INFECTION OF SWEETPOTATO FIBROUS ROOTS BY STREPTOMYCES IPOMOEAE: INFLUENCE OF SOIL WATER POTENTIAL

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Summary—The effect of the matric component of soil water potential (Ψ_m) on infection of fibrous roots of sweetpotato (Ipomoeae batatas) cv. Jewel by Streptomyces ipomoeae and the influence of infection on water extraction by fibrous roots were examined. The severity of disease on fibrous roots was low in plants grown at constant Ψ_m of 0, -1.0 or -2.5 J kg⁻¹ in non-fumigated or fumigated soils infested with S. *ipomoeae*. Disease severity increased with decreasing Ψ_m and was greatest at Ψ_m of -7.5 to -20 J kg^{-1} . Growth of S. ipomoeae in water-filled pores and subsequent infection may have been limited at Ψ_m of 0, -1.0 and -2.5 J kg^{-1} . Root and shoot dry weights of sweetpotato were significantly lower in plants grown in infested soil than in non-infested soils at Ψ_m between -5 and -20 J kg^{-1} , but were not affected by disease at Ψ_m of 0, -1.0 or -2.5 J kg⁻¹. The severity of disease on fibrous roots was low in plants drip-irrigated on a daily schedule, whereas the severity of disease on fibrous roots was significantly greater in plants irrigated on either a 4- or 6-day schedule. Total dry weights of roots were lower in plants grown for 4 weeks in infested than non-infested soil. However, total dry weights of roots were not affected by disease as compared to non-inoculated controls in plants grown for 8 weeks, thus suggesting that roots of cv. Jewel may be able to compensate for disease by production of additional root biomass in soil. Although root dry weight was not affected by disease in plants grown for 8 weeks, diseased plants extracted significantly less water from soil than healthy plants. Therefore, the effect of disease on water extraction from soil was not due solely to a reduction in root biomass. Limited growth of roots to inoculum in saturated soil, limited growth of the pathogen in saturated soil, or altered susceptibility of the host may explain the reduction of disease at high $\Psi_{\rm m}$.

INTRODUCTION

Streptomyces soil rot or pox is a widespread and destructive disease of sweetpotato in the U.S.A. (Clark and Moyer, 1988). The causal agent, Streptomyces ipomoeae (Person and W. J. Martin) Waksman and Henrici, an actinomycete, causes extensive necrotic lesions on fibrous roots and corky scab-like lesions on storage roots that lead to reductions in the yield and marketability of the crop. Severe infections can reduce production of fibrous roots and storage roots and can cause storage root malformation (Person and Martin, 1940; Lorbeer, 1962; Ristaino and Averre, 1992). Management of the disease involves the use of resistant cultivars, soil fumigation, reduction of soil pH with sulfur or crop rotation (Person, 1946; Hooker and Peterson, 1952; Martin, 1958; Lorbeer, 1962; Martin et al., 1975; Moyer et al., 1984). There has been little quantitative research on the ecology of S. ipomoeae or the epidemiology of Streptomyces soil rot on sweetpotato. The influence of soil physical factors such as soil water potential on the development of Streptomyces soil rot on a susceptible sweetpotato cultivar has not been extensively studied (Ristaino and Averre, 1992).

An early study of Streptomyces soil rot on sweetpotato indicated a negative correlation between the amount of soil moisture and disease (Poole, 1925).

There was less disease under saturated soil conditions than when soil was allowed to dry to soil water contents of 2-5%, however, soil water content was not related to the matric component of soil water potential (Ψ_m) in that study (Poole, 1925). Others have noted the relationship between years with low rainfall and increased disease development (Poole, 1922; Manns and Adams, 1925; Person and Martin, 1940; Person, 1946) in the field, but no quantitative studies have been done to evaluate critically the effect of the matric component of soil water potential on infection of fibrous roots. Soil physical factors that affect disease on fibrous roots may ultimately affect disease on storage roots and subsequent yield since the pathogen infects storage roots through lateral fibrous roots on storage roots and does not infect the intact periderm of the storage root (Clark and Matthews, 1987). The severity of disease on fibrous roots is positively correlated with the severity of disease on storage roots in the widely-grown susceptible sweetpotato cv. Jewel (Ristaino and Averre, 1992).

Common scab of potato caused by S. scabies can be effectively controlled through the use of irrigation (Lewis, 1970; Lapwood *et al.*, 1973; Lapwood and Adams, 1975). The potential exists to manipulate soil moisture by irrigation and reduce disease caused by S. *ipomoeae* on sweetpotato. Under field conditions drip irrigation reduced the severity of disease caused by *S. ipomoeae* on fibrous roots, increased the number of storage roots produced per plant, and reduced the number of diseased storage roots produced per plant (Ristaino and Averre, 1992). However, irrigation did not significantly increase yields.

