Effect of Salinity Stress on the Development of Phytophthora Root Rot of Chrysanthemum

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ABSTRACT

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Rooted cuttings of *Chrysanthemum morifolium* 'Paragon' were grown hydroponically in ceramic crocks containing half-strength Hoagland's solution. After 10 days, plants were subjected to pulsed exposures of salinity stress by amending the Hoagland's solution with NaCl to a final concentration of 0.1 M or 0.2 M NaCl. Control plants had no salt added. After 24 hr in the NaCl-amended solutions, both stressed plants and controls were removed from the crocks and inoculated with 10^6 motile zoospores of *Phytophthora cryptogea* by immersing their roots for 1 hr in a measured volume of inoculum prior to returning them to crocks of fresh half-strength Hoagland's, or adding inoculum directly into the crocks of fresh solution. Uninoculated plants subjected to the same stress treatments served as controls to monitor independent effects of the salinity stress. While there was some discoloration of roots following salt stress, and slight stunting of plants exposed to 0.2 M NaCl, all uninoculated plants appeared to recover quickly from the brief stress treatment. When stressed and unstressed plants were inoculated with zoospores of *P. cryptogea*, there was a positive relationship between the degree of stress and the severity of the resulting root rot symptoms. Only 20% of the roots of unstressed plants developed lesions 72 hr after inoculation, whereas 70 and 88% of roots previously exposed to 0.1 M and 0.2 M NaCl, respectively, developed lesions. Lesions that developed on roots exposed to salinity stress spread rapidly and turned large portions of the root system necrotic within 5–7 days. Microscopic examination of roots collected 1 hr after exposure to the zoospore inoculum showed large, statistically significant increases in the number of zoospore cysts attached to roots with each increment increase in salinity stress. The root hair zone was the region of greatest zoospore attachment on stressed roots, and a large proportion of the cysts that attached to stressed roots within 30 min of inoculation were observed by scanning electron microscopy to have germinated and penetrated the host tissue. The severe root rot infection that occurred as a result of NaCl stress could have broad implications in areas where water quality and soil salinity are important problems.

In the soil environment, plant roots are exposed to many forms of physical stress, with opposite extremes in soil-water status probably the most frequent and severe. Although the mechanisms are not yet clearly defined, stresses that result from flooded soil conditions or drought that have been shown to predispose plants to several root diseases. Drought stress has been implicated in charcoal rot of sorghum (9) and cotton (11), and foot rot of wheat (5). In Phytophthora root rot of safflower (8) and Phytophthora root and crown rot of rhododendron (3), drought stresses have clearly been shown to weaken and predispose otherwise resistant plants to disease. Stresses that develop in flooded soils also have been shown to predispose plants to Phytophthora root rots. Kuan and Erwin (16) showed that when alfalfa roots were held in flooded soil for as little as 24 hr prior to inoculation, there was a significant increase in subsequent root infection. Similarly, Blaker and MacDonald (3) showed that exposure of the resistant rhododendron cultivar Caroline to 48-hr flooding periods prior to inoculation resulted in severe root and crown rot symptoms. While the development of Phytophthora root rots under such conditions has historically been attributed to factors influencing movement and activity by the pathogens, it is evident from recent work cited above (3,8,16) that physiological disturbances in the root tissues resulting from stress can be a significant factor in disease development.

Another form of environmental stress to which plants can be exposed is soil salinity, which is a problem in many areas of irrigated agriculture. Indeed, it has been estimated (10) that approximately one-third of the land under irrigation worldwide is affected by excess salinity. In California, the Imperial, Coachella, and Sacramento-San Joaquin valleys, which rank among the most productive agricultural lands in the world, are considered critically affected by soil salinity (10). Many factors contribute to the build-up of salts in irrigated soils. Poor quality of available irrigation water, application of fertilizers or soil amendments, and inadequate leaching of affected soils are among the most important. Many physiological processes are altered in plants grown in saline soils (2,4,17,23), which ultimately reduce their growth and yield. These effects of salinity have been attributed variously to osmotic stresses and specific ion toxicities (10,13). Work recently has been initiated to breed crop plants capable of tolerating salinity stresses (10).

