Soil Water Pressure and *Verticillium dahliae* Interactions on Potato

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ABSTRACT

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Foliar and root growth of potato (cv. Russet Burbank) and colonization of roots and stem vascular sap by *Verticillium dahliae* were monitored weekly for 4 weeks beginning at emergence in soils maintained at different water pressures. A significant soil water pressure × *V. dahliae* interaction resulted in reduced aerial biomass and increased root-to-shoot ratio under excessive soil moisture conditions (–0.01 MPa). At –0.01 MPa, the percent increase in root-to-shoot ratio of plants grown in infested compared with noninfested soil ranged from 40 to 82% over 2 years. In contrast, both root length and colonization of roots by *V. dahliae* were significantly suppressed at –0.01 MPa compared with the lowest soil water pressure (–0.15 MPa). Roots of plants grown at –0.01 compared with –0.15 MPa were 19.6 to 44% shorter at emergence, and suppression of root growth at this high soil water pressure persisted through the observation period. Root colonization by *V. dahliae* was suppressed consistently at –0.01 compared with –0.15 MPa. Reduction in CFU per 100 cm of root length for these respective soil water pressures ranged from 60 to 100%. Soil water pressure had no effect on the population size of *V. dahliae* in stem sap. High soil water pressures may enhance potato early dying caused by *V. dahliae* by slowing root growth and/or by indirectly increasing the rate of microsclerotial germination. Both would facilitate entry of the pathogen into the stele through the vulnerable tissue of the root apex.

Additional keywords: *Solanum tuberosum*, Verticillium wilt.

Potato early dying limits yield of potatoes (*Solanum tuberosum* L.) in many production areas of the world (6,20,21,26). In the arid irrigated region of northcentral Oregon, some growers have reported yield losses of up to 30% in fields that were cropped several times to potato (16). This yield limitation has been attributed to potato early dying which, in this area, is caused primarily by the soilborne fungus, *Verticillium dahliae* Kleb.

Certain cultural practices reduce losses to potato early dying. Studies in Idaho demonstrated that optimization of soil fertility, specifically concentrations of phosphorus and nitrogen, can suppress potato early dying in the cultivar Russet Burbank (8). This effect is presumably the result of enhanced plant health with a resulting increase in resistance to the disease. In another study, Davis and Everson (7) reported that disease severity was lower in furrow- compared with sprinkler-irrigated fields, an effect attributed to enhanced nutrient availability to plants in furrow-irrigated fields.

In irrigated potato production systems, another factor that influences the development of potato early dying is the amount of applied water. In a series of microplot studies in Oregon, Cappaert et al. (3) compared the combined effects of a range in both inoculum density of *V. dahliae* and amount of irrigation water on the severity of potato early dying and tuber yield. Ranges in the amount of applied water were related to estimated consumptive use (ECU) by the plant. Disease severity of plants grown in infested soil was greater under the excessive (150% ECU) than under the moderate (100% ECU) or deficit (50% ECU) irrigation regimes. Also, as inoculum density increased, reductions in tuber yield were greater under excessive than under moderate or deficit irrigation regimes. In a later field study in which similar irrigation treatments were imposed from plant emergence to tuber initiation, disease severity was greater under an excessive compared with a moderate or deficit irrigation regime (4). In both studies, petiole nutrient analyses indicated that the effect of irrigation regimes on disease was not associated with nutrient deficiency. Therefore, the mechanism for increased disease severity in plants grown under wet soil conditions is unknown.

In culture, *V. dahliae* is active at osmotic pressures as low as –12 MPa (15) and matric pressures as low as –10 MPa (18). We estimated that the excessive, moderate, and deficit irrigation regimes of Cappaert et al. (3,4) represent average soil water pressures of approximately –0.01 to –0.03, –0.08, and –0.15 MPa, respectively. Therefore, it is unlikely that an excessive irrigation regime would directly favor pathogen activity over a moderate or deficit soil moisture. High soil moisture, however, may affect the dynamics of root growth, the pathogen's ability to colonize host roots and penetrate the vascular tissue, and/or the host's ability to resist vascular infection.

