Techniques

Wax Partitioned Soil Columns to Study the Influence of Soil Moisture Potential on the Infection of Wheat by *Fusarium graminearum* Group 1

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The first author acknowledges the receipt of a F. H. Loxton postgraduate studentship from The University of Sydney. The authors are grateful to Dr. W. J. Bond for permission to publish the moisture and hydraulic conductivity characteristics of G150 sand.
Accepted for publication 14 August 1987 (submitted for electronic processing).

ABSTRACT

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.

The influence of soil moisture potential on the infection of wheat seedlings by *Fusarium graminearum* Group 1 was examined using a new technique that enables accurate control of the moisture potential of infested soil surrounding the coleoptile. The coleoptile emerged through infested soil sandwiched between two wax layers. The moisture potential of the soil between the wax layers was adjusted by isopiestic or pressure membrane equilibration. The seminal roots grew in a lower soil layer maintained at a constant −105 cm hydrostatic suction. Infection of the coleoptile occurred between saturation and −2.15 MPa soil moisture potential, and maximum infection occurred at −0.5 MPa.

Crown rot, caused by *Fusarium graminearum* Schwabe Group 1 (11), is an important disease of dryland wheat (*Triticum aestivum* L.) in the central and northern regions of the eastern wheat belt of Australia (2). It has also been reported from the Pacific Northwest of the United States (7). In Australia, the disease occurs most commonly on deep, clay soils in regions where the rainfall is summer dominant and spring wheats are grown during winter, using subsoil moisture accumulated during the summer fallow (2). The pathogen persists as hyphae in host residues (20,22) on and in the friable tillage layer of the soil (15,22).

Saprophytic growth of *F. graminearum* Group 1 occurs at osmotic potentials from −0.1 to −13.0 MPa (−1 MPa = −10 bars), with the maximum growth rate at −1.0 to −2.0 MPa (8,23). The maximum growth rate in response to matric potential occurred at −0.2 MPa (the highest potential examined), and the growth rate was 25% of the maximum at −7.7 MPa (the lowest potential examined) (23). The fungus is therefore capable of saprophytic growth over a wider range of potentials than those normally associated with plant growth. In contrast to the deeper, consolidated subsoil, the moisture content of the soil in the tillage layer varies from saturation to air dry within a few days to a few weeks after rainfall (6) and is likely to influence the activity of the pathogen before infection. Thus, the moisture content of the tillage layer is probably a major determinant of the likelihood of infection of susceptible hosts. Infection is also influenced by the moisture status of the host (7), which is mainly dependent on the moisture content of the subsoil and does not vary greatly during the early part of the season (6). Moreover, wheat is planted in the summer dominant rainfall regions only if there is adequate subsoil moisture for crop establishment.

Liddell and Burgess (15) reported that infection of wheat seedling coleoptiles by *F. graminearum* Group 1 occurred in the range −0.1 to −1.5 MPa moisture potential and was maximal at −0.3 to −0.7 MPa, in untreated soil in small pots. Thin wax layers were used to enclose the infested surface soil (soil above the seed) so that the moisture potential of the surface soil could be varied independently of the subsoil, which was maintained in the range −0.1 to −0.3 MPa soil moisture potential. However, critical control of the surface soil moisture potential using this technique

was not possible because it was adjusted on the wetting curve of the moisture characteristic (15). A small loss of moisture from the surface soil during an experiment could therefore cause a rapid decrease in moisture potential as the soil shifted from the wetting to the drying curve.

The technique described in this paper to study the infection of wheat seedling coleoptiles by *F. graminearum* Group 1 ensured that the infested soil surrounding the coleoptile was equilibrated directly to a desired moisture potential and not moisture content. Furthermore, the soil was brought to this equilibrium potential by drying rather than wetting. Thus, a small degree of drying of the infested soil during an experiment would cause only a slight change in moisture potential because the soil remained on the drying curve.

