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Effect of pattern and severity of moisture-deficit stress on stalk-rot incidence in sorghum. II. Effect of source/sink relationships[1]

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ABSTRACT

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Stalk-rot of grain sorghum [*Sorghum bicolor* (L.) Moench] is most commonly associated with weakly parasitic root and stalk-rot fungi when the host plants are subjected to environmental stresses. The incidence of rots is generally more in high-grain-yield environments associated with high plant density or fertilizer application. The effects of time of occurrence and degree of moisture deficit stress (moisture stress) on grain and biomass yields, and the natural incidence of stalk-rots were studied.

Stress during grain-filling had a greater effect on incidence of rots than stress at earlier stages. Grain-yield and disease incidence were differently affected by timing and severity of moisture stress. Stalk-rot incidence was most commonly and strongly associated with moisture stress at the terminal stage of growth. However, stress during panicle development induced changes in the sink size (grain number) or root-growth pattern, which in turn influenced both the timing and extent of stalk-rot incidence. The amount of biomass produced during the later part of the grain-filling period was positively correlated with lower disease susceptibility. The distribution index (i.e., the ratio of grain-yield to biomass produced after flowering) could be generally used to predict disease susceptibility. There were no simple correlations between biomass, grain-yield or yield components, and stalk-rot.

Implications of these findings for sorghum production and for stalk-rot resistance screening are discussed.

INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) grown in stress-free environments is quite healthy at physiological maturity, with 4–8 green leaves and

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solid stalks. Abiotic stress factors, especially during the grain-filling period (growth stage 3 or GS3) cause premature leaf and stalk senescence. Moisture (deficit) stress in particular predisposes sorghum to invasion by one or more species of nonaggressive, facultatively parasitic fungi that attack senescing tissue (Dodd, 1980), resulting in lodging. The causes of premature senescence and lodging are not well understood. Some workers (Chamberlin, 1978) believe that carbon shortage, especially in the stem under moisture stress during rapid grain-filling, causes physiological breakdown of the stem tissue and lodging. Others attribute a more active role to the pathogens causing stem death in adverse environments (Anonymous, 1980; Frederiksen, 1986). It is now well established that several fungi which cause stalk-rot do exist in the roots and stalks of plants from the time the stem begins to elongate during sorghum growth, but infest heavily only after senescence sets in during GS3 (S. Pande, ICRISAT Center, personal communication, 1989). Since both physiological stress and significant colonization of stalks by root and stalk-rot fungi are associated with abiotic stress factors (Pande, 1986), a common basis for disease development based on host/parasite/environment interactions needs to be explored (Jordan et al., 1984).

Experiments withholding irrigation during the dry (post-rainy) season to induce terminal moisture stress, and soil fumigation to reduce initial inoculum level, showed that both the physiological stress and fungi reduce yield (Anonymous, 1984), but quantification of loss due to each of these factors is difficult. Their effects often occur together in the field since the causal fungi are abundant in the soil under dry conditions. The yield loss is likely to be more severe under conditions favoring high potential grain-yield, such as use of high rates of fertilizer or plant population densities, and high-yielding cultivars (Anonymous, 1980; Frederiksen, 1982; Henzell et al., 1984). Therefore it is important to understand how best to manage the crop within the available resources, by optimizing both potential grain-yield and reduction in susceptibility to the disease. The pathogens that cause stalk-rots are ubiquitous. Exclusion of their inoculum in the soil is unlikely (Frederiksen, 1986). The environmental stress factors predisposing the crop to stalk-rots play the major role in disease expression. Hence such factors can be used as a means of altering disease levels and as an experimental technique to study stalk-rots.

Although the incidence of root and stalk-rot in sorghum is associated with moisture stress environments, the relationships between moisture stress and disease levels, and grain-yields, are not straightforward. It is generally acknowledged that field-grown plants with large potential sinks (grain) undergoing severe stress during grain-filling are most predisposed to infection, implying source/sink imbalance as the cause of root and stalk-rots (Dodd, 1980). An understanding of effect of timing and severity of water stress on the net balance between assimilate supply and demand for grain-fill, and disease level, is needed. This is expected to increase the precision and reliability of screening for stalk-rot resistance, and may lead to crop management strategies for increasing both grain-yields and stalk-rot resistance.

The objectives of this study were:

1) to quantify the effect of water supply to dry-season sorghum crops on grain yield, crop growth and source/sink balance;

2) to investigate the vulnerability to stalk-rot of plants in which source/sink relationships were altered at different stages of crop growth as a result of pattern of moisture stress; and

3) to discuss strategies for crop management and stalk-rot-resistance screening based on the literature and our results.

MATERIALS AND METHODS

Field lay-out and treatments

The data were collected from three experiments conducted with an overall objective of studying crop growth and water use during the post-rainy seasons of 1978–1981 at the ICRISAT Center, Patancheru, India. Coordinated Sorghum Hybrid 8R (CSH 8R) was grown on Alfisols at a high plant density (18 plants m^{-2}) in 0.75-m rows with adequate fertilizer (100 kg N, 26 kg P ha^{-1}). This hybrid flowers in about 65 days and matures by about 100 days after sowing (DAS). Carbofuran (40 kg ha^{-1}) was applied at planting to control shootfly and stem borer. The plots were hand-weeded twice. The crops were disease-frêe except for the stalk-rots. Levels of plant water stress were developed during desired stages of crop growth by withholding irrigations, as described below.

