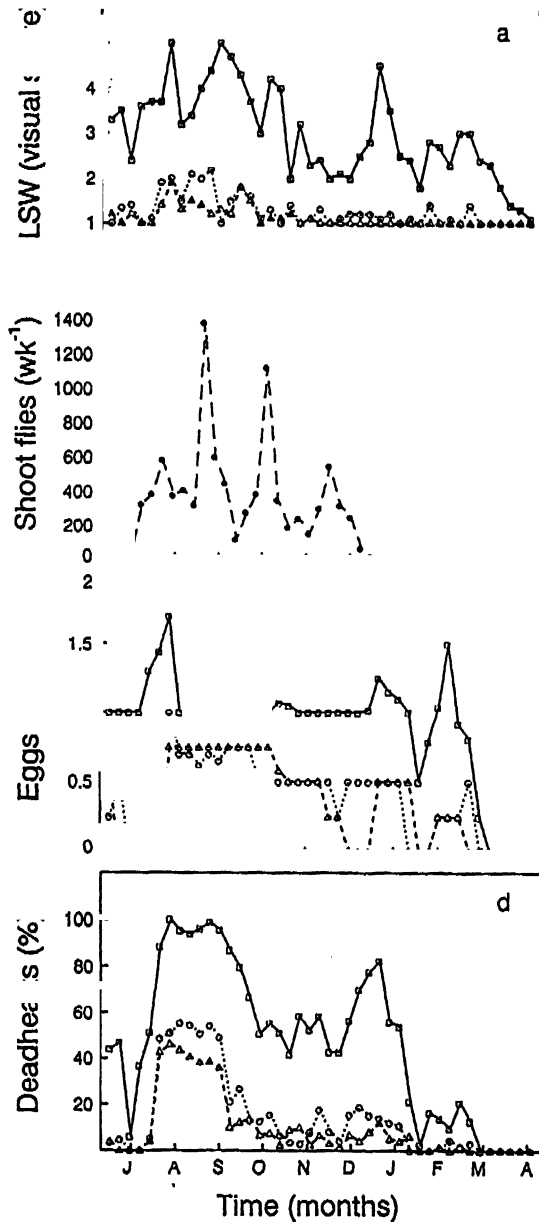


Fig. 5. Annual fluctuation of (a) leaf surface wetness (LSW), (b) shoot fly adult population (c) oviposition and (d) damage (% deadhearts) in 10-day old seedlings of susceptible CSH 1 (□—□) moderately resistant IS 1054 (○—○) and resistant IS 18551 (△—△) between June 1989 and April 1990.

occurring in August/September and a minor peak in October. The population density declined from December onwards and the lowest numbers

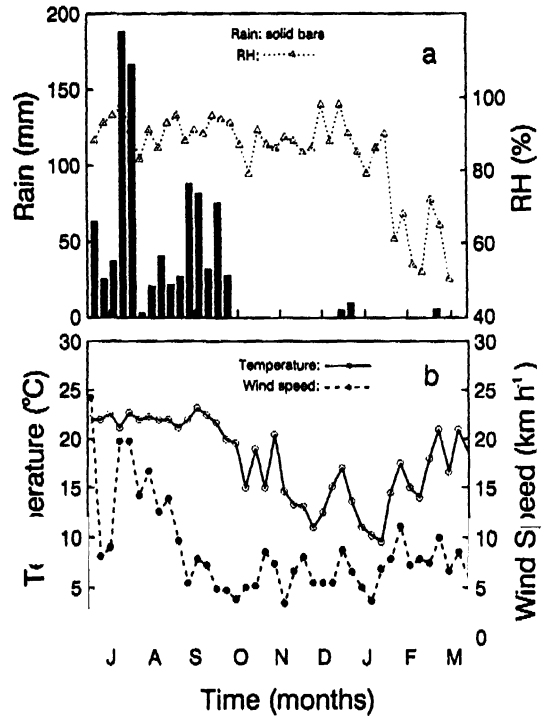


Fig. 6. Annual fluctuation of climatic variables at ICRISAT Centre between June 1989 and April 1990.

(close to zero) were observed from late March to June. The highest mean number of eggs per plant (1.7) was recorded on susceptible CSH 1 during the first week of August (Fig. 5c). Shoot fly damage (deadhearts) also followed a similar pattern to LSW (Fig. 5a and d) and was maximum (100%) on CSH 1 when LSW scores were greatest (Fig. 5d). Some shoot fly damage also occurred on the resistant cultivar, IS 18551 during severe infestations from late July to September.

