Infection of Wheat by *Cephalosporium gramineum* as Influenced by Freezing of Roots

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ABSTRACT

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Exudates collected from wheat roots that had been frozen and thawed increased spore germination, hyphal branching, and conidiogenesis of *Cephalosporium gramineum* more than did exudates from nonfrozen roots. Conidia subjected to soil fungistasis on the surface of nonsterilized soil germinated and penetrated wheat roots in the presence of exudate from roots that had been frozen. Hyphae grew throughout the cortical tissue. Plants with cut roots developed 62% infection following inoculation when roots were dipped into a suspension of conidia of *C. gramineum* and transplanted into soil. Only 0–3% infection developed in plants with cut root systems after they were transplanted into infested soil. Fourteen percent of the plants with intact root systems growing in infested soil became infected after exposure to −15 C, but none became infected when held at a low nonfreezing temperature (2 C). It was concluded that freeze stress may be an important factor affecting the predisposition of wheat plants to active penetration and infection by *C. gramineum*.

Cephalosporium leaf stripe is a vascular disease of winter wheat caused by the soilborne fungus *Cephalosporium gramineum* Nis. & Ika. (= *Hymenula cerealis* Ellis & Everhart). This disease is present in many of the major wheat-growing regions of the world (2,4,8,10,14,15,18,22) including the United States, where it is particularly destructive in Washington (2,3), Kansas (22), and Montana (9). It is generally thought that *C. gramineum* conidia enter passively through roots severed as a result of frost heaving the soil and that they are drawn into the plant via the transpiration stream (8). It is now well established that winter or early spring stresses predispose wheat to infection by *C. gramineum* (3,8,13). However, recent work (1) has provided evidence that forms of winter stress other than frost heaving may play a role in predisposing plants to infection (1). This paper presents evidence that root exudation resulting from freeze stress can promote the germination of *C. gramineum* conidia and result in direct penetration of wheat roots and the development of disease.

MATERIALS AND METHODS

Fungus culture. An isolate of *C. gramineum* obtained from a naturally infested wheat field in East Lansing, MI, was used throughout this work. Stock cultures were maintained on potato-dextrose agar (PDA) at 4 C. The fungus was routinely passed through wheat plants to insure against loss of pathogenicity.

Effect of root exudates on *C. gramineum*. To determine the effect of exuded nutrients from frozen, cut, or intact roots on conidial germination, wheat plants (cultivar Genesee) were grown for 14 days in coarse sand in 10-cm-diameter clay pots (~50 seeds per pot) in a growth chamber with a 16-hr photoperiod (20,000 lux) at 18 C. The plants were removed from the pots and the roots were severed from the shoots. These root systems were treated in one of three ways: frozen in distilled water (−11 C) for 15 hr then allowed to thaw at 22 C for 9 hr (total of 24 hr); cut into 1-cm lengths and soaked at 22 C for 24 hr; or left intact and unfrozen and soaked at 22 C for 24 hr. All root tissue was then removed and the resultant exudate solutions were adjusted with distilled water so that each milliliter represented the exudate from 3.3×10^{-3} g of dry root tissue. Equal volumes (~1.0 ml) of each of these three exudate preparations were added to 1 ml of a conidial suspension (10^6/ml) and placed in individual wells of acid-washed, sterilized depression slides. Germination was determined after incubation overnight at 22 C. Sterile distilled water (22 C) served as a control.