While salinity stress can cause severe disruptions in root physiology and morphology (2,4,20,21), very little is known about how such disturbances might affect their susceptibility to pathogens. In perhaps the only systematic study of the role of salt stresses in plant disease, Beech (1) found that in the greenhouse, excessive amounts of fertilizer salts significantly increased seedling diseases of tomato caused by *Rhizoctonia solani* and *Fusarium oxysporum* f. sp. *lycopersici*, but not *Pythium ultimum*. Beech found his isolate of *P. ultimum* to be more sensitive to salinity than either of the other two pathogens, and similar to a hypothesis concerning temperature effects (18), attributed the increased disease in saline media to a relative growth advantage held by the pathogen over the host under stress conditions, rather than a direct effect of salinity on the host.

Because information regarding host and pathogen interactions in saline environments is needed, the following study was undertaken to determine whether salinity stress, like some other forms of stress (3,8,16), could directly affect the susceptibility of root tissues to pathogen invasion. Phytophthora root rot of chrysanthemum was selected as an example for study.

MATERIALS AND METHODS

Terminal cuttings of *Chrysanthemum morifolium* 'Paragon,' rooted in a perlite/vermiculite mixture (1:1, v/v), were used throughout the experiments. After roots 2–4 cm in length had developed, the cuttings were transferred individually to 2-L ceramic crocks containing half-strength Hoagland's solution (15). The crocks were fitted with opaque plastic lids with holes drilled for the plants, and strips of sponge rubber were used to secure cuttings in the holes with their roots suspended in the nutrient solution. Air

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lines provided continuous aeration and mixing of the nutrient solution, and supplemental lighting was used as needed in the greenhouse to assure 14 hr of continuous light daily. Plants were given 10 days to become established and grow in the nutrient solution, and then visually inspected for uniformity in size and appearance. Insofar as possible, each experiment was initiated with a homogeneous plant population.

Inoculum production and inoculation. A pathogenic isolate of *Phytophthora cryptogea* Pethyb. & Laff., originally isolated from diseased chrysanthemums, was cultured for 7 days on pea-dextrose agar (19), after which disks of aerial mycelium were cut from culture plates with a 7-mm-diameter cork borer and incubated 5 days at 22–24 C in petri dishes containing nonsterile soil extract to a depth of 2–4 mm. Soil extract was made by suspending 20 g of air-dried Yolo clay loam in 1 L of distilled water for 2–3 days and then drawing off the cleared supernatant. Numerous sporangia formed on disks during the incubation period, and zoospore release was stimulated by chilling the petri plates of soil extract to 12 C for 1 hr, followed by rewarming to room temperature. Zoospores were separated from the mycelial disks by filtration through four layers of cheesecloth, and the resulting inoculum suspension was adjusted to 10^4 zoospores per milliliter with distilled water. Plants were inoculated either by adding 100 ml of zoospore suspension to the crocks in which they were growing, or by removing plants from the crocks and placing their roots directly into 100 ml of the zoospore suspension. Although both methods worked equally well, the second method was used in most of the experiments.

Imposition of salinity stress. Plants were subjected to salinity stress by adding NaCl directly to the nutrient solution in which established plants were growing, to amend it to a concentration of 0.1 M or 0.2 M NaCl. Plants were held in the NaCl-amended solutions for 24 hr, after which leaf samples were collected for water potential (Ψ) measurements in an isopiestic thermocouple psychrometer, and returned to fresh, nonsalinized nutrient solution. Plants were inoculated with *P. cryptogea* immediately upon their return to nonsalinized solutions using the methods described above. Plants maintained in nutrient solution in the absence of salinity stress also were inoculated. In each experiment, six plants from each stress level were inoculated, and six were held as uninoculated controls to observe independent effects of the salt stress treatments on root behavior.

Disease evaluation. To examine zoospore attraction to stressed and unstressed roots, the terminal 2–3 cm of five randomly selected roots were excised from each inoculated plant in each treatment 30 or 60 min after exposure to the zoospore inoculum. The root pieces were fixed in 2% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2. For light-microscopic counts of zoospore cysts attached to roots, the fixed tissues were washed in 0.1 M phosphate buffer (pH 7.2), mounted on glass slides, and stained with acid fuchsin. The stained roots then were pressed flat under a glass cover slip to reduce them to a single plane of focus, and the number of zoospore cysts attached along the edges of the pressed roots were counted. Zoospore accumulation was also observed by using a scanning electron microscope (SEM). Fixed root tissues were prepared for the SEM by dehydration in an ethanol series, followed by transfer to isoamyl acetate and critical point drying with CO_2. Root pieces prepared in this manner were mounted on studs with double-stick tape, coated with 40–60 nm of gold in a sputter coater, and examined with a Cambridge Stereoscan Mark II SEM, operating at 10 kV.