MATERIALS AND METHODS

Soil. The soil was collected from the top 15 cm of a black earth at the I. A. Watson Wheat Research Centre, Narrabri, NSW Australia. *F. graminearum* Group 1 could not be isolated from this soil using debris-plating or dilution plating techniques (4). The soil, a vertisol (pH 7.4 in a 1:5 soil suspension in 0.01 M $CaCl_2$), is a high smectite, dark plains soil with a clay content of 51%. Further details of this soil are reported elsewhere (16,21). It was not treated before use beyond sieving through a 2-mm-mesh screen.

Experimental apparatus. Plants were grown singly in untreated black earth in partitioned columns (4 cm diameter) of 10-cm length comprising an 8-cm subsoil column and a 2-cm top-piece, which is located on top of the subsoil column (Figs. 1 and 2). The partitioned columns were placed on a sand tension table maintained at −100 cm suction to supply water for plant growth at a constant potential (Fig. 1). The soil columns were placed directly on the sand bed and were supported by notched PVC rings, which were glued, notches down, to the base of the sand bed. There were six drains in the base of the sand bed; each drain was covered with one layer of 200-μm nylon mesh, which was glued securely over the drain. A 4.25-cm-diameter disk of Whatman No. 50 filter paper was glued over the nylon mesh, and then a single Metricel membrane of 0.45 μm pore size (GN-G, Gelman Instrument Company) was glued over the filter paper using epoxy resin. Before any sand was placed in the sand bed, the baseboard was inverted and each manometer tube was completely filled with water, and the meniscus was maintained approximately 10–20 cm above the baseboard for 10 min to fully saturate the filter paper and the Gelman membrane. The baseboard was then turned upright and placed on supports under fluorescent lights. The manometer tubes were held at $\Delta h = 0$ cm (Fig. 1) for at least 1 hr to ensure that the membrane was fully saturated. After this time the open ends of the manometer tubes were placed in a remote water reservoir, and suction was increased over 8 hr to −100 cm. This suction was left on the drains for 2 wk, to ensure that no air leaks were present in the drain assembly.

A commercially graded silica sand (G150) was chosen for the tension table bed. Before use, the sand was thoroughly washed to remove all particles less than 20 μm in diameter and air dried. A complete characterization of the physical properties of G150 sand was reported by Bond (1). This sand was chosen because it remains saturated at a suction of −100 cm of water on the draining curve (1). Furthermore at −100 cm suction the hydraulic conductivity is relatively high (1.2×10^{-3} cm sec^{-1}) (1), a desirable feature that allows the relatively rapid equilibration of moisture potential throughout the sand bed (Fig. 3).

The manometer tubes were brought up to $\Delta h = 0$ cm before the sand was made into slurry with filtered tap water and poured gently onto the baseboard to a depth of 2.5–3.0 cm so as not to disrupt the exposed membrane over the drain. The slurry was then poured into each of the supports to a depth of 1.5 cm so that the sand bed was continuous over the whole baseboard. A thin, black polyethylene sheet was cut to allow free access to the supports and secured over the sand mass to reduce evaporative losses. The flexible PVC supports were then filled with water that was permitted to drain and come to equilibrium with the applied suction.

The moisture content of the sand was determined gravimetrically at several points around the sand bed each time the bed was remade and put under a tension of −100 cm and again at the end of the experiments. At no time did the moisture content indicate that the sand had drained after the suction was applied. This means that the sand was always at a suction of less than approximately −110 cm (Fig. 3), although it is likely that there were slight gradients in potential within the sand bed leading to the drains. Indeed these gradients would be required for water to move to the plant roots during the experiments. It is anticipated that these gradients would have a minimal effect on the plants and would be taken into account by treatment randomization.