Experiment I (Expt. I)

In this experiment, the soil moisture was varied using a line source (LS) sprinkler irrigation system (Hanks et al., 1976). The field lay-out was similar to that described by Seetharama et al. (1987). The crop was sown on 1 November 1978 in a 130-cm-deep Alfisol with 90 mm of plant-available soil moisture (ASM). The 30-m-long main plots consisted of ten 1.2-m-wide raised (broad) beds separated by 0.3-m furrows parallel to the LS. Two rows of sorghum were grown on a bed at a 0.75-m row spacing. Each broadbed was used as an observational unit for plant measurements.

Flowering in different treatments occurred between 65 and 75 DAS. Beginning at 39 DAS, combinations of a single line source (to create a moisture gradient), uniform irrigation (UI; applied through perforated pipes placed just above canopy height), and no irrigation (NI; uniform moisture stress) were used to create four patterns of water application (treatments), as listed in Table 1. There were two replications.

TABLE 1

Description of irrigation treatments[1] in Experiment I

Treatments	Code Name	Irrigations at (DAS)						
		GS2			GS3			
		39	49	59	69	79	89	99
LS during GS2 and GS3	LS/LS	LS	LS	LS	LS	LS	LS	LS
LS during GS2/ UI during GS3	LS/UI	LS	LS	LS	UI	UI	UI	UI
NI during GS2; LS during GS3	NI/LS	NI	NI	NI	LS	LS	LS	LS
UI in GS2; LS in GS3	UI/LS	UI	UI	UI	LS	LS	LS	LS

[1]Crops in all treatments were uniformly irrigated thrice until 39 days (beginning of GS2) after sowing (DAS). Adequately irrigated plants flowered at 69 DAS and matured at 110 DAS. LS=line-source irrigation; UI=uniform irrigation; NI=No irrigation. GS2, and GS3: periods from panicle initiation to flowering, and flowering to physiological maturity, respectively.

Treatments LS/LS and LS/UI were subjected to an identical gradient of stress (across the different beds) during the panicle-development stage (growth stage 2; GS2), but differed in the stress experienced during GS3 (Eastin, 1971). Similarly, treatments NI/LS and UI/LS experienced a gradient of stress during GS3, but differed in water received during GS2. Each irrigation supplied water equivalent to about 70% of the cumulative class-A pan evaporation rates (mm) during the preceding period. As a result, even in Bed 1 (nearest to the LS), some mild stress resulted. This mild stress varied between the four treatments because of variations in irrigation treatments and crop water requirements at different stages.

Experiment II (Expt. II)

A crop was sown on 24 January 1980 on 160-cm-deep Alfisol (ASM, 120 mm). It received uniform furrow irrigation at sowing, and at 5,15 and 25 DAS (each irrigation nearly recharging the profile water content fully). At 35 DAS, four irrigation treatments were imposed as shown in Table 2. Each plot, 20 m long, consisted of 16 rows. There were two replications.

Experiment III (Expt. III)

This experiment was sown on 24 October 1981 on a medium-deep Alfisol (ASM, 85 mm). Five irrigation treatments (Table 3) were created by with-

TABLE 2

Description of irrigation treatments in Experiment II

Treatments	Code name	Description
Control	CON	Irrigated at 35, 48, 61, and 74 DAS
Late-season (GS3) stress	LTS	Irrigated at 35 and 48 DAS, then stressed till maturity
Mid-season (GS2) stress	MSS	Irrigated at 61 and 74 DAS (stress between 35 and 61 DAS)
Mid-, and late season (GS2 &GS3) stress	M&LS	No irrigation beyond 25 DAS (grown on stored soil moisture)

TABLE 3

Irrigation schedule and the period of water stress in various treatments in Expt. III

Irrigation No.	Growth stage	Stage[1]	DAS[2]	Treatments[3]				
				M0	M1	M2	M3	M4
1.	Sowing	0	0	+	+	+	+	+
2.	5-leaf stage	2	13	+	–	+	+	+
3.	Panicle initiation (PI)	3	27	+	–	–	+	+
4.	9 day after PI	3	37	+	+	–	+	–
5.	Final-leaf visible stage (approx. 50 DAS)	4	46	+	+	–	+	–
6.	Anthesis (50% flowering)	6	70	+	+	+	–	+
7.	Soft dough	7	86	+	+	+	–	–
	Period of stress:			Control	late seedling stage	3–6	6–9	3–5&7

[1]Vanderlip (1972) stages are: 1–3 of Vanderlip's stage corresponds to GS1 of Eastin (1971); 4–6 to GS2; and 6–9 to Gs3.
[2]DAS, Days after sowing (irrigation time).
[3]+, irrigated; –, irrigated withheld. The crop was sown on 24 October 1981.

holding irrigation at different stages of crop growth. Each plot, 20 m long, consisted of 20 rows. There were three replications.

Collection of data

Soil moisture

In Expts. I and II, soil moisture was measured using a neutron probe, except in the top 22.5-cm layer, where moisture was determined gravimetrically. In Expt. I, sets of three access tubes were placed at each of four points along the irrigation gradient in each replication. In Expt. II there were six tubes in each plot. In Expt. III soil moisture was determined gravimetrically.

The soil moisture was measured immediately before and after each irrigation in all experiments. Soil moisture content before irrigation and the class-A pan evaporation rates for the (1–2-day) period between the two measurements were used to calculate the amount of irrigation water required.

