The Influence of Plant Water Stress on Infection and Colonization of Wheat Seedlings by *Fusarium graminearum* Group 1

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ABSTRACT

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The influence of seedling water potential on infection and colonization of wheat seedlings (*Triticum aestivum*) by *Fusarium graminearum* Group 1 was studied using wax partitioning of the soil so that the water potential of the seminal root zone was manipulated independently from the water potential of the infection zone in the subcrown internode region. Eleven days after seeds were sown, water was withheld from the root zone to induce water stress in seedlings, while nonstressed seedlings were watered every 48 h to a soil water content of 0.31 g g^{-1}, favorable for plant growth. In the 1990 experiment, a decrease in seedling water potential of −0.32 to −2.63 MPa in the crown rot-tolerant cv. Suneca and −0.43 to −2.85 MPa in the less tolerant cv. Sunkota as a consequence of stress corresponded with an increase in colonization of wheat seedlings by *F. graminearum* Group 1. The incidence of infection was not related to the tolerance of the host and was similar under both stress and nonstress conditions. *F. graminearum* Group 1 suppressed growth in nonstressed seedlings of both cultivars but not in seedlings subjected to water stress. A trend for *F. graminearum* Group 1 to suppress growth in the stressed seedlings was suggested, but presumably the water stress was so severe that the fungus caused much less suppression by comparison. Suneca seedling water potentials were lower than the water potentials of Sunkota seedlings under stress conditions. These results suggest that low seedling water potential predisposes wheat seedlings to colonization and further damage by the fungus.

Additional keywords: crown rot, drought stress, plant water potential.

Crown rot caused by *Fusarium graminearum* Schwabe Group 1 (10) is a serious disease of dryland wheat (*Triticum aestivum* L.) in the central and northern regions of the eastern wheat belt of Australia (4,16). The disease has also been reported in the Pacific Northwest, United States (5) and in South Africa (24,25).

In sterile soil, *F. graminearum* Group 1 can infect wheat seedlings over a wide range of soil water potentials (12). In contrast, infection of seedlings in natural soil is restricted to a relatively narrow range of soil water potentials between −0.1 and −1.5 MPa (12,14). Antagonistic soil bacteria may be responsible for inhibition of infection in wet soils and antagonistic fungi and actinomycetes for inhibition in dry soil (14). Thus, infection by this pathogen apparently is dependent on a complex interaction among environmental factors, the host plant, the pathogen, and the soil microflora.

The pathogen is removed from the effects of the soil microflora after infection. The water potential of the host then presumably exerts a major influence on parasitic activity (17). The water potential of the host plant, however, is determined largely by the water potential and hydraulic conductivity of the soil. As soil dries, the water potential of the plant decreases gradually unless plant water potential is less than that of the soil (19).

The relationship between plant water stress and the development of foot rot in wheat caused by *Fusarium culmorum* (Wm. G. Sm.) Sacc. grown with different cultural practices in field plots has been studied. Infection, as measured by frequency of isolation of *F. culmorum* from the crown, was similar in all water stress treatments applied (18). However, cultural practices that increased plant water stress increased the severity of disease as measured by browning of the basal portion of the stem and the proportion of tillers with whiteheads (i.e., heads that contain no grain or poorly developed grain, which generally occur if moisture is insufficient for anthesis and grain fill) (15). Therefore, plant water stress may have affected disease development after infection, because infection occurred before the development of differential stress (18).

Field observations and greenhouse studies on the development of crown rot in wheat caused by *F. graminearum* Group 1 also have indicated that dry conditions between anthesis and maturity favor the formation of whiteheads (4,6,12,16). Several studies have been conducted on the role of plant water stress as a predisposing factor to disease (21). In some experiments plant water stress was induced by withholding water from the soil either before or after inoculation (1,9,20,23). The methods used in those studies did not permit independent manipulation of plant water potential and the water potential of the soil in the infection zone. Thus, these results must be interpreted with caution because the responses may not be attributed to a single factor but rather to changes to two factors.

The influence of seedling water potential on infection and colonization of wheat seedlings by *F. graminearum* Group 1 was studied using wax partitioning of the soil to allow manipulation of the water content of soil in the root zone independently of the water content of soil in the infection zone.

MATERIALS AND METHODS

Inoculum preparation. *F. graminearum* Group 1 was isolated from the basal internode of a culm from a wheat plant affected by crown rot from northern New South Wales. A culture derived from a single macroconidium was lyophilized and deposited in the Fusarium Research Laboratory Collection, University of Sydney, under the accession number F7674. The fungus was grown on moist, sterile wheat chaff for 4 wk. Colonized chaff was air-dried, crushed, and passed through a sieve (710-μm mesh) before use as inoculum (3).

