

The Role of Edaphic Factors in Disease Development

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Summary

This paper presents a brief overview of the roles of abiotic stresses in the modification of processes contributing to the growth and grain yield of sorghum in both the absence and presence of biotic (disease) stresses. Water, temperature, and nutrient stresses promote yield losses through their effects on interception of solar radiation and production of photosynthate. Formation and maintenance of active green leaf area is essential for continued production of photosynthate to maintain carbon and energy flow to both developing grain and plant tissues. Abiotic stresses predispose host tissues to pathogen invasion and promote proliferation and spread of disease in plant tissues, but the mechanism(s) are unknown. The association of charcoal rot with stress during grain filling lends support to the view that carbohydrate mobilization from stalk and root tissues may be intimately associated with host resistance. Further research is needed to define the nature of changes induced by stress that predispose host roots to infection. Since infection and proliferation of the pathogen in host tissues seem to be controlled independently, the changes allowing spread should be studied further. Finally, interactions of abiotic stresses should be studied in a manner that will allow formulation of host-pathogen models necessary to explore possible common bases for disease development and resistance.

Edaphic factors such as water, temperature, and nutrition are universally recognized as important in the development and spread of disease in crop plants. Just as atmospheric turbulence, humidity, and other general features of the aerial climate are important to the epidemiology of disease caused by airborne pathogens, issues such as soil water content and potential, soil temperature, and mineral ion availability are central to our understanding of diseases caused by soilborne pathogens.

Relatively few research reports deal specifically with effects of the environment on root and stalk

diseases. In fact, the ICRISAT program appears to be the only major research effort currently dealing with these problems in sorghum. It is our intention not only to review known environmental effects on the development and severity of root and stalk rots in sorghum, but also to provide insights into the effects of specific edaphic factors on the host and pathogen, and their interaction. Because sorghum is a major crop of the semi-arid zones, especially in developing countries, we will concentrate on problems associated with deficiencies in supplies of soil water and mineral nutrients.

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Water in the Soil-Plant-Atmosphere Continuum

Water exists as a continuum from the soil, through the plant, and into the atmosphere. The phase change from liquid water to water vapor within the leaf does not alter this fact. Water moves in such a continuum from regions of high free energy (high water potential) to regions of low free energy (low water potential). Thus, water transpired by a crop flows from moist soil with a relatively high water potential through the plants and into the atmosphere along a water-potential gradient. Typically, soil water potentials (Ψ_s) will range between -0.01 and -15 bars, while leaf water potentials (Ψ_L) of mesophytic plants will range between -1 and -30 bars, and atmospheric water potentials will range between -100 and -1000 bars. Just as typically, Ψ_s may vary from -100 bars or less at the soil surface to -0.01 bars deeper in the soil profile, while the atmospheric water potential may decrease by 1000 bars or more between dawn and midday. At any instant, Ψ_L represents an integration of atmospheric demand and the capacity of the soil to supply water as modulated by the plants' ability to regulate water loss. In this section, we examine soil and plant characteristics that determine rates of water flow through the continuum.

Water Flow in Soils

Over long periods of time, root systems grow to the extremes permitted by physical and chemical constraints, allowing the crop access to water stored deep in the soil profile. However, over short time intervals, it is water movement through soil rather than root growth that allows uptake of sufficient quantities of water to prevent harmful desiccation. Water flow from the bulk soil to the rhizosphere occurs in response to Ψ_s gradients arising from water uptake by roots.

The hydraulic conductivity (H) of a soil is a measure of its capacity to transmit water. A very strong function of Ψ_s , H may change from 10 cm day⁻¹ for a wet soil to as little as 10⁻⁶ cm day⁻¹ at the lower limit of water availability. Reicosky and Ritchie (1976) found that the rate of water flow through soil did not limit water availability to growing crops of maize and sorghum until water extraction caused H to fall below about 10⁻⁶ to 10⁻⁷ cm day⁻¹. When H fell below this value, the roots were no longer able

to absorb water at rates sufficient to satisfy the evaporative demand and water stress (low Ψ_L) resulted. Since the experiments were conducted at different locations and on different soils, their estimate for H may be a general result for well-rooted crops. Unfortunately, the relationship between H and soil water content (θ_v) is unique for each soil (and region of the soil profile); therefore the lower limit of H cannot be translated simply into θ_v , a quantity more frequently available. For sandy and clay soils, H reached 10⁻⁶ to 10⁻⁷ cm day⁻¹ at Ψ_s of -1 and -8 bars, respectively.

Water Flow in Plants

As in the case of soil, water flow in plants occurs in response to a water potential gradient between sites of water absorption in roots and sites of evaporation in leaves. Flow through plant tissues is most conveniently discussed in terms of the familiar electrical analog: water flow is analogous to the flow of electricity as described by Ohm's Law. Thus, the flow (flux) is directly related to the driving force (Ψ gradient in plants) and inversely related to the resistance to flow. Major resistances appear to reside in the radial path of flow between the root surface and the root xylem, and at the stomates. For sorghum, the axial transport of water through healthy roots encounters little resistance (Meyer and Ritchie 1980). Therefore, when soil water is freely available to the crop, high rates of transpiration are maintained with a minimal depression of Ψ_L . Values of Ψ_L for healthy, well-watered sorghum usually range between -8 and -14 bars during peak transpiration periods, increasing to near zero bars before dawn. In some situations, the predawn value of Ψ_L or the Ψ_L of leaves covered to prevent water loss may be taken as an estimate of the Ψ_s surrounding the roots.

Pathogens causing root and/or stalk disease may alter the resistance to water flow through tissues in one of at least four ways:

1. If infection occurs through the root cortex and lesions develop in cortical tissues, the intimate root-soil contact may be destroyed. The net effect is to reduce the total root length in contact with soil, thus increasing the resistance in the radial pathway.
2. If the pathogen produces toxins, the permeability of root tissues to water may be altered, or, if the toxins enter the transpiration stream,

stomates may be affected. This aspect of host-pathogen interaction is not well studied, but either increases or decreases in membrane permeability appear possible.

3. Vessel plugging may occur either with tissues of the pathogen (e.g., fungal mycelia) or by induction of tyloses. This mechanism may result in a dramatic increase in axial resistance of the affected root, but if only a few roots are affected the consequences may be minimal, depending upon the soil water supply.
4. Finally, root deterioration reduces the transport capacity, but from a water supply standpoint, sorghum appears to "overproduce" roots, since loss of up to 50% of the root axis appears to have little impact on Ψ_L so long as water is freely available to the remaining roots. This latter generalization may not hold true for nutrition, and almost certainly would not be true for crops grown in water-limited environments.

