Plant Water Stress and Development of Fusarium Foot Rot in Wheat Subjected to Different Cultural Practices

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ABSTRACT

Fusarium foot rot of winter wheat caused by *F. roseum* f. sp. *cerealis* 'Culmorum' was most severe under dryland conditions (<30 cm annual precipitation) with treatments that caused the greatest plant water stress. These treatments were high N [>60 kg N/hectare (ha)] and high plant densities (1 seed/cm length of row; rows 30 cm apart) with early seeding. Plant water potentials were uniform at −20 to −25 bars for all treatments until May. Infection (as revealed by culture plating) was generally completed at that time and was also uniformly high regardless of treatment, but varied with inoculum density. In plots which received low N, plant water potential dropped only to −30 to −33 bars at plant maturity and disease remained mild. With high N, potentials dropped to −35 to −42 bars, extensive basal culm decay developed at about the dough stage, and tillers died prematurely. In plants in rows 60-90 cm apart (low density) water potentials remained near −30 to −33 bars, even with high N; and disease development slowed accordingly, although it was not prevented.

The development of low plant water potential in June-July was related to high-use rates of soil water reserves in April and early May, presumably because of high transpirational capacity (high leaf area) of the well-nourished plants. Thereafter, soil water supplies became increasingly more limiting and evaporative demand increased; the result was in diminished use rates and lowered plant water potentials. *Fusarium* is apparently a slow-decay organism in wheat that becomes no drier than −30 to −33 bars at plant maturity, but it kills its host by aggressive attack if the plant water potential exceeds −35 to −40 bars at maturity.

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Additional key words: thermocouple psychrometry, dryland winter wheat, nitrogen fertilization.

Root and foot rot of wheat (*Triticum aestivum* L.) caused by *Fusarium roseum* (Lk.) emend. Snyd. & Hans. f. sp. *cerealis* (Cke.) Snyd. & Hans. 'Culmorum,' limits wheat production and indirectly contributes to increased soil erosion in large areas of the low-to-intermediate rainfall, wheat-fallow region of the northwestern USA. Disease is most severe in years of below-normal precipitation and in early fall plantings (6). By comparison, disease is mild or absent with late seedings where plants are small during fall and winter and use less water during the spring-summer season than early plantings. Larger plants from early seeding are desirable both as a ground cover to reduce overwinter soil erosion (5), and also for maximum yield; nevertheless late seeding is practiced to avoid losses from the diseases caused by *Fusarium* spp.

Fusarium root and foot rot has been found to be most severe with high rates of applied nitrogen (N) fertilizer (18). Field observations indicate that the disease is reduced in rows bordered by seeding skips or where the stand was thinned by winter injury. Brown (2) showed that increasing rates of applied N fertilizer increased water use rates and cumulative water use by dryland winter wheat during spring and summer in Montana. Information is generally lacking on water use rates by winter wheat during the spring-summer growing season in Washington. Although cumulative use at harvest does not differ greatly for N-fertilized and nonfertilized wheat in the lower rainfall areas (12), it is highly possible that with high fertility, plants are subjected to greater stress because of higher use rates early in the spring season. Pelton (15) showed that a limited moisture supply was available to spring wheat in Saskatchewan over a longer period in plots with low plant populations; plants at high densities became stressed for water and yields were reduced. Thus, the greater disease with high N, high plant density, and early seeding all point to a relationship between water stress and the onset of severe *Fusarium* root and foot rot.

Chlamydospores of 'Culmorum' germinate at soil matric potentials down to −75 to −85 bars (8). Hyphal growth of this pathogen is actually stimulated when the osmotic potential of the growth medium is lowered to −8 to −10 bars (10). After infection, fungal growth is subject to the internal water status of the plant and thus water stress may favor development of the *Fusarium* in the plant through lowered water potential. Therefore, any studies on the relationship between plant water stress and the *Fusarium* disease must necessarily consider, not only the pattern of soil water use by the crop, but how this relates to plant water potential. This paper reports the results of such a study. Preliminary reports have been published (7, 9, 14).