Soil. Soil was collected from the top 15 cm of a black earth from Narrabri, New South Wales, Australia. *F. graminearum* Group 1 was not detected by the debris-plating and soil dilution plating techniques in this soil (3). The soil was air-dried (moisture content = 0.07 g g^{-1}), crushed, and sieved through a 2-mm-diameter mesh. Properties of this soil, including properties related

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to water relations, have been described (15,22). A fertilizer mix, 22 g of KH_2PO_4, 28.3 g of NH_4NO_3 and 0.123 g of $ZnSO_4$ per 25 kg of air-dried soil, was incorporated into the soil.

Experimental apparatus. A polyvinyl chloride (PVC) pipe (105 mm diameter) was cut into 16-cm lengths, which were capped with PVC caps at one end, and they served as pots without drainage holes (Fig. 1). A hole (12 mm diameter) was drilled into the side of the pot 4.0 cm below the upper rim. A length (20 cm) of plastic tubing (12 mm OD) was inserted into the hole and secured to the pot with silicon sealant. This tube allowed watering of the soil in the infection zone independently of the soil in the surface zone (Fig. 1).

A watering tube was placed in each pot (13). The watering tube (16 cm in length) was constructed from a 20-mm-diameter PVC pipe. Eight holes (0.5 mm diameter) were drilled in a staggered pattern within 7 cm of the base of the watering tube, around which a layer of 200-μm-aperture nylon mesh was glued. The opening at the base of the watering tube was plugged with a rubber bung. The opening at the top of the watering tube also was plugged to reduce evaporation and exclude light from the tube.

Experimental design. The $2 \times 2 \times 2$ factorial experiment was a completely randomized design with five replicates per treatment. Suneca, a crown rot-tolerant cultivar, and the less tolerant cultivar Sunkota (2) were subjected to the following treatments: uninoculated, with root zone maintained at a water content of 0.31 g g^{-1} (equivalent to -0.18 MPa) for the duration of the experiment; uninoculated, with root zone allowed to dry from day 11; inoculated, with root zone maintained at a water content of 0.31 g g^{-1} (equivalent to -0.18 MPa) for the duration of the experiment; and inoculated, with root zone allowed to dry from day 11. Four uninoculated pots were set up at the same time to measure seedling water potential before watering of the surface zone. For each cultivar there was a nonstressed and stressed treatment pot. In addition, four lysimeter pots containing no seedlings were set up to estimate water loss from the soil in the infection zone. The experiment was conducted in March–April 1989 (experiment 1), August–October 1989 (experiment 2), and April–May 1990 (experiment 3).

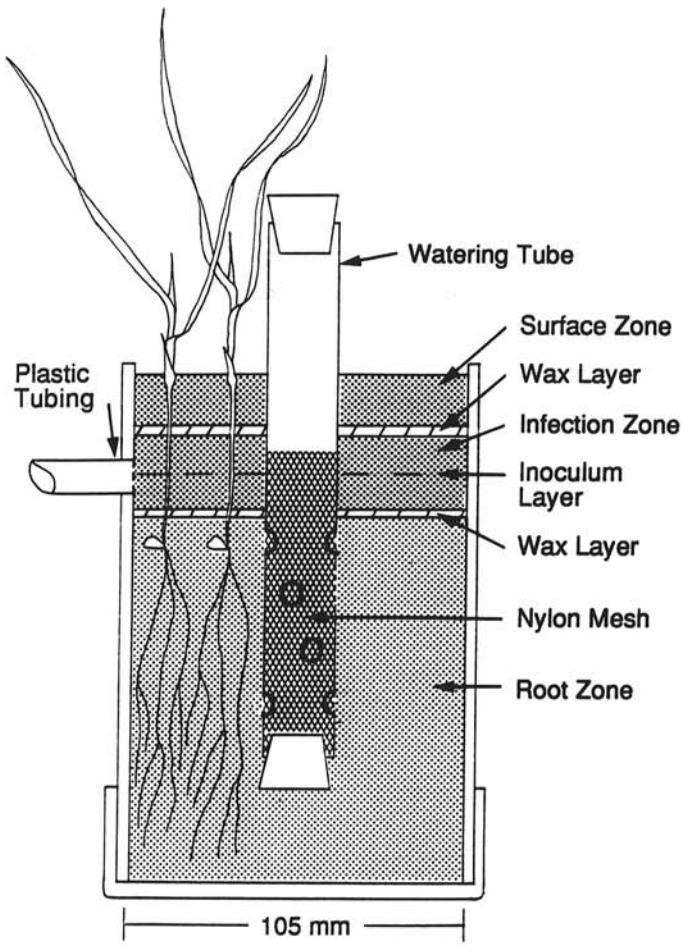

Fig. 1. Diagram of a vertical section through a pot. Wax layers separated the infection zone from the root zone and the infection zone from the air-dry surface zone.