My objective was to evaluate the effect of constant or cyclical changes in Ψ_m on infection of sweetpotato fibrous roots by *S. ipomoeae* under carefully controlled conditions. In addition, the effect of disease on water extraction by roots was evaluated. An abstract of a portion of this work has been published (Ristaino, 1991).

MATERIAL AND METHODS

Inoculum preparation

Stock cultures of S. ipomoeae were maintained on silica gel at 5°C (Sleesman and Leben, 1978). An isolate of S. ipomoeae, No. 78-57 (pathogenic to sweetpotato), isolated from sweetpotato in North Carolina was obtained from C. Clark, Louisiana State University, and used in these experiments. Cultures were grown on Streptomyces growth medium (20 g mannitol, $0.2 \text{ g} \text{ K}_2 \text{HPO}_4$, 0.2 g $MgSO_4 \cdot 7H_2O$, 5.0 g NaCl, 2.0 g CaCO₃, 0.2 mg CoCl₂, 1.0 g yeast extract, 18.0 g agar, 1.0 liter distilled water) at 32°C for 8-10 days prior to transfer (Clark and Lawrence, 1981). Inoculum for use in experiments was prepared by culturing the pathogen at 32°C for 2 weeks in 500 ml of vermiculite and 375 ml of broth (5 g mannitol, 1 g sodium propionate, 0.2 g K_2HPO_4 , 0.2 g $MgSO_4 \cdot 7H_2O$, 1 g yeast extract, 2.0 g CaCO₃, 0.11 mg CoCl₂, 1.0 liter distilled water) contained in 1.0 liter canning jars (C. Clark, pers. commun.). Inoculum consisted of aerial mycelia and spores of the pathogen in the vermiculite-broth carrier.

Stock plants of sweetpotato cv. Jewel were maintained in the greenhouse and fertilized weekly with Miller's solution (20% N, 20% P, 20% K). Terminal vine cuttings with at least three nodes were removed from stock plants and planted in sand in 2.5-cm² cells of styrofoam flats and allowed to root for 1 week before use in experiments.

Soil preparation

Experiments were made in either a sand (87% sand, 9% silt, 4% clay) or a loamy sand soil (80% sand, 13% silt, 8% clay) after sieving (<2 mm sieve). Soil pH was adjusted in each experiment by the addition of dolomitic lime to bring soil pH to *ca* 6.5–7.0. Two additional experiments were done in the two soils that had been fumigated previously with methyl bromide (64 g m⁻³) several weeks prior to infestation of the soil with the pathogen. Soil sterility was confirmed at the time of planting by plating aliquots of soil on potato dextrose agar.

Soil moisture characteristic curves were prepared for each soil with either Büchner tension funnels or a pressure plate to adjust Ψ_m between 0 and $-500 \text{ J} \text{ kg}^{-1}$ (100 J kg⁻¹ = 1 bar) (Klute, 1986). Gravimetric water contents were measured by drying soils to constant weight at 105°C. Gravimetric water contents were converted to volumetric water contents and a soil moisture characteristic curve was prepared for each soil.

Tension funnel experiments

Experiments were arranged in a split block design in the greenhouse. Non-fumigated soil (215 cm³) was placed in each 350 ml tension funnel. Non-fumigated soil in funnels in main plots was either infested with S. ipomoeae in a vermiculite carrier or with the sterile vermiculite at a rate of 27 mg cm⁻³ soil. Rooted cuttings were transplanted into soil immediately after soil infestation and bulk density was adjusted to ca 1.41 g cm⁻³. Soil in all funnels was brought to saturation briefly and then funnels in the subplots were adjusted to $\Psi_{\rm m}$ values of 0, -2.5, -5.0, -7.5, -10 or -20 J kg⁻¹. The vertical distance from the top of the porous plate to the water level in a reservoir was used as the reference distance to determine column heights and adjust Ψ_m values of the soil in tension funnels. Water levels in the reservoirs were adjusted daily to maintain constant $\Psi_{\rm m}$ in the funnels. Soil in the funnels was covered with plastic bags to reduce evaporation. The experiments were repeated twice in non-fumigated sand and twice in non-fumigated loamy sand, and each treatment was replicated four times.

