Stalk Rot of Corn: Mechanism of Predisposition by an Early Season Water Stress

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ABSTRACT

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The incidences of corn stalk rot (probably caused most often by *Fusarium moniliforme*) at the end of the season in field-grown plants exposed to a mild water stress during the pretassel, post pollination, or grain-filling stages of development were 60.3, 25.3, and 7.7%, respectively. The nonstressed control had 24.7% disease. There were no visible symptoms of water deficit during the treatment period. In a separate experiment, infection and systemic colonization of roots by *F. moniliforme* increased significantly following a mild early season water stress compared to nonstressed plants. Diurnal trends in plant water potential (ψ_p) and leaf diffusive resistance (r_l) of previously stressed infected (SI) plants were altered with respect to nonstressed infected (NI) plants and stressed and nonstressed healthy plants. At 3 days after the irrigation that terminated the stress, ψ_p in the SI plants was as much as 5 bars lower and r_l was significantly higher than those of plants that had received the other three treatments for several hours during the day. These trends were amplified at 8 days after the irrigation. By 15 days, when all plants were experiencing water deficits, diurnal trends in ψ_p and r_l in the SI and NI plants were similar. Calculations based on rates of water uptake and ψ_p when soil was at field capacity, indicated that resistance to water flow between roots and leaves was approximately doubled in the SI plants compared to that in plants that had received the other three treatments. Thus, under relatively high evaporative demand, predisposed plants behaved like chronically stressed plants even when adequate soil water was available later in the season; roots proliferated at greater soil depth and stalk and root senescence occurred during the reproductive growth stage. Because *F. moniliforme* is a pathogen of senescing tissues, we conclude that predisposition by a mild early season water deficit permanently increases the likelihood of chronic water stress during periods of relatively high evaporative demand or limited soil water availability, which leads to earlier senescence and increased susceptibility to the stalk rot pathogens. Cultural practices and breeding strategies for disease control are discussed in light of the proposed mechanism.

Fusarium moniliforme (Sheld.) emend. Snyd. & Hans. is probably the most prevalent pathogen causing stalk rot of corn (*Zea mays* L.) worldwide (23,24,34,36,69,71), and it is the primary pathogen in California (28). The disease also may be caused by other species of *Fusarium* and by *Gibberella, Diplodia,* and *Macrophomina* (34). Symptoms, which include internal rotting of the stalk and lodging of the plant, appear as the plant nears maturity (8,44). *F. moniliforme* has been isolated from roots and basal portions of symptomless stalks (24,36). Factors that enable *F. moniliforme* (a weak pathogen [34,36]) and other stalk rotting organisms to cause disease have been the object of much speculation (13,34,40,44,51,52,68). Moisture stress is a major predisposing factor (34,40), but no physiological explanations for this effect have been proposed.

In this paper, predisposition is defined as an induced state of susceptibility to disease caused by an event that occurs before the onset of symptoms. This definition, in contrast to that of Yarwood (70), includes the case of the predisposing event having occurred while the plant was symptomless but latently infected.

The purpose of this study was to determine the importance and physiological basis of a mild early season water stress in predisposing corn plants to stalk rot caused by *F. moniliforme*. A preliminary report has been published (60).

MATERIALS AND METHODS

Field experiment. A plot was established in an infested field in Tulare County, CA. Field corn, cultivar SX17A (P.A.G. Seeds, Minneapolis, MN), was planted in rows 75 cm apart at 2.8 cm intervals to give a final population of ~74,000 plants per hectare. Nitrogen and phosphorus were applied at 194 and 242 kg/ha, respectively. The three treatments consisted of withholding irrigation water until the mean midday leaf water potentials (ψ_l) in the stressed plants were 2 bars lower than those in nonstressed controls at the pretassel, postpollination, and grain fill stages of plant development. Delays in irrigation of approximately 10, 6, and 2 days, respectively, were required to achieve this level of stress. Measurements were made in situ with a modified Scholander pressure chamber (12,61) (Soil Moisture Equipment Corp., Santa Barbara, CA 93105). Except for the experimental treatments, plants were irrigated weekly. Care was taken not to stress any of the plants during pollination because this process is extremely sensitive to water deficits (46). Individual plots were 15 m long by five rows with the center 12 m of the center row being assessed for disease incidence and grain yield. Grain yield and percent moisture were determined and data were adjusted to 15% moisture equivalents. Stalk rot incidence was assessed 138 days after planting by severing stalks at the second internode above the soil surface and determining the percentage of plants with pith discoloration or rot.

Soil tank experiments. Because rooting patterns and plant and soil water parameters in the field were highly variable, an experimental system was devised to eliminate these sources of error and still maintain field meteorological conditions. Corrugated steel cylinders (1.52 m in height and diameter) lined with polyethylene, were placed above ground level on a layer of nylon window screen covering a bed of gravel at Davis, CA. The screen and gravel facilitated drainage and restricted roots from growing into the soil below. The tanks were then filled to within 15 cm of the rim with a Yolo fine sandy loam soil either noninfested or infested with *F. moniliforme*. Inoculum, which consisted of mycelium and microconidia, was prepared by growing the fungus on autoclaved ground barley straw and adding it to the field soil to give a final population of about 700 propagules per gram of soil, a level commonly found in California field soils (28). The soil had been stored outdoors in a pile and had not been cropped for at least 10 years. One week after the last of three weekly irrigations, soil samples were taken for analysis as follows: bulk density, 1.33; pH 7.3; electrical conductivity, 1.2 millimhos per centimeter; nitrate-N, 6.7 μg/g; phosphate-P, 65 μg/g; potassium, 736 μg/g; and textural

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classification, fine sandy loam.

Corn seeds, P.A.G. variety SX98, were planted in a 1.0-m circle in each tank on 5 June 1979. After emergence, seedlings were thinned to 13 equally spaced plants on the circumference of the circle, which corresponded to a population of 71,300 plants per hectare. The circular arrangement allowed for the installation of neutron moisture meter access tubes and tensiometers between plants while maximizing the number of soil sampling sites at the same relative locations. The tanks were fertilized at rates equivalent to those used in the field study.

Treatments consisted of withholding irrigation in each of three infested and noninfested tanks beginning at 5 wk after emergence (eight leaves fully emerged) and continuing until the midday ψ_l was at least 2.0 bars lower than the well-watered controls. This required a 6-day delay in irrigation. Subsequent irrigations, applied at weekly intervals, were identical in all treatments. Thus, there were four treatments with three replications (tanks) each: stressed (S) and nonstressed (N) plants grown in infested (I) and noninfested (N) soil (SI, NI, SN, and NN, respectively). Mean minimum and maximum soil temperatures at a depth of 20 cm during the course of the experiment were 23.7 and 27.6 C, respectively. The experiment was repeated the following year.

Root length density and infection. Root development and infection were assessed periodically during the season. A Veihmeyer soil sampling tube (Hansen Machine Works, Sacramento, CA), 2.54 cm in diameter, was used to extract cores at 15-cm increments to a depth of 1.4 m. Sampling sites between plants were in the same relative position as the neutron moisture meter access tubes. Soil samples were returned to the laboratory, soaked for 1 hr in a 1% solution of sodium hexametaphosphate (HMP) to disperse aggregates, agitated, and decanted through a 1-mm sieve that retained roots.