MATERIALS AND METHODS.—*Field-plot sites.*—Experiments were conducted over three growing seasons (1970-1972) on Ritzville silt loam near Harrington, Lincoln County, in eastern Washington (28-cm mean annual precipitation). The 1970 sites were in two fields separated only by a county road. Both were seeded in early September 1969, one to the club wheat, 'Moro,' and the other to the soft, white winter variety, 'Nugaines.' The Moro field had 200-300 'Culmorum' propagules/g of soil (low infestation) and the Nugaines field had about 2,500 propagules/g of soil (high infestation) in the surface

10 cm. Both fields were characterized by a caliche layer at various depths between 160-180 cm, which restricts water flow and root penetration. The Moro field, traditionally moldboard plowed, contained about 3 cm less total water in the 180-cm profile on 1 April 1970, than the Nugaines field, which was traditionally stubble-mulched.

The 1971 experiments were conducted in one field only, which contained about 800 'Culmorum' propagules/g soil. The 1972 experiments likewise were in one field only; the same field used for the 1970 Nugaines trial, which was fallowed during 1971. Meanwhile, the 'Culmorum' population in this field had increased uniformly to 4,500 to 5,000 propagules/g of soil.

Cultural variables to promote plant water stress.—Conventional rates of N applied for wheat in the dryland areas of Washington average 40-60 kg/ha, but may be as high as 90 kg/ha. The profile may contain as much as 150-200 kg N/ha where heavy applications are made on top of high residual N not used by the previous crop. Seeding rate is about 60 kg seed/ha in rows 30-40 cm apart. N application rates were 56, 112, and 224 kg N/ha in 1970; and 0, 67, and 134 kg N/ha in 1971 and 1972. In addition, the rows were spaced to 90 cm apart to reduce the potential for plant water stress. Seeding rate was held constant at about 1 seed/2 cm of row length so that the wider rows received proportionally less seed.

Measurement of soil water use and plant water potentials.—Soil water contents to the 180-cm depth were measured with a neutron moisture meter at approximately biweekly intervals beginning in early April and continuing until crop maturity. Soil samples for measurement of water potential by thermocouple psychrometry (19) were obtained at different soil depths in June 1970. Rainfall was recorded at the plot locations during the spring in 1971 and 1972.

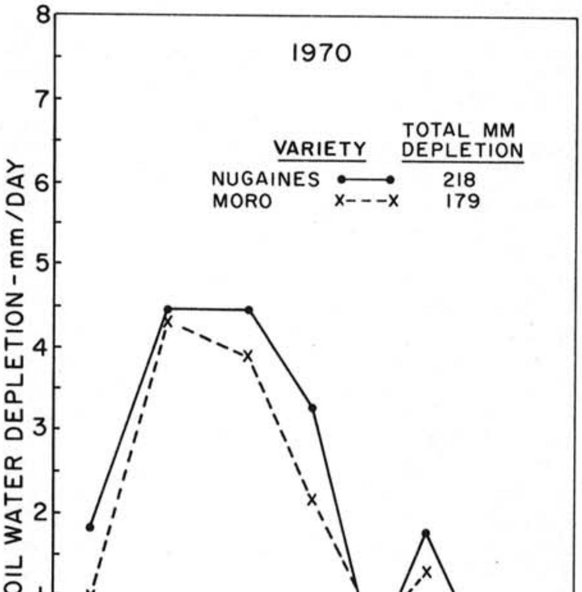

Fig. 1. Soil water depletion rates and total depletion by two winter wheat cultivars during the spring-summer season (1970).

Leaf water potential and osmotic potential measurements were made between 1100 and 1500 hours on uppermost leaves which were fully exposed to the sun. During 1970 and 1971, measurements were made either by punching 6-mm diam leaf disks directly into a sample-changer psychrometer (3), or by mechanically crushing the leaf tissue, squeezing cell sap into 6-mm diam filter paper disks, and measuring the osmotic potential by thermocouple psychrometry. The punched leaf disks were crushed upon insertion into the chambers of the sample changer so osmotic rather than total potential was measured with either method.

Mean values of osmotic potentials of crushed tissue in the sample chamber were generally 3-5 bars lower than those obtained by mechanically extracting the cell sap. Subsequent experiments indicated that rupture of cells with either mechanical method was incomplete, because freezing of the samples on dry ice lowered the measured osmotic potential an additional 2 or 3 bars. For the purposes of this experiment, this offset was not serious, since the important feature was the comparisons between treatments.