In order to determine whether soil microorganisms affected the ability of *S. ipomoeae* to infect at various Ψ_m in soil, experiments were also done in fumigated sand and loamy sand soils. Soil in funnels in main plots was either sand or loamy sand, whereas soil in subplots was adjusted to Ψ_m levels of 0, -2.5, -5.0, -7.5 or -10 J kg⁻¹. Soil in all funnels was infested with the pathogen at the same rate as described above and treatments were replicated four times.

Plants were removed from funnels after 3 to 4 weeks and the severity of disease on fibrous roots was evaluated on individual plants visually using a scale of 0-4 where; 0 = no lesions, 1 = <25% of the fibrous root system with lesions, 2 = 26-50% of the fibrous root system with lesions, 3 = 51-75% of the fibrous root system with lesions, 4 = >75% of the fibrous root system with lesions. Shoot and root dry weights were measured by drying tissue at 60°C to constant weight. Soil pH and gravimetric water content were measured in soil sampled from each funnel at the beginning and end of the experiments. Water contents were similar at a given Ψ_m in each replication of the study.

Drip irrigation experiments

Experiments to evaluate the effect of cyclical changes in soil water potential on infection of sweet-potato fibrous roots by *S. ipomoeae* were done in a growth chamber in the Phytotron Facility at

North Carolina State University. Experiments were arranged in a split block design with inoculum applied to main plots and frequency of drip irrigation applied to subplots. Experiments were done in nonfumigated sand in 11.5 cm dia pots that contained 450 cm³ of soil. Soil was either infested with S. ipomoeae in a vermiculite carrier at a rate of 27 mg cm⁻³ of soil or infested with sterile vermiculite at the same rate. A single rooted cutting was transplanted into each pot and drip emitters were placed on the soil surface. Pots were either irrigated more frequently (once a day) to maintain the $\Psi_{\rm m}$ of soil above $-5.0 \, {\rm J}$ kg^{-1} or less frequently (either every 4 or 6 days) for 5 min. Water was applied at a rate of 100 ml min⁻¹ per emitter at a pressure of 414 kPa. All treatments were replicated four times and there were four pots (subsamples) for each treatment × replicate combination (16 per treatment). Mean data for the four pots were used in the analysis of variance. Plants were harvested after 4 weeks and the severity of disease on fibrous roots was evaluated on the 1-4 scale described above. The dry weight of fibrous roots and shoots was measured after drying tissue at 60°C. Experiments were repeated twice.

Additional experiments were made with 15.0 cm dia pots containing 1500 cm³ of soil. The experiments also were arranged in a split-block design. Soil in pots in the main plots were either infested or not infested with S. ipomoeae whereas, soil in subplots was drip irrigated either more frequently (once a day) or less frequently (every 4 days). All treatments were replicated three times and there were three pots for each treatment-replicate combination (nine per treatment). Plants were harvested after 8 weeks and the severity of disease on fibrous roots, and the dry weight of fibrous roots, storage roots, and shoots were evaluated. Experiments were repeated twice.

The Ψ_m was measured in pots prior to daily irrigation with a pressure transducer (Tensimeter, Soil Measurement Systems Inc., Las Cruces, N.M., U.S.A.) and tensiometers. Tensiometers were 20 cm long and 1.25 cm wide with a 100 J kg⁻¹ porous cup. Soil moisture blocks (Soil Moisture Equipment Corp., Santa Barbara, CA, 93105, U.S.A.) were used to measure the electrical resistance of the soil water in pots prior to less frequent irrigation. Electrical resistance blocks were calibrated in the same soil in a pressure plate over a range of Ψ_m values from 0 to -500 J kg^{-1} . Tensiometers or soil moisture blocks were placed in non-infested soils in each replication of each irrigation treatment in experiments that were carried out for 4 weeks, and in both infested and non-infested soils in experiments that were carried out for 8 weeks. All soil moisture sensors were read just before irrigation in all experiments to measure the lowest Ψ_m of the soil prior to irrigation.

Statistical analysis

Data were tested for homogeneity of variance prior to analysis of variance with the Statistical Analysis System (SAS Institute, Cary, N.C.). Regression analysis was conducted with the SAS general linear models procedures. Second-order polynomial functions were fit to the fibrous root disease data. Least significant difference tests were used to separate appropriate subplot means within or between mainplots (Little and Hills, 1978).

RESULTS

Tension funnel experiments

The volumetric water contents of the sand and loamy sand soils were 0.40 and 0.42 cm³ water cm⁻³ of dry soil at saturation, respectively [Fig. 1(A)]. The loamy sand held more water than the sand at all Ψ_m evaluated. Approximately 16 or 17% of the water was released from the sand or loamy sand soils at Ψ_m of $-5 J kg^{-1}$ and pores $> 58 \mu m$ dia. were drained at this Ψ_m [Fig. 1(B)].