In addition to relative differences in zoospore cyst attachment, the crock lids were periodically raised and the roots were examined over a 7–10 day interval after inoculation to evaluate differences in symptom development. The root systems of all plants were examined 72 hr after inoculation, with 50 roots counted at random on each plant to estimate the percentage of roots with visible lesions. At the termination of each experiment, the root systems of all plants were harvested, dried at 95 C, and dry weights (DW) were determined. In one experiment, intact plants were removed from the plastic lids and their total fresh weights (FW) were determined at the start of the experiment, and at each 48-hr interval thereafter for 12 days.

RESULTS

The solute potentials of the half-strength Hoagland's, 0.1 M NaCl- and 0.2 M NaCl-amended solutions used in these experiments were −2.0 to −2.5, −6.5 to −7.0, and −10.5 to −11.0 bars, respectively. Plants given a 24-hr pulse exposure to 0.1 M NaCl-amended solution developed a slight brown root discoloration, but otherwise did not appear to be adversely affected by the brief treatment. Following removal of the salt stress they resumed normal growth, and in terms of FW accumulation, were indistinguishable from unstressed controls (Fig. 1). In addition to a slight discoloration of roots, plants exposed to 0.2 M NaCl wilted during the stress period, and although they quickly regained turgidity upon relief of the stress, were stunted by the treatment, as evidenced by their smaller FW relative to other treatments at each subsequent measurement (Fig. 1). At the end of the 24-hr stress period, plants exposed to 0.2 M NaCl had leaf Ψ values ranging from −19 to −22 bars, whereas those held an equivalent time in unsalted or 0.1 M NaCl solutions, had leaf Ψ values ranging −10 to −12.5 and −14 to −15.5 bars, respectively.

The stress treatments resulted in marked differences in the severity of disease symptoms in plants inoculated with motile zoospores of *P. cryptogea*. Examination of the root systems 72 hr after inoculation showed that only 20% of the roots of unstressed plants had visable lesions, while 70 and 88% of the roots of plants exposed to 0.1 M and 0.2 M NaCl, respectively, had lesions. Furthermore, lesions that developed on salt-stressed roots appeared to be much larger than those on unstressed roots at 72 hr, and they coalesced rapidly and resulted in necrosis of large portions of the root system (Fig. 2). The increased severity of disease at each level of salinity was reflected in significant differences in the dry weights of the harvested roots (Fig. 3).

Although sporangia were seen on infected roots within 24–48 hr of inoculation, secondary inoculum cycles did not appear to play a significant role in disease development. The lesions that formed initially on unstressed roots did not increase greatly in size or number over the subsequent 8–12 day period, and lateral roots that formed nearby remained symptomless. Furthermore, adventitious roots that developed from the crowns of stressed plants 4–6 days after relief of stress also remained symptomless, even though large portions of the original root system were infected. Indeed, the severe symptoms of massive, rapidly spreading root infections observed in these experiments (Fig. 2) appeared to be dependent on the salinity stress.

The number of zoospore cysts attached to roots 1 hr after inoculation were counted by light microscopic examination of each

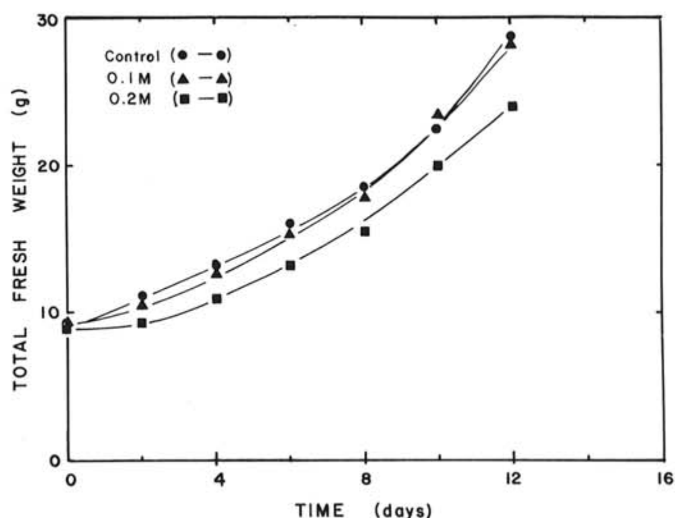

Fig. 1. Total fresh weight of chrysanthemums at intervals following a 24-hr pulse exposure to half-strength Hoagland's solution amended to 0.1 M and 0.2 M NaCl. Weights were measured immediately following relief of stress and every 48 hr thereafter.