Sowing and infestation. Before sowing, the subsoil columns were inserted into the flexible PVC supports, the sand surface was roughened, and then air-dry black earth was placed in each column. The columns were filled to within 1 cm of the top and then the soil was saturated to allow drainage into the sand bed. After 24 hr of equilibration, wheat seeds (cultivar Timgalen), which had been surface disinfested (1.8% hypochlorite for 1 min) and pregerminated for 72 hr on moist, sterile filter paper in a humid chamber at 20 C in the dark, were sown on the moist subsoil. One healthy, germinating seed, with a radicle length of 2–10 mm, was

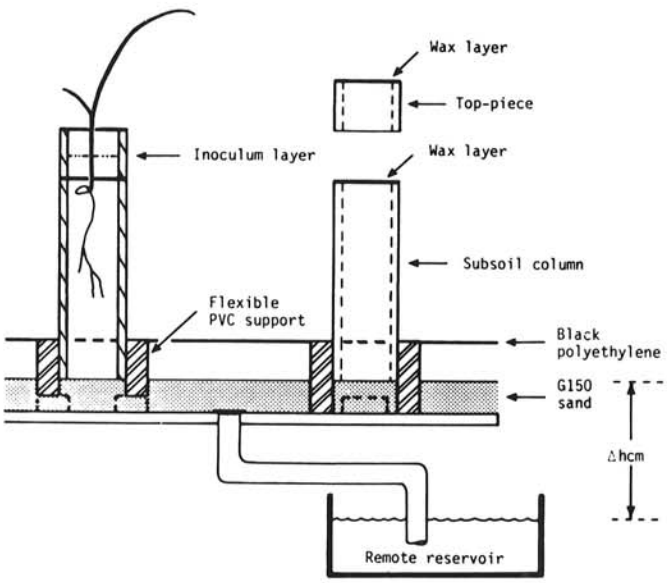

Fig. 1. Diagram of partitioned columns and sand tension table.

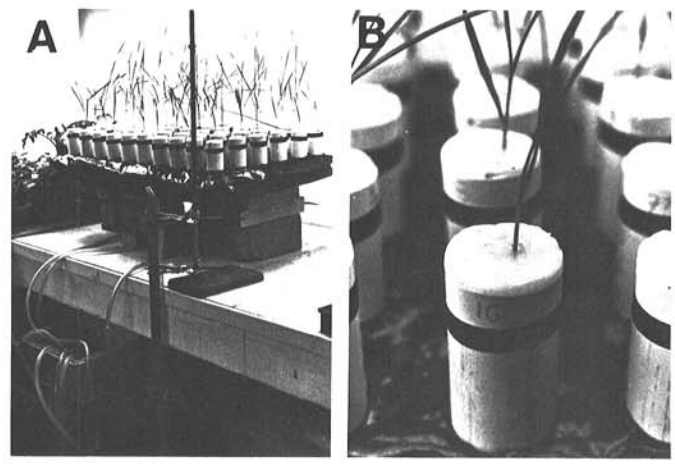

Fig. 2. View of the sand tension table and partitioned columns containing wheat plants. **A,** Sand tension table at −50 cm tension and partitioned columns with young seedlings. **B,** Seedlings emerging through wax layers.

sown in each subsoil column. The seed was then covered with air-dry soil to the top of the column and carefully watered with an atomizer to saturate the soil above the seed. A layer (2–3 mm thick) of Ceratak 165 wax mixture (2 parts Ceratak 165 to 1 part paraffin oil, v/v) (17) was then poured over the soil surface using a circular mold and sealed to the top of the subsoil by gentle pressure around the edge.

The soil in the top-piece was infested with 0.05 g of inoculum of *F. graminearum* Group 1 (isolate DAR 52453) using the layer method (16) as a fine band midway between the top and bottom of the top-piece (Fig. 1). The inoculum density within the layer was 4 mg cm^{-2}, about an order of magnitude higher than the density used in large pot experiments (16). The inoculum was derived from cultures of *F. graminearum* Group 1 grown on wheat chaff (fragments of stem internodes and nodes). Colonized chaff was air dried, crushed, and sieved (710 μm diameter) before infestation (16).

Moisture potential adjustment. The moisture potential of the soil in the top-piece was adjusted by one of two methods depending on the experimental design. Both methods of adjusting moisture potential enabled the precise adjustment of the moisture potential directly on the drying curve. The two methods used were the pressure membrane technique (18,19) and isopiestic equilibration over saturated salt solutions (5,12). All operations were carried out at constant 20 C.