The effect of exudates from frozen roots of aseptically grown wheat plants was also determined. Wheat seeds were sterilized by treating them for 5 min in 70% ethanol followed by 5 min in 5.25% sodium hypochlorite. After four washes in sterile distilled water, seeds were germinated in 5 ml of sterile 0.1% nutrient agar in petri dishes. Uncontaminated seedlings were placed in 30-ml plastic disposable syringe barrels (OD 2.5 cm) containing 3 ml of sterile Hoagland's solution (5). Sterile serum bottle caps covered the small orifice and sterile cotton plugged the large orifice. When the first true leaf had reached the cotton plug, the cotton was removed, and the seedlings were elevated so that the shoot was outside the syringe, but the seed and root remained within. The cotton was then aseptically replaced and syringes containing the plants were racked in "Conetainer" trays (Ray Leach's "Conetainer" Nursery, Canby, OR 97013). The plants were first grown for 20 days at 18 C in a growth chamber with a 15-hr photoperiod (10,000 lux), then were hardened for 20 days at 2 C in a growth chamber under continuous light (27,000 lux). The plants were then frozen in a freezing chamber (11) (supplied by C. R. Olien) in which the temperature was lowered at the rate of −0.5 C/hr. A minimum air temperature of −10 C was followed by a slow thaw (0.5 C/hr).

Root exudate from each plant was collected aseptically 3 days before and 3 days after freezing, by using a sterile hypodermic syringe to withdraw it by puncturing the serum bottle cap. These solutions were tested for sterility by plating 0.5 ml on PDA, then were adjusted to contain the equivalent of exudate from 2.0×10^{-3} g of dry root per milliliter of water. Agar was added to make a 2% solution (w/v), and the mixture was autoclaved and poured into petri plates (10 ml per plate). One milliliter of a conidial suspension (~10^6 conidia per milliliter) was added to disks (8 × 1 mm) of exudate agar and incubated at 22 C for 1.5 days. Germination, length of germlings, hyphal branching, and production of conidia were determined at the end of the incubation period.

Effect of exudate from frozen wheat roots on germination of *C. gramineum* in soil-imposed fungistasis. Nonsterilized soil was employed in a system that maintained the sterility of conidia of *C. gramineum* and wheat roots (Fig. 1). The center of a 'ring' cut from 10 ml of solidified 2% water agar, with a central opening 2.5 cm in

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diameter, was filled with saturated (31% moisture), nonsterile Capac clay loam soil. A sterile Millipore filter (0.22 μm, 4.7 cm in diameter) was placed over and in contact with the soil with its edge extending beyond the outer edge of the agar ring. Disks of water agar (8 × 1 mm) bearing conidia of *C. gramineum* on the upper surface were placed on the center portion of the filter over the soil.

Sterile, 4-day-old wheat seedlings, whose roots had been frozen immediately before use, were placed on the disks in contact with the conidia. Freezing was done by covering the roots of intact seedlings in sterile 50 ml beakers with sterile distilled water, covering the beakers with Parafilm (American Can Co., Greenwich, CT 06830), and placing them in a stirred ethanol bath. The temperature of the ethanol was lowered by the addition of liquid nitrogen. The water temperature dropped from 20 to −5 C in 12 min. After an additional 3 min at −5 C beakers were removed and allowed to thaw at room temperature. Nonfrozen roots were treated as above, except that they were incubated at 20 C for 15 min. The spores were examined by using Nomarski differential interference contrast optics.

Electron microscopy of the infection process. Roots of 7-day-old seedlings, incubated on agar disks with conidia of *C. gramineum* (see previous section), were examined. Studies were also made with roots of 21-day-old unhardened seedlings growing in syringe barrels (as described above), and frozen to −10 C at the rate of −0.5 C/hr in a chest freezer in which the lid had been replaced with a 1.9-cm-thick plywood board into which 2.5-cm-diameter holes had been cut. The syringes were inserted into the holes so that only the roots were frozen. After thawing, Hoagland's solution was replaced with a suspension of conidia of *C. gramineum* (3×10^5/ml) in distilled water. After 10 days, the roots were cut into short (1–2 cm) segments and soaked in 5% glutaraldehyde solution at pH 4.2 overnight. After two washes in 0.1 M phosphate buffer (pH 7.2) the root tissue was soaked in 1.0% osmium tetroxide overnight. Two more washes in 0.1 M phosphate buffer (pH 7.2) preceded dehydration in an ethanol series. The tissue was frozen in liquid nitrogen and freeze-fractured by striking it repeatedly with a razor blade until all pieces were approximately 2–3 mm in length. The tissue pieces were critical-point dried by using a Sorvall Critical-Point Drying System (Ivan Sorvall, Inc., Newtown, CT 06470), fixed to stubs, and gold-coated using a sputter coater (Mini-Coater, Film-Vac, Inc., Englewood, NJ 07631). A Super MINI II scanning electron microscope (International Scientific Instruments, Santa Clara, CA 95050) was used to visualize the samples.