Soil preparation and sowing. In the root zone, the watering tube was centered on 400 g of soil in the pot, and an additional 600 g of soil was placed around the watering tube (Fig. 1). This soil was packed to a bulk density of 1.0 g cm^{-3}. The soil was then watered to a moisture content of 0.31 g g^{-1}, which is an appropriate level for plant growth and is equivalent to -0.18 MPa on the drying boundary curve. The pot was then enclosed in a plastic bag, and the soil was allowed to equilibrate for three days.

Seeds of the cultivars Suneca and Sunkota were sieved through 200-μm-aperture mesh. Uniform, large seeds retained on the sieve were selected for sowing. Seeds were surface-sterilized (1% sodium hypochlorite in an aqueous solution of 10% ethanol) for 30 s, air-dried, and sown (15 seeds per pot) in the root zone. The seeds were covered with 100 g of air-dry soil and watered with an atomizer to bring this air-dry soil to a water content of 0.31 g g^{-1}. A 2- to 3-mm wax layer was then poured onto the surface of the root zone. The wax was prepared by melting and blending Techniwax (Dussek Campbell Pty Ltd, Sydney, Australia) and paraffin oil 2:1, v/v. In the infection zone, air-dry soil (0.75 cm) was placed over the wax layer. Inoculum (0.3 g) of *F. graminearum* Group 1 was spread evenly over the soil, and more soil (0.75 cm) was added (Fig. 1). A second wax layer was poured onto the soil in the infection zone. A further layer of soil (1.0 cm), defined as the surface zone, was placed over the wax and maintained in an air-dry state for the duration of the experiment to inhibit crown root formation (Fig. 1).

Growth conditions. The pots were placed in a glasshouse with 18 C/13 C, day/night alternating temperatures. The mean day length was 12 h in experiment 1; 11 h 44 min in experiment 2; and 10 h 52 min in experiment 3. The mean radiation level was $1,250 \pm 671$ W m^{-2} in experiment 1; $1,835 \pm 369$ W m^{-2} in experiment 2; and $1,062 \pm 418$ W m^{-2} in experiment 3.

The root zone was watered in all pots via the watering tube every 48 h to a predetermined weight corresponding to a moisture content of 0.31 g g^{-1} (-0.18 MPa). Water was withheld from pots that were to be stressed, and seedlings were thinned in all pots to 11 per pot on day 11. The infection zone in all pots was watered to 0.31 g g^{-1} moisture content via the plastic tubing to initiate infection (13) when all seedlings in the stress treatment were visibly stressed in all pots. Estimates of evaporative losses of moisture from the infection zone were derived from lysimeter pots. These estimates were used to correct the predetermined weight. The infection zone was moistened to 0.31 g g^{-1} every 48 h for 28 days, and then all plants were harvested.

Assessment. The water potentials of five seedlings from each of the four uninoculated treatment pots were measured by a sample chamber psychrometer (PMS Instrument Company, Corvallis, OR) when the infection zone was first watered, and one seedling from each pot was also measured at the termination of the experiment. The moisture contents of the soils in the root zone and surface zone at the final sampling were determined gravimetrically by drying soil at 105 C.

All seedlings were removed gently from each pot at harvest. The severity of disease was assessed using the following index: 0 = symptomless plant; 1 = slight browning of the subcrown internode (<25%); 2 = more obvious browning of the subcrown internode (25–75%); 3 = extensive browning of the subcrown internode (75–100%) and slight browning of the basal portion of stem (<25% of total plant); 4 = extensive browning of subcrown internode, stem, and leaf sheath (25–75% of total plant); and 5 = totally necrotic seedling. Disease severity was expressed as

a weighted average of the disease index per pot. This was calculated by the following equation:

$$\text{Disease severity} = \frac{\Sigma\ (\text{disease index} \times \text{number of seedlings})}{\text{total number of seedlings in pot}}$$

Sections were cut from each seedling at the junction of the subcrown internode and crown and at 2.0, 4.0, and 6.0 cm above the crown. These were washed under a fine spray of filtered tap water for 30 min. The sections were then surface-sterilized (1% sodium hypochlorite in an aqueous solution of 10% ethanol) for 30 s, rinsed for 30 s in sterile water, and allowed to dry for 20 min in a flow of filtered air. The sections were then plated on modified potato-dextrose agar (3). All plates were incubated for 4 days in a growth room with a 12-h photoperiod and 25 C/20 C, day/night alternating temperatures. The frequency of isolation of *F. graminearum* Group 1 was determined.