2–3 cm length of root. Each root was visually separated into three distinct zones: the root cap zone (as delimited by the presence of root cap cells), the root hair zone (as delimited by the presence of root hairs), and the smooth root zone (which included all portions of the root not covered by root cap cells or root hairs). The location and relative size of the root hair zone and smooth root zone were variable from root to root, so all comparisons were based on the number of attached cysts per centimeter of each root zone. In these comparisons, there were large and statistically significant differences in the numbers of zoospore cysts attached to roots from the various stress treatments (Fig. 4). Unstressed roots had the fewest attached cysts, those previously exposed to 0.2 M NaCl had the most, and roots previously exposed to 0.1 M NaCl had an intermediate number of attached cysts. The salinity stress effect (increasing the number of attached cysts) was greatest in the root hair zone.

Both uninoculated and inoculated roots were collected from unstressed and 0.2 M NaCl-stressed plants 30 min after the start of inoculation and examined with an SEM. Although there were no apparent breaks or ruptures in the epidermal tissues of roots given a pulse exposure to 0.2 M NaCl, the root cap cells appeared to have collapsed (Fig. 5A and B). When the inoculated roots from these treatments were examined, a few cysts could be seen attached to unstressed roots (Fig. 5C), while large numbers were attached to stressed roots (Fig. 5D to F). The cysts did not attach randomly or uniformly along the surface of stressed roots, but instead occurred in clusters, sometimes of great size (Fig. 5E). Within these clusters, high proportions of the cysts had germinated and penetrated the epidermal cells (Fig. 5F), even though only 30 min had passed from the time roots were exposed to the motile zoospores until they were excised and fixed.

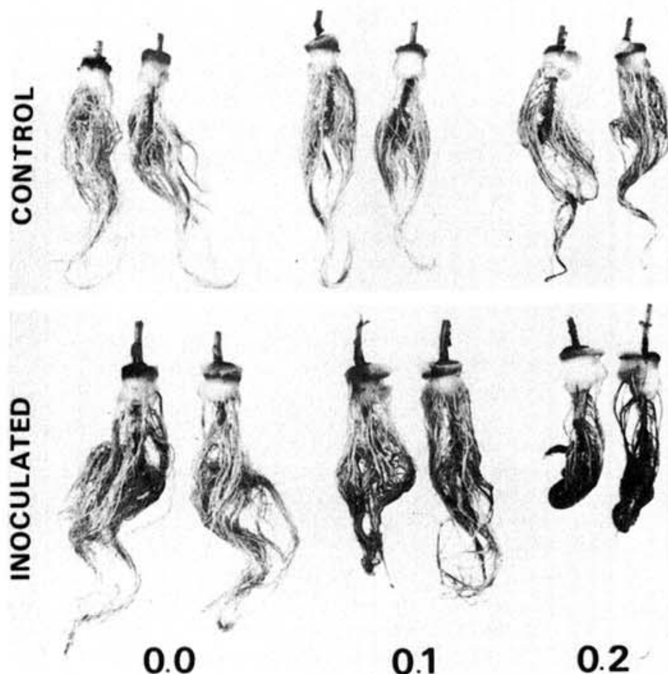

Fig. 2. Chrysanthemum roots grown in half-strength Hoagland's solution and given a 24-hr pulse exposure to (from left to right) 0.0, 0.1, or 0.2 M NaCl-amended solution. Root systems across the top are uninoculated controls, while those across the bottom were inoculated with 10^6 motile zoospores of *Phytophthora cryptogea* immediately upon relief of the stress.