Disease incidence in relation to mechanical injury. Wheat seedlings grown for 10 days in sand in 11-cm-diameter pots were carefully removed and washed in tap water. One-half of the root system was removed by cutting with a razor blade perpendicular to the axis of the plant. The plants were transplanted into sieved (5 mm) Capac clay loam soil after one of the three following treatments: planted in soil with no additional conidia; root-dipped for 1–2 min in a conidial suspension (2.4×10^6 conidia per milliliter) before planting; and planted directly in an area (~2.5 cm in diameter × 1.0 cm deep) of soil to which 5 ml of the conidial suspension had been mixed. The naturally occurring population of *C. gramineum*, as determined by using a selective medium (20), was approximately 8.3×10^2 colony-forming units (cfu) per gram of soil. Plants were grown in a greenhouse and observed for symptom development during 8 wk. Results were confirmed by isolations of *C. gramineum* from wheat leaves (20).

In another experiment, 10-day-old wheat seedlings were grown and root-injured as described above, and the seedlings were planted in Capac clay loam that contained $1–6 \times 10^3$ cfu of *C. gramineum* per gram of soil. The population consisted of the naturally occurring propagules of *C. gramineum* with additional conidia added from liquid cultures grown in the laboratory. Symptom development was recorded approximately weekly during 8 wk of growth in a greenhouse.

Disease incidence in relation to freeze-induced injury. Wheat plants grown for 6 wk in sand in 1-L pots (10 plants per pot) in a growth chamber at 20 C, a 15-hr photoperiod and 27,000 lux were hardened for 3 wk in a growth chamber at 2 C under continuous light (10,000 lux). Roots were cut by severing the lower half of the sand/root ball without otherwise disturbing the root system. *C. gramineum* conidia were added as a drench to each pot (67×10^3 conidia per gram of sand). Pots were then maintained either in the growth chamber at 2.0 C, or were subjected to decreasing temperatures for 24 hr in the freeze chamber as described previously. In the latter treatment, pots were placed in an unlighted refrigeration chamber where the ambient air temperature was initially −3.0 C. The air temperature was decreased approximately 0.5 C per hour for 24 hr until it reached −15.0 C. The refrigeration was then turned off and the pots were allowed to thaw for approximately 24 hr in the closed chamber. Plants were moved to a greenhouse and observed for symptom development. This procedure has been established as an approximate simulation of winter stress encountered in Michigan (12).

RESULTS

Effect of exudates from frozen roots on conidial germination and germ tube growth. Exudate from severed frozen wheat roots stimulated germination of conidia of *C. gramineum* and germ tube growth, compared to exudate from unfrozen, cut or uncut roots, or sterile distilled water (Table 1).

Agar containing root exudate from axenically grown, hardened, and frozen wheat seedlings supported greater production of hyphal branches and conidia than agar containing exudate from nonfrozen roots or water alone (Table 2). Germling length, though tending to be greater in the presence of exudate from frozen roots, was not significantly different ($P = 0.05$) among the three treatments.

Unsterilized soil was fungistatic to conidia of *C. gramineum* on agar disks (Fig. 2A). Conidia placed on water agar alone without soil readily germinated and produced copious conidia (Fig. 2B). However, conidia placed in sterile distilled water germinated poorly or not at all. Nonfrozen roots stimulated sparse germination (Fig. 2C), whereas frozen wheat seedling roots (−5 C) placed on agar disks over soil stimulated abundant germination of *C. gramineum* conidia and vigorous growth of mycelium (Fig. 2D).