Our objectives were to monitor early foliar and root growth of potatoes planted in soil noninfested or infested with *V. dahliae* over a range of soil water pressures and to quantify the colonization of roots and stems by *Verticillium*.

MATERIALS AND METHODS

Treatments and experimental design. Three soil water pressures were combined factorially with two inoculum densities of

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V. dahliae for a total of six treatments. The three soil water pressures, determined from a soil water release curve (Soil Analysis Laboratory, Department of Crop and Soil Science, Oregon State University, Corvallis) (Fig. 1), were –0.01, –0.08, and –0.15 MPa. These soil water pressures corresponded to 17.5, 5, and 3.5 g of H_2O/100 g of oven-dried soil, respectively. In 1991, the –0.01 MPa treatment was replaced with –0.03 MPa 3 weeks after emergence. Inoculum densities of *V. dahliae* were established at 0 and 10 CFU/g of soil in 1991, and at 0 and 25 CFU/g of soil in 1992. Each of the six inoculum density × soil water pressure treatments was replicated ten or eight times for each of 4 harvest weeks in 1991 and 1992, respectively.

Soil. Soil (Quincy fine sandy loam; mixed with mesic xeric Torripsamment), fumigated with methyl bromide/chloropicrin (3:2, vol/vol) at 488 kg/ha, was obtained from the Hermiston Agricultural Research and Extension Center in Hermiston, OR. Prior to use, the soil was pasteurized with aerated steam at 60°C for 1.25 h and air-dried. In 1992, soil also was sieved through a 4-mm mesh screen to increase its uniformity and to remove rocks and organic debris.

Inoculum and seed tubers. A mixture of four isolates of *V. dahliae*, obtained from symptomatic potato plants, was used in this study. Single-spore isolates were cultured on potato-dextrose agar (Difco Laboratories, Detroit). Cultures were flooded with sterile distilled water and scraped gently with a glass rod to release conidia. Aliquots (1 ml) of the resulting conidial suspension were transferred onto minimal agar medium (27) overlain with sterile, uncoated cellophane (Bio-Rad Laboratories, Richmond, CA). After 3 weeks of growth, the cellophane was removed and processed in a blender with distilled water. The resulting suspension was washed through a nested series of three screens (1.18-, 0.425-, and 0.075-mm mesh) to separate microsclerotia from the cellophane and to remove conidia and mycelial fragments. The microsclerotia, which were air-dried at room temperature for 2 to 3 days, were mixed for 3 min with air-dried soil in a twin shell blender. This blend of soil and inoculum was used as an inoculum concentrate. Infestation of soil was accomplished by mixing the inoculum concentrate with the dried soil in a cement mixer. Noninfested soil was not mixed in the cement mixer in 1991, which may have resulted in a bulk density difference between the noninfested and infested soil. To eliminate this possible variable, infested and noninfested soil were mixed in the cement mixer in 1992. Plastic 5-liter pots (21-cm diameter by 19.5-cm height) were filled with approximately 7,100 g of dry soil. Water, in amounts appropriate to achieve desired soil water pressures, and a liquid fertilizer were added to the soil. The fertilizer consisted of KH_2PO_4 (115 mg), $(NH_4)_2SO_4$ (56 mg), $Ca(NO_3)^2{\cdot}4H_2O$ (100 mg), and $MgSO_4{\cdot}7H_2O$ (21 mg) per kilogram of soil. Soil was allowed to equilibrate for 5 days between initial watering and planting.

Nuclear seed potatoes (cv. Russet Burbank) were obtained from Alpine Spuds, Enterprise, OR. Melon ball seed pieces were scooped from around potato eyes with a 29-mm-diameter melon ball scooper, air-dried for 18 h, and presprouted in moist vermiculite for 1 week. One melon ball seed piece was planted in each pot. A layer of perlite, approximately 3-cm deep, was then spread evenly over the soil to reduce evaporative water loss. Soils were maintained at desired water pressures by weighing pots periodically (daily, 1 week after emergence) and adding tap water as necessary. Greenhouse temperatures were maintained at 13 to 27°C, and plants were grown under natural daylight. In both years, the experiment was initiated in March and terminated in May.