Water Flow in the Integrated Soil-Plant System

Several references were made in preceding sections to the dynamic nature of water potentials, both spatially and temporally, but visualization of the interdependence of soil, atmosphere, and plant is difficult. The question remains as to how soil and plant properties act in concert to regulate the flow of water through the system so the plant can remain relatively stress free. One means of examining this problem is through use of simulation models based on descriptions of flow in soil and plants as presented by Jordan and Miller (1980). An example of a sorghum crop growing in a drying clay soil is illustrated in Figure 1. If we assume that Ψ_L remains constant at -15 bars (minimal plant stress) and the average root-length density is $1.0 \text{ cm root } (\text{cm}^3 \text{ soil})^{-1}$, then a flow rate equivalent to 0.8 mm h^{-1} can be met only if the average Ψ_s is above about -1.5 bars. This flow rate is in the range of those experienced in semi-arid field environments. If, on the other hand, flow rates are as low as 0.2 mm h^{-1} (cloudy, humid situation), then these rates could be met from a drier soil at a Ψ_s of about -4.5 bars. Although this treatment and example are simplistic, they serve to illustrate the complex interaction of system components under realistic environmental conditions. An understanding of

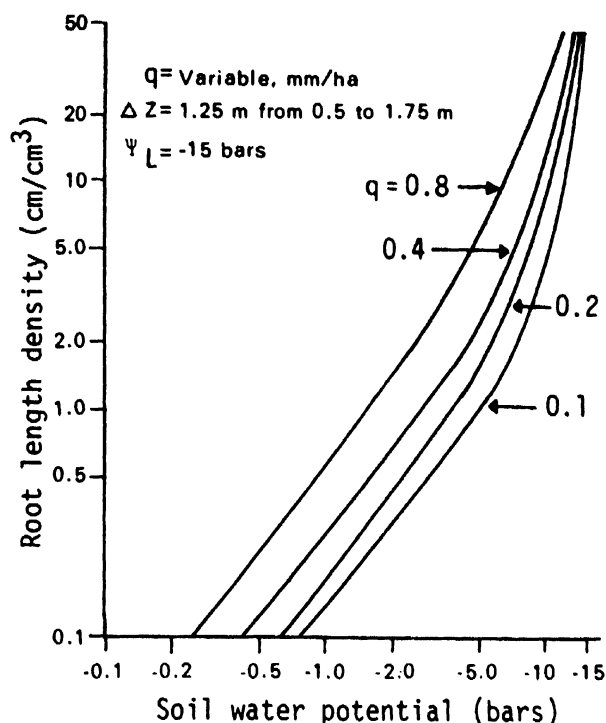


Figure 1. Predicted relations among root length density, soil water potential, and transpiration rate (q) for sorghum plants at a constant leaf water potential of -15 bars. Water uptake is assumed to come from a 1.25-m soil layer (Δz) between 0.5 m and 1.75 m deep. (Source: Jordan and Miller 1980.)

these interactions is central to understanding plant performance in both healthy and diseased conditions.

Soil Water Deficit and Crop Productivity

Sorghum is grown in large areas of the semi-arid tropics because of its ability to produce grain under water-limited conditions. Factors contributing to sorghum's drought resistance have been detailed elsewhere (Jordan and Monk 1980, Jordan et al. 1983, Seetharama et al. 1982, Simpson 1981), but the fact remains that serious yield losses result from moderate to severe soil water deficits (Blum 1970, Garrity et al. 1982). Eastin et al. describe the sensitivities of sorghum to environmental stresses in these proceedings, and hence only a brief discussion of the effects of soil water deficits on development, activity, and duration of various

carbohydrate sources and sinks is presented to examine how root and stalk diseases effect yield reductions. For a more complete treatment of water relations of sorghum, readers are referred to recent reviews by Jordan (1983), Turner and Burch (1983), and Krieg (1983).

So long as cultural and environmental constraints are minimal, total dry matter production appears to be linearly related to the total solar radiation intercepted by a crop during the growing season (Monteith 1977). Light interception depends primarily on the seasonal distribution of the leaf area index (LAI); therefore factors that modify rates of leaf area development and maintenance may also modify the potential for grain yield.

On a whole-plant basis, the leaf area present at any time is a complex function of leaf numbers, leaf sizes, and leaf longevity. Leaf number is fixed within relatively narrow limits by the maturity of the cultivar, and the ultimate number of leaves formed per plant appears to be relatively unaffected by soil water deficits (Kannangara et al. 1983; W.R. Jordan and G.F. Arkin, Blackland Research Center, Temple, Texas, USA, unpublished data, 1982), although rates of leaf appearance are reduced. Since leaf appearance is strongly dependent on cellular expansion, and expansion is inhibited by water deficits (Boyer 1970; Hsiao et al. 1976a, 1976b), the reduction in leaf appearance rates is believed to result primarily from an inhibition of expansion. The net result from soil water deficits that develop progressively during vegetative growth is an overall reduction in leaf area per plant, as illustrated in Figure 2 (Jordan 1983), due primarily to reductions in final leaf sizes. During severe drought, formation of new leaf area may stop completely, giving the appearance that the crop is in a state of suspended animation (growth) while awaiting rainfall.

Reports dealing with the longevity of leaves during periods of drought are both sketchy and contradictory. Much of the confusion arises from failures to consider crop phenology and the rate and severity of water stress when evaluating effects of drought on leaf longevity. Recent results suggest that the longevity of individual leaves is not seriously altered by water deficits that develop gradually over long periods during vegetative growth stages, but rapid development of water deficits may accelerate senescence of lower leaves (Wilson and Allison 1978, Stout et al. 1978, Jordan 1983). However, if water deficits develop after anthesis, leaf senescence may be accelerated due to translocation of carbohydrates and

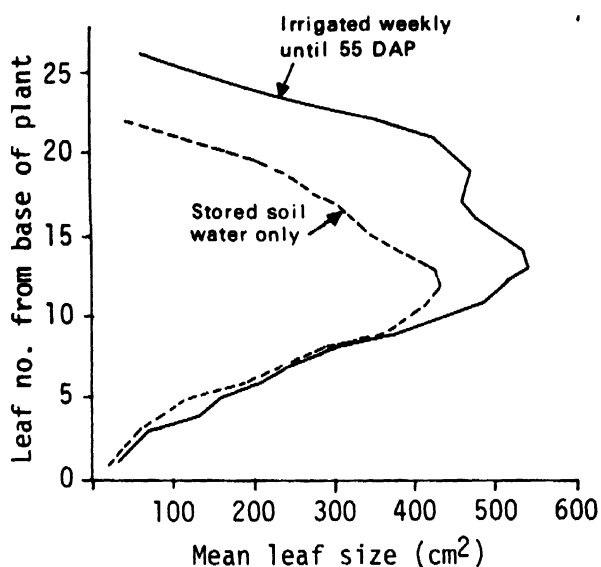


Figure 2. Vertical distribution of leaf area for 100 M sorghum plants grown on stored soil water or irrigated weekly until 55 days after planting (DAP). (Source: J.T. Ritchie, R.G.C. Smith, J.E. Begg, and W.E. Lonkerd, Blackland Research Center, Temple, Texas, USA; unpublished data, 1978.)

nitrogenous compounds to developing grain. This aspect of dry matter redistribution will be enlarged upon in following sections.