The severity of disease on fibrous roots was significantly affected by the Ψ_m of the non-fumigated sand during infection (Ψ_m main effect significant at P < 0.01) [Fig. 2(A)]. The severity of disease on fibrous roots was low in plants held in non-fumigated sand at constant Ψ_m above -5.0 J kg^{-1} and increased with decreasing (more negative) Ψ_m [Fig. 2(A)]. A similar relationship between disease severity on fibrous roots and Ψ_m (Ψ_m main effect significant at P < 0.01) was observed in the non-fumigated loamy sand [Fig. 2(A)]. The relationship between the

2 1 0.5 Sand ి 0.2 Loamy sand 0.1 Ô -1.0 -2.5 -5.0 -7.5 -10 -15 Matric potential (J kg-1) 291 58.2 29.1 Effective pore diameter (µm)

Fig. 1. Soil moisture characteristic curve for the sand and loamy sand soils used in the experiments described.



Fig. 2. The severity of disease on fibrous roots caused by S. *ipomoeae* on sweetpotato cv. Jewel as a function of the matric component of soil water potential (Ψ_m) in: (A) non-fumigated sand or loamy sand soil or (B) fumigated sand or loamy sand soil. Solid circles represent the mean values for each treatment in sand, and open triangles represent the mean values for each treatment in loamy sand.

severity of disease on fibrous roots and Ψ_m of the non-fumigated sand or loamy sand soils was best described by the second-order polynomial functions $y = -0.24 + 0.04x - 0.0002x^2$ ($r^2 = 0.76$) and $y = -0.0017 + 0.04x - 0.0001x^2$ ($r^2 = 0.76$), respectively, where $x = \Psi_m$ and y = the severity of disease on fibrous roots [Fig. 2(A)].

The severity of disease on fibrous roots was also affected by the Ψ_m in fumigated sand and loamy sand soils [Fig. 2(B)]. Disease on fibrous roots was low in plants held in either fumigated sand or loamy sand at Ψ_m above -5 J kg^{-1} . Disease increased with decreasing Ψ_m in fumigated soils [Fig. 2(B)] and the response between 0 and -7.5 J kg^{-1} was linear and similar to the response in non-fumigated soils [Fig. 2(A)]. Disease was not measured at Ψ_m of -20 J kg^{-1} in the experiments with fumigated soils.

In non-infested soils the dry weight of sweetpotato fibrous roots grown in non-fumigated sand increased with decreasing Ψ_m [Fig. 3(A)]. Disease significantly reduced the dry weight of fibrous roots by 48–59% as compared to non-inoculated controls at Ψ_m values between -5.0 and -20 J kg^{-1} (inoculum $\times \Psi_{\text{m}}$ interaction was significant at P < 0.05) [Fig. 3(A)]. Disease did not affect root dry weights in soils at Ψ_{m} above -5.0 J kg^{-1} . There was a significant negative correlation between the severity of disease on fibrous roots and root dry weight (r = -0.61).

In non-infested soils, the dry weights of shoots grown in non-fumigated sand was not greatly affected by Ψ_m between 0 and -20 J kg^{-1} [Fig. 3(B)]. However, disease reduced shoot dry weight by 29–48% as compared to non-inoculated controls at Ψ_m values between -5.0 and -20.0 J kg^{-1} (inoculum $\times \Psi_m$ interaction significant at P < 0.01) [Fig. 3(B)]. There was also a significant negative correlation between the severity of disease on fibrous roots and shoot dry weight (r = -0.59).

Drip irrigation experiments

The severity of disease on fibrous roots in plants harvested after 4 weeks was significantly lower in plants irrigated on the daily schedule, than in plants irrigated every 4 or 6 days (irrigation effect was significant at P < 0.05) (Table 1). The severity of disease on fibrous roots in inoculated plants irrigated every 4 or 6 days was uniformly high (Table 1). Plants harvested after 8 weeks showed a similar response

Fig. 3. The dry weight of: (A) fibrous roots and (B) shoots (vines plus leaves) of sweetpotato cv. Jewel as a function of the matric component of soil water potential (Ψ_m) in non-fumigated sand infested (cross-hatched bars) or not infested (open bars) with *S. ipomoeae*. For comparison of means within and between bar clusters, $LSD_{0.05} = 0.19$ and 0.18, for root dry weights and shoot dry weights, respectively.







Fig. 4. The change in the matric potential component of soil water potential (Ψ_m) over time in: (A) non-infested (open squares) or infested (solid squares) soils irrigated daily for 8 weeks; (B) in non-infested (open circles) or infested (solid circles) soils irrigated every 4 days for 8 weeks.

with less disease on fibrous roots of plants irrigated daily than every 4 days (irrigation effect significant at P < 0.05) (Table 1).