In 1972, leaf water potentials were measured in the field by means of pressure chamber (1, 16). The leaves were then frozen in stoppered segments of Tygon tubing on dry ice (solid CO_2) and transported to the laboratory where some of the cell sap was squeezed onto filter paper disks for osmotic potential measurement with a thermocouple psychrometer.

By the time treatment effects became discernible, midday turgor pressures were at or near zero and osmotic potential measurements indicated leaf water potentials. Water potentials at the basal portion of the stem (in the vicinity of the fungus) were undoubtedly higher than those in the leaf; but measured soil water potentials approached midday leaf water potentials so the stem potential must have been within a few bars of the leaf potential. Therefore, the leaf osmotic potential was taken as a valid indicator of plant water energy. The sample standard deviation of a set of measurements (4-6 per plot) was generally less than 2.5 bars. Some leaf water potential measurements were made in 1970 with a portable freezing-point meter similar to that described by Cary and Fisher (4). These measurements gave the same trends as those with psychrometry, although the absolute values of water potential with the freezing point meter were consistently 20-30% lower.

Disease assessment.—Percentage plant infection was estimated in early April (when plants were still in the rosette stage) by culturing internal crown tissue (6) of at least 100 random plants per treatment on acid cornmeal agar, and recording the proportion which yielded 'Culmorum.'

A second assessment was made in June-early July (at the early dough stage) to determine percentage of tillers killed or dying because of infection by 'Culmorum.' Counts were made by direct inspection of 80-100 standing tillers in each of three representative areas per plot. Diseased tillers were recognized either by a white head, or a severely chlorotic and rolled flag leaf which indicated

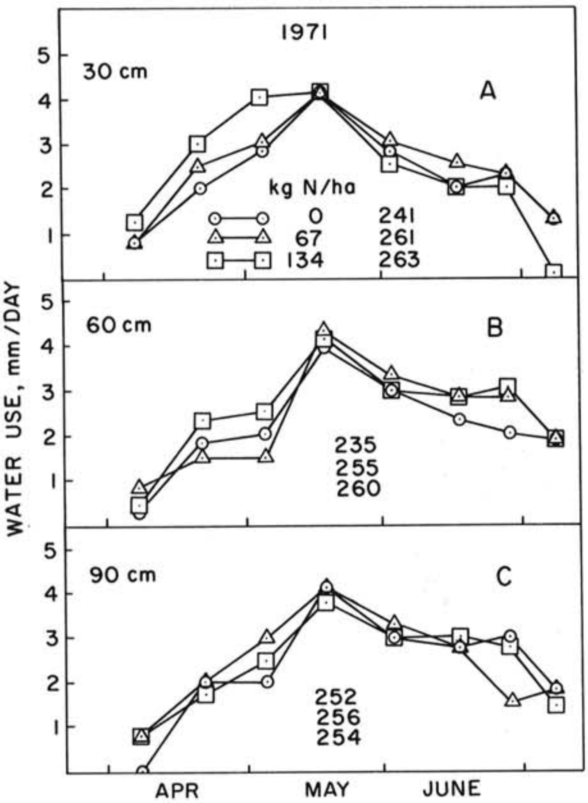

Fig. 2. Water use (including rainfall) during the spring-summer season by 'Nugaines' wheat planted in 30, 60, or 90 cm rows and fertilized with 0, 67, or 134 kg N/hectare. The numbers opposite the N rates are total water use for that treatment. Seeding rate per unit length of row was identical for all row widths (1971).

extensive basal stem browning and impending death. Disease incidence was low in 1971, and counts on a percentage basis were not practical. Therefore, the second assessment that year was based on diseased tillers per meter of row length in each of three places per plot. The counts were adjusted to allow for differences in numbers of tillers per m of row as follows: diseased tillers per m row per gm mature tillers per m row × 100 = disease index.