Electron microscopy of the infection process. Electron

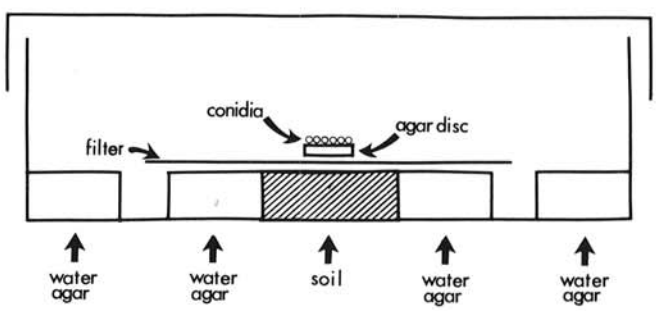

Fig. 1. Sterile chamber used to study soil-imposed fungistasis. All components within the petri dish (100 × 15 mm) are sterile except the soil. The membrane filter maintained the sterility of the agar disk and was in direct contact with the soil beneath it.

TABLE 1. Effect of exudate from frozen and nonfrozen wheat roots on conidial germination and growth of *Cephalosporium gramineum* on sterile depression slides

Exudate source[x]	Germination (%)[y]	Germ tube length (μm)[y]
Frozen intact roots	23 b	27.0 d
Nonfrozen intact roots	3 a	0.5 b
Nonfrozen cut roots[z]	5 a	2.5 c
Water	0 a	0.0 a

[x] Exudate was collected from roots of 14-day-old wheat seedlings, excised from the plant, and frozen in distilled water for 15 hr at −11 C; all other roots were held at 22 C. All roots were in water for a total of 24 hr.

[y] Values in each column followed by the same letter do not differ significantly ($P = 0.05$).

[z] Roots were cut to 1-cm lengths before being placed in water for 24 hr.

micrographs of freeze-fractured, 7-day-old frozen (−5 C) wheat roots showed hyphal penetration and growth deep into the cortical tissues (Fig. 2E-G).

Further electron microscopic studies were conducted on roots frozen to −10 C in syringe barrels into which conidia were introduced after thawing. After germination, hyphae grew randomly along the surface of the root before penetrating the epidermis, either intracellularly or intercellularly (Fig. 3A). Penetration of the epidermis was usually preceded by an appressoriumlike swelling of the hypha (Fig. 3B) at the point of entry. In some cases, a somewhat pointed projection from the hyphae, similar to a penetration peg, was observed entering the epidermal cell (Fig. 3B). Direct entry by hyphae without such structures was also seen. Once in the epidermis, hyphal growth was generally directed through the cortex toward the axis. Upon contacting endodermis the hyphae spread over the surface of this tissue layer. Hyphal growth through the endodermis was not observed at the time intervals sampled. There was no evidence of freezing-induced ruptures large enough to allow conidia to passively enter the root. Occasionally hyphae were observed in epidermal cells of nonfrozen roots, but these did not penetrate beyond the epidermis.

TABLE 2. Response of *Cephalosporium gramineum* to exudates from frozen and nonfrozen axenically grown wheat roots[x]

Exudate source[y]	Length of germlings (μm)	Hyphal branches (no.)	Conidial production index[z]
Nonfrozen roots	151.7 a	1.6 a	0.37 ab
Frozen roots	239.6 a	2.5 b	2.00 c
Control (water agar)	199.8 a	0.5 a	0.60 b

[x]Washed conidia were pipetted onto disks of root exudate agar and incubated for 1.5 days before counts were made. Values in each column followed by the same letter do not differ significantly ($P = 0.05$).