The seasonal pattern of dry-matter accumulation in sorghum is illustrated in Figure 3 (Krieg 1983). The period between panicle initiation and flowering, usually referred to as growth stage 2 (GS2), is a time of rapid increases in leaf area and dry matter and is the period when the potential grain number is determined. It is during GS2 that the crop expresses maximum sensitivity to environmental stresses, including water, heat, and light (Eastin et al., these proceedings). The causes underlying yield reductions from water deficit during GS2 are not fully understood, but Fischer's analytical framework of wheat growth and yield under water-limited conditions suggests that a functional balance exists between viable leaf area (source) and potential grain numbers (sink), provided that water deficits develop slowly (Fischer 1979). If this analysis also holds true for sorghum, some sort of feedback regulation between source (leaves) and sink (panicle) is implied. Whether this "communication" between source and sink arises from disruptions in the flow of organic energy and carbon sources from leaves to panicle, or from

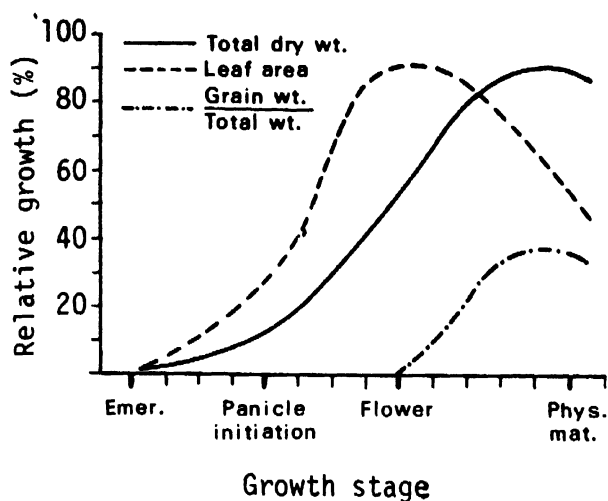


Figure 3. Fractional total dry weight, green leaf area, and harvest index of sorghum grown for grain as a function of growth stage. (Source: Krieg 1983.)

changes in the hormone balance of the panicle, is unknown (Krieg 1983). Regardless of the basic causes, the net effect of water deficit is expressed soon after anthesis as fewer grains per panicle, as evidenced by small panicles in general or by sterile branches within panicles (head blasting). In extreme cases the entire panicle may be sterile, either because the florets failed to develop or because they aborted.

Actual yields under favorable conditions are limited by source activity: that is, by the photosynthetic capacity of the leaves, stem, and panicle (Krieg 1983). Overall source activity is limited by soil water deficit through its inhibitory effect on total plant dry weight at anthesis, green leaf area remaining after anthesis, and production and translocation of photosynthate during the grain-filling period (GS3). As illustrated in Figure 3, grain filling occurs during a period when green leaf area is decreasing. It is not clear how much dry matter is translocated from senescing sorghum leaves, but in cases of crops well supplied with water, the loss of lower leaves probably has little impact on grain yield. However, if LAI is already low and the loss of leaf area after anthesis is accelerated by drought, serious source limitations may result from an inability to intercept sufficient radiation. In addition, the production of photosynthate may be reduced by stomatal closure during periods of peak evaporative demand when Ψ_L is low, further reducing the flow of materials required to maintain grain growth.

While some preanthesis assimilate is translocated from stem and leaves to grain under normal conditions, proportionately more may be translocated as photosynthate production rates fall due to drought during GS3. Results with most commercial sorghum hybrids suggest that the harvest index (HI) is maintained at relatively constant values as yields are reduced up to 50% by soil water deficits (Garrity et al. 1982), but that HI falls at extremely low grain yields (Blum 1970).

The total amount of dry matter stored in stem and leaves that is capable of translocation to developing grain is not known, but recent results with senescent and nonsenescent cultivars suggest that genotypic variability for this trait does exist for sorghum. Depletion of stem (and root?) reserves during GS3 may predispose senescent cultivars to infection by soilborne pathogens, especially *Macrophomina phaseolina*, the causal organism of charcoal rot, but a direct causal relationship has not been established. However, it is clear that development of root or stalk diseases that interfere with absorption or transport of water will create internal water deficits, with consequences similar to those described above for soil water deficits.

Disease Development and Soil Water Supply

Root and stalk rot diseases of sorghum often develop most dramatically during GS3, when water is in short supply and soil temperatures are high. Charcoal rot, a serious disease of sorghum and maize, is expressed in this circumstance, but research reports on the causal pathogen and its interaction with the soil environment and host are indeed few. Even considering this paucity of information, the charcoal rot problem appears to be the best studied example of a stalk or root disease causing serious crop losses in sorghum (Mughogho and Pande, these proceedings). The discussion in the following sections will concentrate on those reports dealing with the effects of soil water deficits on *M. phaseolina* and the development of charcoal rot.

Effects of Ψ_s on *M. phaseolina*

Effects of low water potential on the germination of sclerotia and growth of mycelia have apparently been studied in detail only in the laboratory, using

artificial media (Dhingra and Sinclair 1978). Sclerotial germination in culture occurs over a wide range of water potentials and temperatures, including those expected in the field during drought (Odyssey and Dunkle 1979, Shokes et al. 1977). The sclerotia appear well adapted for survival for long periods in dry soil, but exposure to wet soil (-0.01 bar) at 30°C for 2 weeks decreased survival in one test (Shokes et al. 1977).