Crop growth and development

Growth stages as defined by Vanderlip (1972) were recorded regularly in all experiments. These were translated to growth stages as defined by Eastin (1971) for simplicity of presentation. Eastin growth stage 1 (GS1) corresponds to Vanderlip stages 1–3, GS2 to stages 4–6, and GS3 to stages 6–9. Yield and yield components were determined at harvest using large plots of 9 (Expts. I and II) or 18 m^2 (Expt. III).

Growth analysis and yield estimation

Leaf area and dry-weights were determined at about 10-day intervals in all experiments. All plants in a 1.2-m^2 area were cut at ground level and separated into green leaves, dead leaves, culm and panicles. Green-leaf area was determined by a LI-COR 3100 (LI-COR Inc., Lincoln, NE, USA) leaf-area meter. Samples were dried in a forced-air oven at 70°C for 48 h before weighing.

Leaf water-potential

Leaf water-potential (ψ_l) was measured as described by Seetharama et al. (1987).

Root studies

Roots were sampled on four dates after the boot stage in Expts. I and II. For each treatment, soil cores were taken at intervals of 10 cm down to 70 cm. Two cores were taken in the centre of each row, and two more were taken exactly between the rows (37.5 cm from rows). Few roots were detected at depth >70 cm. After washing the cores, the length of roots was measured using the line-interception method (Newman, 1976). Dry-weights of roots were determined after drying at 80°C for 24 h.

Monitoring stalk-rot incidence

At physiological maturity, ten plants from a 74-cm row length (subsamples) were monitored for soft stalks by the method of Rao et al. (1980) in Expt. I. Three subsamples per plot were used in the other experiments. In Expt. III, disease was assessed soon after physiological maturity (110 days), and at 117 and 124 DAS, to investigate the differences in the rates of disease development between physiological maturity and harvest.

The incidence of stalk-rot was expressed as the percentage of plants affected, i.e., those with soft stalks (Rao et al., 1980). As the natural incidence of stalk-rot was expected to be adequate, no artificial inoculation was undertaken (Seetharama et al., 1987). *Macrophomina phaseolina* (Tassi) Goid. was identified as the causal pathogen based on the symptoms observed on vertically split stems in randomly selected plots in all experiments. For the sake of brevity, the levels of stress or plant growth parameters are mentioned in a few cases only to indicate the relative effect of different stress treatments. Detailed data on crop growth, root profiles and plant water status will be published elsewhere.

RESULTS

Expt. I

As expected, there was a linear decrease in soil moisture availability during the LS irrigation period as the distance from the LS sprinkler line increased in all four LS irrigation treatments ($P<0.001$), resulting in linear decline in grain yield (Fig. 1A). The grain-yield response of the LS/LS, LS/UI and UI/LS treatments to decreasing amount of water supplied through the LS was similar. A *t*-test showed no significant differences ($P<0.05$) between the intercepts of these three regression lines. Similarly, the slopes of these three regressions did not differ significantly.

Treatment LS/UI had no effect on stalk-rot incidence (mean of 30%), as there was no water stress during GS3. In the LS/LS and NI/LS treatments, which received gradient irrigation during GS3, the disease was absent in the first few beds adjacent to the LS (Fig. 1B), beyond which it increased rapidly with distance, approximately 8–10% for each consecutive bed (5–7% m^{-1}) away from the LS.

When the irrigation gradient was imposed only during GS3, as in UI/LS, the disease incidence was greater in all beds in this treatment than those in others (Fig. 1B). Even in the first bed, the incidence was about 55%, approaching 100% at the far end. As this treatment was regularly irrigated until flowering, both the panicle (sink) size and the leaf area were maximum (*L* of 3.2; Table 4). As a consequence, the plants suffered from greater water stress than those in other treatments, especially at the end of the irrigation gradient (leaf-water potential of −2.31 MPa; Table 4). The root system in UI/LS was also shallower than in NI/LS (Fig. 2) and less soil moisture was extracted from the lower layers.