[y]Exudates were collected from aseptically grown, hardened wheat plants that had been freeze-stressed at −10 C. Exudates were collected from the same roots 3 days before and 3 days after freezing. They were adjusted to contain the equivalent of exudate from 0.002 g of dry root per milliliter and solidified with agar.

[z]Conidial production indices were 0 = no new conidia, 1 = 0–5, 2 = 5–10, and 3 = >10 new conidia per germling.

Disease incidence in relation to mechanical injury. Root severing predisposed plants to infection when roots were subsequently dipped in a conidial suspension before being transplanted into soil. Disease incidence, as determined by isolation of *C. gramineum* from wheat leaves, was 62%. By contrast, transplanting plants with cut roots into naturally or artificially infested soil gave only 3 and 2% infection, respectively. In a similar experiment in which laboratory-grown conidia were mixed in a naturally infested field soil, no disease developed on root-severed seedlings.

Disease incidence in relation to freeze-induced injury. Nine-week-old hardened wheat plants growing in sand were frozen at −15 C or exposed to 2 C immediately following inoculation with a conidial suspension of *C. gramineum*. Plants whose roots were cut before inoculation had the highest percentage of infection, with those held at 2 C having more infection (77%) than those at −15 C (39%) (Table 3). In addition, symptoms developed more rapidly on plants with cut roots; plants exposed to 2 C showed symptoms after 21 days and those exposed to −15 C, after 32 days. Of the inoculated plants with uncut roots, only those subjected to −15 C developed symptoms (14%), which appeared after 46 days. The population density of *C. gramineum* in soil after incubation at −15 C did not differ significantly from that in soil incubated at 18 C. The