Sampling and assays. After 90% emergence, plants were harvested weekly for 4 weeks. Foliage (leaves and stems) of each plant was cut at the soil line, dried at 40°C for several days, and weighed. Roots of each plant were removed from the soil. In 1991, root systems were placed in separate sacks made of nylon screen, and washed overnight in a running water bath. In 1992, root systems were washed individually by hand under running tap water over a fine mesh sieve. Following washing, roots were blotted dry, weighed, placed in a plastic bag containing a moist paper towel, and refrigerated until processed.

Root lengths were estimated using the line-intercept method of Newman (23) as modified by Marsh (19). In 1991, root lengths were determined for the entire root system for weeks 1, 2, and 3. In 1992, root lengths were determined for 100, 20, and 10% of each root system in weeks 1, 2, and 3.

Roots were cut into 1.5- to 2.5-cm-long segments and approximately 100 cm of roots were plated onto either streptomycin water agar (22) in 1991 or NP-10 medium (29) in 1992, to determine number of CFU per centimeter of root. In 1992, sap was extracted from stems with a garlic press, serially diluted, and aliquots spread onto NP-10 agar plates. Plates were incubated at room temperature for approximately 10 days before determining the number of colonies of *V. dahliae*.

Data analysis. Significance of treatment differences was determined on SAS version 6.04 (SAS Institute Inc., Cary, NC) by Analysis of Variance (ANOVA) using PROC GLM. When the ANOVA residuals were examined, data were transformed using the natural log or square root transformation, as necessary. Because plants grown in noninfested soil were not assayed for *V. dahliae*, one-way analysis was performed on CFU data with soil water pressure as the independent variable. Means were separated by Fischer's protected least significant difference. Because of the exponential increase in CFU per milliliter of stem sap between weeks 1 and 4 of 1992, analysis was performed on natural log transformed data.

RESULTS

Plant growth. Significant pathogen × soil water pressure interactions were detected in aerial biomass in both 1991 (Fig. 2A) and 1992 (Fig. 2B). Growth suppression of *Verticillium*-infected plants was greater in wet soil (–0.01 MPa) than in drier soils (–0.08 and –0.15 MPa). In contrast, in soil noninfested with *Verticillium*, the range in soil water pressures evaluated had little effect on aerial biomass (Fig. 2C and D).

In 1991 and 1992, there was a significant pathogen × soil water pressure interaction ($P \leq 0.01$) for root-to-shoot ratio. At –0.01 MPa, the root-to-shoot ratio of plants grown in infested compared with noninfested soil was 40 and 82% higher in 1991 and 1992,

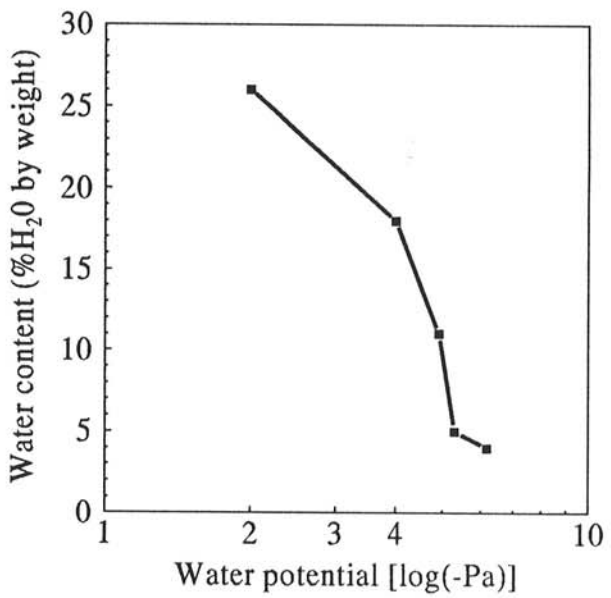

Fig. 1. Water release curve for Quincy fine sandy loam soil.