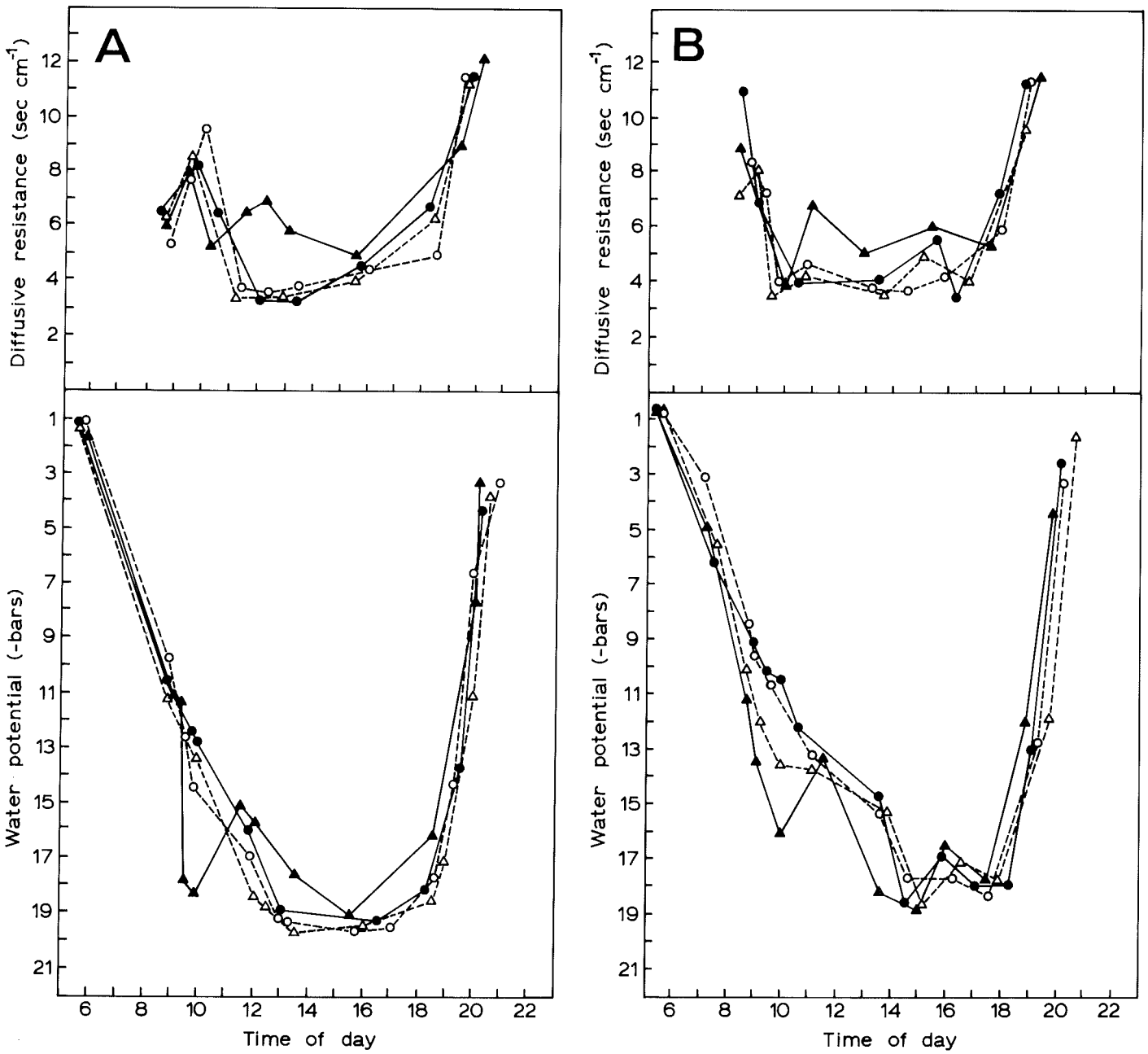
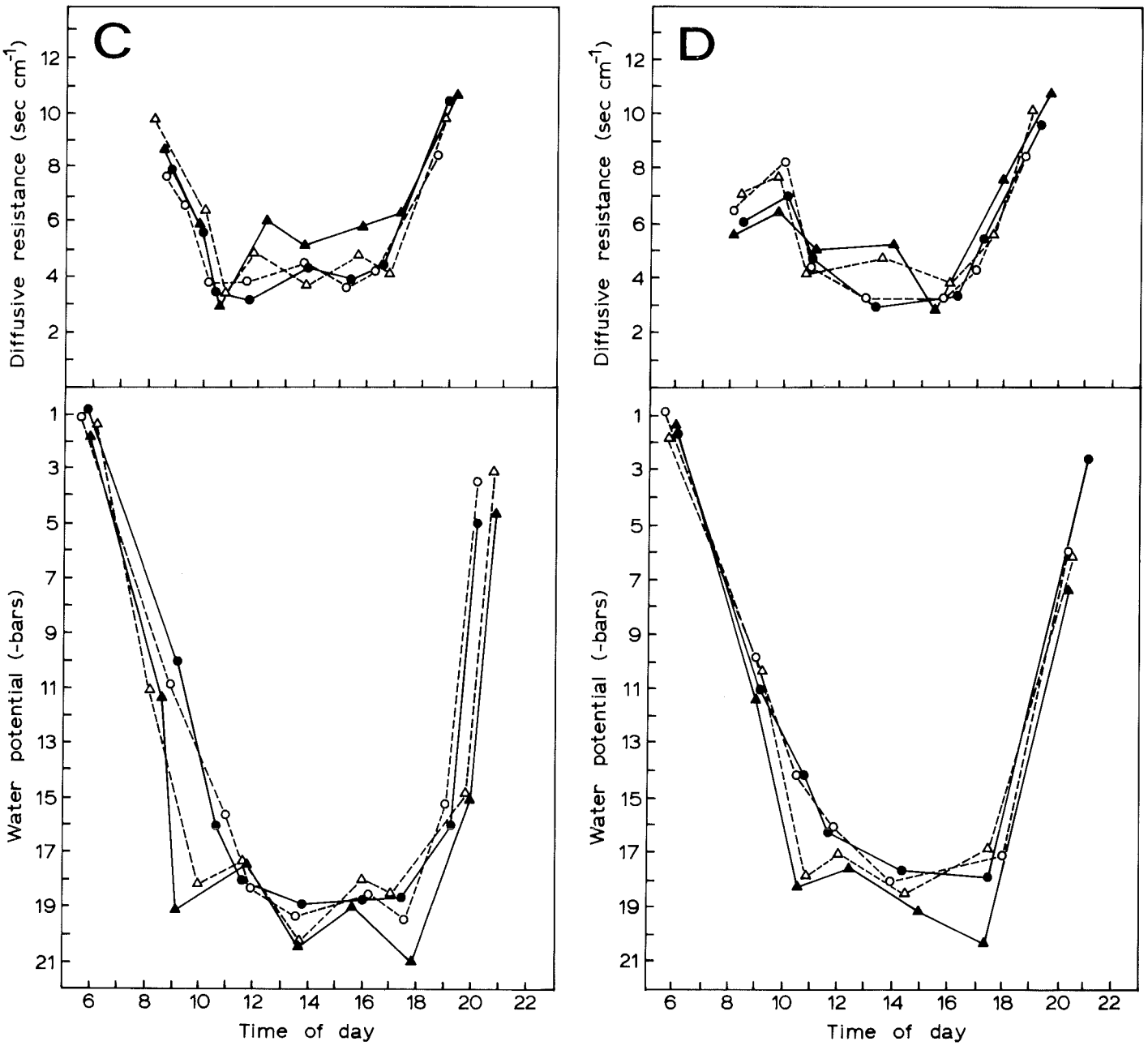


Fig. 1. Diurnal trends in leaf water potential and diffusive resistance in corn plants grown in soil either noninfested or infested with *Fusarium moniliforme* and either exposed to a mild early season water stress or nonstressed as follows: noninfested, nonstressed (o------o); noninfested stressed (•——•); infested, nonstressed (△------△); and infested, stressed (▲——▲). Measurements were made at **A,** 3 days; **B,** 8 days; and (see next page) **C,** 15 days after the irrigation which terminated the stress treatment and again at **D,** 3 days after the next irrigation. Each point is the mean of five determinations. Mean standard error over all treatments and days when water potential was below −11 bars is 2.2 bars.