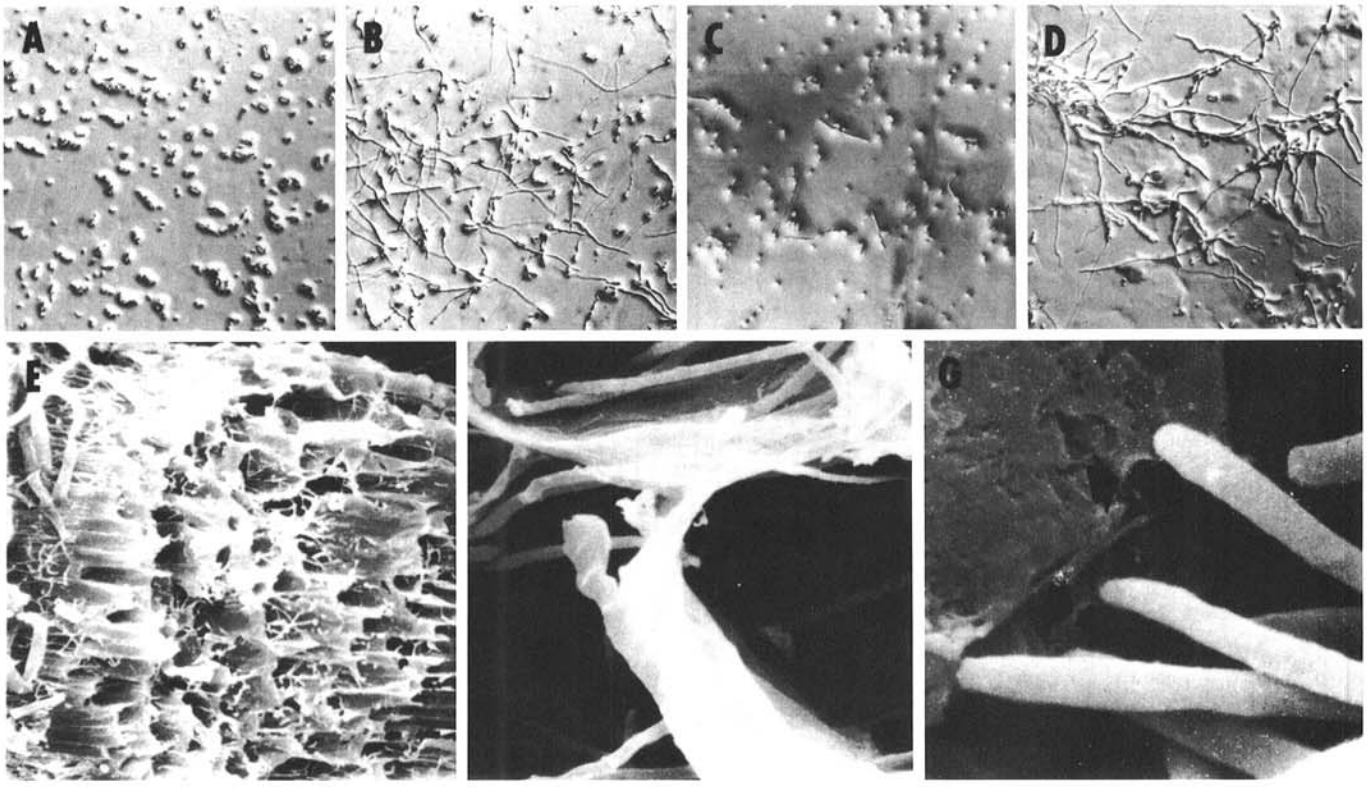

Fig. 2. Light and scanning electron micrographs of *Cephalosporium gramineum* germination on agar covering soil, and growth through wheat root tissues. **(A to D)** Nomarski interference contrast micrographs of conidia of *C. gramineum* on agar disks, which were placed on a membrane filter resting on unsterilized soil and incubated for 24 hr (×145). **A,** No wheat roots present; conidia remained ungerminated. **B,** As in A, except that no soil was present below the filter; conidia germinating. **C,** As in A, but with a sterile, nonfrozen wheat root stimulating some conidial germination. **D,** As in C, except that the wheat root had been frozen (−5 C). Note the vigorous hyphal growth. **(E to G)** Scanning electron micrographs showing penetration of previously frozen (−5 C) wheat roots by *C. gramineum*, and growth within a previously frozen wheat root after 3 days of incubation. **E,** Cross section of a wheat root that had been frozen. Hyphae have penetrated the epidermis and cortex, but the stele has not been colonized (×117). **F,** Hyphae penetrating the cell walls of the cortex (×1,187). **G,** Hyphal tips displaced from original point of contact (arrows) with a cortical cell wall during sample preparation, showing apparent sites of penetration (×4,880).

means of three experiments were 1.3×10^5 and 8×10^4 propagules per gram of soil for the 18 C and −15 C treatments, respectively, as determined by using a selective medium (20).

DISCUSSION

Under natural conditions, either insect damage (16) or freezing winter temperatures (3,8,13) predispose wheat plants to infection by *C. gramineum*. It has been hypothesized that *C. gramineum* conidia passively enter the root systems of wheat plants in the spring after freezing and thawing cycles have severed the roots, thus creating infection sites (8). Such a mode of infection would, in a fundamental way, distinguish *C. gramineum* from other vascular pathogens such as *Fusarium* and *Verticillium* species, which gain entry by active penetration and growth into root tissues. Several workers have demonstrated that wheat plants may become readily infected when severed roots are exposed to a conidial suspension of the pathogen (6,8,9,19). In the present work, plants with clipped roots either dipped in a conidial suspension before planting, or drenched with a conidial suspension after being transplanted into porous sand, resulted in a high incidence of diseased plants within 2–3 wk. However, similarly injured plants transplanted into a clay loam soil containing conidial inoculum of *C. gramineum* had little or no infection. The low infection incidence in the clay loam soil may reflect difficulty in conidial transport in soil water of fine-textured soils.