Root and shoot dry weights of plants harvested after 4 weeks were significantly greater in plants irrigated daily than in plants irrigated every 4 or 6 days (irrigation effect significant at P = 0.004 and 0.0004) (Table 1). Disease reduced fibrous root dry weights as compared to non-inoculated controls from 560 to 370 mg plant⁻¹ and reduced shoot dry weights from 1.51 to 1.14 g plant⁻¹ at all irrigation frequencies in plants harvested after 4 weeks (inoculum effect significant at P < 0.05 and 0.05, for root or shoot dry weights respectively). Fibrous root and shoot dry weights of plants harvested after 8 weeks were also greater in plants irrigated daily than in plants irrigated every 4 days, however, treatment differences were only significant for shoot dry weights (irrigation effect significant at P < 0.01) (Table 1). Plants irrigated daily for 8 weeks produced greater dry matter

Table 1. The effect of irrigation frequency on the severity of disease on fibrous roots, and fibrous root, shoot and storage root dry weight in cultivar Jewel grown for either 4 or 8 weeks in soil

infested with S. ipomoede				
Irrigation frequency	Severity of disease on fibrous roots ^a	Fibrous root dry weight (g plant ⁻¹) ^b	Shoot dry weight (g plant ⁻¹) ^c	Storage root dry weight (g plant ⁻¹) ^d
Harvested afte	er 4 weeks			
Daily	0.94	0.57	1.56	ND
4-day	2.00	0.45	1.36	ND
6-day	2.10	0.38	1.04	ND
Harvested afte	er 8 weeks			
Daily	0.66	2.63	7.40	9.20
4-day	2.33	1.69	4.80	0.60

*The severity of disease on fibrous roots evaluated on a scale of 1–4. For comparison of mean severity of disease on fibrous roots after 4 or 8 weeks, LSD_{0.05} = 0.59 and 0.65, respectively.
^bFor comparison of mean fibrous root dry weights between irrigation levels after 4 or 8 weeks

 $LSD_{0.05} = 0.7$ and 3.04, respectively. "For comparison of mean shoot dry weights between irrigation levels after 4 or 8 weeks $LSD_{0.05} = 0.12$ and 1.45, respectively.

^dFor comparison of mean storage root dry weights between irrigation levels after 8 weeks LSD_{0.05} = 1.69. ND = not determined. in storage roots than plants irrigated every 4 days (irrigation effect significant at P < 0.01) (Table 1). Discase did not reduce fibrous root dry weights, shoot dry weights, or storage root dry weights in plants harvested after 8 weeks as compared to non-in-oculated controls.

The Ψ_m of non-infested soils planted with sweetpotato was highest in soils irrigated daily and remained above -10 J kg^{-1} for the duration of the 4and 8-week experiments. Non-infested soils planted with sweetpotato and irrigated either every 4 or 6 days dried to a greater extent than soils irrigated daily and lowest Ψ_m values ranged from -64 to -71 Jkg⁻¹ after 4 weeks (data not shown).

Disease significantly reduced the ability of roots to extract water from soil in plants grown for 8 weeks in S. ipomoeae-infested soils [Fig. 4(A) and (B)]. Healthy plants irrigated daily extracted water to $\Psi_{\rm m}$ of -9 J kg^{-1} , whereas diseased plants extracted water only to $\Psi_{\rm m}$ of $-3 \,{\rm J}\,{\rm kg}^{-1}$ over the 8 weeks [Fig. 4(A)]. In contrast, inoculated plants irrigated every 4 days had higher amounts of disease on fibrous roots than plants irrigated daily (Table 1), and subsequently roots of these plants extracted significantly less water from soil over the 8 week experiment than noninoculated plants [Fig. 4(B)]. The Ψ_m was similar in both infested and non-infested soils irrigated every 4 days until 21 days after planting [Fig. 4(B)]. Thereafter, diseased plants extracted significantly less water from soil and by 32 days after planting, Ψ_m readings in infested soils following irrigation were significantly higher than in non-infested soils.