The use of pressure membrane apparatus was described by Richards (18,19). It was applied to the following experiments by wetting air-dry soil in a plastic bag with a fine spray of water and constant mixing until the soil was at a moisture content of 0.275 g g^{-1}. This soil was then allowed to equilibrate for 3 wk in the dark at 20 C with kneading every 3 or 4 days. After equilibration the soil was packed into top-pieces with inoculum, at a bulk density of 1.0 g cm^{-3}. The top-pieces were then placed on the ceramic plates of the pressure chambers (Soil Moisture Equipment Co., Santa Barbara, CA). The soil was then gently flooded and saturated. The appropriate pressure was applied until all water extraction had ceased, at which time the top-pieces were placed on the subsoil columns and covered with a wax layer as described below.

Isopiestic equilibration involved the use of a saturated solution of the appropriate salt to establish infested soil in the top-pieces at a particular total moisture potential. Air-dry soil was placed in a plastic bag and wet with a fine spray of water while being mixed continuously. The soil was wet to a moisture content well above the moisture content on the drying curve equivalent to the desired moisture potential. This soil was allowed to equilibrate for 3 wk in the dark at 20 C with kneading every 3 or 4 days. After equilibration the soil was packed into top-pieces with inoculum at a bulk density of 1 g cm^{-3} with a layer of 200 μm nylon mesh strapped to the base. These were placed in a vacuum desiccator containing the appropriate saturated solution. The desiccator was evacuated and placed in a constant temperature water bath at 20 C in the dark for 4 wk until constant weight was achieved. The nylon mesh was removed at this time, and the top-piece was placed on the subsoil column and covered with a wax layer as described below.

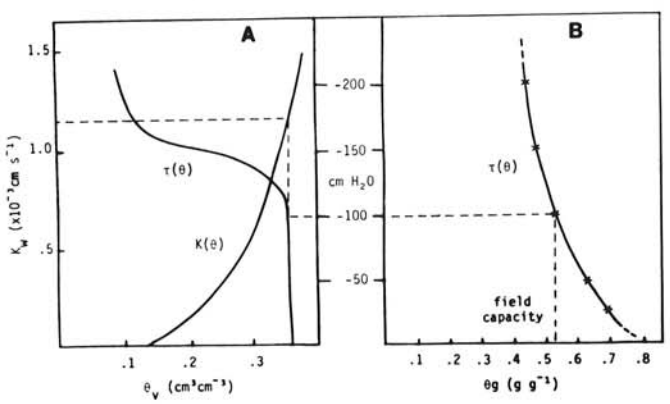

Fig. 3. Moisture characteristics $\tau(\theta)$ of **A,** G150 sand and **B,** a Narrabri black earth from 0 to −200 cm suction and the hydraulic conductivity $K(\theta)$ of G150 sand over the same range. Soil hydraulic conductivity on the y-axis expressed as K_w; volumetric moisture content expressed as θ_v in **A**; and gravimetric moisture content expressed as θ_g on the x-axis in **B.**

Placement of top-pieces and growth conditions. When the top-piece was packed with soil and the layer of inoculum and equilibrated to the appropriate moisture potential they were carefully placed on top of the wax layer on a subsoil column and taped to the column with black, polyethylene adhesive tape. A layer of wax (2–3 mm) was then poured onto the surface of the soil in the top-piece using a circular mold and also between the soil and the wall of the top-piece if the soil had shrunk during equilibration.

The tension table was located below a bank of 10 fluorescent lights (5 × 40W Gro-lux and 5 × 40W cool-white) with a photoperiod of 9 hr at a constant 20–22 C. The lights were 60 cm above the top of the top-piece. All experiments were conducted under these conditions. Water was continuously supplied to the base of the subsoil at −100 cm suction through the sand table. Experiment 1 was conducted four times and experiment 2 was conducted twice.

Influence of soil moisture potential on infection: saturation to air-dry. In this experiment, the general relationship between moisture potential (from saturation [0.0 MPa] to air-dry [approximately −75.0 MPa]) and infection of wheat by *F. graminearum* Group 1 was examined.