Root length density (centimeters of root per cubic centimeter of soil) was determined 7 days after the termination of the stress treatment as follows: All of the roots extracted from a 15-cm core were suspended in water retained in a large Büchner funnel with a filter paper disk that was attached to a vacuum flask. After clumps of roots were teased apart, vacuum was applied to quickly drain the water. The filter paper bearing the roots was then removed and placed under a plexiglass sheet that had been etched with a grid. Root length was then determined by Newman's (48) line intersect method as modified by Torssell et al (63). Counts of discolored and healthy-appearing roots were recorded separately.

A duplicate sample was extracted as previously described and quantitatively assayed for infection by *F. moniliforme*. Portions of the roots collected from the sieve were either rinsed in sterile HMP or surface sterilized by immersion in 0.2% sodium hypochlorite for 4 min, rinsed in sterile water, and plated on Komada's medium (35), which is selective for *Fusarium* spp. *F. moniliforme* is easily recognized on this medium by its distinctive colony morphology and chains of microconidia. Root length on each plate was determined, and, after incubation for 7 days at 23 C, the number of colonies of the pathogen was determined on each plate. In addition, the total length of systemically infected root was estimated in each plate by measuring those portions of surface-sterilized root segments that had oval colonies larger than 0.5 cm (maximum diameter). Data are expressed as number of colonies or centimeters of systemic infection per 100 cm of root.

Plant and soil water relations. Measurements of ψ_l and leaf resistance to diffusion of water vapor (r_l) were made at approximately 2-hr intervals from predawn until after dark on the third, eighth, and 15th days after the stress was relieved. An additional set of measurements was made at 3 days after the next irrigation. A diffusion porometer (32) (LI 60 meter with LI 20S sensor, Lambda Instruments, Lincoln, NE), calibrated daily according to the manufacturer's recommendations, was used to measure r_l on the adaxial and abaxial surfaces of each of five upper leaves that were exposed to direct sunlight. Assuming individual surface resistances acted in parallel (56), total r_l was calculated by $1/r_l = 1/r_a + 1/r_b$ in which r_a and r_b are the adaxial and abaxial resistances, respectively. The same leaves were used for determining ψ_l as previously described. Some of these leaves, which were collected while ψ_l was declining, were quickly sealed in vials and stored on ice for transport to the laboratory for determination of relative water



content (RWC) as described by Barrs (4).

Pith density of the second internode above the soil surface was determined 3 days after the last irrigation before the imposition of the stress treatment and again 3 days after an irrigation when plants were in the dough stage of development about 30 days after silking. Two plants in each tank were severed at the soil surface and at the third node. The stalk segments were sealed in polyethylene bags and stored on ice for transport to the laboratory. The rind of the second internode was removed and pith density was determined according to the methods of Craig and Hooker (10).

Soil moisture was monitored at 23, 38, 53, 68, 84, 99, and 114 cm with a neutron probe (Campbell Pacific Nuclear Corp., Pacheco, CA) that had been calibrated in the tanks. A moisture release curve was constructed so that readings of volumetric water content obtained with the probe could be converted to soil water potential (ψ_s).

RESULTS

Field experiment. Incidences of stalk rot in the field plot for the adequately watered control and pretassel, postpollination, and grain fill stress treatments were 24.7, 60.3, 25.3, and 7.7%, respectively (LSD = 11.5, $P = 0.05$). Symptoms were not apparent until about 2 wk before harvest, about 11 wk after the imposition of the first stress treatment. There was a statistically significant positive correlation ($r^2 = 0.542$, $P = 0.05$) between disease incidence and yield.

Tank experiments. Diurnal trends in ψ_l and r_l at 3 days after the experimental stress treatment was relieved indicated that the water relations of plants in the SI treatment had been drastically affected (Fig. 1A). Between 0530 (before sunrise) and 0930 hours plants in all four treatments exhibited about the same rate of decline in ψ_l, which reached −11 bars. At 0930 hours, ψ_l in the SI treatment fell precipitously and by 1000 hours averaged −18.5 bars, but by 1130 hours it had increased to about −15 bars. Diffusive resistance also was affected in this treatment; a sudden increase occurred at about the same time that ψ_l was recovering. Compared to the other three treatments, r_l remained high until about 1530 hours. There were no such cycles in ψ_l or r_l in the other treatments.

Based on midday ψ_l, all treatments normally would have been irrigated at 7 days to avoid stress. However, the drying cycle was allowed to continue for an additional 22 days so that the effects of the predisposing treatment could be evaluated under conditions of

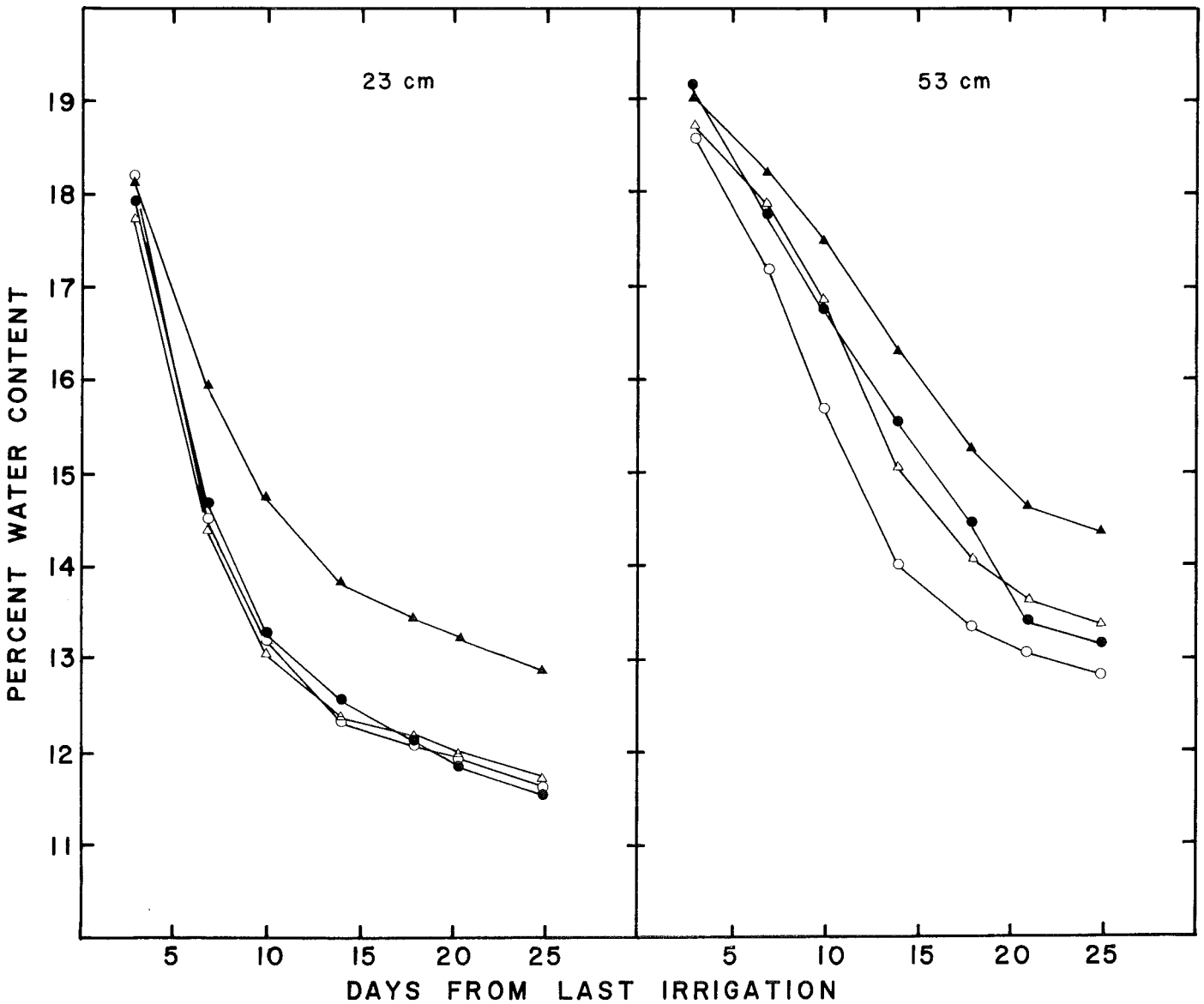


Fig. 2. Relationships of soil water content as a function of time after the irrigation that terminated the experimental stress treatment at depths of 23 and 53 cm for corn plants grown in soil either noninfested or infested with *Fusarium moniliforme* and either exposed to a mild early season water stress or nonstressed as follows: Noninfested, nonstressed (o——o); noninfested, stressed (•——•); infested, nonstressed (△——△); and infested, stressed (▲——▲). Each point represents the mean of five neutron moisture meter readings in each of three replications. The standard error averaged over all treatments and times at both depths is 0.8%.

severe water deficit.