The oven-dry weight of the plant tops (excluding the sections removed for plating) from each pot was determined by drying at 70–80 C for 24 h.

Statistical analysis. The frequency of isolation of *F. graminearum* Group 1 was expressed as a proportion of the plants per pot, transformed (arcsine) and analyzed by ANOVA as a completely randomized design (CRD). Data from uninoculated seedlings were omitted from the analyses as *F. graminearum* Group 1 was not isolated from these seedlings. Disease severity was expressed as a weighted average of the disease index per pot, transformed (square root) and analyzed by ANOVA (CRD). ANOVAs (CRD) also were performed on dry weights and seedling water potential data before initiation of infection and seedling water potential at termination of the experiments. A test for heterogeneity of variance was conducted for the three experiments, and the ANOVAs for each experiment were combined. The ANOVAs for seedling water potentials at initiation of infection and at termination of the experiments could not be combined. At termination, only the seedling water potential ANOVAs for experiments 1 and 2 could be combined. An LSD ($P = 0.05$) was used for comparison between means.

RESULTS

Soil water content. In both stress and nonstress treatments, the water content of soil in the root zone was uniform within treatments for both cultivars before initiation of infection. The water content of the soil in the root zone in the stress treatment pots was lower than the water content of pots of the nonstress

TABLE 1. Water contents of soil from the root zone before initiation of infection and at termination of the experiments

	Soil water content ($g\ g^{-1}$)					
	Before initiation of infection			Termination		
Treatment	Experiment 1[w]	Experiment 2[w]	Experiment 3[x]	Experiment 1[y]	Experiment 2[z]	Experiment 3[y]
Suneca						
Nonstress						
Uninoculated	0.29 ± 0.02	0.29 ± 0.01	0.29	0.29 ± 0.02	0.31 ± 0.03	0.29 ± 0.01
Inoculated				0.30 ± 0.02	0.28 ± 0.02	0.29 ± 0.00
Stress						
Uninoculated	0.21 ± 0.01	0.18 ± 0.03	0.20	0.15 ± 0.01	0.15 ± 0.01	0.12 ± 0.00
Inoculated				0.16 ± 0.01	0.16 ± 0.01	0.14 ± 0.01
Sunkota						
Nonstress						
Uninoculated	0.32 ± 0.03	0.28 ± 0.02	0.32	0.29 ± 0.02	0.31 ± 0.02	0.28 ± 0.01
Inoculated				0.32 ± 0.02	0.32 ± 0.01	0.28 ± 0.02
Stress						
Uninoculated	0.18 ± 0.00	0.21 ± 0.01	0.20	0.17 ± 0.03	0.16 ± 0.01	0.13 ± 0.01
Inoculated				0.16 ± 0.01	0.16 ± 0.01	0.14 ± 0.01

[w] Value shown is a mean of three replicates.
[x] Value shown is one measurement.
[y] Value shown is a mean of five replicates.
[z] Value for the uninoculated is a mean of four replicates and value for the inoculated is a mean of six replicates.

TABLE 2. Water potential of wheat seedlings before initiation of infection and at termination of the experiments

	Seedling water potential (MPa)[y,z]					
	Before initiation of infection			Termination		
Treatment	Experiment 1	Experiment 2	Experiment 3	Experiment 1	Experiment 2	Experiment 3
Suneca						
Nonstress						
Uninoculated	−0.37 a	−0.45 a	−0.32 a	−0.36 a	−0.26 a	−0.36 a
Inoculated				−0.32 a	−0.28 a	−0.32 a
Stress						
Uninoculated	−0.84 d	−1.55 b	−0.73 d	−3.24 bcd	−3.60 b	−3.00 b
Inoculated				−2.97 de	−3.46 bc	−2.63 c
Sunkota						
Nonstress						
Uninoculated	−0.41 a	−0.40 a	−0.36 a	−0.32 a	−0.28 a	−0.32 a
Inoculated				−0.43 a	−0.36 a	−0.43 a
Stress						
Uninoculated	−1.26 c	−1.54 b	−0.70 d	−2.67 e	−3.00 cde	−2.55 c
Inoculated				−2.64 e	−3.00 cde	−2.85 d

[y] Water potential of seedlings measured in a sample chamber psychrometer. Value shown is a mean of five replicates. Means followed by the same letter indicate no significant difference according to the LSD ($P = 0.05$).
[z] Water potentials of seedlings before initiation of infection and at termination were not combined. At termination, seedling water potentials in experiments 1 and 2 were combined, but not in experiment 3.

treatment before initiation of infection. The same trend was observed between pots from stress and nonstress treatments at termination of the experiment. The final water content of soil from the stress treatments was similar in both cultivars (Table 1).