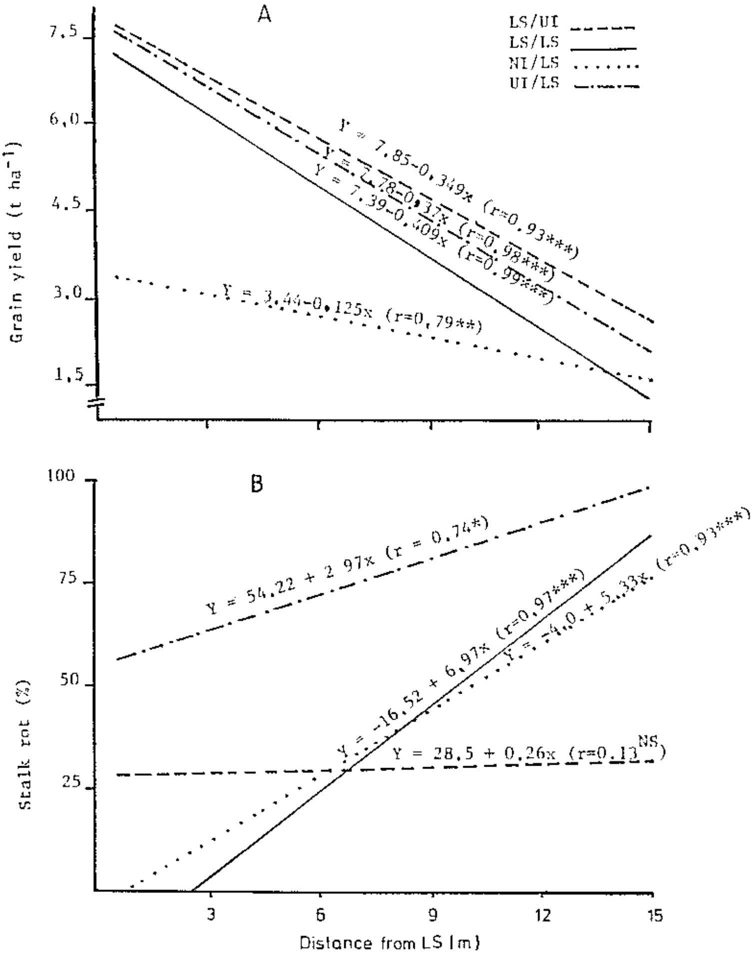

Fig. 1. Expt. I: Relationships between distance from the line source (decrease in water supply) and A) grain-yield, and B) incidence of stalk-rot in different treatments. Significance of linear regressions: *, $P<0.05$; ***, $P<0.005$; n.s., not significant.

Expt. II

Dry-matter and grain-yields, and grain number m^{-2} were highest in the irrigated control treatment (CON; Table 5). Withholding irrigations later in the season (LTS) reduced yields more than doing so before flowering (MSS). The treatment M&LS yielded least.

There were significant differences in stalk-rot incidence (Table 5), mid-season stress (MSS) giving the least (10%). Even the control treatment had 68% incidence, since the last irrigation was given at 74 DAS, 16 days before physiological maturity. Thus plants undergoing this treatment were vulnera-

TABLE 4

Midday leaf-water potential (ψ_l) and leaf-area index (L) at the extreme ends of LS treatments NI/LS and UI/LS in Expt. I

Treatment	ψ_l [1] (MPa)			L		
	Bed 1	Bed 10	Mean	Bed 1	Bed 10	Mean
NI/LS	−1.58	−2.01	−1.80	1.96	1.54	1.75
UI/LS	−1.65	−2.31	−1.98	3.20	1.40	2.3
$LSD_{0.05}$ for bed No.			−0.31			1.1
for irrigation treatment		−2.1			0.73	

Leaf-area data for 94 DAS, approximately 10 days before physiological maturity at 105 DAS.
[1] ψ_l was measured at 01:30 h, on six dates between 94 and 105 DAS.

ble at the very end of GS3. Plants in MSS had less disease than those in CON and their leaf area and sink strength (seed number) were both reduced by early stress (Table 5).

The capacity of dry-matter production during GS3 to meet the sink (grain growth) demand can be represented by the distribution index (DI), the ratio of grain-yield to dry-matter produced during GS3. It was less than 1.0 only for the MSS crop. There were negative relationships between dry-matter production during the later weeks in GS3 and stalk-rot incidence (Table 6). The correlation between dry-matter produced during GS3, and disease, was also negative ($r=-0.546$; DF$=6$). There were no significant correlations between stalk-rot and grain- or dry-matter yields or their components (Table 7).

Disease incidence did not follow the soil moisture extraction patterns. At harvest, plots of MSS, followed by those of CON, contained more water in the soil profile than the other two treatments (Fig. 3). Soil moisture profiles in M&LS (which missed the last four irrigations) were drier than in LTS (missing only the last two; Fig. 3). At maturity, there were no significant differences among treatments in the soil moisture content of the top 0.5 m. There was significant loss of soil moisture in MSS and CON plots between 73 and 82 DAS. Evapotranspiration between 82 and 87 DAS was low in all treatments as both the leaf area, and therefore the crop demand for water, were low during this period just before maturity.

Expt. III

Withholding irrigations reduced both grain and biomass yields in all treatments (Fig. 4A). Greater reductions were recorded for treatments missing irrigations during GS3 (M3 and M4) than during GS2 (M1 and M2). Though