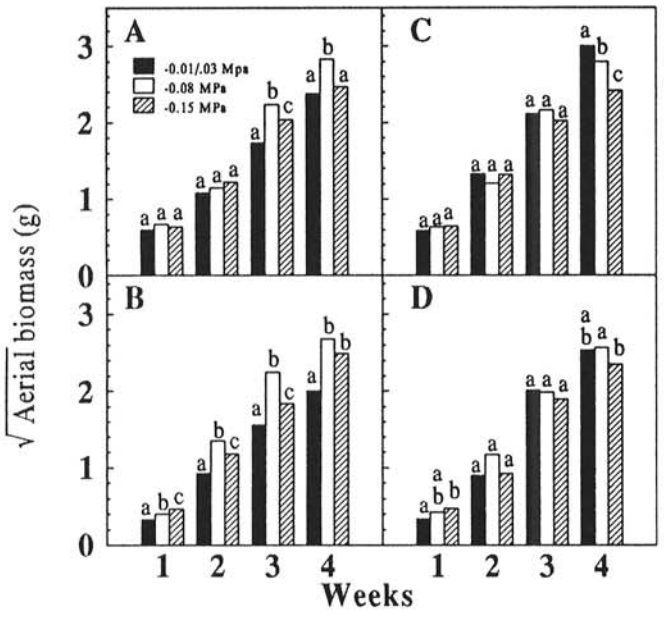

Fig. 2. Soil water pressure × week × *Verticillium dahliae* interactions in aerial biomass of potato in **A,** 1991, *V. dahliae*-infested soil; **B,** 1992, *V. dahliae*-infested soil; **C,** 1991, noninfested soil; and **D,** 1992, noninfested soil. Within weeks, bars with the same letter were not significantly different according to Fisher's protected least significant difference (LSD) test ($P \leq 0.05$). LSD values for weeks 1 to 4 are: **A,** 0.0748, 0.1712, 0.123, and 0.1231; **B,** 0.0425, 0.1326, 0.1756, and 0.2456; **C,** 0.1016, 0.1717, 0.1967, and 0.1594; and **D,** 0.1089, 0.26, 0.2178, and 0.1829, respectively.

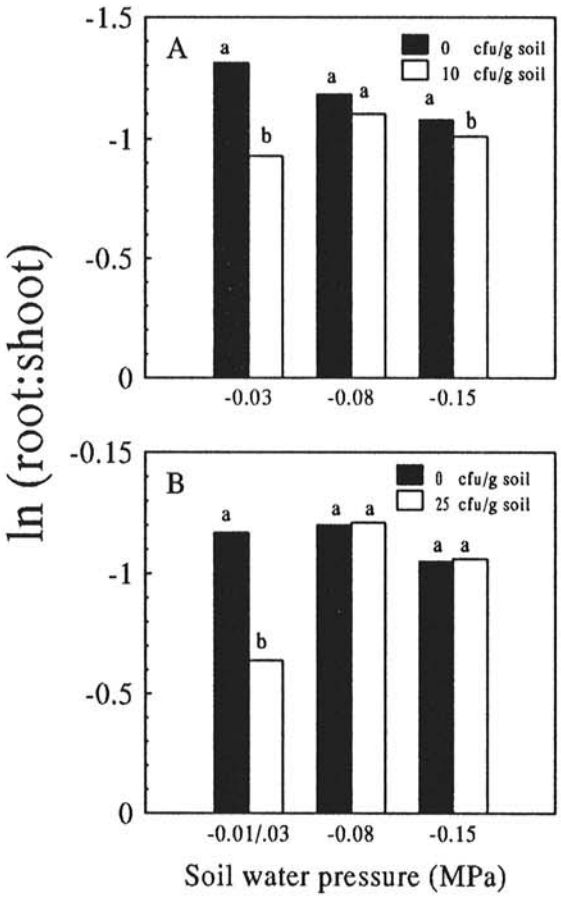

Fig. 3. Soil water pressure × *Verticillium dahliae* interactions in root-to-shoot ratio of potato in **A,** 1991 and **B,** 1992. Within soil water pressures, bars with the same letter did not differ significantly according to Fisher's protected least significant difference (LSD) test ($P \leq 0.05$). LSD values for soil water pressures –0.01/0.03, –0.08, and –0.15 MPa are **A,** 0.297, 0.091, and 0.03; and **B,** 0.221, 0.1509, and 0.1996, respectively.

respectively (Fig. 3A and B). There was also a significant soil water pressure × week interaction for root-to-shoot ratio, but the results were not consistent across years (data not shown).