At 8 days after termination of the predisposing stress, diurnal trends in ψ_l in the four treatments were similar to the third-day measurements except that plants in the NI treatment also were beginning to show a steep decline at about 0900 hours (Fig. 1B). Stomatal cycling, a sudden increase in r_l, was again evident in the SI treatment (Fig. 1B).

Plants in the SI and NI treatments exhibited the same diurnal trends in ψ_l and r_l at 15 days (Fig. 1C). By 1000 hours, ψ_l in both infested treatments had fallen to −18 to −19 bars then increased to about −17.5 bars at 1130 hours. There were two additional cycles in these treatments with ψ_l of −20 bars at 1330 hours and −21 bars at 1730 hours in the SI treatment. Stomatal cycling also was evident at this time (Fig. 1C).

Ten days after the 15-day readings all tanks were irrigated to saturation and allowed to drain to field capacity for 3 days. At this time another set of measurements was made (Fig. 1D). The noninfested treatments showed the same diurnal trends in ψ_l and r_l as those recorded 3 days after the previous irrigation (compare Figs. 1A and D). However, plants in the NI treatment showed the same precipitous decline in ψ_l as the SI treatment reaching about −18 bars by 1030 hours and making a slight recovery by 1230 hours. Plants in the SI treatment then declined to about −20.5 bars by 1730 hours. As before, there were differences in r_l between the two treatments (infested and noninfested) (Fig. 1D).

Inasmuch as rates of transpiration, hence plant water relations, are determined in part by atmospheric evaporative demand (58), the following meteorological data are provided as a reference for the tank study. Rates of evaporation from a standard meteorological pan located about 2 km from the tanks were, respectively, 1.37, 1.09, 1.07, and 0.83 cm/day for the 4 days during which diurnal measurements were made. Maximum temperatures and minimum relative humidities for each of the 4 days were, respectively, 41.1, 35.5, 34.4, and 32.2 C; and 10, 15, 13, and 24%.

Soil water extraction patterns measured at depths of 23 and 53 cm for 25 days following the termination of the experimental stress showed that rate of water uptake by plants in the SI treatment was significantly lower than those in plants that received the other three treatments (Fig. 2). Rates of extraction in all four treatments decreased substantially at about 13 days after irrigation at 23 cm (notice the time at which the curves become linear in Fig. 2A). However, in relating water content to ψ_s by using the moisture release curve, the reduced rate of water extraction by plants in the SI treatment began at ψ_s of −0.53 bars while soil water availability became limiting in the other three treatments at about −0.88 bars. The same trends were observed at 53 cm (Fig. 2).

There were no significant differences among the four treatments in the internal water relations of the leaves as determined by relating ψ_l to r_l (Fig. 3), and RWC (Fig. 4).

Root infection, root length density, and pith density. Root infection was assessed at 3 days after the termination of the experimental stress in the two infested treatments at 23 cm (Table 1). There was no significant difference in root colonization by the pathogen when roots were not surface sterilized. However, after surface sterilization, there were about 7- and 14-fold increases in nonsystemic and systemic infections in the SI as compared to the NI treatments, respectively.

Root length density was determined at depths of 23, 53, and 83 cm at the same time that root infection was assessed (Table 2). At 23 cm, there were significantly less healthy roots with a significantly larger percentage of discolored roots in the SI treatment compared to the other three. At 53 cm, there were no significant differences in total root length density, but the proportion of discolored roots was two- to threefold greater than the other three treatments. Total root length density at 83 cm in the SI treatment was about twice the value for the other three treatments, which averaged 2.8 cm/cm^3. There were no detectable differences in percentage discolored roots at this depth.

Pith density was determined 3 days after the last irrigation before

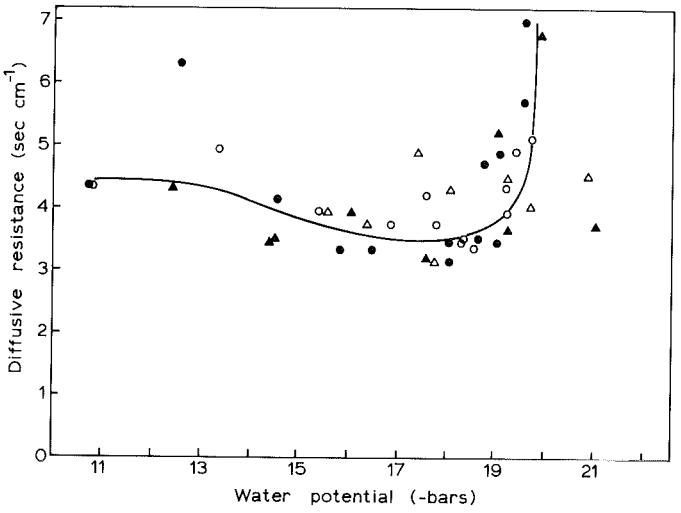


Fig. 3. Relationship between water potential and diffusive resistance in leaves of corn plants grown in soil either noninfested or infested with *Fusarium moniliforme* and either exposed to a mild early season water stress or nonstressed as follows: Noninfested, nonstressed (o); noninfested, stressed (•); infested, nonstressed (△); and infested, stressed (▲). Each point represents the mean of five determinations, which were made while leaf water potential was declining. The line was visually fitted to the data points.

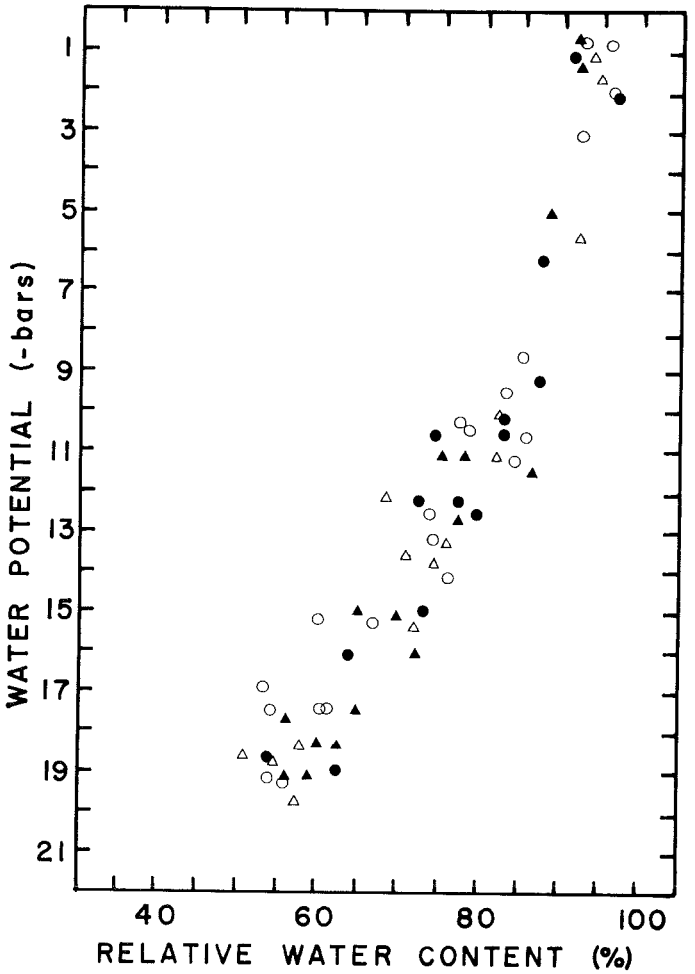


Fig. 4. Relationship between water potential and relative water content in leaves of corn plants grown in soil either noninfested or infested with *Fusarium moniliforme* and either exposed to a mild early season water stress or nonstressed as follows: Noninfested, nonstressed (o); noninfested, stressed (•); infested, nonstressed (△); and infested, stressed (▲). Each point represents the mean of three determinations, which were made while leaf water potential was declining.