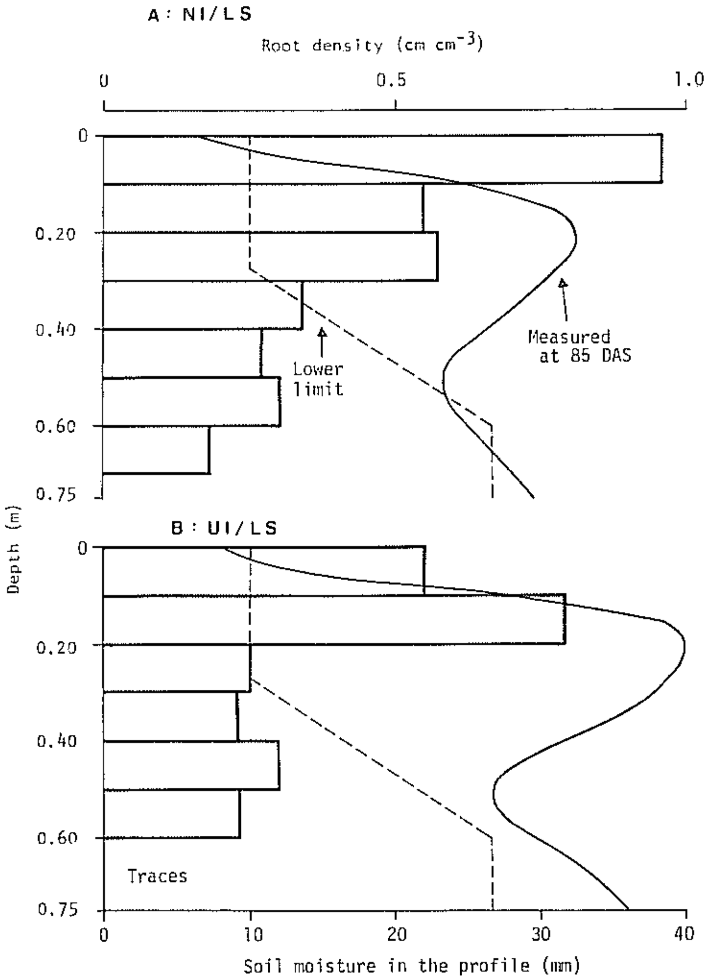

Fig. 2. Expt. I: Root density (histogram) distribution and measured soil water-content 6.75 m away from the LS at 85 days after sowing (DAS). A) treatment NI/LS; B) treatment UI/LS. The bars represent root density, the solid lines denote volumetric water content measured at 85 DAS, and broken lines, lower limit of plant available water in the soil profile.

the harvest index (HI) ranged from 45 to 50%, the differences were not significant ($P<0.05$).

Stalk rot measured at the end of the season (124 DAS) depended on the stress conditions during the later part of the life-cycle (Fig. 4B). Treatment M3, which experienced terminal stress for the longest time (Table 3), had the highest incidence, followed by M4. In M0 (control), M1 and M2 the final irrigation was applied at the soft-dough stage, which might have imposed some terminal stress during the later part of GS3, and plants in these treatments

TABLE 5

Effect of different Irrigation treatments on agronomic traits and incidence of stalk-rot in sorghum (Expt. II)

Irrigation treatment	Total dry-matter ($t\ ha^{-1}$)	Grain-yield ($t\ ha^{-1}$)	Seeds m^{-2}	Seed size (mg)	Stalk-rot (%)	*L* at flowering
CON	7.43	2.71	10179	26.6	68	2.72
LTS	5.83	1.25	5046	24.8	72	2.17
MSS	7.32	2.50	8432	29.8	10	2.24
M&LS	4.03	0.84	5613	15.0	43	1.92
$LSD_{0.05}$	1.30	0.46	2697	6.5	25	0.93

TABLE 6

Correlation coefficients (*r*) between dry-matter produced during each of first four weeks after flowering and the severity of stalk-rot at maturity (Expt. II)

Week	
1	0.350
2	0.158
1+2	0.311
3	−0.774
4	−0.829
3+4	−0.848
1+2+3+4	−0.546

TABLE 7

Simple correlation coefficients[a] between stalk-rot incidence or grain-yield, and growth and yield attributes in Expts. II and III

	Stalk-rot		Grain-yield	
	Expt. II	Expt. III	Expt. II	Expt. III
Grain weight	−0.273	−0.281	1.000	1.000
Total dry-weight at harvest	−0.160	−0.295	0.931***	0.990***
Harvest index (HI)	−0.336	−0.313	0.966***	−0.477
Dry matter produced before flowering	0.450	0.445	0.546	0.524
after flowering	−0.601	−0.567+	0.718*	0.893***
Distribution index	0.550	0.856**	−0.374	−0.504
Seed number m^{-2}	−0.215	−0.070	0.924**	0.868***
Seed size	−0.213	−0.465+	0.789*	0.176

[a] +, $P<0.10$; *, $P<0.05$; **, $P<0.01$; $n=8$ in Expt. II; $n=15$ in Expt. III.