A soil water pressure × week interaction ($P \leq 0.01$) was detected in root length in both years (Fig. 4A and B). For the first and third sampling dates in 1991, roots were 19.6 and 27.7% shorter in plants grown at –0.01 compared with –0.15 MPa. The same trend was observed in 1992, although the percent reduction in root length was twice that observed in 1991.

Root colonization. In 1991, the fungus was first recovered from roots of plants grown in infested soil at week 2 at –0.08 and –0.15 MPa and at week 3 at –0.01 MPa. The proportion of root systems from which *V. dahliae* was recovered was consistently lower at –0.01 MPa compared with the other soil water pressures, and never approached 100% at any soil water pressure. In contrast, the pathogen was recovered from virtually all root systems in 1992, beginning at week 1 (data not shown).

In both years, colonization of roots by *V. dahliae* was consistently suppressed in the wettest soil (–0.01 MPa) (Fig. 5A and B). In 1991, the population size of *V. dahliae* was 100 and 87% lower at –0.01 compared with –0.15 MPa in weeks 2 and 4. For weeks 1 and 4 in 1992, and comparing the same respective soil water pressures, the reduction in number of CFU of *Verticillium* was 60 and 63%.

Vascular colonization. Soil water pressure had no consistent effect on the population size of *V. dahliae* in the stem vascular sap. *Verticillium* was recovered at the first sampling date at all soil water pressures, and the population size ranged from 0.8 to 1.6 ln (CFU/ml) of sap. By the fourth sampling date, populations had increased fourfold and ranged in size from 4.4 to 5.2 ln (CFU/ml) of sap.

DISCUSSION

Soil water pressure and *V. dahliae* interacted to reduce aerial biomass and to increase the root-to-shoot ratio of potato, but under excessive soil moisture conditions (–0.01 MPa); however, there were no corresponding significant increases in root or vascular colonization by *V. dahliae* at this soil water pressure. In fact, there was a significant decrease in root colonization at this soil water pressure. It is paradoxical that despite no significant increase in root or vascular colonization by *V. dahliae* at –0.01 MPa, aerial biomass was reduced and the root-to-shoot ratio was increased at this soil water pressure. Evidently, the wet soil enhanced the ability of the fungus to detrimentally affect potato early in its development in a manner not directly related to the extent of root and vascular colonization.

The disparity between the amount of root colonization and apparent effect of *V. dahliae* on aerial biomass and root-to-shoot ratio at –0.01 MPa might be understood, in part, by considering the possible histological origins of the colonies recovered in our root assays. For *Verticillium* to systemically infect its host and cause symptoms, it must gain entrance to the host's stele. It has been widely demonstrated, however, that most root infections by *V. dahliae* do not successfully enter the vascular tissue (11,25). In fact, the susceptibility of a plant to systemic invasion by *V. dahliae* does not appear to be a function of the ability of the fungus to colonize the root cortex (9). Huisman and Gerik (14) estimated that in cotton there are approximately 5,000 cortical invasions of the root by *V. dahliae* for every vascular infection.

Although the root systems in our study were washed in running water, a procedure which should have removed most fungal tissue from the root surface, they were not surface sterilized. Depending on the concentration of the sterilant and the duration of sterilization, sterilizing can eliminate fungal growth from subsurface root tissues (13). Huisman (13) reported a 50% reduction in colony growth from plated cotton roots that were surfaced sterilized in NaOCl for 5 to 15 s. Because our roots were not sterilized, colo-

nies appearing on the medium could have originated from any layer of root tissue. It is almost certain that the vast majority of colonies recovered in our assays did not originate from the vascular tissue. Nevertheless, it is reasonable to assume that a higher frequency of cortical root infections should lead to a higher incidence of vascular infection and, consequently, accelerated symptom development. This relation could be altered, however, by conditions that enhance fungal invasion of the vascular tissue.