the imposition of the stress treatment and again at 3 days after the next irrigation (Table 3). At the first sampling date, there were no differences in pith density among the four treatments. However, after the stress, pith density in the SI treatment was significantly lower than the other three. Pith in the SI treatment at the second sampling was more spongelike and white as compared to the other three treatments, which were still succulent.

Calculations of rate of water uptake and resistance to water flow in plants. Rates of water uptake at depths of 23 and 53 cm were calculated by first determining the volume of water extracted per cubic centimeter of soil in a 24-hr period with the neutron probe then dividing this value by the root length density at the appropriate depth. Values are expressed as cubic centimeters of water per centimeter of root per day. Mean rates of water uptake at the two depths for treatments NN, SN, and NI were about 70% greater than the SI treatment (Table 4).

Although absolute values of resistance to liquid water flow in plants can be obtained only under steady state conditions (9), for comparative purposes, we present values that were determined during a diurnal cycle for all treatments. Whole-plant resistance was calculated according to the transposed equation of Kaufman and Hall (33):

$$r_{sl} = (\psi_l - \psi_s)/F$$

where r_{sl} is resistance to flow between soil and leaf and F is rate of flow, which was determined as previously described. Calculations were made for the third day after the irrigations that terminated the experimental stress at which time ψ_s was about -0.1 bars for all treatments. Resistance to water flow through soil was eliminated as a variable (see Hsiao et al [27] for a complete discussion) in the calculations in that r_s is negligible with respect to r_{sl} at field capacity (6,19,49).

Estimates of r_{sl} for the SI treatment were about twofold larger than the other three treatments at 23 and 53 cm depths (Table 4). There were no significant differences among treatments NI, SN, and NN at either depth. Estimates of r_{sl} at 53 cm were about twice as large as the values at 23 cm in all four treatments.

In an effort to determine the primary site of increased r_{sl} (ie, roots or stalks) ψ_l was determined for leaves from the tops and bottoms of one plant from each replication at midday. Differences between the two leaves did not exceed 2 bars in any treatment.

TABLE 1. Influence of a mild early season water stress on root infection and systemic colonization of corn roots by *Fusarium moniliforme*

Treatment	Root infection (colonies per 100 cm of root)		Systemic colonization[c] (cm per 100 cm of root)
	Before surface sterilization[a]	After surface sterilization[b]	
Nonstressed	79	6*[d]	
Stressed	92	42	14

[a] After a thorough washing, known lengths of root were plated on Komada's medium (35) and numbers of colonies of *F. moniliforme* were determined after 7 days of incubation at 23 C.
[b] Roots were washed, surface sterilized in 0.2% sodium hypochlorite for 4 min, then plated as described above.
[c] Total length of oval colonies longer than 0.5 cm growing from surface sterilized roots plated as described above.
[d] Asterisk indicates significant difference ($P = 0.05$) between treatments according to student's t-test.

DISCUSSION

Several observations have been made concerning the role of water stress as an environmental determinant in stalk rot of corn (34,40,45); however, this factor has not been critically evaluated under field conditions. Results from our field study clearly show the predisposing effect of an early season water deficit on disease development, the predisposing event having occurred 11 wk prior to the onset of symptoms. It should be noted that stressed plants in the present study were not wilted during the predisposing water deficit or at any time during the experiment.

Even though symptoms were not apparent for many weeks after predisposition, immediate effects were observed in enhanced rate of infection and systemic colonization of roots. This in itself is significant in that Whitney and Mortimore (68,69) demonstrated that stalk infection originates from infected roots. Thus, we would expect that, for a given cultivar, there would be a direct correlation between rate of root infection and systemic colonization early in the season and subsequent disease incidence.

Hornby and Ullstrup (24,25) proposed that resistance to stalk rot in corn is first manifested in restricted root infection, and that resistance to root infection and colonization during the vegetative phase of plant growth is associated with maintenance of a certain level of physiological vigor. Their experimental control of root vigor involved removing leaves and the use of different genotypes that were either maintained in the vegetative state by interrupting pollination or allowed to develop into the reproductive phase. In our studies, root senescence was experimentally manipulated by imposition of a mild water deficit during vegetative development. Nevertheless, our results substantiate their hypothesis by clearly showing that an environmental stress accelerated root senescence of plants in the noninfested treatment and resulted in enhanced infection and systemic colonization of plants in the infested treatment. The lack of significant difference in root colonization as measured before surface sterilization between the stressed and

TABLE 2. Root length density of healthy appearing and discolored corn roots at three depths as affected by an early season water stress and infection by *Fusarium moniliforme*

Treatment[a]	Root length density (cm of root per cm^3 of soil) at the indicated depths											
	23 cm				53 cm				83 cm			
	H[b]	D[c]	Total	%D[d]	H	D	Total	%D	H	D	Total	%D
Nonstressed, noninfested	8.3	0.8	9.1	8.8	4.4	0.3	4.7	6.4	2.7	0.1	2.8	3.6
Stressed, noninfested	7.3	1.8	8.3	19.8	5.4	0.5	5.9	8.5	2.9	0.1	3.0	3.3
Nonstressed, infested	7.0	1.4	8.4	16.7	4.0	0.6	4.6	13.0	2.7	0.1	2.8	3.5
Stressed, infested	5.4	2.7	8.1	33.3	5.2	1.3	6.5	20.0	6.2	0.2	6.4	3.2
LSD ($P = 0.05$)	1.3	0.8	NS[e]	8.5	NS	0.8	NS	11.1	2.8	NS	3.1	NS

[a] Treatments consisted of imposing a mild water stress by withholding irrigation water beginning at 5 wk after emergence until mean midday plant water potential was 2 bars lower than the nonstressed treatments. This was done in soil either noninfested or infested with *F. moniliforme*.
[b] Healthy appearing roots.
[c] Discolored roots.
[d] Percent of total root length that was discolored.
[e] No significant differences among treatments ($P = 0.05$).

nonstressed treatments indicates that predisposition did not have a direct effect on the pathogen in the soil; rather it was mediated through the host.

Recently, Kommedahl et al (36) suggested that most stalk infections probably do not originate from roots. Their conclusion was based on sequential samplings of roots and stalks from, which according to their report, during the latter part of the season, the frequency of isolation of *Fusarium* spp., including *F. moniliforme*, decreased in roots while it increased in stalks. They did not indicate if they included discolored or senescing roots in their samples. Because senescing roots, particularly those colonized by saprophytes such as *Fusarium* spp., would soon be decomposed (25,69), it is possible that most of the roots remaining by the end of the season would be vigorous and relatively free of infection.

The foregoing discussion was concerned with the initial root infection process that occurred shortly after predisposition. Inasmuch as stalk rot symptoms were not apparent until 11 wk after predisposition, plants were well irrigated for the duration of the season, and root infections are generally restricted during the vegetative stage of plant development (25), we now discuss the influence of enhanced early season root infection on subsequent plant water relations and disease development.