Since sclerotia germinate readily in culture over a wide range of conditions, the question of control of germination under favorable soil conditions naturally arises. Some form of nutrient-dependent fungistasis is most often alluded to as a germination control (Ayanru and Green 1974). Odyssey and Dunkle (1979) observed higher germination on potato dextrose agar at low osmotic potentials (< -40 bars) than on water agar, but germination was similar at higher osmotic potentials. This suggests that endogenous nutrients should support germination under most conditions. However, they also reported that sclerotia isolated from soil did not germinate when incubated on water agar in the presence of contaminating soil particles, but germinated readily when they were surface-sterilized, suggesting some type of active fungistasis associated with contaminating microorganisms. In other studies, the fungistatic properties of nonsterile soil were reduced or eliminated by additions of nutrients such as amino acids (Ayanru and Green 1974) or additions of root exudate (Smith 1969), suggesting large supplies of appropriate organic compounds can overcome propagule dormancy.

The relationship of low Ψ_s to sclerotial germination is not clear, but based on current evidence at least three hypotheses may be proposed. First, low Ψ_s near the soil surface may differentially inhibit the soil microflora, thereby reducing the endogenous or exogenous fungistasis so that germination can occur. A body of evidence suggests that growth and activity of bacteria are inhibited at much higher Ψ_s than several fungi (Griffin 1981, Harris 1981). In fact, growth of many fungi, including *M. phaseolina*, appears to be stimulated by reductions in the osmotic potential of culture media by -5 to -20 bars (Shokes et al. 1977, Odyssey and Dunkle 1979, Cook and Duniway 1981). However, stimulation by equivalent matric potentials in soils is often not observed (Cook and Duniway 1981). Wilson and Griffin (1975) reported that bacterial respiration was negligible at Ψ of -20 bars, while total soil respiration was constant to -30 bars, presumably because fungal respiration was

unaffected.

A second hypothesis involves the effects of low Ψ_s on chemical composition and/or amount of root exudate (Kerr 1964, Cook and Flentje 1967) and the distance these nutrients move from roots. Cook and Duniway (1981) suggest that the availability of nutrients may confine propagule germination to the relatively high water potentials suitable for growth of the host plants, but that low Ψ_s near the surface will not restrict growth or activity of the host if sufficient root length exists in wetter, lower regions. Exudates produced by roots in dry regions may raise the Ψ_s in the rhizosphere, but the distance this influence might extend into the soil is not known.

The third hypothesis is related to the growth and senescence of roots induced by low Ψ_s . A recent review on the relationships between root growth dynamics and epidemiology of root-invading fungi (Huisman 1982), indicates that the information available on this topic is inadequate. Roots of most species will not grow in soils drier than about -2 bars. Taylor and Klepper (1974) reported the disappearance of roots growing against rhizotron windows when Ψ_s fell below -2 to -3 bars. Presumably these roots had deteriorated and, in doing so, could have provided a nutrient source for the microflora. A recent study with maize (Schneider and Pendery 1983) found enhanced root senescence when plants were exposed to mild water stress, even though symptoms of stress were not visible. The total amount of nutrients that could be supplied by root decomposition is not known because only the fine roots appear to be so affected (W.R. Jordan, personal observations). Root proliferation in surface horizons occurs rapidly and repeatedly as soils are rewet by rainfall or irrigation; therefore the potential amount of nutrients available from this source may be larger than expected.

Water Deficit and Disease Development

The association of soil water deficit with increased severity of stalk and root rots caused by normally weak pathogens (including species of *Fusarium*, *Gibberella*, *Diplodia*, and *Macrophomina*) is well established, although the underlying mechanism(s) remain unclear. Recently, Schneider and Pendery (1983) presented evidence that stalk rot of maize at season's end was strongly enhanced by mild stress during earlier growth stages. Mild

stress, insufficient to cause visible symptoms, resulted in pith discoloration or stalk rot in 60.3% of the plants during the pretassel stage of development, 25.3% during postpollination, and 7.7% during grain filling. Even though the stress was mild (Ψ_L about 2 bars lower than well-watered controls), root senescence was accelerated in uninfested treatments and enhanced infection and root colonization occurred in infested treatments, causing the resistance to water flow to increase about twofold. The causal organism was believed to be *Fusarium moniliforme*.

Similar results were obtained with sorghum growing in pots infested with sclerotia of *M. phaseolina* (Odvy and Dunkle 1979). When water-stressed during the soft dough stage, 83% of the fertile CK60 plants developed charcoal rot symptoms, while male-sterile plants were symptomless. Since both fertile and male-sterile plants had high rates of root infection, male-sterile plants apparently possessed some mechanism to retard spread of the infection. Also, since nonstressed plants growing in infested soil remained relatively infection free, stress appeared to promote initial infection of host roots.

Studies at ICRISAT provide evidence that charcoal rot development is related to the severity as well as the timing of soil water deficits. Using a line-source sprinkler system to establish a gradient in soil water deficit, Seetharama et al. (unpublished data, 1983) examined the relationship between the amount of water applied during GS3 (distance from the line source) and the fraction of plants developing soft stalks following toothpick inoculation (Fig. 4). A linear response between distance from the line source and disease development is clearly illustrated for both years, supporting the view that disease severity and drought severity are coupled during the period when the sink demand from developing grain is large. Grain yield decreased linearly with distance from the line source in both years. Additional observations provided evidence that the rate at which disease spread from the point of inoculation increased with time after flowering, as well as with stress severity, supporting earlier findings by Edmunds (1964) and Livingston (1945).

While the concept of edaphic factors in "preconditioning" or "predisposition" of host plants to disease is certainly not new (Schoeneweiss 1978; Yarwood 1976; Dodd 1980a, 1980b), underlying mechanisms remain largely unknown. Recently, Dodd (1980a, 1980b) proposed an explanation of predisposition based on the carbohydrate status of

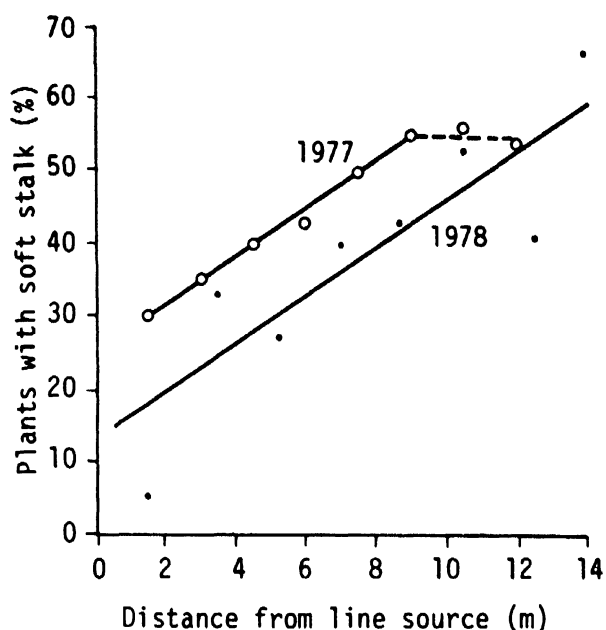


Figure 4. Relation between charcoal rot development (plants with soft stalk) and soil water supply after anthesis (distance from line source) for CSH-6 sorghum grown at Hyderabad, India, in 1977 and 1978. (Source: Seetharama et al., ICRISAT; unpublished data, 1983.)