A third and final assessment was made after maturity, by directly inspecting the basal portions of tillers of 5-10 plants pulled from each of five places per plot. The leaf sheaths were stripped back to reveal the presence or absence of basal stem decay. At least 100 random tillers were examined from the samples from each plot and categorized as either disease free, mildly diseased (brown discoloration no higher than first node above ground), or severely diseased (brown discoloration as high as third or fourth nodes and tiller often shriveled).

RESULTS.—*Water use and plant water potentials.*—In spite of variability and irregularities in climate and stand between sites and years, patterns of water use had certain similarities; i.e., low (0.5-1.0 mm/day) early in the season, maximal (3-4 mm/day) in May or early June, and then low again towards maturity (Fig. 1 and 2). Water use results in 1972 provided no information different from that in 1971 and are not reported. When water was more plentiful, peak use occurred later in the season; peak use occurred in early- and mid-May for low (1970) and average (1971) soil water contents, respectively (Fig. 1 vs. Fig. 2). With low soil water reserves, use rates generally decreased with increase in evaporative demand. In 1970, for example, daily maximum temp during early- to mid-June were above normal (35-38 C) and water use during this period virtually ceased (Fig. 1).

TABLE 1. Influence of nitrogen (N) fertilization rate and row spacing on leaf osmotic potentials of two winter wheat varieties on selected dates in 1970

	Leaf osmotic potential (bars)				
	'Moro'		'Nugaines'[a]		
	5/22	6/6	5/22	6/5	6/19
N applied (kg/ha)					
56	−23.2	−23.2	−21.8	−26.6	−32.2
112	−28.9	−32.7	−22.8	−28.9	−33.6
224	−27.6	−42.5	−25.2	−34.5	−35.5
Row spacing (cm)					
30			−24.7	−31.0	−35.1
60			−21.7	−28.9	−32.3

[a]For the N application rates the osmotic potentials are means for all row spacings; for the row spacings the potentials are means for all N-fertilizer application rates.

In 1970, both sites showed marked plant water stress, based on leaf osmotic potentials. The Moro wheat (where available soil water was low from the outset) showed stress in late May-early June, 2 to 3 wk earlier than the adjacent Nugaines site where soil water supply was less critical. Water potentials as low as −35 to −40 bars were recorded just before maturity or plant death. Cumulative use for the Moro site from April 14 to June 30 was 179, 152, and 145 mm of water for the 56, 112, and 224 kg N/ha applications, respectively. Following the same order, grain yields were 1,585, 1,402, and 1,083 kg/ha. Plants were larger and grew faster early in the season with the higher N rates, but subsequently ceased growth rather abruptly, as evidenced by less total water use as compared to the low-N rate. Osmotic potentials for the Moro wheat were lowest with the two higher N rates, beginning in late May (Table 1). Daytime wilting was evident by this time, and by early June leaves of plants fertilized with 112 and 224 kg N/ha remained wilted even overnight.

Water use (Fig. 1) and grain yield (average 2,400 kg/ha) on the adjacent Nugaines site in 1970 were not significantly different among N rates and row spacings. However, leaf osmotic potentials by late May through mid-June were progressively lower with increased N, and narrower row spacing (Table 1). Soil water potentials in the profiles of both sites in early June (Fig. 3) further substantiated the lower moisture reserves with increased N application.

In 1971 (a cool, wet growing season), increased N increased the water use rate in April and early May for the 30-cm row spacing (Fig. 2-A), but less so (or not

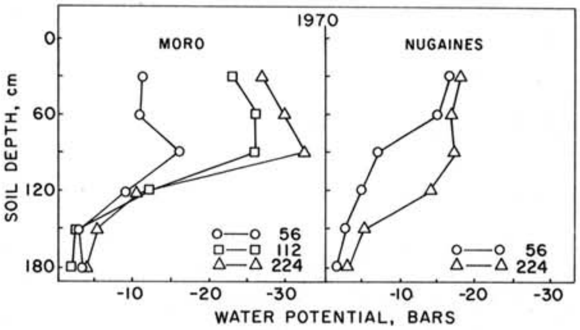

Fig. 3. Water potentials at different depths in the profile for Moro and Nugaines wheat at different rates of N fertilization. Sampling date was 5 June 1970.

consistently) with the wider row spacing (Fig. 2-B, C). Late-season use rates diminished more rapidly with the high N-narrow row spacing, than with low N or wide row spacing. Total water use was 20 mm higher or more with high N as compared with no N applied, except for the 90-cm row spacing where total use was similar for all N rates (Fig. 2).