In comparing the diurnal trends in ψ_l and r_l for the four treatments, it is obvious that the predisposing treatment profoundly affected the manner in which these plants reacted to the environment. At 3 days after the irrigation that terminated the water stress, ψ_l was as much as 6 bars lower for 3 hr, and r_l was significantly increased for about 6 hr during the day in the SI as compared to the other three treatments. These trends were amplified at 8 days after the irrigation. At 15 days, both infested treatments were stressed for water and were showing the same diurnal trends. Thus, at 3 days after the next irrigation, both infested treatments had been previously stressed and were showing identical diurnal trends in ψ_l and r_l.

The similar relationships among treatments in ψ_l, r_l, and RWC indicate that the factor causing stress in leaves was a reduced supply of water rather than an alteration in the solute relationships of the tissue (2,4). These trends are comparable to those reported by other workers (1,64). Barrs (5) concluded that stomatal cycling, as observed in this study, may be caused by unusually high or variable resistance to water flow in roots. Furthermore, the small differences in ψ_l between top and bottom leaves indicated that the stem was not a major contributor to r_{sl}. Our estimates of r_{sl}, which are similar to those reported by other workers (27) but which cannot be considered absolute because they were not determined at steady state, indicate that root resistance was approximately doubled in the SI treatment. This explains why plants in this treatment, compared to the other three, could not extract as much water from the soil profile, thus becoming far less efficient in using stored soil water. Such an increase in resistance is not drastic when one considers that other vascular wilt and root diseases cause increases ranging from 14- to several hundredfold (14,15,57,59).

The trends discussed above indicate that predisposed plants were forced to behave like chronically stressed plants for the duration of the season even when soil water was at field capacity. Furthermore, in corn and other plants in the vegetative state, increased root proliferation in the lower soil stratum is a characteristic response to long-term soil moisture deficits (21,26,39,53). During vegetative growth, corn roots act as the largest sink for photosynthate (22) and grow at the expense of other organs during water stress (3). In addition, our results show that root growth and senescence vary within the profile indicating that assimilates may be mobilized from roots in the upper dry stratum to those at lower depths where more moisture is available. However, during reproductive growth, roots as well as stalks are poor competitors for assimilates during periods of water deficits and, in fact, serve as sources of assimilates for the developing grain, thus accelerating senescence in these tissues (30,38,66). Boyer and McPherson (7) reported that net photosynthesis in corn was reduced by 85% at ψ_l of −18 to −20 bars while translocation from vegetative organs (ie, accelerated senescence) to developing kernels was relatively unaffected and that symptoms of water stress during this time were not obvious. In the present study, stalk senescence, or cell death, was associated with low pith density as described by Pappelis and co-workers (51,52) and root senescence was associated with discoloration. The relatively low pith density of plants that received the SI treatment, as compared to the NI treatment, was within the range of stalk rot-susceptible inbreds as reported by Craig and Hooker (10).

In view of the water relations of predisposed plants and the fact that stalk rot is a disease of senescing root (25,45) and stalk (10,44,51,52,65) tissues, we propose the following mechanism to explain predisposition by an early season water deficit. Water stress during vegetative growth causes an acceleration of root senescence in the upper soil strata. These senescing roots are more susceptible to infection and limited spread by the pathogen, are inefficient in water uptake, and, under meteorological conditions of high evaporative demand, lead to chronic water stress in the plant. During reproductive growth, such stress results in a remobilization of stored assimilates and senescence and death of cells in roots and stalks, all of which are requisite for systemic spread by stalk rotting organisms. Thus, the direct correlation between yield and disease incidence in our field experiment, which confirms reports by others (13,34), can be attributed to enhanced susceptibility caused by accelerated translocation of assimilates from vegetative organs to

TABLE 3. Influence of a mild early season water stress and *Fusarium moniliforme* on pith density in corn determined before and after the imposition of stress

Treatment[b]	Pith density ($g \cdot cm^{-3}$)[a]	
	Before stress[c]	After stress[d]
Nonstressed, noninfested	0.86	0.79
Stressed, noninfested	0.90	0.76
Nonstressed, infested	0.80	0.72
Stressed, infested	0.81	0.59*[e]

[a] Determined according to the method of Craig and Hooker (10).
[b] Treatments consisted of imposing a mild stress by withholding irrigation water beginning at 5 wk after emergence until mean midday plant water potential was 2 bars lower than the nonstressed treatments. This was done in soil either noninfested or infested with *F. moniliforme*.
[c] Determined at 3 days after the last irrigation before the imposition of stress.
[d] Determined at 3 days after an irrigation about 30 days after silking.
[e] Significantly different ($P = 0.05$) from other three treatments.

TABLE 4. Rate of water uptake and resistance to water flow in corn plants as affected by a mild early season water stress and infection by *Fusarium moniliforme* at two soil depths

Treatment[b]	Rate of water uptake (cm^3 per cm root per day) at indicated depth[a]		Resistance to water flow between soil and leaf (bars per cm^3 per cm of root per day) at indicated depth	
	23 cm	53 cm	23 cm	53 cm
Nonstressed, noninfested	0.19	0.11	60.2	115.7
Stressed, noninfested	0.16	0.09	68.7	126.8
Nonstressed, infested	0.16	0.09	71.9	127.7
Stressed, infested	0.10*[c]	0.05*	116.1*	320.0*

[a] See text for assumptions and method of calculating rate of water uptake and resistance to water flow.
[b] Treatments consisted of imposing a mild stress by withholding irrigation water beginning at 5 wk after emergence until mean midday plant water potential was 2 bars lower than the nonstressed treatments. This was done in soil either noninfested or infested with *F. moniliforme*.
[c] Significantly different ($P = 0.05$) from other three treatments.

seed.

Our studies were conducted under microclimatic conditions of high evaporative demand such that small increases in resistance to liquid water flow in the soil or plant would result in significant decreases in ψ_l and alterations in assimilate partitioning. These physiological responses by the plant would not be so pronounced under meteorological conditions, which are not as conducive to high rates of transpiration. Under these conditions, even though predisposition may have occurred early in the season, disease severity would not increase unless there was a deficit in soil moisture availability later in the season.

Recently, Dodd (13) proposed a "photosynthetic stress-translocation balance concept" for stalk rot of corn, which states "predisposition is associated with carbohydrate shortage in root tissue, which is caused by the combination of reduction of photosynthesis and intraplant competition for carbohydrate by developing kernels of grain. Consequently, root tissue has a weakened cellular defense system allowing invasion and degeneration by soil microorganisms." The only evidence offered in support of this hypothesis was an association of numbers of kernels produced by rotted or healthy stalks at the end of the season at two plant spacings at which time he reported that diseased plants had 11–13% more kernels. From this, he deduced that increased grain yield had occurred at the expense of stalk and root reserves, which he did not measure. Another plausible explanation for these findings is that CO_2 exchange rate per unit leaf area may have increased in response to the larger sink demand (20). He reported no determinations of root or stalk condition, rates of photosynthesis or translocation, pith density, root infection trends, water relations, or any other stress-related physiological processes at any time during the season even though all of these factors were incorporated into the hypothesis. In view of these inadequacies, we reject Dodd's hypothesis as being far too broad to explain a single predisposing factor such as early season water stress. Because plants respond to different environmental stresses in various ways, each stress factor that may act as a predisposing agent, such as water deficit, soil compaction, nutritional imbalance, inadequate light, etc., must be studied separately before a unifying concept can be proposed.

