Probable Involvement of Thaxtomin A in Pathogenicity of *Streptomyces scabies* on Seedlings

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ABSTRACT

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Inoculation with *Streptomyces scabies* significantly ($P < 0.05$) reduced shoot height of seedlings in 11 of 14 plant species tested. Reduction in shoot height was 53 to 89% in crucifers and 35 to 67% in legumes, whereas effects on monocot seedlings were more variable. Other symptoms on seedlings included necrosis of roots and thickening of roots and shoots. *S. scabies* strain 87-22 was more virulent on seedlings than was strain 84-34. A nonpathogen, *S. lividans* strain TK24, did not consistently reduce the seedling height of any plant species and did not produce growth abnormalities or necrosis. Both supernatants of cultures of *S. scabies* strains and thaxtomin A, a phytotoxin produced by *S. scabies*, reproduced the symptoms of pathogenic strains on seedlings. Concentrations of 50 to 100 µM thaxtomin A greatly reduced the total length of radish seedlings and caused tissue necrosis and death, whereas concentrations of 10 to 25 µM caused shoot and root stunting and thickening. Cross sections of roots and shoots demonstrated that tissue thickening was due to cell hypertrophy, rather than cell hyperplasia. Thaxtomin A is a broad-spectrum phytotoxin and may be responsible for plant pathogenicity in *S. scabies*.

Additional keywords: root diseases, streptomycetes.

Streptomyces scabies is a causal agent of common scab of potato (*Solanum tuberosum* L.). Infection occurs through lenticels on immature, expanding potato tubers (1). Initial symptoms are necrosis around the infection site and usually a developing, unsuberized lenticel (3). Mature lesions may be raised or pitted and are usually corky, accounting for the name of the disease. *S. scabies* also produces lesions on expanding tap roots of radish, beet, turnip, and carrot.

Fibrous roots of seedlings also can be infected by *S. scabies* strains that are pathogenic on potato tubers. The fresh weight of roots of soybean, pea, wheat, radish, and beet seedlings grown in soil agar infested with *S. scabies* was reduced compared with the fresh weight of roots grown in noninfested soil agar (5). Symptoms included necrosis on root tips and reduced development of lateral roots. In that study, Hooker (5) reported that disease symptoms could not be attributed to extracellular toxins. In contrast, Sakai et al. (13) reported that a toxin, extracted from cultures of *Streptomyces* species that were pathogenic on potato and sugar beet, reduced root growth of rice seedlings. This toxin was never identified.

Thaxtomins, a class of phytotoxins produced by strains of *S. scabies* pathogenic on potato tubers, were described by King et al. (10). Thaxtomin A is the most abundant of these unique 4-nitroindol-3-yl-containing 2,5 dioxopiperazines in tuber tissue infected by *S. scabies* (10). Thaxtomin A has been reported to produce cell proliferation, expansion, and necrosis when applied to the immature periderm of potato tubers (11). There was a positive correlation between pathogenicity on potato tubers and the production of thaxtomin A in tuber tissue by 23 strains of *Streptomyces* (9). In addition to *S. scabies*, two other pathogenic species produce thaxtomins in host tissue: *S. acidiscabies*, causal agent of acid scab on potato (12), and *S. ipomoeae*, causal agent of soil pox of sweet potato (8).

Thaxtomins are produced in oatmeal broth (OMB) cultures of *S. scabies* and *S. acidiscabies* during late log and early stationary growth (2,12). *S. ipomoeae* does not produce thaxtomins in OMB or other media (8). The amount of thaxtomin A produced by strains of *S. scabies* in OMB is variable and may be related to the virulence of the strain (12).

The objectives of this research were to evaluate the pathogenicity of *S. scabies* on seedlings of diverse crop species and to test the hypothesis that thaxtomin A is involved in disease development on seedlings. In this report, we confirmed that *S. scabies* is indeed pathogenic on seedlings of a wide variety of monocot and dicot crops. We also demonstrated that the range of symptoms produced by *S. scabies* on seedlings can be reproduced with purified thaxtomin A at concentrations of 10 to 100 µM.