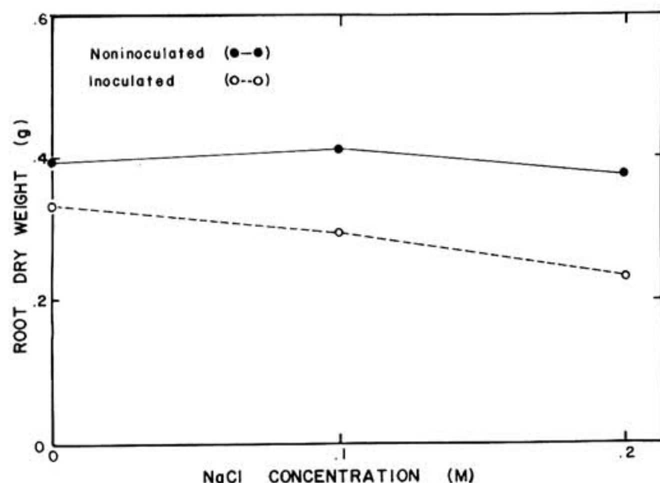

Fig. 3. Dry weight of chrysanthemum roots 12 days after relief of a 24-hr pulse exposure to different levels of NaCl in half-strength Hoagland's solution. Inoculated plants were exposed to 10^6 motile zoospores of *Phytophthora cryptogea* immediately upon relief of the salt stress (LSD = 0.092 g at $P = 0.05$).

DISCUSSION

The results of this research clearly show that salinity stress can predispose chrysanthemums to Phytophthora root rot. In his early work with fertilizer salts and tomato seedlings, Beech (1) attributed increased disease under osmotic stress to growth advantages of the pathogens over the host. However, by using solution culture techniques in these experiments, it was possible to avoid exposing the pathogen to salinity stress. Thus, the increased root rot that resulted following exposure to salinity stress can be attributed directly to the effect of salinity on the host without any concomitant effect of salinity on the pathogen, and salinity stress fits the definition of a predisposing factor (24) by acting on the host to increase its susceptibility to disease. Furthermore, it was evident

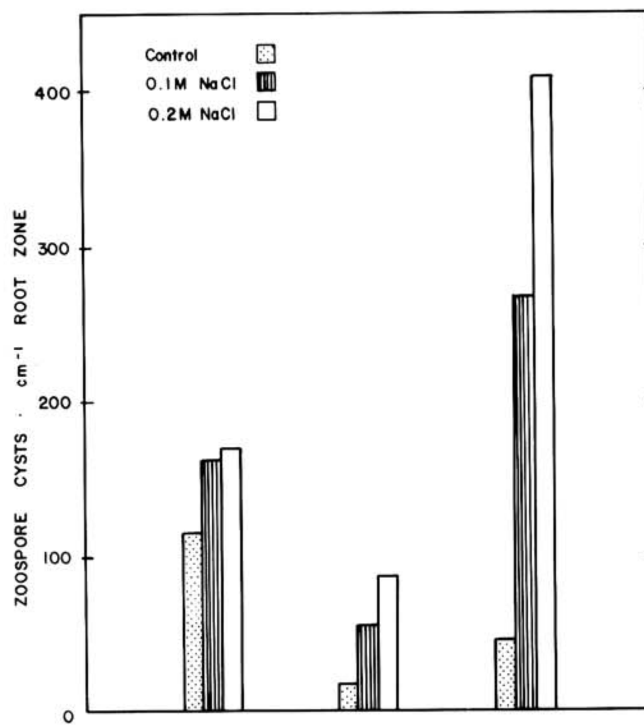

Fig. 4. Numbers of zoospore cysts attached to various regions of chrysanthemum roots 1 hr after exposure to 10^6 motile zoospores of *Phytophthora cryptogea*. Roots had previously been exposed for 24 hr to different concentrations of NaCl in half-strength Hoagland's solution. Counts were based on light microscopic examination as described in text (LSD = 62 at $P = 0.05$).