DISCUSSION

The severity of disease on fibrous roots caused by S. ipomoeae on sweetpotato cv. Jewel was significantly affected by the Ψ_m at which the soil was held. Disease severity was low at Ψ_m above -5 J kg^{-1} in both soils, and disease severity increased with decreasing Ψ_m . Poole (1925) demonstrated that less disease occurred under saturated soil conditions than when soil was allowed to dry to soil water contents of 2-5%. However, the Ψ_m was not critically controlled in Poole's work and soil water contents can vary between soils of different textures held at similar $\Psi_{\rm m}$. The data presented here demonstrate that $\Psi_{\rm m}$ during infection can have large effects on the severity of disease on fibrous roots in cv. Jewel. Disease was severe over the range of $\Psi_{\rm m}$ from -5.0 to -20 J kg⁻¹ and root and shoot growth was significantly reduced as compared to non-inoculated controls.

The reduction in infection of sweetpotato fibrous roots by S. *ipomoeae* at Ψ_m above -5 J kg^{-1} may be due to reduced growth of the pathogen in water-filled pores. The pore size distributions of the two soils used in this study were similar as indicated by the cumulative water loss curves for the sand and loamy sand soils [Fig. 1(B)]. Little infection occurred at Ψ_m above -5.0 J kg^{-1} when the proportion of water-filled pores in soil was high. Most of the soil water was released from pores > 58.2 μ m at Ψ_m of -5 J kg⁻¹ and little additional water was released from both soils at Ψ_m below -5 J kg^{-1} . The growth and survival of Streptomyces species in soil is limited in waterfilled pores (Williams et al., 1972). Populations of total Streptomyces species in two different soils detected by dilution plate assays were greatest at $\Psi_{\rm m}$ between -10 and -100 J kg^{-1} (Williams et al., 1972), and were greatly reduced in wet soils at $\Psi_{\rm m}$ between 0 and $-1 J kg^{-1}$. In soils at Ψ_m lower than -1×10^3 J kg⁻¹ growth of Streptomyces species is severely limited. However, some species of Streptomyces can grow on agar media at osmotic potentials as low as -1.5×10^4 J kg⁻¹ (Wong and Griffin, 1974) and spores can survive for prolonged periods under dry conditions (Meiklejohn, 1957; Williams et al., 1972, 1984). In my study, population densities and growth of the pathogen in soil were not quantified because a selective soil assay was not available. We have developed a selective soil assay for S. ipomoeae which should prove useful in future work to monitor population dynamics of the pathogen in soil under conditions of changing soil water status (Weicht et al., 1992).

Low amounts of infection of fibrous roots by S. *ipomoeae* at Ψ_m of 0, -1.0 and -2.5 J kg^{-1} also could have been due to alterations in the susceptibility of the host to infection in wet soils. Rates of gaseous diffusion of O₂ or CO₂ are considerably reduced in soils at high Ψ_m when soil pores are water-filled (Griffin, 1963; Papendick and Campbell, 1985). Anaerobic conditions in saturated soil due to reduced O₂ or increased CO₂ may have limited colonization of roots by the pathogen. On the other hand, limited root growth under saturated conditions may have reduced pathogen contact with inoculum in soil. In non-infested soils, root dry weights were lowest at Ψ_m of 0 and -1.0 J kg^{-1} and increased with decreasing Ψ_m . Thus, root growth was reduced by high Ψ_m .

Frequent drip irrigation reduced the severity of disease caused by S. ipomoeae on sweetpotato fibrous roots. When plants were irrigated to maintain $\Psi_{\rm m}$ above -10 J kg^{-1} on a daily schedule, fibrous root disease was significantly reduced. Lapwood and Lewis (1967) and Lapwood et al. (1970, 1973) have demonstrated that timing irrigations to maintain the $\Psi_{\rm m}$ of soil above $-10 \,{\rm J \, kg^{-1}}$ during 5-weeks of tuber initiation significantly reduced the incidence of common scab caused by S. scabies on potato in the field. Potatoes are susceptible to common scab caused by S. scabies during tuber initiation (Lapwood and Lewis, 1967; Lapwood et al., 1970; Lapwood, 1973). Unlike common scab, sweetpotato storage roots are believed to be susceptible to Streptomyces soil rot caused by S. ipomoeae throughout the entire growing season (Clark and Moyer, 1988). However, infections that originate early in the season can cause storage root malformations and more severe lesions than those that develop later in the season (Person and

Martin, 1940). Thus, irrigations on sweetpotato would probably need to be applied for a longer period during the growing season than on potatoes.

The response of disease caused by S. *ipomoeae* on fibrous roots to Ψ_m was similar in both fumigated and non-fumigated sand or loamy sand soils. Lewis (1970) and Adams and Lapwood (1978) suggested that increased infection of potato tubers in dry soils was related to a decrease in the number of antagonistic bacteria in the lenticels of tubers. In my study, the fumigated soil did not contain antagonistic microorganisms at the time of planting. However, I did not assay the soil at harvest to determine if antagonistic bacteria recolonized the fumigated soil. Competition from antagonistic microorganisms was probably not involved in suppression of disease on fibrous roots at Ψ_m above -5 J kg^{-1} in my study, however, further experimentation is necessary to confirm this.