Leaf osmotic potentials were −20 to −23 bars in early June 1971, regardless of row spacing or N rate (Fig. 4). With low N or wide rows, they dropped to about −30 bars by July 1; with high N and narrow rows, they approached −40 bars (Fig. 4). With no N applied, leaf osmotic potentials were slightly lower with the wider rows, and plants obviously were not lacking in N as evidenced by their deep green color.

Leaf osmotic potentials in 1972 were similar to those measured in 1971, again being progressively lower with increased N, and lowest with high N and narrow row spacing (Table 2). Treatment effects were apparent only after mid-June, at which time combined pressure bomb measurements of leaf water potential and osmotic potential of the cell sap indicated very low turgor potential during midday. Plant wilting, however, was minimal. In contrast to 1971, there was little difference between wide and narrow row spacing where no N was applied.

Incidence and severity of disease.—In 1970, 50-60% of the Nugaines plants yielded 'Culmorum' upon culture plating on April 1, with no difference among treatments. In the adjacent Moro field which contained about one-tenth the 'Culmorum' population, percentage of infection was 27-33, regardless of treatment. A somewhat inconspicuous brown-pink internal crown necrosis characterized most infected plants at that time, but outward symptoms were nonexistent. Similar results of uniform infection regardless of treatment were obtained in 1971 and 1972.

Differentiation between treatments in foot rot severity was first evident at abouth the early-dough stage. Tillers and whole plants began to die and were characterized by a sudden and rapid onset of basal browning, collapse, and decay of the tillers with accompanying white heads. Dead or dying tillers were most numerous in plots where early water use rates had been highest, and plant osmotic potentials lowest; i.e., where both N and plant density were high (compare Tables 1 and 2 with Tables 3 and 4).

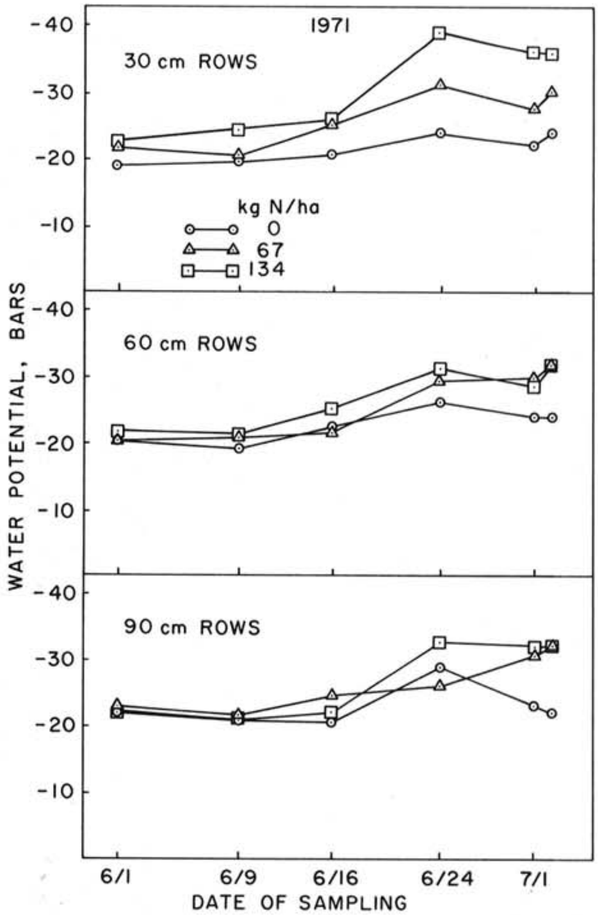

Fig. 4. Water potentials of crushed wheat leaf disks for three row spacings and three rates of N fertilization determined on selected days in 1971.

Increasing the row spacing from 30-40 cm to 60-90 cm tended to nullify the N effect on plant disease (Tables 3 and 4).

A major problem each year was poor fall stand establishment, or winter injury, with the result that some plots had low plant densities. Another was high residual nitrogen measured in the soil profile, presumably from fertilizer applications of previous years. Where stands were thin, disease severity was low regardless of rate of nitrogen application, just as with wide rows. Where residual N was high, there was little additional response to applied N, and disease was high.