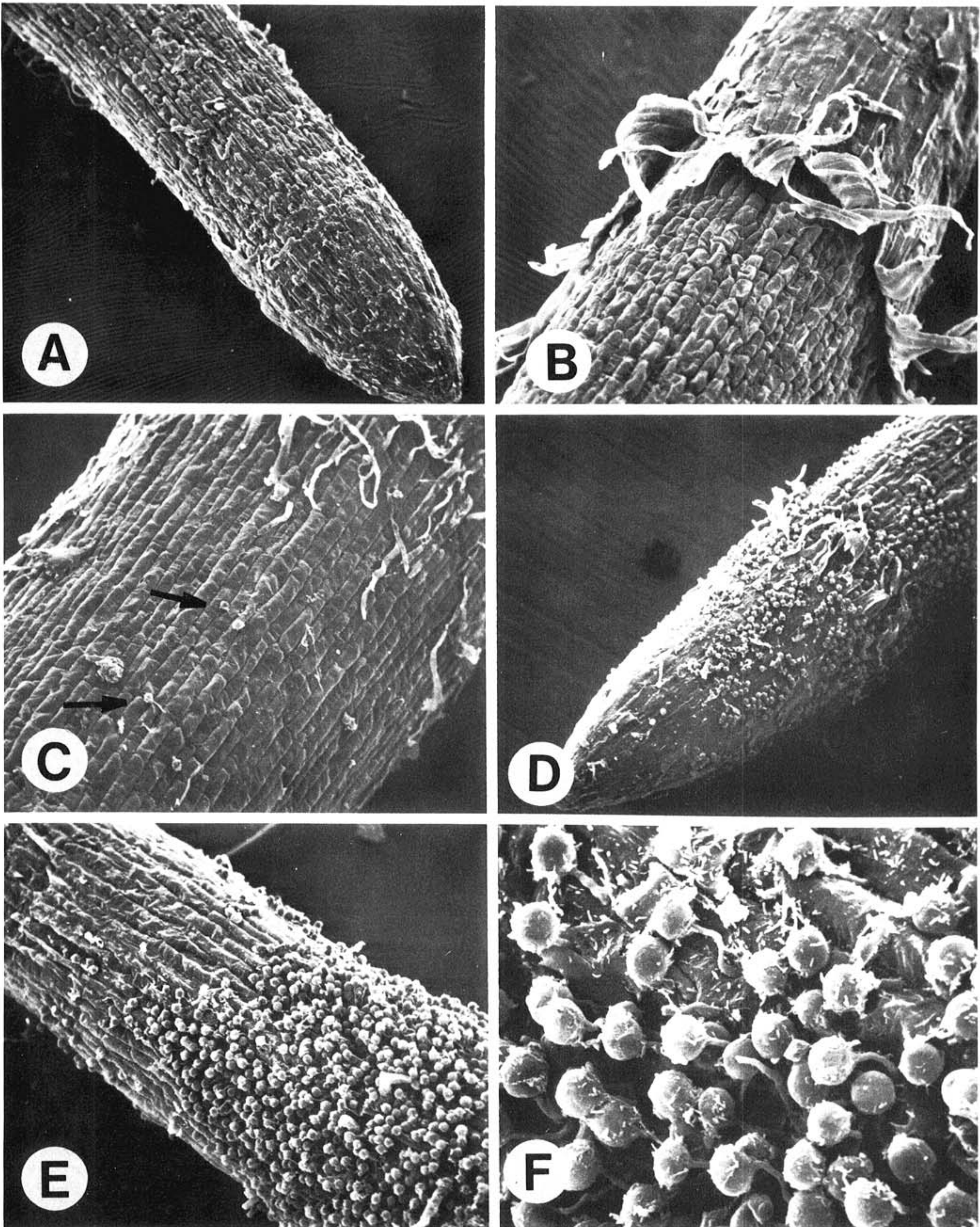

Fig. 5. Scanning electron micrographs of solution-grown chrysanthemum roots. **A,** Uninoculated root grown in half-strength Hoagland's solution (×95) **B,** Uninoculated root exposed for 24 hr to 0.2 M NaCl-amended Hoagland's solution, followed by 30 min in fresh half-strength Hoagland's solution (×190) (apex out of view in upper right corner). **C,** Zoospore cysts attached to unstressed root 30 min after inoculation with motile zoospores of *Phytophthora cryptogea* (×200). **D** and **E,** Zoospore cysts attached to salt-stressed roots 30 min after inoculation with motile zoospores of *P. cryptogea* (×110 and ×180, respectively). **F,** Germinated zoospore cysts on salt-stressed root 30 min after inoculation (×900).

that increasingly severe salinity stresses resulted in increasingly severe disease symptoms (Figs. 2 and 3). In this regard, the results agree generally with those of Beech (1), who found disease in tomato seedlings cased by *R. solani* and *F. oxysporum* f. sp. *lycopersici* to be most severe at the highest level of stress, least severe at the lowest level of stress, and intermediate at the middle levels of stress. Although it is not possible to compare the results of the two studies directly, the levels of stress employed in these pulse-exposure experiments correspond to roughly the lowest, intermediate, and highest levels of stress used by Beech. With only three treatments, it was not possible to determine whether there is a stress threshold below which salinity has no effect on disease development.