Plant water potential. The water potentials of both Suneca and Sunkota seedlings in the stress treatments were significantly lower at both sampling times than the water potential of seedlings in the nonstress treatments. The water potential of the seedlings in the stress treatments were lower at termination than when infection was initiated. Before initiation of infection, the water potentials were significantly lower in experiment 2 than experiment 1, which in turn were significantly lower than experiment 3. There were significant interactions between cultivar and experiment ($P < 0.01$), water and experiment ($P < 0.01$), and cultivar, water, and experiment ($P < 0.05$). In experiment 1, Sunkota seedlings had significantly lower water potentials than Suneca seedlings, however, in experiments 2 and 3 both cultivars had the same water potentials. In experiment 2, seedlings under water stress had significantly lower water potentials than in experiment 1, which in turn had significantly lower water potentials than experiment 3. In the nonstress treatment, water potentials of seedlings were the same in all three experiments. At termination, there were significant interactions between cultivar and water ($P < 0.05$), cultivar and inoculation ($P < 0.01$), and cultivar, water and inoculation ($P < 0.01$) in experiment 3. At termination, Suneca seedlings in the stress treatment had lower water potentials than Sunkota seedlings. In the stress treatment, the presence of the fungus lowered seedling water potential in Sunkota seedlings but increased seedling water potential in Suneca seedlings. This effect due to the presence of the fungus was not observed in experiment 1 or 2. The seedling water potentials in experiments 1 and 2 were lower than in experiment 3 and could not be analyzed together. In experiments 1 and 2 there were significant interactions between cultivar and water ($P < 0.01$) and water and experiment ($P < 0.01$), however, the same trends were observed in 1989 as in 1990 (Table 2).

Frequency of isolation of *F. graminearum* Group 1. *F. graminearum* Group 1 was isolated from the crown, subcrown internode, and the stem at 2.0, 4.0, and 6.0 cm above the crown in nonstress and stress inoculated treatments of both cultivars (Table 3). The frequency of isolation of the fungus from seedlings was greater in experiment 3 than in experiments 1 and 2. No significant difference occurred in frequency of isolation of *F. graminearum* Group 1 at the subcrown internode and crown in the nonstress and stress treatments of both cultivars in all three experiments. The frequency of isolation of *F. graminearum* Group 1 from the stem decreased with increasing height from the crown. There were significant interactions between water and experiment ($P < 0.01$), height and experiment ($P < 0.01$), height and water ($P < 0.01$), and height, water, and experiment ($P < 0.05$). Isolation of *F. graminearum* Group 1 from seedlings in the stress treatment was significantly greater in experiment 3 than in experiments 1 and 2. In all three experiments, the fungus was isolated more frequently from the crown than from the stem segments 2.0, 4.0, and 6.0 cm above the crown. In all three experiments, the fungus was isolated at the same frequency from the stem at 2.0 and 4.0 cm above the crown, which in turn was significantly greater than from the stem at 6.0 cm above the crown. However, in experiment 3 there was no significant difference in the frequency of isolation of the fungus from the stem at 4.0 and 6.0 cm above the crown. *F. graminearum* Group 1 was isolated more frequently from seedlings in the stress treatment than in nonstressed treatments from the stem at 2.0, 4.0, and 6.0 cm above the crown. However, in experiment 2 the fungus was isolated at the same frequency from Sunkota seedlings in the stress treatment and nonstressed treatments. *F. graminearum* Group 1 was not isolated from seedlings in uninoculated treatment pots.

Disease severity. Subcrown internode and basal stem browning were noted in all treatments (Table 4). Seedlings of both cultivars grown in pots with no inoculum showed significantly less severe subcrown internode and basal stem browning than seedlings in the inoculated treatments. The mild symptoms on some uninoculated seedlings can be attributed in part to infection by *Bipolaris sorokiniana* (Sacc.) Shoemaker, which was isolated from these seedlings. There were significant interactions between water and inoculation ($P < 0.01$), inoculation and experiment ($P < 0.05$), and cultivar and experiment ($P < 0.01$). Seedlings of both cultivars in the inoculated stress treatment showed a greater degree of browning than seedlings in the inoculated nonstress treatment. In experiment 3, disease symptoms were more severe than in experiment 1, which in turn were more severe than in the experiment 2. In experiment 3, there were no differences in disease severity between cultivars, however, in experiment 1 symptoms in Sunkota seedlings were more severe than in Suneca seedlings, but in experiment 2 the reverse was true.