Our findings suggest several possibilities for disease control. Inasmuch as plant water stress induces susceptiblity to otherwise weak stalk-rotting pathogens, control of plant water status under field conditions might have potential. Papendick and Cook (50) arrived at the same conclusion following their studies on foot rot of wheat. This could be achieved by: altering soil structure to increase soil water availability (55) and to encourage deeper rooting (62); closely monitoring soil water status and using appropriate irrigation techniques (55,67) including mist (54); and using antitranspirants (17,18,37) and reflectants (42). The recent development of remote sensing techniques to identify periods of moisture stress (41) and models for estimating water requirements under different meteorological conditions (11,31,43) now make it possible to implement control strategies involving manipulation of plant ψ_l at the appropriate time.

Breeding strategies must take into account the associations among chronic water stress, altered assimilate partitioning, and induced senescence and susceptibility to stalk rot. Our results indicate that corn plants capable of photosynthesizing at reduced ψ_l and maintaining vigor in roots and stalks during periods of water deficit should be resistant to the disease. Interestingly, Johnson and Tanner (29) demonstrated that corn inbreds maintain a higher proportion of soluble carbohydrates in their stems than do more productive hybrids and that inbreds and hybrids are equal in vegetative yield, but that rate of grain fill is up to 50% higher in the hybrids. Thus, the very trait that makes hybrids more productive than their inbred parents, translocation of a greater proportion of soluble solids from vegetative organs, also conditions them for susceptibility to stalk-rotting fungi, particularly under stress conditions. Furthermore, Evans and Wardlaw (16) stated that although stored carbohydrates in vegetative plant organs are of value as an insurance against late stresses, they nevertheless represent unused yield potential that should be exploited by plant breeders. We conclude that such breeding strategies must be used with caution and that drought tolerance mechanisms other than induced senescence of roots and stalks should be evaluated for corn. Recently, Mtui et al (47) showed that there are differences in yield characteristics and water-use efficiency among corn genotypes under conditions of high transpirational demand, but they did not determine if grain dry matter was accumulated at the expense of vegetative organs. Evaluations of inbreds and hybrids under stress conditions as described by Mtui et al (47) plus determinations of photosynthate partitioning characteristics should be useful in identifying sources of resistance to stalk rot.

LITERATURE CITED

1. Acevedo, E., Fereres, E., Hsiao, T. C., and Henderson, D. W. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. Plant Physiol. 64:476-480.
2. Ayres, P. G. 1978. Water relations of diseased plants. Pages 1–60 in: Water Deficits and Plant Growth. Vol. V. Water and Plant Disease. T. T. Kozlowski, ed. Academic Press, New York. 323 pp.
3. Barlow, E. W. R., Boersma, L., and Young, J. L. 1976. Root temperature and soil water potential effects on growth and soluble carbohydrate concentration of corn seedlings. Crop Sci. 16:59-62.
4. Barrs, H. D. 1968. Determination of water deficits in plant tissues. Pages 235–368 in: Water Deficits and Plant Growth. Vol. I. Development, Control and Measurement. T. T. Kozlowski, ed. Academic Press, New York. 390 pp.
5. Barrs, H. D. 1971. Cyclic variations in stomatal aperture, transpiration, and leaf water potential under constant environmental conditions. Annu. Rev. Plant Physiol. 22:223-236.
6. Blizzard, W. E., and Boyer, J. S. 1980. Comparative resistance of the soil and the plant to water transport. Plant Physiol. 66:809-814.
7. Boyer, J. S., and McPherson, H. G. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-28.
8. Christensen, J., and Wilcoxson, R. D. 1966. Stalk rot of corn. Phytopathological Monogr. 3. Am. Phytopathol. Soc., St. Paul, MN. 59 pp.
9. Cowan, I. R., and Milthorpe, F. C. 1968. Plant factors influencing the water status of plant tissues. Pages 137–193 in: Water Deficits and Plant Growth. Vol. I. Development, Control and Measurement. T. T. Kozlowski, ed. Academic Press, New York. 390 pp.
10. Craig, J., and Hooker, A. L. 1961. Relation of sugar trends and pith density to Diplodia stalk rot in dent corn. Phytopathology 51:376-382.
11. De Bruyn, L. P., and De Jager, J. M. 1978. A meteorological approach to the identification of drought sensitive periods in field crops. Agric. Meteorol. 19:35-40.
12. De Roo, H. C. 1969. Leaf water potentials of sorghum and corn, estimated with the pressure bomb. Agron. J. 61:969-970.
13. Dodd, J. C. 1980. Grain sink size and predisposition of *Zea mays* to stalk rot. Phytopathology 70:534-535.
14. Duniway, J. M. 1976. Water status and imbalance. Pages 430–449 in: Physiological Plant Pathology. R. Heitefuss and P. H. Williams, eds. Springer-Verlag, New York. 890 pp.
15. Duniway, J. M. 1977. Changes in resistance to water transport in safflower during the development of Phytophthora root rot. Phytopathology 67:331-337.
16. Evans, L. T., and Wardlaw, I. F. 1976. Aspects of the comparative physiology of grain yield in cereals. Adv. Agron. 28:301-359.
17. Fuehring, H. O. 1973. Effect of antitranspirants on yield of grain sorghum under limited irrigation. Agron. J. 65:348-351.
18. Gale, J., and Hagan, R. M. 1966. Plant antitranspirants. Annu. Rev. Plant Physiol. 17:269-282.
19. Gardner, W. R., and Ehlig, C. F. 1962. Impedence to water movement in soil and plant. Science 138:522-523.
20. Gifford, R. M., and Evans, C. T. 1981. Photosynthesis, carbon partitioning and yield. Annu. Rev. Plant Physiol. 32:485-509.
21. Hoffman, G. J., Rawlins, S. L., Garber, M. J., and Cullen, E. M. 1971. Water relations and growth of cotton as influenced by salinity and relative humidity. Agron. J. 63:822-826.
22. Hofstra, G., and Nelson, C. D. 1969. The translocation of photosynthetically assimilated ^{14}C in corn. Can. J. Bot. 47:1435-1442.
23. Hooker, A. L., and White, D. G. 1976. Prevalence of corn stalk rot fungi in Illinois. Plant Dis. Rep. 60:1032-1034.
24. Hornby, D., and Ullstrup, A. J. 1967. Fungal populations associated with maize roots. Quantitative rhizosphere data for genotypes differing in root rot resistance. Phytopathology 57:76-82.
25. Hornby, D., and Ullstrup, A. J. 1967. Fungal populations associated with maize roots. Composition and comparison of mycofloras from