In histopathological studies in which staining and electron microscopy were used to examine artificially inoculated Russet Burbank roots, *V. dahliae* seldom penetrated beyond the epidermis (25). In response to invasion by the fungus, the exodermis of the root produced lignitubers that were highly effective at preventing further penetration. When *V. dahliae* succeeded in penetrating the cortex, the endodermis did not appear to be an effective barrier against invasion of the vascular tissue. Beckman and Talboys (1) suggested that the portion of the root most vulnerable to invasion that will ultimately lead to vascular colonization is the zone of elongation where such resistance mechanisms have yet to take effect.

In general, nutrient leakage occurring at the growing root tip, specifically the zone of elongation, greatly exceeds that of older root tissue (28). Furthermore, nutrients that are released by the root are used up rapidly by the microbial community of the rhizosphere, dramatically reducing the sphere of influence of root exudates around the mature root (24). Therefore, stimulation of a fungal propagule is most likely to occur when the growing root, specifically the root tip, first reaches the vicinity of the propagule. If an approaching root stimulates a microsclerotium to germinate, the proximity of the point of initial contact between the two organisms should be a function of the rate of root elongation and the speed with which the propagule responds to root exudates. Roots of most cultivated plants grow at a rate of 3 to 10 mm/day depending on the plant species and the type of root (12). In addition, environmental and nutritional factors can affect the root elongation rate. In our experiments, total root length was reduced at –0.01 MPa compared with roots of plants grown at lower water pressures (Fig. 4A and B). If this reduction in total root length reflected an actual reduction in the elongation rate of the root, the point of initial contact of the fungus with the root could have been closer to the root apex at high rather than at low soil water pressures. It is this region that is thought to be most vulnerable to invasions that might ultimately reach the vascular tissue.

Observations on the general mode of infection of roots by *V. dahliae* are limited and rather conflicting. Bowers et al. (2) examined potato (cv. Superior) roots using an immunoenzymatic stain and observed that invasion of the vascular tissue by *V. dahliae* occurred exclusively via the root apex. Using an assay, similar to the one employed in our study, in which cotton roots were plated on agar, Huisman and Gerik (14) found that colonies were detected as close as 1 mm from the root apex, but colonies this close to the apex were rare. They were detected with increasing frequency farther away from the apex, reaching a plateau at approximately 1 cm from the root tip, a region well behind the region of undifferentiated tissue. Colony density then remained stable for most of the remaining root length. Therefore, the region of most extensive colonization and the region of greatest vulnerability to infection are evidently not equivalent.

In a soil environment, the sphere of influence of a root tip on a microsclerotium is small, e.g., only 30 to 100 μm for cotton (10).

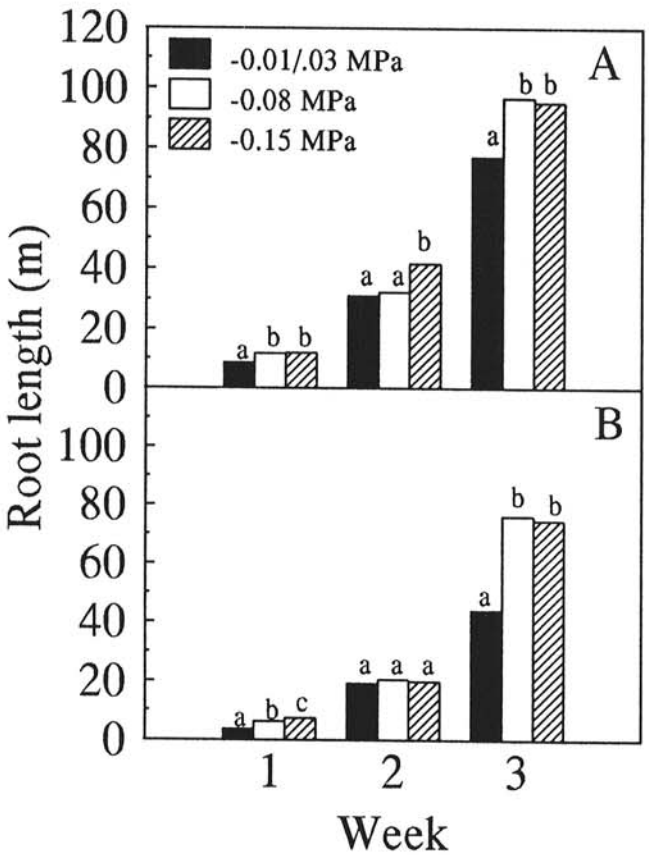

Fig. 4. Soil water pressure × week interactions in root length of potato grown in soil infested with *Verticillium dahliae* in **A,** 1991 and **B,** 1992. Within weeks, bars with the same letter were not significantly different according to Fisher's protected least significant difference (LSD) test ($P \leq 0.05$). LSD values for weeks 1 to 3 are **A,** 1.91, 6.52, and 12.9; and **B,** 0.88, 4.58, and 12.19, respectively.