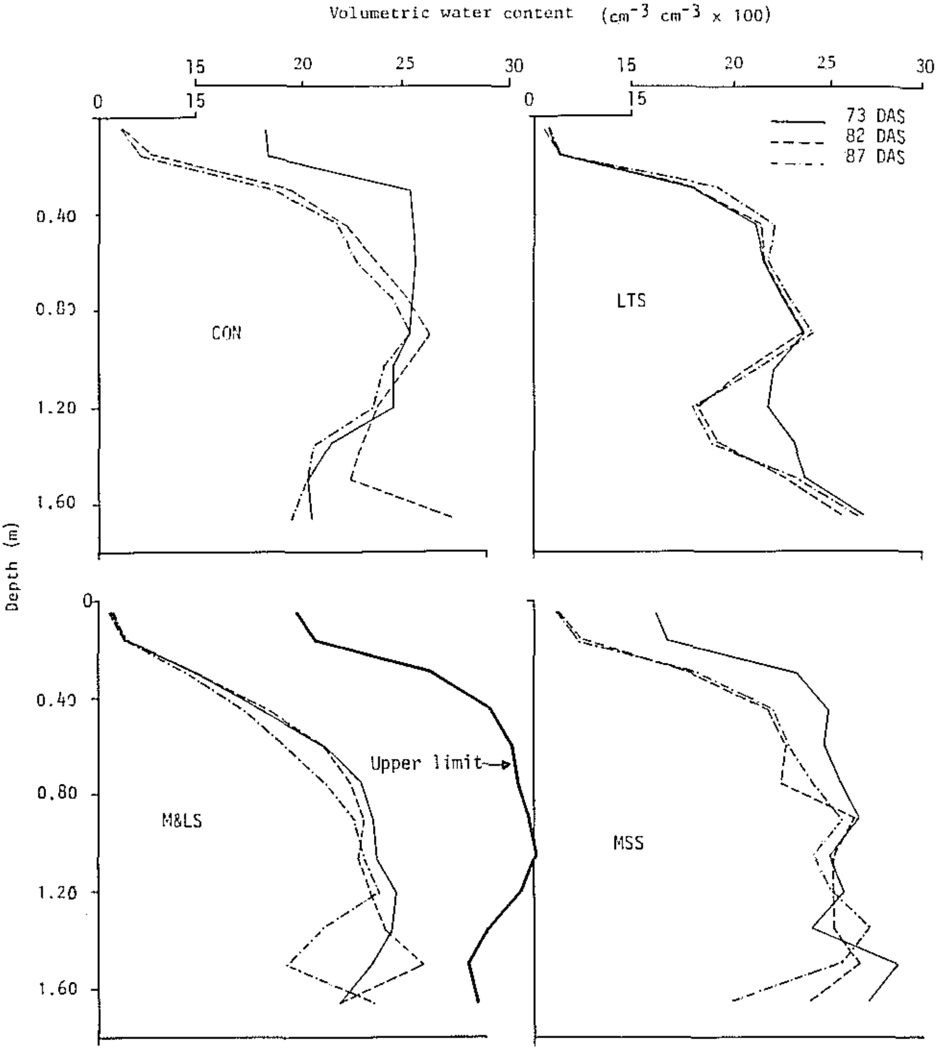

Fig. 3. Expt. II: Soil moisture profile under various irrigation treatments immediately after the last irrigation in CON and MSS (73 DAS), and twice thereafter at 82 and 87 DAS. The last measurement was made immediately after harvest. Note the difference in scale for volumetric water content in the ranges 0–15% and 15–40%. The mean upper limit of water-holding capacity of the profile is shown in the lower left-hand side.

showed some incidence of stalk-rot. Of these, M1 and M2 crops had smaller sinks (late GS1 or GS2 stress), and lower yields and stalk-rot incidence than the M0 crop.

The interaction between irrigation treatment and the time of disease occurrence was significant ($P<0.05$), indicating differences in disease spread be-

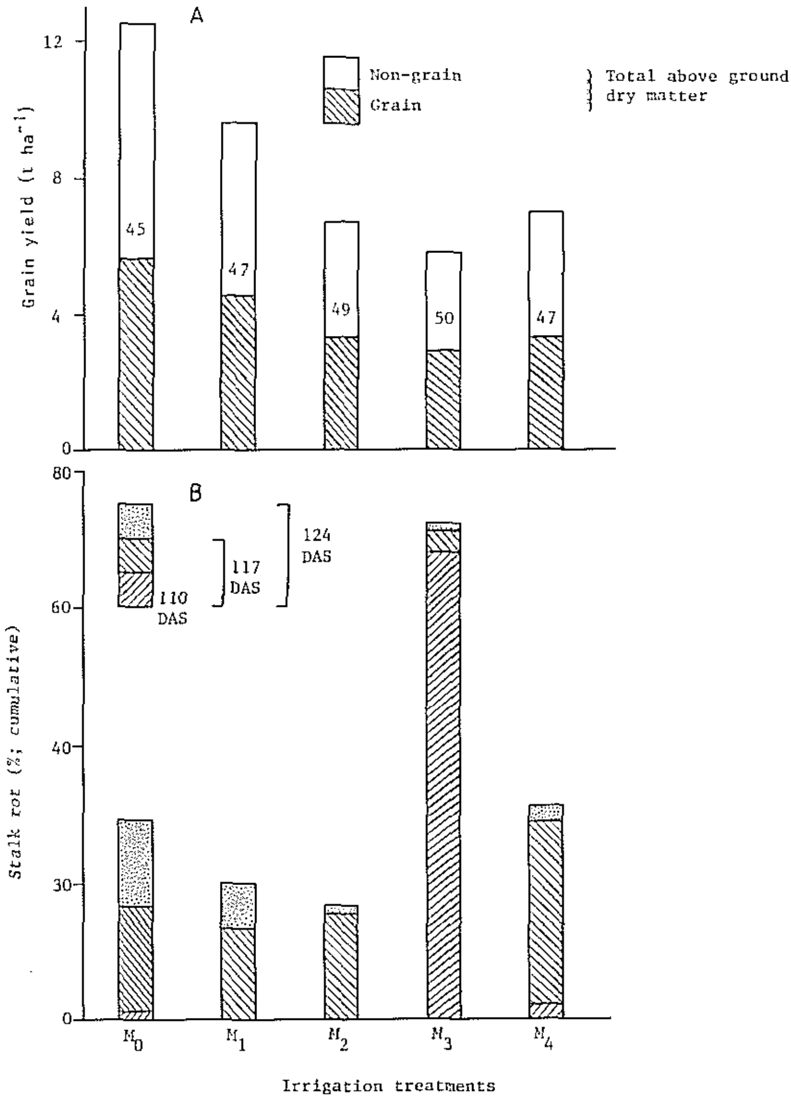

Fig. 4. Expt. III: Effect of five irrigation treatments imposed at different growth stages on A) grain and total dry-matter yields (the number within each unshaded bar represents harvest index in percentage LSD (0.05) for grain and dry-matter are 0.3 and 0.5 respectively) and B) stalk-rot incidence at three stages (DAS); LSD 0.05 for comparing irrigation treatments is 4.

tween treatments soon after physiological maturity. In M3, the disease developed rapidly before 110 DAS, while others showed significant increases only at 117 DAS. The further increase in disease after 117 DAS was significant only for M0 (control) and M1, which underwent the least amount of stress during their life-cycles. Treatments M0 and M1 showed significant increase in disease only at the later stages around maturity.