The second disease assessment presented a source of error; namely, that a tiller might have basal stem browning due to upward progression of 'Culmorum,' but decay might not yet be sufficient to cause outward symptoms. Several hundred random and apparently healthy tillers were, therefore, checked at early dough by stripping back the lower leaf sheaths. Essentially none showed basal symptoms of the disease. This supported the observation that, once underway, disease progression is abrupt and rapid. For all practical purposes, outward appearance at early dough stage was an accurate means of

TABLE 2. Influence of N fertilization rate and row spacing on leaf osmotic potentials of 'Nugaines' wheat on selected dates in 1972

N rate (kg/ha)	Row spacing (cm)	Leaf osmotic potential on selected days (bars)				
		5/11	5/24	6/6	6/21	7/5
0	30	---	---	−20.9	−24.0	−33.3
	90	---	---	−21.9	−24.7	−31.9
67	30[a]	−21.7	−19.9	−21.0	−26.3	−37.9
134	30	−22.6	−20.2	−24.4	−27.5	−39.9
	90	---	---	−24.0	−26.4	−32.6

[a]Data obtained only for the 30-cm row spacing fertilized at 67 kg N/hectare.

TABLE 3. Influence of row spacing and nitrogen (N) fertilization rate on development of foot rot in wheat at two stages of plant growth in 1970 and 1972

Year	N rate (kg/ha)	Row spacing (cm)	Percentage of tillers with severe foot rot	
			Early dough[a]	Maturity[b]
1970				
	56	30	15.7	83
		60	7.9	89
	112	30	13.0	89
		60	4.0	76
	224	30	6.7	83
		60	8.1	89
1972				
	0	40	5.2	19.6
		80	2.0	21.1
	67	40	8.0	31.9
		80	2.8	25.3
	134	40	20.2	28.9
		80	3.9	32.0

[a]Percentage based on examination of 200-300 standing tillers in each of three reps.

[b]Percentage based on examination of about 100 tillers representing 25-50 uprooted plants from each of three reps in 1970 and four reps in 1972.

TABLE 4. Influence of row spacing and rate of nitrogen (N) on development of foot rot in wheat caused by *Fusarium roseum* f. sp. *cerealis* 'Culmorum' and on wheat yields (1971)

N rate (kg/hectare)	Row spacing (cm)	Disease index[a]	Grain yield (kg/hectare)
0	30	1.1	2,970
	60	3.2	2,923
	90	3.3	2,876
67	30	7.4[b]	3,730
	60	2.0	3,750
	90	3.2	3,293
134	30	7.1[b]	3,756
	60	4.2	3,683
	90	2.2	3,259

[a]Number of severely infected tillers per meter row at dough stage × 100: total tiller wt (g) per meter row. Each value is average of four reps, three samplings per rep.

[b]Significantly different from all other readings, $P = 0.01$.

estimating percentage tillers with basal stem decay at that time.

Differences between treatments tended to disappear by the third and final disease assessment, made at plant maturity. In general, a nitrogen effect was still detectable, but not a row-spacing effect (Table 3). In 1970, percentage of diseased tillers in Nugaines grown in soil with 2,500 'Culmorum' propagules/g was 83-89 regardless of row spacing or N rate (Table 3). In the adjacent Moro, a variety normally affected less than Nugaines by this disease, with one-tenth the 'Culmorum' population, but where plant water stress developed earliest because of lower soil moisture reserves, disease percentages were 76, 85, and 84 for 56, 112, and 224 kg N/ha, respectively. In other words, the greater stress on Moro apparently resulted in as much disease as in the adjacent more susceptible Nugaines with a slight N effect being present. In 1971, final disease percentages (average for all row spacings) for Nugaines growing in soil with 800 propagules/g and with more plentiful seasonal rainfall was 6.2, 12.5, and 17.3 for 0, 67, and 134 kg N/ha, respectively. Disease percentages for row spacings (average for all N rates) in that same trial were 11.7, 10.3, and 14.0 for 30, 60, and 90 cm, respectively. The greater disease severity with high N and narrow rows reduced the anticipated yield advantage afforded by these treatments in a year when water was less limiting (Table 4). In 1972, the N effect on disease tended to persist, but not the row-spacing effect. Moreover, final disease readings in 1972 were less than half those recorded in the same field in 1970 when inoculum was less, but when plant water stress occurred earlier and more acutely.