Most rainfall occurred between July and September when there were 37 rainy days (Fig. 6a). Relative humidity at 07.15 h usually ranged between 80 and 95%, from June to December and dropped to below 60% in January. Minimum air temperature varied between 20 °C and 25 °C during the rainy period but dropped to below 15 °C between November and January (Fig. 6b). Wind speed (daily mean) was greatest (range of 8–24 km/h) during the months of July and August and lowest (range of 3–8 km/h) in October.

Discussion

In our earlier study (Nwanze *et al.*, 1990), we showed that LSW was much higher in susceptible CSH 1 than in resistant IS 2146. This difference was confirmed in the present study and in addition there was a similarity in the seasonal variations of shoot fly population, deadheart and LSW. Our results agree with earlier studies by Taneja and Leuschner (1985) and Taneja *et al.* (1986) who reported a peak in shoot fly infestation in August.

While our earlier study showed that LSW was highest in 10-day old seedlings in August, the present study also showed that in November, LSW was highest in 14-day old seedlings. This may be explained by the lower temperatures in November which result in slower plant growth. We observed that seedlings at the 5-leaf stage were 10 days old in August but 14 days old in November. It therefore appears that LSW measurements should be related to phenological growth stage rather than chronological age.

Slavik (1974) indicated that moisture accumulation on leaves may result from condensation or from guttation due to pressure in the xylem. The VPG values (Fig. 4e and f) indicate whether water is likely to have condensed on the leaf or evaporated. Condensation would occur only if the VPG is less than or equal to zero. This condition is clearly not met in July–August, and may be met only transiently in November. Periods of rapid increase in LSW between 18.00 and 24.00 h always coincided with times when the VPG was substantially greater than zero, that is, when water would be expected to evaporate. This suggests that water is not originating from the atmosphere and that leaf surface water of the central whorl leaf originates from the plant. The decrease in LSW after 02.00 h is surprising, and confirms that water is indeed evaporating from the plant during the night. During periods of increasing LSW, the rate of supply must exceed the rate of evaporation of water.

Further support to the idea that water originates from the plant is given by the different amounts of LSW on susceptible and resistant

cultivars with similar microclimatic conditions. It should be noted that the leaf temperatures of both cultivars were similar, so the VPGs would also be similar. This suggests that there are differences in the genetic potential (probably physiological) between cultivars in the rates of supply of LSW. Since other possibilities are unlikely, we conclude that water is exuded onto the surface of the whorl leaf and that this merits further investigation. Furthermore, the nature of the leaf surface microstructure may also affect the evaporation/retention of exuded moisture as well as larval behaviour. This hypothesis is related to question (b) in the introduction of this paper and is currently being investigated with studies of the leaf cuticle, epicuticular wax and trichomes. These studies will be reported elsewhere.

Previously Nwanze *et al.* (1990) showed that shoot fly eggs usually hatch in the early hours of the morning. This period corresponds with peak LSW of the central whorl leaf which is the path of the newly hatched larva as it moves towards the growing point. This synchronisation between the insect's biology and the physiology of its host indicates a highly evolved and closely integrated insect-host relationship which is an evolutionary process that guarantees the survival of the pest species.

There are seasonal changes in both the amount of LSW and the time that maximum LSW occurs diurnally. Experimental plants were irrigated each day in pots and in the field, so seasonal differences in soil moisture, if any, would have been small. The good agreement between results from potted and field plants supports our belief that differences in soil moisture were not large enough to markedly affect LSW. Seasonal changes in LSW might arise from differences in plant water potential. In the rainy season, small daytime vapour pressure deficits would result in less negative plant water potentials than occur in the post-rainy season (when vapour pressure deficits are large). In the night, recovery of plants from daytime water stress would be different in the two seasons, and may account to some extent for the seasonal change in LSW. The amount of LSW at night would be expected to be less in plants which

had undergone more severe water stress during the previous day. Further experimentation with different soil moisture regimes as indicated in question (c) of the introduction is needed to test this hypothesis.

The high degree of correspondence between visual estimates and quantitative measurements of LSW indicate that an acceptable level of accuracy can be achieved when the former method is employed. This method, which is less tedious and less time consuming, can easily be used for the rapid screening of a large collection of sorghum genotypes for resistance to the shoot fly. However, Figure 1 shows that small amounts of water cannot be detected visually. Also, the threshold for visual detection is different for CSH 1 and IS 18551. The quantitative method would be more appropriate in detailed studies for the identification of minor differences between genotypes. Similarly, the high correspondence in LSW between potted seedlings and field plants will also facilitate the rapid screening for shoot fly resistance.

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