The experiment was of a randomized complete block design with five different moisture potentials of the infested soil contained in the top-pieces, replicated 12 times. The different moisture potentials were: 0.0 MPa, saturated by placing soil with the layer of inoculum contained in top-pieces in 1 cm depth of water for 3 wk, in the dark at 20 C; −0.3 MPa and −1.0 MPa, obtained by pressure membrane equilibration; −2.15 MPa, obtained by isopiestic equilibration over saturated $K_2Cr_2O_7$; and approximately −75.0 MPa, air-dry soil with a moisture content of 0.072 g g^{-1}.

Pregerminated seeds of cultivar Timgalen were sown in the subsoil columns, and all top-pieces were positioned within 2 days of sowing. The moisture content of soil samples equilibrated at the same time as the top-piece soil was determined at this time. Twenty days after sowing the experiment was terminated.

Emergence was assessed daily. At the termination of the experiment, the number of plants that had emerged through one or both wax layers was determined, and the total height of the plant above the top wax layer was recorded. Each plant was carefully removed and washed free of soil. The plant was then washed under filtered tap water for 1 hr, and the coleoptile was removed. The coleoptile was air dried and plated on YDA (1 g L^{-1} of yeast extract, 5 g L^{-1} of dextrose, and 20 g of agar in 1 L) after air drying. The remainder of the plant was surface sterilized (1.8% hypochlorite and 10% ethanol in aqueous solution) and air dried. Small segments of tissue from the seminal roots, scutellum, subcrown internode, leaf sheaths, and vegetative shoot apex were plated on YDA. The plates were incubated under fluorescent lights for 4–6 days (4) before the frequency of isolation of *F. graminearum* Group 1 was recorded. The gravimetric moisture content of the soil in the top-piece also was determined at the termination of the experiment.

Total height data and final moisture content data were analyzed with a one-way analysis of variance. Discrete data, such as emergence and isolation data, were analyzed by calculating homogeneity χ^2 values for the proportion of total plants from all possible pairs of treatments.

Influence of soil moisture potential on infection: −0.1 MPa to −1.0 MPa. Experiment 2 was designed to identify the optimal soil moisture potentials for infection more precisely by assessing the incidence of infection in the range −0.1 to −1.0 MPa matric potential.

The experimental design and methods for this experiment were as for experiment 1. The soil in the top-pieces was prepared at five moisture potentials by pressure membrane equilibration and the potentials used were −0.1, −0.3, −0.7, and −1.0 MPa. This experiment was terminated 19 days after sowing.

RESULTS

Influence of soil moisture potential on infection at saturation to air dry. The mean height of all plants above the top wax layer was 290.2 mm in experiment 1, and there was no significant difference between any of the moisture potentials. The emergence of plants through the top wax layer began 5 days after sowing, and all plants that finally emerged had done so by 9 days (Table 1). There was no significant difference in the rate of emergence. The moisture content of the soil in the top-pieces at the end of the experiment was not significantly different from that determined at the beginning of the experiment (Table 2). This indicates that containment of moisture by the wax layers was within acceptable limits.

F. graminearum Group 1 was isolated more frequently from plants that emerged through top-pieces containing soil at a moisture potential of −0.3 MPa (Table 1). The frequency of isolation was low at saturation, −1.0 MPa and −2.15 MPa, and *F. graminearum* Group 1 was not isolated from any plants that emerged through top-pieces containing air-dry soil (Table 1).

Influence of soil moisture potential on infection at −0.1 MPa to −1.0 MPa. The mean height of all plants above the top wax layer was 308.4 mm in Experiment 2, and there was no significant difference between any of the matric potentials. The emergence of plants through the top wax layer began 5 days after sowing, and all plants that finally emerged had done so by 11 days (Table 3). There was no significant difference in the rate of emergence, although one plant did not emerge through the top wax layer at −0.5 MPa because of preemergent death caused by *F. graminearum* Group 1. The moisture content of the soil in the top-pieces at the end of the experiment was not significantly different from that determined at the beginning of the experiment.