root tissues and the influence of soil water deficits on deposits and withdrawals from the sink. In this concept, carbohydrate depletion in root tissues weakens the cellular defense mechanisms, allowing the invasion and spread of disease. The effects of soil water deficit on production and redistribution of photosynthate were discussed in earlier sections, and Dodd's concept is supported by work of Edmunds and Voigt (1966), Edmunds et al. (1964, 1965) and Odvy and Dunkle (1979). However, although no alternative explanations of this predisposition phenomenon enjoy wide acceptance, it seems unlikely that any concept based on simple changes in carbohydrate status of roots or stalks will hold up to critical examination. McBee discusses the question of stem reserves in greater detail in these proceedings.

Disease Development and Temperature

Throughout the sorghum-growing regions, high temperatures normally accompany droughts, but

seldom have the effects of high temperature per se been separated from those due to water deficits. A C₄ species, sorghum is adapted to hot, high-radiation regimes, but these same conditions are often cited as facilitating disease incidence and development. In the following sections we explore the effects of high temperatures on the host and pathogen and speculate on the role of this stress on host-pathogen interaction.

Sorghum Response to High Temperature

The effects of both super- and supraoptimal temperatures on sorghum have been recently reviewed (Peacock 1982), with the conclusion that consequences of high temperatures are most serious when they coincide with the critical growth stages of the crop. Thus, germination and emergence are viewed as critical to obtaining an adequate plant population, development and maintenance of leaf area as critical to photosynthate production, and panicle development and growth as critical to yield potential. Since root and stalk rots are normally associated with late-season stresses, we will consider only those effects observed during GS2 and GS3.

The importance of leaf-area development and maintenance has already been discussed with respect to water. Numerous reports document the fact that the general effects of moderate increases in temperature are reflected in faster growth rates in general, as evidenced by earlier maturity. This fact is incorporated in several plant growth models in which process rates are governed by heat-unit accumulation rates. The question of optimum temperature or leaf-area development remains unresolved because much of the growth data collected in controlled environments is not directly applicable to crops grown in a field environment. Data from ICRISAT (Peacock 1982) suggest that leaf extension rates are greatest at an air temperature of about 34°C and that final leaf number and leaf area increase as temperatures increase from 25/20°C (day T/night T) to 35/25°C. Although Quinby et al. (1973) reported genetic variation in leaf growth in relation to air temperature, little use seems to have been made of this information and little effort appears to be directed toward identification of genotypes capable of growth maintenance at high temperatures. Escalada and Plucknett (1975) reported enhanced tillering as temperatures

were increased from 23.9/15.5°C to 32.2/23.9°C, so long as daylengths also increased, suggesting a link between tiller development and total photosynthate supply.

The effects of temperature on yield and yield components have been studied at several locations, with the conclusion that grain numbers per panicle are not reduced by growth at temperatures as high as 35/25°C. However, yield is markedly reduced by these high temperatures due to a reduction in weight per grain. Excessively high temperatures during panicle development often result in head blasting or localized abortion within the panicle, but these effects have not been well documented, nor have the effects of temperature been separated from those due to dehydration.

Leaf firing occurs in the field in response to hot, dry conditions, and variability in both the extent and pattern of firing appears to be under genetic control. Peacock (1979) reported firing in hybrid P6610 when leaf temperatures exceeded 43°C, but at least some germplasm will tolerate leaf temperatures as high as 55°C (Peacock 1982). Leaf firing is one component used in the Texas Agricultural Experiment Station breeding program as a selection criterion for drought tolerance (Rosenow et al. 1983).

The causes underlying heat-induced firing are not known, but other evidence also suggests that genetic variability exists for heat tolerance. In one test, grain yields of M35-1 conversion hybrids growing under conditions of heat stress in Nebraska were correlated with an estimate of heat tolerance based on electrolyte leakage from damaged leaf cells (Sullivan and Ross 1979). Other reports document the existence of substantial genotypic variability for heat tolerance based on this method (Sullivan 1972, Jordan and Sullivan 1982). Genetic variability in the ability to maintain high photosynthetic rates at temperatures between 40° and 43°C also exists (Norcio 1976), but present evidence suggests that photosynthetic rates would be greatly reduced in the range of 44° to 48°C, well below the temperature causing firing in some Indian cultivars.

Temperature and Host-Pathogen Interaction

Even though hot, dry conditions enhance charcoal rot on susceptible sorghum cultivars, there is little evidence that heat stress per se plays a role in

disease incidence or development. At least one causal organism seems well adapted to the high temperatures that exist near the surface of dry soils. Mycelia of *M. phaseolina* are capable of growth to at least 40°C in culture (Odvody and Dunkle 1979), as are many other soilborne fungi. Although unexplained, the growth optimum of the fungus shifts to lower water potentials at higher temperatures, suggesting a unique form of adaptation to the high T-low Ψ_s conditions expected near the surface as the soil dries.

Bell (1982) recently proposed a model showing how temperature may differentially affect the rate of pathogen colonization and active host resistance to differences in relative resistance. His Model A, illustrated in Figure 5, is cited as an example applicable to charcoal rot caused by *M. phaseolina*. In this case, host resistance reaches its maximum at temperatures near or slightly below its optimum for growth, but lower than temperatures for maximum rates of pathogen colonization. Since relative resistance is the ratio of the two rates, increases in temperature result in a decline in relative resistance. While these general predictions appear superficially plausible, there is no

direct experimental evidence to support this hypothesis.

Disease Development and Mineral Nutrition

Specific Element Effects on Disease

Each mineral element essential to plant growth has been implicated in disease incidence or severity, as have many not considered essential. The body of literature dealing with interactions between mineral elements and plant disease in general is extensive (e.g., reviews by Graham 1983, and Huber 1978, 1980), but few reports deal specifically with sorghum. Reported effects of specific elements on some of the organisms associated with root and stalk rots are summarized in Table 1.