In light microscopic and SEM examination of roots, it was clearly evident that each increment increase in salinity stress resulted in a corresponding increase in the number of zoospores attached to roots within 1 hr of inoculation (Fig. 4). In this respect, the results are similar to those of Kuan and Erwin (16) who found that the longer alfalfa roots were held in flooded soil, the more zoospores that subsequently encysted on them. However, while they attributed the increased attraction of zoospores to a release of chemotactically active substances from cracked and ruptured epidermal cells of flooded-stressed roots, no such injury was evident on roots exposed to salinity stress (Fig. 5). While older cells of the root cap appeared to have collapsed or separated from the root following the 0.2 M NaCl treatment, underlying epidermal cells appeared completely intact. Thus, if the greater number of zoospores attached to regions other than the root cap zone of salt-stressed roots resulted from a greater exudation of chemotactically active substances, the release of such substances must be attributed to physiological disturbances or less obvious forms of mechanical injury. There is evidence that high levels of sodium increase the permeability of cell membranes (4), and that extreme NaCl stresses can disrupt cellular organization (21). Effects of salinity on the integrity or permeability of the plasmalemma could result in greater exudation of chemotactically active substances from stressed roots and need to be investigated. However, it is not clear whether the attachment of large numbers of zoospore cysts to salt-stressed roots (Figs. 4 and 5) was simply the result of increased attraction caused by release of chemotactically active substances. In the vigorously aerated solutions, there would have been little opportunity for establishment of chemical gradients, which could explain the failure of zoospores to attach in large numbers to the zone of elongation of roots as has been reported with other examples (16,27). On the other hand, opportunities for random, nondirected contact between the motile zoospores and host roots would have been increased as a result of the mixing and aeration of the solutions. Recent work with corn (14) indicates that adhesion of *P. cinnamomi* zoospores to roots depends on carbohydrate components of root slime, and a stress-induced change in adhesion properties of roots could be as important in disease as any change in their chemotactic properties. Because the germination of chlamydospores of *Fusarium* and the formation of infection cushions of *R. solani* are known to be affected by host exudates (6,26) it is possible that quantitative or qualitative changes in host exudates under osmotic stress also could account for the enhancement of disease observed by Beech (1).

The use of pulsed-exposures to salinity stress in these experiments exposed roots to two episodes of osmotic shock: the first as they were transferred to saline solutions, and the second as they were returned to nonsaline solutions. This raised the question whether the imposition or the relief of salinity stress was of greater importance in predisposition. In one experiment (data not shown), a group of plants was inoculated immediately after imposition of a 0.2-M salinity stress (plasmolytic shock), and another group in the usual manner upon relief of the salinity stress (deplasmolytic shock). While it is not possible to exclude potential salinity effects on the zoospore inoculum in the plasmolytic shock treatment, the deplasmolytic shock appeared far more effective in predisposing roots to infection. Evidence obtained with slowly permeating osmotica (12) indicates that deplasmolysis is more damaging to the metabolism of highly vacuolated root cells than nonvacuolated cells. Although the osmotica used in the experiments described here can be transported readily by cells during osmotic adjustment, a greater sensitivity of highly vacuolated root hair cells to deplasmolytic shock injury might explain the preferential attachment of zoospore cysts to those cells (Fig. 4).

Solution culture techniques allowed the uniform application of carefully controlled stresses to entire root systems. While it is difficult to determine precisely, I believe that the levels of stress employed here are a reasonable approximation of stresses to which roots would be subjected in naturally saline soils. The electrical conductivity of the 0.1 M and 0.2 M solutions was 10.5–11.0 and 21–25 mmho/cm, respectively. A saline soil is defined (22) as one in which the saturation paste extract has an electrical conductivity ≥ 4 mmho/cm. However, while the soil solution at saturation would have an electrical conductivity ≥ 4 mmho/cm, removal of water from saline soil by evaporation and transpiration would greatly concentrate solutes in the remaining soil solution. Thus, between cycles of irrigation, roots in saline soils may be exposed to soil solutions that could approach the levels of salinity used here. Furthermore, immediately following irrigation, the roots could be subjected to deplasmolytic shocks similar to those employed here. The conditions of soil saturation that would generate a deplasmolytic shock, also correspond to conditions considered optimal for the release and motility of zoospores in soil (7,19). Although evidence is limited (19,25, and *unpublished*), levels of salinity similar to those used here do not appear to adversely affect the processes of mycelial growth, sporangium formation, or zoospore release by several species of *Phytophthora*. Thus, it seems likely that root diseases of plants growing in salt-affected soils may be substantially enhanced by salt stress predisposition.

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