Freezing injury involves more than a mechanical breakage of the roots (7). In our work, freezing resulted in germination in the presence of fungistatic conditions and increased hyphal branching and conidium production by *C. gramineum,* presumably due to increased root exudation. After conidial germination, runner hyphae grew over the root surface and initiated penetration points on the epidermis. Once penetration had occurred, the epidermis and root cortex did not appear to serve as barriers to colonization. Details of endodermal and xylary penetration are not known since this process was not microscopically visualized. Root breakage apparently was not the cause of exudation enhancement, since exudates from cut roots did not stimulate germination. Plant tissues that are subjected to freezing temperatures are known to release more exudates than do nonfrozen tissues (7).

Smith and Olien (17) found that freezing predisposed the crown tissues of winter barley to disease caused by *Fusarium roseum* f. sp. *cerealis*. Crown lesions, caused by ice crystals, were believed to be the sites of penetration. It is not known if increased root exudation alone was primarily responsible for increased disease in the present work, or if structural or physiological changes due to freeze injury were also involved.

The potential number of root infections would be much greater for direct than for passive penetration. Growing roots colonizing the soil would encounter a much larger proportion of inoculum than would root wounds caused by soil heaving. Moreover, the volume of soil contributing inoculum for direct penetration would encompass that distance from the root surface in which root exudates stimulate spore germination and hyphal growth. This volume would be expected to be larger than that sampled in the case of passive infection, which would be the distance from the exposed xylem elements that transpiration water can draw in conidia. The low infection incidence obtained when plants with severed roots were transplanted into soil containing a high population density of conidia of *C. gramineum* suggests that conidia are not readily transported in soil, at least in the clay loam soil used. Moreover, wheat stem nodes have been shown to screen out colloidal particles of gold (W. V. Single, *personal communication*) moving through the xylem. If broken roots are unselectively sampling soil particles at least the size of *C. gramineum* conidia, it would be of interest to

TABLE 3. Effect of exposure of wheat plants growing in sand to freezing conditions, on development of Cephalosporium leaf stripe symptoms

Root treatment[y]	Temperature (C)	Infected leaves (%)[z]	Days from addition of conidia to first symptoms[z]
Noncut	+2.0	0 a	...
Cut	+2.0	77 d	21 a
Noncut	−15.0	14 b	46 c
Cut	−15.0	39 c	32 b

[y] Roots were cut by severing the lower half of the sand/root ball without otherwise disturbing the root system. Roots were drenched with conidia just before placing the plants in a freezing chamber. Plants were frozen by reducing the ambient air temperature approximately 0.5 C/hr until −15.0 C was reached.

[z] Values are the means of three separate experiments. Values in each column followed by the same letter do not differ significantly ($P = 0.05$).