Macronutrients (N, P, K, Ca, Mg, and S) generally have no effects on disease resistance at supraoptimal levels, but usually have their effects only at low or deficient levels. On the other hand, the micronutrients (Cu, B, Mn, Fe, and Zn) have pro-

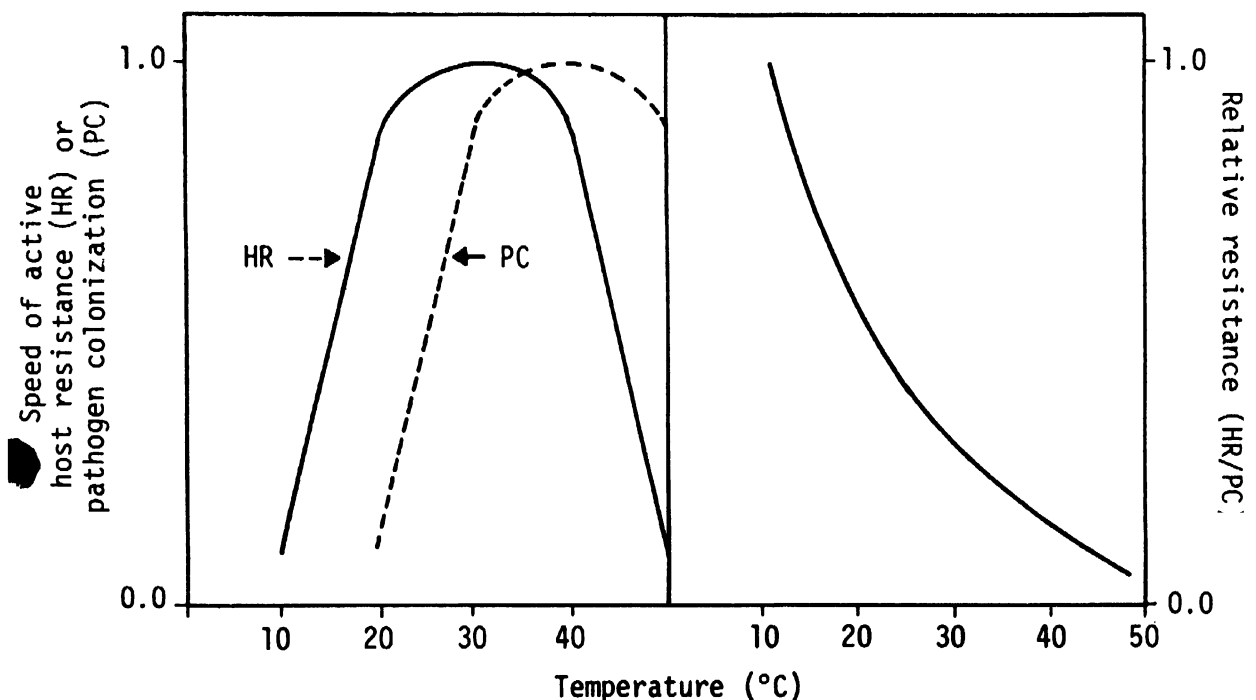


Figure 5. Illustrations of how temperature affects the relative resistance of a host based on its effects on the speed of pathogen colonization and speed of active host resistance. The resultant pattern of decrease in relative resistance at increasing temperatures fits observations of charcoal rot of sorghum caused by *Macrophomina phaseolina*. (Adapted from Bell 1982.)

Table 1. Summary of reported interactions of mineral elements and disease for some root/stalk rot pathogens.
(Source: Huber 1980.)

Pathogen	Mineral element												
	NH ₄	NO ₃	P	L	Ca	Mg	S	Na	Mn	Fe	Zn	B	Cu
<i>Diplodia zeae</i>	D ^a	I	I	D									
<i>Fusarium colmarum</i>									D	D	D		D
<i>Fusarium moniliforme</i>	I	D		D									
<i>Fusarium nivale</i>				D			D						
<i>Fusarium roseum</i>	I	D			D								
<i>Gibberella zeae</i>	D	±	±	D									
<i>Ophiobolus graminis</i>	D	±	D	D	I		D						
<i>Phythium arrhenomanes</i>	D	±	D										
<i>Rhizoctonia solani</i>	I	D	D	I	D	D	D	D	D				

a. Incidence of disease decreased (D), increased (I), or dependent on hosts or environmental conditions (+).

nounced effects on disease resistance at supraoptimal levels as well as at low or deficient levels. These responses are probably because the macronutrients are involved in compositional, structural, conformational, and osmotic functions in plants, and micronutrients usually function as catalysts, cofactors, and inhibitors. Increasing the supply of an element in deficient or low supply generally increases the resistance of plants to pathogens.

Many factors, interactions, and responses are involved in mineral element relationships to disease resistance. The effects of mineral elements on plant yield may involve not only the plant requirements for a specific element, but also the ways in which the element may change the host's defense mechanism against disease. Mineral elements may also have direct toxic effects on invading pathogens. Lignin and phenol synthesis seem to be more affected by certain elements (N, Cu, B, and Mn) than by others; phytoalexin synthesis also appears to be affected by certain other elements (Zn, Fe, and Ni); certain biochemical pathways for disease defense may also require specific elements (Si, Li, and Ni); competition between host and pathogen may occur with certain of the elements (Fe); and interactions and toxicities appear with almost all elements. The mechanisms for mineral-element defenses in disease resistance are multiple, and the function of each element in metabolism or plant disease resistance processes must be understood separately. So little is understood about the function of mineral elements in disease resistance that similarities of element functions and disease resistance may be coincidental.

Mycorrhizae and Mineral Element Uptake

Mycorrhizal fungi play important roles in assuring sufficient and constant supplies of nutrients to host plants under all conditions, but their importance may be magnified during drought. The importance of mycorrhizae in enhancing uptake of mineral elements became evident only in recent years (Tinker 1980, Tinker and Gildon 1983). Increased uptake of N by plants infected with ectotrophic mycorrhizae (ECM) has been suggested, but proof has not been conclusive. ECM fungi have been found to enhance Zn and K uptake, and their mycelia translocate Ca. On the other hand, vesicular-arbuscular fungi (VAM) have been found to enhance P, Zn, Cu, K, Si, and S uptake by host plants, and also to translocate Ca. VAM fungi are highly involved with enhancing P uptake by plants, especially under conditions of low P. The relationships between VAM fungi and P have been the subject of numerous investigations since their discovery.