Influence of plant water stress and colonization on dry matter production of wheat. Seedlings in the nonstress treatment produced more dry matter than seedlings under water stress (Table

TABLE 3. Influence of seedling water potential on the frequency of isolation of *Fusarium graminearum* Group 1 from the crown and subcrown internode and from a segment of the stem at heights of 2.0, 4.0, and 6.0 cm above the crown of wheat seedlings

Treatment	Frequency of isolation of *F. graminearum* Group 1[z]			
	Subcrown internode and crown	At 2.0 cm above crown	At 4.0 cm above crown	At 6.0 cm above crown
Experiment 1				
Suneca				
Nonstress	87.5 bcde	18.9 mnopqr	6.1 opqrstu	0.0 u
Stress	81.0 cdef	43.5 hijk	39.5 hijklm	19.7 kmnopqr
Sunkota				
Nonstress	71.7 defg	24.7 klmn p	13.1 nopqrs	0.0 u
Stress	72.6 defg	56.4 fghij	45.5 ghijk	34.7 jklmn
Experiment 2				
Suneca				
Nonstress	80.2 cdef	19.7 lmnopqr	4.8 rstu	1.0 stu
Stress	91.2 abcd	63.3 fghi	36.6 jklm	5.7 op rstu
Sunkota				
Nonstress	87.5 bcde	24.7 klmno	7.1 pqrstu	1.9 stu
Stress	71.7 defg	33.8 jklmn	22.1 klmnopq	7.1 qrstu
Experiment 3				
Suneca				
Nonstress	99.2 ab	12.4 nopqr t	0.8 s u	0.4 u
Stress	99.2 ab	80.2 cdef	65.2 efgh	40.5 ijklm
Sunkota				
Nonstress	96.8 abc	6.6 opqrstu	3.9 rstu	0.5 u
Stress	99.6 a	60.4 fghij	58.4 fghij	43.5 hijk m

[z]Value shown is a mean of five replicates. Retransformed means followed by the same letter indicate no significant difference according to LSD ($P = 0.05$) on transformed data.

TABLE 4. Influence of plant water stress and colonization by *Fusarium graminearum* Group 1 on disease severity of wheat seedlings

Treatment	Disease severity[z]		
	Experiment 1	Experiment 2	Experiment 3
Suneca			
Nonstress			
Uninoculated	0.07 hij	0.02 ij	0.10 hi
Inoculated	1.06 de	0.76 ef	1.49 bcd
Stress			
Uninoculated	0.02 ij	0.11 hi	0.15 ghi
Inoculated	2.22 b	1.88 bc	3.61 a
Sunkota			
Nonstress			
Uninoculated	0.02 ij	0.00 j	0.06 hij
Inoculated	1.42 cd	0.45 fg	1.80 bc
Stress			
Uninoculated	0.19 gh	0.00 j	0.19 gh
Inoculated	3.17 a	1.88 bc	3.46 a

[z]Figure shown is a mean of five replicates. Retransformed means followed by the same letter indicate no significant difference according to LSD ($P = 0.05$) on transformed data.

5). In experiment 2, more dry matter was produced than in experiment 1, which in turn was greater than in experiment 3. There were significant interactions between water and inoculation ($P < 0.05$), water and experiment ($P < 0.01$), inoculation and experiment ($P < 0.01$), and water, inoculation, and experiment ($P < 0.05$). In experiment 1, the presence of the fungus suppressed growth in nonstress seedlings; in experiment 3, the fungus suppressed growth in nonstressed Sunkota seedlings only; however, in experiment 2, the presence of the fungus had no effect on seedling growth. In the stress treatment, both cultivars produced the same amount of dry matter when uninoculated or inoculated with the fungus in all three experiments. However, there is a trend for *F. graminearum* Group 1 to suppress growth in the stressed seedlings.

DISCUSSION

The technique described herein enabled the independent manipulation of the moisture content of soil in the root zone, zone of infection, and surface zone. Thus, the influence of seedling water potential on infection, colonization, and symptom development could be assessed while the water potential of the soil in the infection zone was maintained at near-optimum levels for infection. The soil in the surface zone was maintained in an air-dry state throughout the experiment to prevent the growth of crown roots into the moist soil of the infection zone. Such root growth would provide an alternative source of soil moisture and alleviate seedling water stress induced by manipulation of water in the root zone.

The incidence of infection by *F. graminearum* Group 1 was similar in stressed and nonstressed seedlings. The fungus was able, however, to colonize stressed seedlings to a greater height than seedlings grown under nonstress conditions. These results support the suggestion (18) that the influence of plant water stress on disease is on development of disease rather than initial establishment of the pathogen in the host.