Disease caused by S. ipomoeae significantly reduced root dry weights in plants held at constant Ψ_{m} between -5 and -20 J kg^{-1} for 3 weeks as compared to non-inoculated controls. Disease also reduced root dry weights at all irrigation frequencies in plants grown in infested soils for 4 weeks as compared to non-inoculated controls. However, in experiments conducted for 8 weeks in infested soils exposed to cyclical changes in Ψ_m , disease did not significantly reduce root dry weights. These data indicate that plants of cv. Jewel may be able to compensate for disease by producing additional root dry matter. Irrigation frequency had the largest effect on root dry weight in cultivar Jewel in my experiments. Plants irrigated more frequently produced larger root systems which also may have helped them to compensate for root loss due to disease. Carlson and Struble (1960) proposed that sweetpotato breeding lines with higher rates of root growth may be more resistant to disease than plants with lower rates of root growth. However, this mechanism may not explain resistance in current resistant cultivars such as Beauregard since fibrous root growth over time is significantly less in "Beauregard" than the susceptible cv. Jewel (Ristaino, 1992).

Although disease did not affect root dry weights in plants grown in infested soils for 8 weeks, disease had a large effect on the ability of fibrous roots to extract water from soil. These data suggest that the effect of disease on water extraction from soil was not due solely to a reduction in root biomass. Increased resistance to water uptake or water flow in roots may explain the results observed. Phytophthora root rot on safflower and Phymatotrichum root rot on cotton can cause large increases in resistance to water flow in roots (Duniway, 1977; Olsen et al., 1983). S. scabies produces the toxin thaxtomin which may play a role in symptom expression (Lawrence et al., 1990). The isolate of S. ipomoeae used in my study produces a modified form of thaxtomin A (M. Clark, pers. commun), but the effect of the toxin on water uptake by sweetpotato roots has not been examined. Acknowledgements—The technical assistance of G. Parra and A. Schepps is appreciated. This work was funded in part by the North Carolina Agricultural Research Service and in part by the North Carolina Sweetpotato Commission.

REFERENCES

- Adams M. J. and Lapwood D. H. (1978) Studies on the lenticel development, surface microflora and infection by common scab (*Streptomyces scabies*) of potato tubers growing in wet and dry soils. *Annals of Applied Biology* 90, 335-343.
- Carlson L. W. and Struble F. E. (1960) Methods for determining the reaction of sweetpotato lines to soil rot. *Phytopathology* 50, 822-826.
- Clark C. A. and Lawrence A. (1981) Morphology of spore-bearing structures in *Streptomyces ipomoeae*. *Canadian Journal of Microbiology* 27, 575–579.
- Clark C. A. and Matthews S. W. (1987) Histopathology of sweetpotato root infection by *Streptomyces ipomoeae*. *Phytopathology* 77, 1418-1423.
- Clark C. A. and Moyer J. W. (1988) Compendium of Sweet Potato Diseases. American Phytopathological Society Press, St Paul.
- Duniway J. M. (1977) Changes in resistance to water transport in safflower during the development of Phytophthora root rot. *Phytopathology* **61**, 331-337.
- Griffin D. M. (1963) Soil moisture and the ecology of soil fungi. Biological Reviews 38, 141-166.
- Hooker W. J. and Peterson L. E. (1952) Sulfur soil treatment for control of sweetpotato soil rot incited by *Streptomyces ipomoeae*. *Phytopathology* 42, 583-591.
- Klute A. (1986) Water retention: laboratory methods. In Methods of Soil Analysis Part 1: Physical and Mineralogical Methods (A. Klute, Ed.), 2nd Edn, pp. 635-662. American Society of Agronomy, Madison.
- Lapwood D. H. (1973) Streptomyces scabies and potato scab disease. In Actinomycetales: Characteristics and Practical Importance (G. Sykes and F. A. Skinner, Eds), pp. 253-260. Academic Press, New York.
- Lapwood D. H. and Adams M. J. (1975) Mechanisms of control of common scab by irrigation. In *Biology and Control of Soil-borne Plant Pathogens* (G. W. Bruehl, Ed.), pp. 123–129. The American Phytopathological Society, St Paul.
- Lapwood D. H. and Lewis B. G. (1967) Observations on the timing of irrigation and the incidence of potato common scab (Streptomyces scabies). Plant Pathology 16, 131-135.
- Lapwood D. H., Wellings L. W. and Hawkins J. H. (1973) Irrigation as a practical means to control common scab (*Streptomyces scabies*): final experiment and conclusions. *Plant Pathology* 22, 35-41.
- Lapwood D. H., Wellings L. W. and Rosser W. R. (1970) The control of common scab by irrigation. Annals of Applied Biology 66, 397-405.
- Lawrence C. H., Clark M. C. and King R. R. (1990) Induction of common scab symptoms in aseptically cultured potato tubers by the vivotoxin, Thaxtomin. *Phyto*pathology 80, 606-608.
- Lewis B. G. (1970) Effects of water potential on the infection of potato tubers by *Streptomyces scabies* in soil. *Annals of Applied Biology* 66, 83-88.
- Little T. M. and Hills F. J. (1978) Agricultural Experimentation. Wiley, New York.
- Lorbeer J. W. (1962) Control of soil pox of sweetpotato in California. *Phytopathology* 49, 544 (abstract).
- Manns T. F. and Adams J. F. (1925) Diseases of sweetpotato and their control in Delaware. University of Delaware Agriculture Experiment Station Bulletin 141, 24-26.
- Martin W. J. (1958) Reaction of sweetpotato varieties and seedlings to soil rot. *Phytopathology* 48, 445-448.