In M3, GS3 lasted only for 36 days (40 days in all other treatments), and thus the earlier termination of demand for assimilates, and probably reduced competition between the fewer remaining disease-free plants for water, would have prevented further disease development at 117 or 124 DAS (Fig. 4B). The relationships between stalk-rot and various components of yield in Expt. III were similar to those in Expt. II, except that the correlation with DI was stronger (Table 7).

DISCUSSION

Effects of water stress on grain-yield and disease incidence

Although both grain-yield and incidence of stalk-rot are affected by plant and soil water stress, their responses to moisture stress at different stages were quite dissimilar. In Expt. I, in both LS/LS and NI/LS, the disease was absent near the LS (least moisture stress) but increased with increasing stress (increasing distance from the LS). The assimilate supply seemed to be adequate to meet the (grain) sink demand of plants near LS, but as the level of stress increased continuously (increasing distance from LS) a progressive increase in assimilate shortage and disease incidence occurred (Seetharama et al., 1987).

Although the amount of water applied to the bed nearest to the LS in UI/LS was the same as that applied to corresponding beds nearest to LS in the other treatments, the disease incidence was much higher (Fig. 1). In UI/LS the plants were well irrigated until flowering, and the grain number (sink) and the leaf area (source) were largest (Table 4). The slightest amount of stress during GS3 made the plants in this treatment more vulnerable to stalk-rot than those in NI/LS. This may be partly due to less extensive deep-root development in UI/LS than in NI/LS (Fig. 2), resulting in less-efficient water extraction from the lower layers of the soil. Additionally, the HI in UI/LS (47% at 6.75 m from LS) was higher than in LS/LS and NI/LS (46 and 38%, respectively), which may be due to a greater remobilization of stem reserves to fill the larger sink potential established during GS2.

It does not necessarily follow, therefore, that stress which reduces grain-yield increases stalk-rot incidence. Stress before flowering will result in a slightly smaller sink and hence a small reduction in yield, but at the same time significantly decreases the vulnerability to stalk-rot. In Expt. II, MSS led to 17% fewer seeds than CON, but in MSS the seeds were slightly larger (less competition for assimilates amongst the fewer grains), while disease incidence was also far less. The same relationship held for the lower disease incidence observed in M1 and M2 than in M0 in Expt. III.

TABLE 8

Simple linear-regression equations[a] describing the relationship between total water received during crop growth-period (X; mm) and A) grain-yield, or B) stalk-rot incidence in Expt. I

	A) Grain-yield (t ha^{-1})				B) Stalk-rot (%)			
	Io	*b*	RSE	*r*	*Io*	*b*	RSE	*r*
LS/LS	−0.22	0.017	0.273	0.991	95.14	−0.217	10.03	0.932
LS/UI	−15.62	0.055	0.733	0.914	48.58	−0.048	9.72	0.146
NI/LS	−0.79	0.008	0.467	0.788	130.02	−0.454	8.20	0.971
UI/LS	−3.16	0.025	0.332	0.984	140.07	−0.196	13.06	0.739

[a] *Io*, intercept; *b*, slope; *r*, Simple correlation coefficient; RSE, Residual standard error; *, **, ***, $P \leq 0.05$, 0.01, 0.001, respectively.

Though the yield and stalk-rot responses to applied water in the four treatments in Expt. I were exactly opposite (rank correlation of −1.0), the rates of increase in grain-yield and reduction in disease in response to applied water were different. Although it is difficult to compare the absolute responses (rates of change) as the range of water received differed among treatments, grain-yield increase ranged from 8 to 55 kg ha^{-1} mm^{-1}, compared to the decrease in stalk-rot from 0.05–0.45% mm^{-1} (Table 8). Thus, with 350 mm of water application, the predicted grain-yields of LS/LS and UI/LS were nearly the same (5.6 t ha^{-1}), but the stalk-rot percentages were 19 and 71, respectively. Similarly with 350 mm water, LS/UI and NI/LS yielded 3.7 and 2.1 t ha^{-1} of grain with 32 and 0% stalk-rot, respectively.

Photosynthetic stress and translocation balance

In all three experiments, severe stalk-rot was associated with a relatively large sink size (grain-yield) when this was not supported by adequate levels of dry-matter production during grain-filling.

The sorghum plant can adjust its seed number by either producing fewer spikelets per panicle or setting fewer seeds when significant stress develops during the respective ontogenetic stages. Should the conditions improve later during grain-filling, part of the loss in seed number can be compensated for by an increase in seed size as in treatment MSS of Expt. II (Table 5). In such situations, assimilates stored before seed-set are made available from the stem reserves; hence the conditions are not congenial for stalk-rot development (Dodd, 1980). The production of assimilates during the later part of GS3 is far more important than during earlier stages for lowering disease incidence, as indicated by the highly significant correlation between dry-matter produced during the 4th week in GS3 and stalk-rot incidence (Table 6).