Improvement of host plant nutrition by mycorrhizal infection should occur whenever the uptake rate of the specific element by the host root is restricted by transport mechanisms of the element in soils (diffusion and mass flow) below that required for optimum plant growth allowed by the environment, if mycorrhizae can absorb and transfer that particular element. Yield improvements are difficult to predict, but growth responses have been large in some cases. For example, the amount of soluble P fertilizer required to give the same growth response as VAM infection for several plants was around 100 kg P/ha, and as high as 500 kg P/ha for a citrus crop (Menge et al. 1978).

since micronutrients such as Cu, Zn, and Mn have very low soil mobility, mycorrhizae-enhanced plant uptake has been observed. The mechanisms for uptake and transfer of micronutrients within the mycelia are not fully known, but could be associated closely with P compound complexes such as polyphosphate.

The beneficial effects of VAM on apparent drought resistance of plants (Maronek et al. 1981) may result from two sources. Hyphae from VAM-infected roots extend some distance into the soil mass, effectively increasing the root length density and thereby reducing the distance water must flow through soil (Allen 1982, Gerdemann 1970, Safir et al. 1972). These root extensions could become important in maintaining high water uptake rates as Ψ_s and H fall due to evapotranspiration. Equally important, however, may be the continued growth of roots made possible by the enhanced uptake of P described above (Sieverding 1981). Continued or stimulated growth of root axes places larger root areas in contact with unexplored, wetter soil, thereby delaying the onset of stress. Since mineral nutrients added as fertilizers are usually concentrated in the upper 15 cm of the soil profile, mycorrhizal-enhanced uptake of mineral elements from soil too dry to support root growth may be very important to crop health and productivity, and deserves more extensive study.

Influence of Water- and Nutrient-Stress Interactions on Disease Development

Deficiencies of both water and nutrients, especially N, are the rule rather than the exception in many sorghum-producing regions in developing countries. Even in highly productive dryland systems, water availability has a strong influence on the uptake efficiency and recovery of added nutrients and may influence management decisions dealing with the amount and timing of fertilizer applications.

The total and seasonal nutrient requirements of a sorghum crop have been presented in detail (Lane and Walker 1961, Vanderlip 1972) and will not be repeated here except to point out that large quantities of N, P, and K are required during the relatively brief GS3. For example, at maturity, grain contains 67% of the plant's total N, 76% of its P, and 26% of its K. Much of the grains' total requirement can be supplied by uptake from soil, so long as the surface

remains moist or is frequently wetted. However, as the surface dries, root activity is forced to deeper strata that are normally low in nutrients, and grain demands are met by remobilizing elements stored in leaves, roots, and stalks. Under drought conditions it is not known whether senescence or firing of lower leaves is triggered by translocation of carbohydrates or mobile nutrients such as N.

High grain yields require high plant populations and large inputs of N, but these conditions also increase disease severity. Sachan et al. (ICRISAT, unpublished data, 1983) found a strong interaction between grain yield, N fertility, and stalk rot for sorghum hybrid CSH-6 subjected to water stress after anthesis with the line source system (Fig. 6). High N fertility resulted in both higher grain yield and greater incidence of stalk rot. The range of water supplies that resulted in a linear increase in grain yield also resulted in a linear decrease in disease incidence for both fertility levels.

Conclusions and Research Needs

Edaphic factors such as water availability, temperature, and mineral nutrient supply have been shown to have a large influence on both infection and disease development by normally weak pathogens causing root and stalk rots. Fungi are among the members of the soil microflora most resistant to low soil water potentials, making them ideally suited to the ecosystem of the near-surface soil horizon. Even mild water stresses trigger changes in host-root resistance, allowing infection at an earlier stage of growth than expected based on symptom expression. Disease spread in host tissues is associated with an increasing demand for carbohydrates and nutrients by the developing grain. Since soil water deficits during grain filling may reduce photosynthate production, greater disease incidence observed under these conditions suggests a causal relationship between the carbohydrate status of roots and stems and disease severity. The generality of this association has not been examined in detail. High supplies of N fertilizer also promote disease, but are required for high grain yields.

The line-source sprinkler system is an important tool for screening for resistance to both drought and disease. It provides a relatively simple means to establish a dependable, multilevel stress condi-