DISCUSSION.—This study reveals a distinct relationship between increased plant water stress during the growing season (as indicated by lowered leaf osmotic potentials) and increased incidence of severe *Fusarium* foot rot in wheat. Stress was earliest and greatest with cultural practices that hastened early spring depletion of water; i.e., high N fertility, and particularly high N combined with high plant densities. Severe foot rot similarly developed earliest and in highest incidence in these plots. Early planting would also promote stress where water is limiting, which accounts for the increased disease long associated with this practice. With soil water more plentiful, plant osmotic potentials remained relatively high later into the season and, accordingly, there was less disease. The 'Culmorum' population above a certain minimum was apparently less important than water stress in determining disease severity. Moreover, the influence is on disease development after infection, since infection occurred before differential stress development and was independent of the treatments.

The plant water potential, which is a measure of the internal water deficit of the plant tissue, is determined first by the soil water potential of the root zone, and second by the extent that water absorption by the roots lags transpiration (17). Accordingly, where continued dry weather resulted in low soil water reserves by mid-May, wilting was severe only at osmotic potentials of −38 to −42 bars; wilting symptoms were not apparent at −33 to −35 bars. These driest plants showed the highest incidence of severe *Fusarium*-caused disease. In associated work, we observed that, during hot weather, plants supplied with relatively high soil moisture reserves wilted in the daytime at osmotic potentials considerably higher than −35 bars. Thus, the "stress" in a plant due to temporary wilting may not be as important to disease as exceptionally low plant water potential that develops with low soil moisture, whether or not the plant shows symptoms of wilting. Perhaps the strain on a plant drier than −33 to −35 bars predisposes it to aggressive attack by the pathogen already established in its tissues, which otherwise would be a slow-decay organism.

Nitrogen fertilization increases the rooting depth and root density in soil, and also the leaf area index, thereby increasing the transpirational capacity of the plant. Plants with low N apparently do not develop the low osmotic potentials characteristic of well-fertilized plants, even when water is limiting, and presumably will wilt and die at higher soil water potentials than well-fertilized plants. The lower osmotic potentials of N-fertilized plants may explain why these deplete soil water to lower levels than do low-N plants (11, 13)—they exert a greater suction. This aspect may also explain the increased disease severity with high N-fertility where water was less limiting; e.g., with wide row-spacing.

Basal culm decay would also promote stress and raises the question of whether disease is the cause or the result of lowered plant water potentials. In other words, does N stimulate disease development other than through increased water stress and then as disease progresses the low potentials develop? Probably not, since the incidence of foot rot was too low (maximum of 13-15 tillers/m of row, even in the most dense stands) to account for the consistently low osmotic potential of random tillers from high N-narrow row plots. The chances of picking a diseased tiller every time was virtually nil. Moreover, in the early stages of foot rot development, the flag leaf became chlorotic. These chlorotic leaves had consistently higher water potentials than healthy green leaves until later stages of chlorosis when the leaf began to dry up. The low potential must, therefore, have resulted from the treatments themselves, although a nutritional influence of N on the fungus itself cannot be ruled out completely as a contributing factor. However, if N-nutrition were important, it seems unlikely that disease could be reduced or delayed in the presence of high N simply by widening the rows; nevertheless, this was so in our trials.

From the practical standpoint, growers should carefully avoid excessive N application in relation to plant population and available water supply where foot rot is a problem. In particular, they must adjust their N rates according to residual N in the profile to avoid overfertilizing their crops. Excess N may not be detrimental to the wheat crop in pathogen-free soils, but it is highly hazardous in fields infested with 'Culmorum.' These results also suggest that wheat varieties that are economical in their use of the limited water supply (have low transpiration rates and sensitive control of transpiration as water becomes limiting) would be less susceptible to foot rot disease. There is some indication that this may be true; and this is the subject of another study now in progress.

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