F. graminearum Group 1 was isolated more frequently from plants that emerged through top-pieces containing soil at a matric potential of −0.5 MPa (Table 3). The frequency of isolation was significantly lower only at −0.1 MPa and −1.0 MPa, indicating that the optimum matric potential for infection is in the range of −0.3 MPa to −0.7 MPa.

DISCUSSION

The results indicate that infection of wheat by *F. graminearum* Group 1 occurs over the range of 0.0 to −2.15 MPa moisture potential and that the optimal moisture potential for infection is between −0.3 and −0.7 MPa. These findings are in agreement with earlier experiments (15), which indicated that the optimal moisture potential for infection was approximately −0.3 to −0.7 MPa, although no significant difference was detected between the incidence of infection at −0.1, −0.3, −0.5, and −0.7 MPa. The present experiments have shown a significant reduction in the rate of infection at −0.1 MPa as well as at −1.0 MPa, −2.15 MPa, and no infection at −75.0 MPa. This means that the results do not greatly differ from those of Liddell and Burgess (15) despite the greater precision of the technique used in the current studies. Therefore, the influence of hysteresis of the soil moisture content and soil moisture potential relationship is not important in the study of infection of wheat by *F. graminearum* Group 1. This is due to the relatively wide range of potentials that are favorable for infection and the low resolution of the limits of this range of potentials using the present technique. Higher resolution of the relationship between moisture potential and infection would be hard to attain because of the difficulties in maintaining a truly homogeneous constant soil moisture potential.

The inhibition of infection under saturated soil conditions is noteworthy and may be due to microbiological antagonism or oxygen depletion. This inhibition of infection at high moisture potentials (0.0 to −0.1 MPa), which was also observed earlier (15), supports the hypothesis that bacterial antagonism becomes important at these potentials. The high frequency of isolation of bacteria from the coleoptiles of plants that emerged through saturated soil provides further support for this possibility (Liddell and Burgess, *unpublished*).

Liddell (14) showed that the infection rate in sterile soil at a moisture potential as low as −5.0 MPa was 100%, and Wearing and Burgess (23) demonstrated that *F. graminearum* Group 1 can grow saprophytically in culture at a matric potential as low as −7.7 MPa. Thus, it appears that wheat has little or no inherent resistance to infection by *F. graminearum* Group 1 and that infection rates below 100% in untreated soil are probably caused by microbiological suppression of *F. graminearum* Group 1. This may take the form of antagonism or nutritional competition. Griffin (13) suggests that fungi, such as *Aspergillus* spp. and *Penicillium* spp., are most active at these potentials. Assuming a low level of available nutrients, then *F. graminearum* Group 1 would be required to compete with these fungi that are more adapted to growth at low moisture potentials (13). As the moisture potential increases, the metabolic demand for osmoregulation presumably decreases and *F. graminearum* Group 1 would be able to compete more successfully for the available nutrients, reaching a peak of activity before the onset of maximum bacterial activity at above −0.1 MPa (13). Duniway and Gordon (10) also suggest that actinomycetes active at low potentials (below −1 MPa) may be responsible for the suppression of infection at lower potentials, which are still favorable for saprophytic growth.

Growth of *F. graminearum* Group 1 out of the inoculum layer into adjacent soil during the equilibration period was noted in some of the moist soil treatments (−0.3, −0.5, and −0.7 MPa). It was not extensive but indicates that *F. graminearum* Group 1 was active in the soil at these potentials. This observation indicates that infection may have been more common at −0.3, −0.5, and −0.7 MPa partly because the fungus was already active.

The partitioned column technique represents a considerable advance in the study of the influence of low soil moisture on soilborne diseases. A number of techniques have been developed for studies on fungi such as *Phytophthora* spp. at high moisture potentials (9). These depend on tension plates that allow accurate control of matric potential from saturation to a suction of about −300 cm of water, which means that such studies are restricted to matric potentials above field capacity (−0.03 MPa).