In vitro growth of *F. graminearum* Group 1 can occur over a wide range of osmotic and matric water potentials and is stimulated only slightly by lowering the osmotic water potential of the agar from −0.36 MPa to approximately −1 to −2 MPa (26). The fungus colonized the seedlings extensively in this study when seedling water potential was lowered from −0.43 to −2.85 MPa in cv. Sunkota and −0.32 to −2.63 MPa in cv. Suneca in April–May 1990. Thus, the greater colonization of stressed seedlings by *F. graminearum* Group 1 cannot be explained as a direct stimulatory effect of lowered water potential of the seedling on the growth of the fungus. Low seedling water potential presumably disrupts host physiological processes, including defense mechanisms. Such disruptions would enhance colonization of the host by *F. graminearum* Group 1 and increase severity of symptoms. Although considerable information on the effects of water deficits on host processes is available, the processes that influence host susceptibility are unknown (11).

The severity of symptoms differed between cultivars in all three experiments. Differences between cultivars in respect to disease symptoms have been observed previously in field trials (8) and in pot trials (7). Variations in disease severity in the same cultivar have been attributed to such factors as changes in seasonal conditions, inoculum levels, time of planting, soil type, and nutrient status (8).

The difference in seedling water potential between experiments is due in part to the level of radiation for each period. At high radiation levels, transpiration is increased and ultimately lowers the water potential of the leaf (19). In 1989, seedling water potentials were lower than in 1990 and the corresponding radiation levels were greater. In 1989, the presence of the fungus had no effect on seedling water potential, however, in 1990 the presence of the fungus in Sunkota seedlings reduced seedling water potential. It seems likely that at 4 wk the presence of the fungus in stem tissue had not disrupted seedling water potential. At optimum water potentials, there is evidence that the fungus suppressed dry matter accumulation in seedlings. This trend was also seen in stressed seedlings, but presumably the fungus caused much less suppression by comparison.

In summary, low water potential in wheat seedlings probably disrupted host physiological processes including defense mechanisms to *F. graminearum* Group 1, thus predisposing seedlings to colonization and further damage by the fungus. The results support the hypothesis that the effect of low seedling water potential on disease is more likely to be related to host susceptibility to the fungus than to growth of the pathogen per se.

The effect of water stress in wheat and other cereals and grasses on diseases caused by soilborne pathogens can be studied under controlled conditions using the technique described in the present study for manipulation of moisture in soil layers. Further development and application of the technique described herein would facilitate research on predisposition of mature plants to disease.

TABLE 5. Influence of plant water stress and colonization by *Fusarium graminearum* Group 1 on dry matter production of wheat seedlings

Treatment	Dry matter production (g)[z]		
	Experiment 1	Experiment 2	Experiment 3
Suneca			
Nonstress			
Uninoculated	4.37 c	4.71 abc	3.10 ef
Inoculated	3.38 d	4.89 ab	2.92 f
Stress			
Uninoculated	0.90 hi	0.60 hi	0.88 hi
Inoculated	0.81 hi	0.54 i	0.83 hi
Sunkota			
Nonstress			
Uninoculated	4.50 bc	4.93 a	3.14 ef
Inoculated	3.35 e	5.12 a	2.41 g
Stress			
Uninoculated	0.87 hi	0.56 i	1.01 h
Inoculated	0.72 hi	0.61 hi	0.78 hi

[z]Figure shown is a mean of five replicates. Means followed by the same letter indicate no significant difference according to LSD ($P = 0.05$).