MATERIALS AND METHODS

***Streptomyces* strains.** Strains 84-34 (ATCC 49173) and 87-22 of *S. scabies* and strain TK24 of *S. lividans* were used. Both strains of *S. scabies* were isolated from scab lesions on potato tubers collected in the United States, are pathogenic on potato, and produce thaxtomin A in OMB culture. *S. lividans* strain TK24 is a nonpathogen and does not produce thaxtomin A (12).

Spores of *Streptomyces* were produced by culturing strains on yeast malt extract agar (15). Strains were stored as spore suspensions (7) in 20% glycerol at –20°C or on slants of yeast malt extract agar at 4°C. Inoculum was produced by inoculating OMB (12) with spore suspensions and incubating at 28 to 30°C for 4 to

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6 days on a rotary shaker (160 to 180 rpm). Culture supernatants of OMB cultures of *Streptomyces* strains were prepared by filter sterilization, using microspin filters with a 0.2-μm pore size (Schleicher & Schuell, Inc., Keene, NH).

Thaxtomin A purification. Methods used for production and purification of thaxtomin A were similar to those of Babcock et al. (2) and Loria et al. (12). To obtain large quantities of thaxtomin A, 200 ml of OMB amended with trace elements (7) was inoculated with 200 μl of a concentrated spore suspension of *S. scabies* strain 87-22. The spore suspension was prepared as described by Hopwood et al. (7). To obtain good aeration, the cultures were then incubated at 28°C at 180 rpm for 4 days in a 1-liter Erlenmeyer flask. Cultures were filtered to remove mycelium, and the filtrate was extracted twice with equal volumes of chloroform. The combined chloroform extracts were evaporated to dryness, and the yellow residue was taken up in methanol. Thaxtomin A was purified by reverse-phase thin-layer chromatography on Whatman LKC-18F plates (20 × 20 cm, 250 μM) (Whatman, Inc., Maidstone, England) using an acetone and water (3:2) solvent system. A deep yellow band comigrated with the thaxtomin A standard that was graciously supplied by R. R. King. The yellow band was scraped off and eluted with methanol. Thaxtomin A was further purified by passing the solution through a SEP-PAK PLUS C18 cartridge (Waters Chromatography Div., Milford, MA) in methanol before drying and weighing. Cell-free aqueous solutions of thaxtomin A were used in radish seedling assays.

Seedling assays. In experiment 1, seeds of 14 crop plants were assayed for susceptibility to *S. scabies*. Plant species included crucifers (cauliflower [*Brassica oleracea* L. cv. Snowball 34], radish [*Raphanus sativus* L. cv. Champion], rapeseed [*Brassica napus* L. cv. Cascade], and turnip [*Brassica rapa* L. cv. Purple Top White Globe]), legumes (alfalfa [*Medicago sativa* L. cv. Oneida VR], pea [*Pisum sativum* L. cv. Progress 9], and red clover [*Trifolium pratense* L. cv. Arlington]), grasses (barley [*Hordeum vulgare* L. cv. Lud], corn [*Zea mays* L. cv. Pioneer 3590], rye [*Secale cereale* L. cv. Aroostook], and wheat [*Triticum aestivum* L. cv. Geneva]), and others (beet [*Beta vulgaris* L. cv. Detroit Dark Red], buckwheat [*Fagopyrum esculentum* Moench], and cucumber [*Cucumis sativus* L. cv. Marketmore 76]).