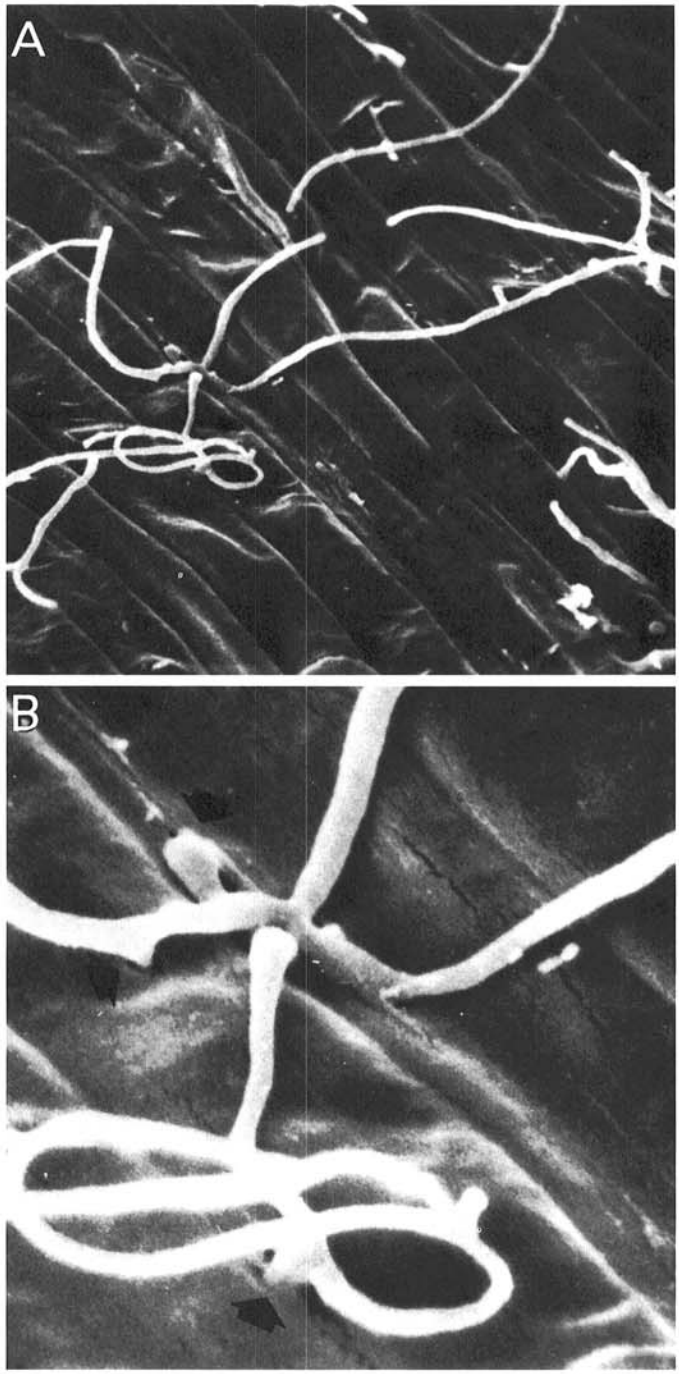

Fig. 3. Scanning electron micrographs of *Cephalosporium gramineum* penetrating wheat root epidermis following freezing (−10 C) of the tissue and after 10 days of incubation with conidia of *C. gramineum*. **A,** Hyphal growth along the surface of a wheat root (×675). **B,** A close-up of a portion of (A) (×2,380). Note the appressoriumlike swellings and structures resembling penetration pegs at the points of entry (arrows).

TABLE 4. Comparison of direct and passive infection process by *Cephalosporium gramineum*

Trait	Direct	Passive
Infection court	Entire rhizoplane	Severed root xylem
Predisposition factor	Freezing	Heaving (diurnal freezing)
Latent period (time from predisposition to symptom expression)	30–50 days	10–30 days
Relationship to snow cover	Should take place under snow (does not require active transpiration)	Probably can't take place under snow (requires active transpiration)
Relationship to population peak of *C. gramineum*	Can occur at any time after initial freeze, normally encompassing the peak population period	Can occur only after heaving (or other mechanical injury), usually in spring, well after the peak population period

know how long a newly broken root would maintain a suction pressure before becoming plugged with debris.

Cephalosporium gramineum populations in soil change radically with time, reaching a peak between December and January, then dropping to very low densities by April (21). Snow cover, which is common in Michigan wheat fields during periods of peak *C. gramineum* populations, greatly reduces an already slow transpiration rate. Consequently, this would reduce the efficiency of an infection mechanism that depends on conidial uptake via the transpiration stream. Conversely, snow cover allows the soil to warm, increasing the proportion of the root which is at temperatures compatible for growth of *C. gramineum*. Although *C. gramineum* grows slowly even at its optimum temperature (20 C), its ability to grow at low temperatures (5–7 C) (3) may afford a competitive advantage when the soil is beginning to thaw. Under conditions of thin snow cover, reflection of light could increase the temperature of exposed wheat leaves during daylight hours, thus increasing transpiration and water demand by the roots, possibly favoring passive uptake of conidia.

Our work provides evidence that *C. gramineum* can infect wheat roots by direct penetration. Table 4 outlines the differences between direct and passive infection. The relative importance of these two mechanisms is yet to be determined.

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