Stalk-rot was not significantly correlated with grain-yield (Table 7), but

TABLE 9

Simple linear regressions[a] describing the relationships between stalk-rot incidence (Y) and distribution index (DI; X in regressions) in Expts. I–III

Expt/ treatment	Regression equation		RSE		Stalk-rot when DI = 1.0 (%)
	Intercept (a)	Slope (b)			
Expt. I					
LS/LS	−21.7	25.5	18.0	0.68**	3.8
LS/UI	39.2	−7.1	9.7	0.14$^{\text{n.s.}}$	32.1
NI/LS	13.4	35.6	24.6	0.70**	22.2
UI/LS	46.6	19.0	17.4	0.50$^{\text{n.s.}}$	65.6
Expt. II	−12.7	47.3	22.5	0.76**	34.6
Expt. III	−4.1	40.6	9.9	0.91**	36.5

[a]Means for the two (Expt. I) or three (Expt. III) replications were used.
*, **, $P<0.05$ and 0.01 respectively; n.s., not significant.

showed an inverse relationship with dry-matter produced during GS3. A satisfactory linear relationship is found between the ratio of the above two variables (DI) and stalk-rot incidence (Table 9) in most cases. The computed DI in Expt. II was less than 1.0 only for MSS, suggesting that, in all other treatments, plants would have suffered from source/sink imbalance between dry-matter accumulation in grain and its production during GS3.

The upper range of DI calculated for severely stressed plots in all experiments was rather high. For example, a DI of 2 would indicate that 50% of the grain dry-matter was derived from the pre-flowering assimilates. However, normally one does not expect remobilization to exceed 30% in sorghum (Seetharama et al., 1982). This anomaly might have arisen for any of the following reasons: a) severe loss of dead leaf tissues under stress; b) sampling errors [e.g., before flowering only 1.2 m^2 was harvested, whereas at harvest maturity 9–18 m^2 was harvested in the various experiments for dry-matter measurements, and sampling date did not exactly coincide with flowering in some plots as flowering occurred earlier under mild stress, than under severe stress]; and c) the stalk-rot spread under severe stress would have reduced stem dry-weight considerably.

Correlations between stalk-rot incidence and DI support the photosynthetic-stress/translocation-balance hypothesis of Dodd (1980). However, it is clear from Table 9 that stalk-rot incidence cannot be estimated by computing DI alone; nor it is possible to predict any critical DI for disease incidence.

Soil moisture, root growth, and stalk-rot

Comparison of root profiles in NI/LS and UI/LS treatments showed that the former had proportionately a more extensive root system; it was not only deeper, but also had greater density in the top layers. However, disease incidence cannot be related to soil water content (or root extraction) alone, independently of source-sink relationships. In Expt. II, treatment LTS had more stalk-rot than M&LS, although the moisture deficit was greater in the latter. Similarly, MSS and CON had similar amounts of water available during later parts of grain filling, but their vulnerability to stalk-rot was vastly different, as described above. Continued root growth during GS3 (Rao and Venkateshwarulu, 1974) is expected to ensure both satisfactory plant water-status and delayed senescence, by supplying both nutrients and cytokinins and other growth regulators to the shoot (Kende, 1965; Itai and Vaadia, 1971). However, this is possible only when the lower layers have enough soil moisture and nutrients, and the shoot is able to supply photoassimilates, and possibly auxins (Bever and Woolhouse, 1974).

Severe root infection prior to stem infection has been shown to affect stalk-rot and lodging (Rosenow, 1980; Mughogho and Pande, 1984). Earlier drying of the upper layers of the soil profile, along with the resultant increase in soil temperature, may be conducive to better multiplication of the fungi below ground, and for the fungi to attack the senescing lower internodes through the root system (Seetharama et al., 1987). This may partly explain the observed differences in the time of severe stalk-rot incidence between M3 and other treatments in Expt. III (Fig. 4).

Implications for crop management, and stalk-rot-resistance screening

Elucidation of the biological and physical basis of disease development in crops is essential for establishing effective screening procedures to identify resistant cultivars or to evolve strategies for disease control. If the amount of water is limiting, regulating the water use both before and after flowering will help in balancing transpiration and growth during each period to get the highest yield with the least stalk-rot.

Cultural methods may be employed to conserve water in the profile for later use if the soil can store sufficient amounts: e.g., use of wider row spacing (Blum and Naveh, 1976), or lower plant populations (Mughogho and Pande, 1984), or by choice of planting date or cultivar such that GS3 coincides with low atmospheric demand for water. If the roots are confined to the upper layers of soil only, then stalk-rot may develop rapidly under terminal stress. Thus, promoting denser root development in the deeper layers of soil is important. This could be achieved by exposing the plants to mild stress during the vegetative growth period, without unduly sacrificing yield potential, and by ensuring adequate nutrients and soil physical conditions for root growth.

The wide range in disease incidence within a cultivar under different patterns and intensities of stress (e.g. 0–100% in Expt. I) highlights the difficulty in screening cultivars for stalk-rot resistance. However, cultivars with low disease susceptibility, showing least degree of stalk-rot incidence only during the later stages of crop growth, or with a low incidence and no significant reduction in yield, do exist (Rosenow, 1980). For screening, cultivars should be grown under conditions which promote formation of a large sink (grain number per unit land area). After this, required intensities of water stress should be imposed, so as to predispose the plants to this disease.

CONCLUSIONS

High grain-yields and high disease incidence need not be inversely related. Irrigation or rainfall events capable of increasing yield potential of a crop may not be equally effective in suppressing stalk-rot incidence. There seems to be greater buffering capacity in plants against yield loss due to water stress than for stalk-rot susceptibility.

Although stalk-rot incidence is most sensitive to environmental stress around physiological maturity, events occurring earlier during development can influence disease development through their effect on source/sink relationships.

Differences exist in rates and time of disease development which are inversely related to the ability of plants to produce assimilates during the later part of the grain-filling period. As significant levels of resistance to root and stalk-rots are unlikely because of the broad and non-specific host range of pathogens, more research should be directed towards efficient crop management strategy to delay and minimize the effect of rots.

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