TABLE 1. Effects of oatmeal broth cultures of *Streptomyces scabies* strains 87-22 and 84-34, the nonpathogen *S. lividans* strain TK24, or noninoculated oatmeal broth (control) on shoot height (mm) of seedlings growing in water agar

	Inoculum			
Plant	Control	TK24	84-34	87-22
Crucifers				
Cauliflower	19.6 a[z]	21.0 a	7.6 b	5.4 b
Radish	35.2 ab	36.8 a	16.4 bc	8.8 c
Rapeseed	45.7 a	51.8 a	6.0 b	5.0 b
Turnip	27.6 a	36.2 a	4.8 b	3.8 b
Legumes				
Alfalfa	10.2 a	11.5 a	5.3 b	4.2 b
Pea	41.7 a	29.5 ab	27.0 ab	16.7 b
Red clover	12.8 a	13.8 a	4.8 b	4.2 b
Grasses				
Barley	115.0 a	145.6 a	116.2 a	34.8 b
Corn	56.8 a	71.2 a	58.0 a	50.7 a
Rye	145.8 a	129.6 a	118.4 a	20.4 b
Wheat	165.2 a	143.7 b	106.0 c	75.0 d
Others				
Beet	10.8 a	13.7 a	8.0 a	4.8 a
Buckwheat	51.2 a	61.5 a	18.8 a	17.3 a
Cucumber	35.0 a	32.4 a	25.2 ab	11.2 b

[z] Shoot height, measured as vertical height above the agar, is the mean of five to six replicates from one experiment. Means followed by the same letter within a row are not significantly different, using Tukey's studentized range test (experimentwise $P = 0.05$) for means separation.

Seeds were surface disinfested in a solution of 0.26% NaOCl and 0.1% Tween 20 (Sigma Chemical Co., St. Louis) for 3 min. Seeds were then rinsed twice in sterile, distilled water and germinated on 1.5% water agar for 1 day. Germinated seedlings were selected for uniformity and individually placed in glass culture tubes (25 mm in diameter) containing 10 ml of either 1% water agar or 0.5% Gelrite (Scott Laboratories, Inc., West Warick, RI).

Seedlings were inoculated with either 125 μl of *Streptomyces* cultures, grown for 4 to 6 days as described previously, or a control treatment of noninoculated OMB. Treated seedlings were grown under lights (12-h photoperiod) at 24°C for 6 days. Shoot height was measured as vertical height above the medium, without removing the seedlings from the culture tubes, using five to six replicate seedlings per treatment. Seedlings were also observed for necrosis and abnormalities in root and shoot morphology.

The effects of extracellular compounds produced by *S. scabies* were investigated in experiment 2. Radish and alfalfa seedlings were treated with 4- to 6-day-old OMB cultures of the three *Streptomyces* strains, culture supernatants of those cultures, or noninoculated OMB using the procedure described for experiment 1. Shoot and root length were measured after removing each seedling from its culture tube, using six replicate seedlings per treatment.

The effects of extracellular compounds on disease development were further investigated in experiment 3. Radish seedlings were treated with decreasing concentrations of a 4- to 6-day-old OMB culture of strain 87-22, decreasing concentrations of the culture supernatant, or noninoculated OMB using the procedure described for experiment 1. Concentrations of 1, 0.5, 0.25, 0.125, 0.1, 0.063, 0.031, 0.016, 0.001, and 0 of the culture and the culture supernatant were prepared with sterile, distilled water. Shoot and root length were measured and combined to obtain the total length of each seedling, using five replicate seedlings per treatment.

The effects of purified thaxtomin A on radish were investigated in experiment 4. Radish seedlings were treated with thaxtomin A at concentrations of 0, 1, 10, 25, 50, and 100 μM. Additional treatments included an OMB culture of *S. scabies* strain 87-22, a culture supernatant of that culture, and filtered and unfiltered OMB. The procedure described for experiment 1 was used with several modifications. Radish seeds were surface disinfected in 70% ethanol for 30 s prior to treatment with 0.26% NaOCl solution. Seeds were germinated on sterile, moist filter paper rather than water agar. Culture supernatants and filtered OMB were centrifuged prior to filtering. Shoot and root length were measured and combined to obtain the total length of each seedling, using seven to ten replicate seedlings per treatment. Cross sections of seedlings treated with 0 or 10 μM thaxtomin A were examined microscopically for effects on cellular morphology. Sections were made by hand without fixing or imbedding the tissue.