LITERATURE CITED

1. Blaker, N. S., and MacDonald, J. D. 1981. Predisposing effects of soil moisture extremes on the susceptibility of Rhododendron to Phytophthora root and crown rot. Phytopathology 71:831-834.
2. Burgess, L. W., Klein, T. A., Liddell, C. M., and Brewster, C. 1987. Breeding for resistance in wheat to *Fusarium graminearum* Group 1. Pages 62-75 in: Breeding Cereals for Disease Resistance. D. R. deKantzow and N. Derera, eds. AIAS Occasional Publication No. 34.
3. Burgess, L. W., Liddell, C. M., and Summerell, B. A. 1988. Laboratory Manual for Fusarium Research. 2nd ed. Department of Plant Pathology and Agricultural Entomology. University of Sydney, Australia. 156 pp.
4. Burgess, L. W., Wearing, A. H., and Toussoun, T. A. 1975. Surveys of Fusaria associated with crown rot of wheat in eastern Australia. Aust. J. Agric. Res. 26:791-799.
5. Cook, R. J. 1968. Fusarium root and foot rot of wheat in Pacific Northwest. Phytopathology 58:127-131.
6. Cook, R. J., and Christen, A. A. 1976. Growth of cereal root-rot fungi as affected by temperature-water potential interactions. Phytopathology 66:193-197.
7. Dodman, R. L., and Wildermuth, G. B. 1987. Inoculation methods for assessing resistance in wheat to crown rot caused by *Fusarium graminearum* Group 1. Aust. J. Agric. Res. 38:473-486.
8. Dodman, R. L., Wildermuth, G. B., Klein, T. A., and Ellison, F. W. 1985. Field resistance of wheat cultivars to crown rot (*Fusarium graminearum* Group 1). Pages 167-168 in: Ecology and Management of Soilborne Plant Pathogens. C. A. Parker, A. D. Rovira, K. J. Moore, P. T. W. Wong, and J. F. Kollmorgan, eds. The American Phytopathological Society, St. Paul, MN.
9. Duniway, J. M. 1977. Predisposing effect of water stress on the severity of Phytophthora root rot in safflower. Phytopathology 67:884-889.
10. Francis, R. G., and Burgess, L. W. 1977. Characteristics of two populations of *Fusarium roseum* 'Graminearum' in eastern Australia. Trans. Br. Mycol. Soc. 68:421-427.
11. Hsaio, T. C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.

12. Liddell, C. M., and Burgess, L. W. 1985. Wax layers for partitioning soil moisture zones to study the infection of wheat seedlings by *Fusarium graminearum*. Pages 206-208 in: Ecology and Management of Soilborne Plant Pathogens. C. A. Parker, A. D. Rovira, K. J. Moore, P. T. W. Wong, and J. F. Kollmorgan, eds. The American Phytopathological Society, St. Paul, MN.
13. Liddell, C. M., and Burgess, L. W. 1987. A technique for manipulating the time of infection of wheat by *Fusarium graminearum* Group 1. Plant Prot. Q. 2(3):103-107.
14. Liddell, C. M., and Burgess, L. W. 1988. Wax partitioned soil columns to study the influence of soil moisture potential on the infection of wheat by *Fusarium graminearum* Group 1. Phytopathology 78:185-189.
15. Liddell, C. M., Burgess, L. W., and Taylor, P. W. J. 1986. Reproduction of crown rot of wheat caused by *Fusarium graminearum* Group 1 in the greenhouse. Plant Dis. 70:632-635.
16. McKnight, T., and Hart, J. 1966. Some field observations of crown rot of wheat caused by *Fusarium graminearum*. Qld. J. Agric. Anim. Sci. 23:373-378.
17. Papendick, R. I., and Campbell, G. S. 1975. Water potential in the rhizosphere and plant and methods of measurement and experimental control. Pages 39-49 in: Biology and Control of Soil-borne Plant Pathogens. G. Bruehl, ed. The American Phytopathological Society, St. Paul, MN.
18. 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.
19. Ray, P. M. 1972. The Living Plant. 2nd ed. Holt, Rinehart and Winston, Inc. New York. 206 pp.
20. Ristaino, J. B., and Duniway, J. M. 1989. Effect of preinoculation and postinoculation water stress on the severity of Phytophthora root rot in processing tomatoes. Plant Dis. 73:349-352.
21. Schoeneweiss, D. F. 1975. Predisposition, stress, and plant disease. Annu. Rev. Phytopathol. 13:193-211.
22. Stace, H. C. T., Hubble, G. D., Brewer, R., Northcote, K. H., Sleeman, J. R., Mulcahy, M. J., and Hallsworth, E. G. 1968. A Handbook of Australian Soils. Rellim Technical Publications. Glenside. 435 pp.
23. Trimboli, D. S., and Burgess, L. W. 1983. Reproduction of *Fusarium moniliforme* basal stalk rot and root rot of grain sorghum in the greenhouse. Plant Dis. 67:891-894.
24. Van Wyk, P. S., Los, O., Pauer, G. D. C., and Marasas, W. F. O. 1987. Geographic distribution and pathogenicity of *Fusarium* species associated with crown rot of wheat in the Orange Free State, South Africa. Phytophylactica 19:271-274.
25. Van Wyk, P. S., Los, O., Rheeder, J. P., and Marasas, W. F. O. 1987. *Fusarium* species associated with crown rot of wheat in the Humansdorp district, Cape Province. Phytophylactica 19:343-344.
26. Wearing, A. H., and Burgess, L. W. 1979. Water potential and the saprophytic growth of *Fusarium roseum* 'Graminearum'. Soil. Biol. Biochem. 11:661-667.