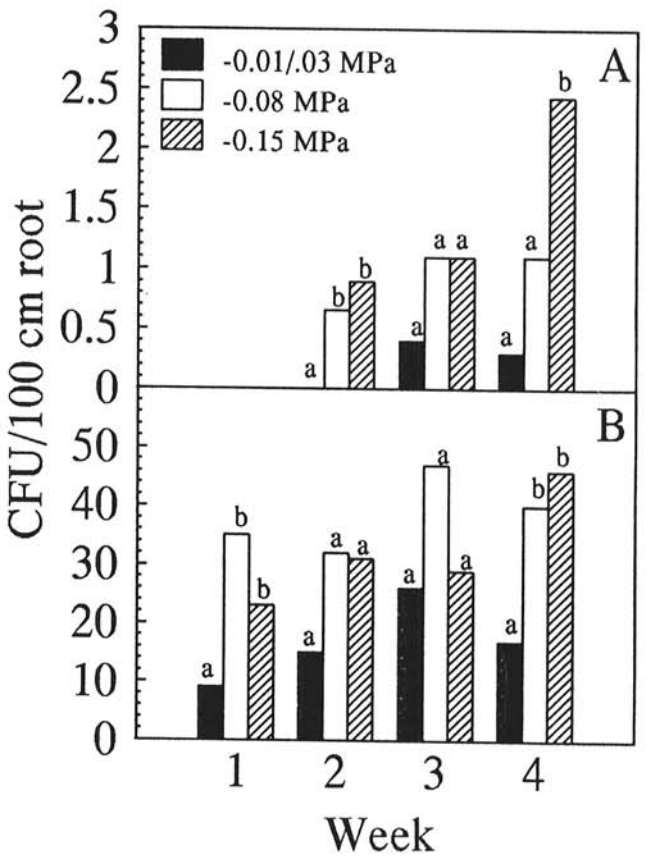

Fig. 5. Soil water pressure × week interactions in mean population estimates of *Verticillium dahliae* on potato roots in **A,** 1991 and **B,** 1992. Within weeks, bars with the same letter were not significantly different according to Fisher's protected least significant difference (LSD) test ($P \leq 0.05$). LSD values for weeks 1 to 4 are **A,** no data, 0.5, 1.0, and 1.5; and **B,** 15, 3, 26, and 20, respectively.

The speed at which the fungus can begin colonizing a root is more restricted by the amount of time it requires to germinate than by the time required for the germ tube to reach the root. Germination periods are greatly reduced when soils are amended with plant extracts (10). Kuan and Erwin (17) demonstrated that the leakage of amino acids and carbohydrates from alfalfa roots increased by 2 to 4.5 times in saturated soil. If increased soil water facilitates leakage of nutrients from roots, thereby increasing the concentration of germination stimuli reaching a microsclerotium, the germination period for the microsclerotium could be reduced. This would reduce the distance of the initial contact point from the root tip, possibly placing the initial point of contact between root and fungus at or near the location of maximum vulnerability of the root to vascular infection.

It is well recognized that vascular wilt diseases are favored by moist soils. Moist soils, coupled with an arid atmosphere, favor rapid transpiration that results in a rapid unrestricted flow of water and conidia through stems and leaves of the plant (5). We suggest that wet soils also increase the severity of potato early dying by facilitating conditions that enhance the ability of the fungus to penetrate the vascular tissue. Specifically, wet soils could increase the likelihood that a fungal germ tube will initially encounter a root at the root's point of maximum vulnerability to vascular invasion by inhibiting root growth and/or by indirectly increasing the rate of microsclerotial germination.

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