The growth tube technique permits studies over the entire range of matric or total potentials encountered in soil. It is, however,

TABLE 1. Frequency of isolation of *Fusarium graminearum* Group 1 from the plant tissue indicated, of plants that emerged through soil with a layer of inoculum of five moisture potentials from saturation to −75.0 MPa after 20 days (Experiment 1)

Moisture potential (MPa)	Isolation frequency[x]						Plants infected[x,y] (no.)	Plants emerged through lower wax layer (no.)	Plants emerged through upper wax layer (no.)
	Coleoptile	Seminal roots	Scutellum	Sub-crown internode	Leaf sheaths	Shoot apex			
0.0	2 a[z]	0 a	0 a	0 a	0 a	0 a	2	12	12
−0.3	7 b	0 a	1 a	6 b	4 b	0 a	11	12	11
−1.0	3 a	0 a	1 a	1 a	1 a	0 a	3	12	11
−2.15	2 a	0 a	0 a	0 a	0 a	0 a	2	12	11
−75.0	0 a	0 a	0 a	0 a	0 a	0 a	0	12	12

[x] Maximum number of 12.

[y] *F. graminearum* Group 1 isolated from any tissue.

[z] Values followed by the same letter indicate no significant difference within columns according to homogeneity χ^2 test ($P = 0.05$).

most suitable for use with emerging coleoptiles or other subterranean stem tissues that do not extract soil moisture. The technique depends on static equilibrium for the control of the moisture potential of the soil in the top-pieces. Consequently any loss of moisture results in a lack of precision. The wax layers prevent loss of moisture, but may reduce oxygen availability over longer experiments. For this reason all experiments were kept as short as possible.

Further possible problems with the technique relate to the long equilibration period for the soil with the layer of inoculum in the top-pieces. A pathogen may either proliferate or fail to survive through the equilibration period, resulting in variation in inoculum levels at different moisture potentials. At moisture potentials in the range from saturation to −0.1 MPa, the activity of antagonistic microorganisms is likely to be high, and a pathogen may not survive the equilibration period. However, the data of Burgess and Griffin (3) indicated that *F. graminearum* Group 1 should survive up to 12 wk under these conditions. Furthermore, this fungus was isolated from the chaff inoculum at each moisture potential both after equilibration and after the experiments were terminated. However, these isolation procedures could not detect small changes in inoculum levels between treatments. We recommend that the equilibration time at high moisture potentials be as brief as possible to minimize such changes. Fortunately equilibration at these moisture potentials is very rapid using the pressure membrane apparatus.

TABLE 2. Gravimetric moisture content of soil contained between wax layers in the top-pieces before and after Experiment 1 (20 days)

Moisture potential of soil contained in top-piece (MPa)	Gravimetric moisture content g g^{-1}	
	At start of experiment	At termination of experiment
0.0	0.675[a]	0.627
−0.3	0.275	0.272
−1.0	0.223	0.221
−2.15	0.164	0.167
−75.0	0.072	0.074

[a] No significant differences between means in each row.

TABLE 3. Frequency of isolation of *Fusarium graminearum* Group 1 from the plant tissue indicated, of plants that emerged through soil with a layer of inoculum of five moisture potentials between −0.1 and −1.0 MPa after 19 days (Experiment 2)

Moisture potential (MPa)	Isolation frequency[x]						Plants infected[x,y] (no.)	Plants emerged through lower wax layer (no.)	Plants emerged through upper wax layer (no.)
	Coleoptile	Seminal roots	Scutellum	Sub-crown internode	Leaf sheaths	Shoot apex			
−0.1	2 a[z]	0 a	0 a	2 a	1 a	0 a	4	12	12
−0.3	7 b	0 a	0 a	8 b	4 ab	0 a	8	12	12
−0.5	5 b	0 a	1 a	9 b	6 b	1 a	11	12	11
−10.7	2 a	0 a	0 a	4 ab	5 b	0 a	7	12	12
−1.0	1 a	0 a	1 a	1 a	0 a	0 a	2	12	12

[x] Maximum number of 12.

[y] *F. graminearum* Group 1 isolated from any tissue.

[z] Values followed by the same letter indicate no significant difference within columns according to homogenity χ^2 test ($P = 0.05$).

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