- Martin W. J., Hernandez Travis P. and Hernandez Teme P. (1975) Development and disease reaction of Jasper, a new soil rot-resistant sweetpotato variety from Louisiana. *Plant Disease Reporter* **59**, 388–391.
- Meiklejohn J. (1957) Numbers of bacteria and actinomycetes in a Kenya soil. Journal of Soil Science 8, 240-247.
- Moyer J. W., Campbell C. L., Echandi E. and Collins W. W. (1984) Improved methodology for evaluating resistance in sweetpotato to *Streptomyces ipomoeae*. *Phytopathology* 74, 494–497.
- Olsen M. W., Misaghi I. J., Goldstein D. and Hine R. B. (1983) Water relations in cotton plants infected with *Phymatotrichum. Phytopathology* **73**, 213–216.
- Papendick R. I. and Campbell G. S. (1985) Theory and measurement of water potential. In *Water Potential Relations in Soil Microbiology* (J. F. Parr, W. R. Gardner and L. F. Elliot, Eds), pp. 1–22. Soil Science Society America, Madison.
- Person L. H. (1946) The soil rot of sweetpotatoes and its control with sulfur. *Phytopathology* 36, 869–875.
- Person L. H. and Martin W. J. (1940) Soil rot of sweetpotato in Louisiana. *Phytopathology* 30, 913-926.
- Poole R. F. (1922) Recent investigations on the control of three important field diseases of sweetpotato. New Jersey Agriculture Experiment Station Bulletin 365, 4-39.
- Poole R. F. (1925) The relation of soil moisture to the pox or ground rot disease of sweetpotatoes. *Phytopathology* 15, 287-293.

- Ristaino J. B. (1991) Effect of soil matric potential on infection of sweetpotato fibrous roots by *Streptomyces* ipomoeae. Phytopathology 81, 1186 (abstract).
- Ristaino J. B. (1993) Effect of host resistance to *Strepto-myces ipomoeae* on disease, yield, and dry matter partitioning in sweetpotato. *Plant Disease* 77. Accepted for publication.
- Ristaino J. B. and Averre C. W. (1992) Effects of irrigation, sulfur, and fumigation on Streptomyces soil rot and yield components in sweetpotato. *Phytopathology* 82, 670-676.
- Sleesman J. P. and Leben C. (1978) Preserving phytopathogenic bacteria at -70°C or with silica gel. Plant Disease Reporter 62, 910-913.
- Weicht T. R., Moyer J. W. and Ristaino J. B. (1992) Detection of *Streptomyces ipomoea* in mixed cultures, soil, and sweetpotato fibrous roots with a serological assay. *Phytopathology* 82 (abstract), 1145.
- Williams S. T., Lanning S. and Wellington E. M. H. (1984)
 Ecology of Actinomycetes. In *The Actinomycetales* (M. Goodfellow, M. Mordarski and S. Williams, Eds).
 Academic Press, New York.
- Williams S. T., Shameemullah M., Watson E. T. and Mayfield C. I. (1972) Studies on the ecology of actinomycetes in soil. VI. The influence of moisture tension on growth and survival. Soil Biology & Biochemistry 4, 215-225.
- Wong P. T. W. and Griffin D. M. (1974) Effect of osmotic potential on Streptomycete growth, antibiotic production, and antagonism to fungi. Soil Biology & Biochemistry 6, 319-325.