genotypes differing in root rot resistance. Phytopathology 57:869-875.
26. Hsiao, T. C., and Acevedo, E. 1975. Plant responses to water deficits, water-use efficiency, and drought resistance. Pages 59–84 in: Plant Modification for More Efficient Water Use. J. F. Stone, ed. Elsevier Scientific Publishing Co., New York. 320 pp.
27. Hsiao, T. C., Fereres, E., Acevedo, E., and Henderson, D. W. 1976. Water stress and dynamics of growth and yield in crop plants. Pages 281–305 in: Water and Plant Life. Problems and Modern Approaches. O. L. Lange, L. Kappen, and E. D. Schulze, eds. Springer-Verlag, New York. 536 pp.
28. Hsieh, W. H. 1975. Biology of *Fusarium (Gibberella) moniliforme* and its pathology on cereals. Ph.D. thesis. University of California, Berkeley. 120 pp.
29. Johnson, D. R., and Tanner, J. W. 1972. Comparisons of corn (*Zea mays* L.) inbreds and hybrids grown at equal leaf area index, light penetration, and population. Crop Sci. 12:482-485.
30. Jurgens, S. K., Johnson, R. R., and Boyer, J. S. 1978. Dry matter production and translocation in maize subjected to drought during grain fill. Agron. J. 70:678-682.
31. Kanemasu, E. T., Rasmussen, V. P., and Bagley, J. 1978. Estimating water requirements for corn with a pocket calculator. Kansas Agric. Exp. Stn. Bull. 615. (Unpaged).
32. Kanemasu, E. T., Thurtell, G. W., and Tanner, C. B. 1969. Design, calibration and field use of a stomatal diffusion porometer. Plant Physiol. 44:881-885.
33. Kaufman, M. R., and Hall, A. E. 1975. Plant water balance—Its relationship to atmospheric and edaphic conditions. Pages 85–98 in: Plant Modification for More Efficient Water Use. J. F. Stone, ed. Elsevier Scientific Publishing Co., New York. 320 pp.
34. Koehler, B. 1960. Cornstalk rots in Illinois. Ill. Agric. Exp. Stn. Bull. 658. 90 pp.
35. Komada, H. 1975. Development of a selective medium for quantitative isolation of *Fusarium oxysporum* from natural soil. Rev. Plant Protection Res. 8:114-125.
36. Kommedahl, T., Windels, C. E., and Stucker, R. E. 1979. Occurrence of Fusarium species in roots and stalks of symptomless corn plants during the growing season. Phytopathology 69:961-966.
37. Lipe, W. N., and Wendt, C. W. 1978. Effects of antitranspirants on yield, grade distribution, and water use of potatoes. Am. Potato J. 55:203-209.
38. McPherson, H. G., and Boyer, J. S. 1977. Regulation of grain yield by photosynthesis in maize subjected to a water deficiency. Agron. J. 69:714-718.
39. Merrill, S. D., and Rawlins, S. L. 1979. Distribution and growth of sorghum roots in response to irrigation frequency. Agron. J. 71:738-745.
40. Michaelson, M. E. 1957. Factors affecting development of stalk rot of corn caused by *Diplodia zeae* and *Gibberella zeae*. Phytopathology 47:499-503.
41. Millard, J. P., Jackson, R. D., Goettelman, R. C., Reginato, R. J., and Idso, S. B. 1978. Crop water-stress assessment using an airborne thermal scanner. Photogramm. Engin. Remote Sens. 44:77–85.
42. Moreshet, S., Stanhill, G., and Fuchs, M. 1977. Effect of increasing foliage reflectance on the CO_2 uptake and transpiration resistance of a grain sorghum crop. Agron. J. 69:246-250.
43. Morgan, T. H., Biere, A. W., and Kanemasu, E. T. 1980. A dynamic model of corn yield response to water. Water Resources Res. 16:59-64.
44. Mortimore, C. G., and Wall, R. E. 1965. Stalk rot of corn in relation to plant population and grain yield. Can. J. Plant Sci. 45:487-492.
45. Mortimore, C. G., and Ward, G. M. 1964. Root and stalk rot of corn in southwestern Ontario. III. Sugar levels as a measure of plant vigor and resistance. Can. J. Plant Sci. 44:451-457.
46. Moss, G. I., and Downey, C. A. 1971. Influence of drought stress on female gametophyte development in corn (*Zea mays* L.) and subsequent grain yield. Crop Sci. 11:368-372.
47. Mtui, T. A., Kanemasu, E. T., and Wasson, C. 1981. Canopy temperatures, water use, and water use efficiency of corn genotypes. Agron. J. 73:639-643.
48. Newman, E. I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3:139-145.
49. Newman, E. I. 1969. Resistance to water flow in soil and plant. II. A review of experimental evidence on the rhizosphere resistance. J. Appl. Ecol. 6:261-272.
50. Papendick, R. I., and Cook, R. J. 1974. Plant water stress and development of Fusarium foot rot in wheat subjected to different cultural practices. Phytopathology 64:358-363.
51. Pappelis, A. J., and Boone, L. V. 1966. Effect of planting date on stalk rot susceptibility and cell death in corn. Phytopathology 56:829-831.
52. Pappelis, A. J., and Smith, F. G. 1963. Relationship of water content and living cells to spread of *Diplodia zeae* in corn stalks. Phytopathology 53:1100-1105.
53. Pearson, R. W. 1966. Soil environment and root development. Pages 95–126 in: Plant Environment and Efficient Water Use. W. H. Pierre, D. Kirkham, J. Pesek, and R. Shaw, eds. Am. Soc. Agron. and Soil Sci. Soc. Am., Madison, WI. 295 pp.
54. Reicosky, D. C., Campbell, R. B., and Doty, C. W. 1975. Diurnal fluctuation of leaf-water potential of corn as influenced by soil matric potential and microclimate. Agron. J. 67:380-385.
55. Reicosky, D. C., Campbell, R. B., and Doty, C. W. 1976. Corn plant water stress as influenced by chiseling, irrigation, and water table depth. Agron. J. 68:499-503.
56. Ritchie, J. T. 1973. Influence of soil water status and meteorological conditions on evaporation from a corn canopy. Agron. J. 65:893-897.
57. Roberts, B. R., and Schreiber, L. R. 1977. Influence of Dutch elm disease on resistance to waterflow through roots of American elm. Phytopathology 67:56-59.
58. Rosenberg, N. J. 1974. Micro-climate: The Biological Environment. John Wiley & Sons, New York. 315 pp.
59. Safir, G. R., and Schneider, C. L. 1976. Diffusive resistances of two sugar beet cultivars in relation to their black root disease reaction. Phytopathology 66:277-280.
60. Schneider, R. W., 1981. Predisposition of corn to stalk rot by early-season water stress. (Abstr.) Phytopathology 71:253.
61. Scholander, P. F., Hammel, H. T., Bradstreet, E. D., and Hemmingsen, E. A. 1965. Sap pressure in vascular plants. Science 148:339-346.
62. Taylor, H. M. 1971. Soil conditions as they affect plant establishment, root development, and yield. Pages 292–312 in: Compaction of Agricultural Soils. K. K. Barnes, W. M. Carleton, H. M. Taylor, R. I. Throckmorton, and G. E. Vanden Berg, eds. Am. Soc. Agric. Engin., St. Joseph, MI. 471 pp.
63. Torssell, W. R., Begg, J. E., Rose, C. W., and Byrne, G. F. 1968. Stand morphology of Townsville lucern (*Stylosanthes humilis*). Seasonal growth and root development. Aust. J. Exp. Agric. Anim. Husb. 8:532-543.
64. Turner, N. C. 1974. Stomatal behavior and water status of maize, sorghum, and tobacco under field conditions. II. At low soil water potential. Plant Physiol. 53:360-365.
65. Wall, R. E., and Mortimore, C. G. 1965. The growth pattern of corn in relation to resistance to root and stalk rot. Can. J. Bot. 43:1277-1283.
66. Wardlaw, I. F. 1976. Assimilate partitioning: Cause and effect. Pages 381–391 in: Transport and Transfer Processes in Plants. I. F. Wardlaw and J. B. Passioura, eds. Academic Press, New York. 484 pp.
67. Wendt, C. W., Onken, A. B., Wilke, O. C., Hargrove, R., Bausch, W., and Barnes, L. 1977. Effect of irrigation systems on the water requirements of sweet corn. Soil Sci. Soc. Am. J. 41:785-788.
68. Whitney, N. J., and Mortimore, C. G. 1957. Root and stalk rot of field corn in southwestern Ontario. I. Sequence of infection and incidence of the disease in relation to maturation of inbred lines. Can. J. Plant Sci. 37:342-346.
69. Whitney, N. J., and Mortimore, C. G. 1961. Root and stalk rot of field corn in southwestern Ontario. II. Development of the disease and isolation of organism. Can. J. Plant Sci. 41:854-861.
70. Yarwood, C. E. 1959. Predisposition. Pages 521–562 in: Plant Pathology: An Advanced Treatise. Vol. 1. J. G. Horsfall and A. E. Dimond, eds. Academic Press, New York. 674 pp.
71. Young, T. R., and Kucharek, T. A. 1977. Succession of fungal communities in roots and stalks of hybrid field corn grown in Florida. Plant Dis. Rep. 61:76-80.