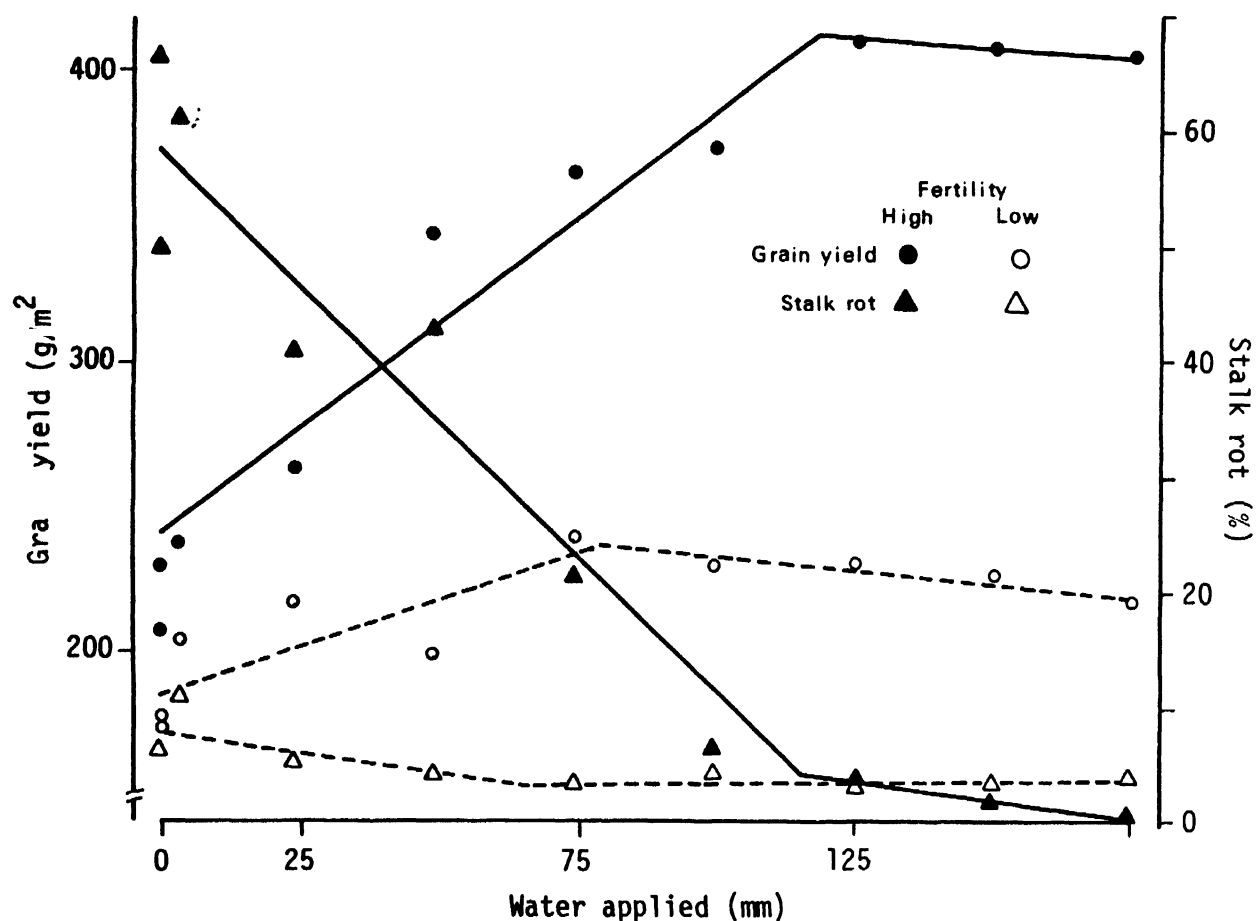


Figure 6. Influence of nitrogen fertility on the interaction among grain yield, charcoal rot incidence, and water applied after anthesis. Low fertility plots received 20 kg N ha⁻¹, while high fertility plots received 100 kg N ha⁻¹. (Source: Sachan et al., ICRISAT, unpublished data, 1983.)

tion in the field and overcomes many of the experimental limitations in studies of soilborne pathogens. Results from the line source system also suggest strategies of water management that may be effective in disease delay or prevention. Maintenance of high plant water potentials, at least during grain fill, are effective in prevention of yield losses due to disease and may be achieved by a variety of cultural and water management techniques. The introduction of drought- and disease-resistant cultivars into farming systems will present new opportunities for management for high yield.

Several important problems should receive added research emphasis. The role of water stress in the production and composition of root exudates should be examined in greater detail because of the possible importance of this source of organic and mineral nutrients to germination of propagules and growth of pathogens. Also, stress-induced

changes in root physiology should be studied closely because of the apparent role of even mild stress in the infection process. Root senescence is an almost unexplored area of research that has importance to both drought and disease resistance. The total amount of dry matter lost as exudates and during root degeneration is unknown.

Information about the importance of individual mineral nutrient elements to the pathogen and to disease development is badly needed, especially for sorghum. Little is known about interactions between water and nutrient availability near the soil surface. The importance of root growth in near-surface regions of the profile should be explored because of the large requirements for mineral elements and their concentration in that region. Finally, the importance of mycorrhizal fungi in enhancing sorghum resistance to drought and nutrient stresses remains to be defined.

• In summary the following is a list of specific topics for future research:

I. Effects of abiotic stresses on the host

- A. Optimum root system and rooting pattern
 - 1. Define "optimum" in terms of the soil-plant-atmosphere system.
 - 2. What is the role of root resistance?
 - 3. Determine efficient use of water resources.
- B. Root senescence and regeneration
 - 1. Determine the effects of low soil water potential on growth and survival, especially in the near-surface regions of the soil profile.
 - 2. What quantity of root dry matter is lost or remobilized?
 - 3. What is the role of root deterioration in microflora ecology?
 - 4. How much regeneration of roots is necessary for efficient water and nutrient uptake?
- C. Root exudates; quantity and composition
- D. Leaf firing
 - 1. What is the mechanism—heat or desiccation? To what degree does the retranslocation of carbon and minerals from the leaf affect its longevity?
 - 2. Determine genotypic differences.
 - 3. Determine progressive vs general firing.
- E. Floret abortion
 - 1. What controls head blasting—heat stress, growth inhibition due to water stress, involvement of hormones, etc.?
 - 2. What are the limits to recovery via seed size adjustment?
- F. Capacity and consequences of redistribution of stem and root reserves
 - 1. Is there some redistribution under all conditions?
 - 2. What is the relationship of reserves to yield under stress?
- G. Interactions of biotic stresses
- H. Role of individual nutrient elements and water x nutrient interactions on host growth, vigor, and senescence.

II. Effects of abiotic stresses on pathogens

- A. Confirmation of synthetic media results in soil system
 - 1. Most media studies use osmotic stress. What is the impact of soil water deficits through matric effects?
- B. Basis for apparent drought resistance
 - 1. Investigate stress levels at which propagules are resistant to heat and desiccation.
 - 2. What is the role of osmoregulation in maintenance of growth?
- C. Specific nutrient effects
- D. Temperature tolerance at low soil-water potential
 - 1. What is the effect of high temperatures near soil surface?
 - 2. Determine growth optimum shifts to higher temperature as water potential decreases in media studies.
- E. Investigate the relation between soil physical properties and fungal survival

III. Host/pathogen interactions

- A. Role of root exudates on germination, growth, and pathogenicity of fungi
- B. Effect of pathogen on exudates
- C. Mechanisms of infection
- D. Mechanisms for control of pathogen activity and spread in host tissues
- E. Mechanisms for yield reduction

IV. Edaphic stress/host stress/pathogen interactions under field conditions

- A. Inorganic nutrient availability to host and pathogen, including the role of mycorrhizal fungi
- B. Mechanisms for stress-induced predisposition to infection
- C. Direct vs indirect control of pathogen spread in tissues
- D. Separation of effects of abiotic stresses from biotic stresses on grain yield

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Questions

Partridge:

In your conclusion you state that "stress triggers changes in host root resistance, allowing infection at an earlier stage of growth than expected...." Do you have or can you elucidate data to support this conclusion?

Jordan:

Reports by Schneider and Pendery [1983] with maize and Odvody and Dunkle [1979] present evidence that mild water stress during some period before anthesis promotes colonization of roots by organisms reported to cause root and stalk rots.

Partridge:

Do you have or can you elucidate data to support your conclusion that "disease spread is associated with an increasing demand for CHO...."

Jordan:

Disease spread (symptom expression in stalk) is associated with CHO deposition in grain. The assumption is that the presence of developing grain creates an increased demand for CHO, but in reality this may just be a competing sink. Disease spread into the stalk during grain fill of fertile, but not sterile isolines appears to be the best example of this presumed increased CHO demand. References are cited in the text.

Partridge:

Dr. Clark, have phytoalexins been demonstrated in sorghum, and if so, have they been shown to affect stalk rot?

Clark:

I saw no literature on phytoalexins in sorghum. However, my literature search was not directed to phytoalexins, but to nutrient elements.