All experiments were repeated with similar results. Measurements of seedling growth were compared for treatment effects. Data for each plant species were analyzed using SAS (SAS Institute Inc., Cary, NC) analysis of variance or general linear models, and Tukey's studentized range test for means separation, with the experimentwise $P = 0.05$. In experiments 3 and 4, total length of seedlings were regressed with concentrations of the cultures, or thaxtomin A concentration, to calculate the best-fitting line.

RESULTS

Inoculation with one or both strains of *S. scabies* significantly ($P < 0.05$) reduced shoot height for all plant species except corn, beet, and buckwheat (Table 1). Shoot heights were reduced by 53 to 89% in crucifers and by 35 to 67% in legumes by treatment with *S. scabies* strains. Effects of *S. scabies* strains on monocot seedlings were more variable, with growth ranging from 14 to 102% of the control. The shoot height of barley, rye, and wheat seedlings treated with strain 87-22 was significantly less than that

of seedlings treated with strain 84-34. Shoot heights of barley, rye, and cucumber seedlings treated with strain 84-34 did not significantly differ from those treated with noninoculated OMB. The nonpathogen, *S. lividans* strain TK24, significantly ($P < 0.05$) reduced the shoot height of wheat (13%) in one of the experiments (Table 1) compared with the noninoculated control. However, this reduction was not repeatable in another experiment (data not shown).

S. scabies also caused necrosis on roots and thickening of the shoots and roots of some seedlings. Occasionally, corky lesions on the hypocotyl or leaf epinasty were observed. None of these symptoms were evident in seedlings treated with the nonpathogen *S. lividans* or with noninoculated OMB.

Shoot and root length of radish and alfalfa were significantly ($P < 0.05$) reduced by treatment with either whole culture or culture supernatant of *S. scabies* strain 87-22 (Table 2). These treatments were similar in their effects on plant growth, but seedlings treated with whole culture exhibited more necrosis and were often flaccid, whereas hypocotyls of seedlings treated with culture supernatant were generally swollen and turgid. Culture supernatant of strain 84-34 generally reduced plant growth less than did whole culture of that strain. However, treatment with culture supernatant of strain 84-34 did significantly reduce the length of radish shoots and roots compared with the OMB control.

OMB cultures of strain 87-22 reduced seedling growth more than did cell-free culture supernatants at the same concentration (Fig. 1). Total length was reduced by treatment with whole cultures, even at low concentrations. However, the effects of culture supernatant quickly diminished with decreasing concentrations. When total seedling length was regressed with concentration, the slope of the regression line was significantly ($P < 0.01$) greater than 0 for each of the two concentration series.

Treatment with thaxtomin A reduced the growth of radish seedlings (Fig. 2). Seedling growth decreased with increasing thaxtomin A concentrations, and the slope of the regression line was significantly ($P < 0.01$) less than 0 in all experiments. Seedlings treated with 10 µM toxin were always similar in appearance and length to those treated with culture supernatants of strain 87-22 cultures (Figs. 2 and 3). Hypocotyl and root swelling was evident in these treatments. Seedlings treated with 50 to 100 µM thaxtomin A were always similar in appearance to seedlings treated with unfiltered OMB cultures of strain 87-22. Seedlings were necrotic and flaccid in these treatments, and swelling of roots and shoots was not evident. However, seedlings treated with 25 µM thaxtomin A varied in symptom severity. In some experiments, 25 µM thaxtomin A had the same effect as 50 to 100 µM (Fig. 3). In other experiments, 25 µM was similar in effect to 10 µM (Fig. 2). Seedlings treated with ≥10 µM thaxtomin A did not develop root hairs, if root hairs were not present at the time of treatment.

TABLE 2. Effects of oatmeal broth cultures and culture supernatants (CS) of *Streptomyces scabies* strains 87-22 and 84-34, the nonpathogen *S. lividans* strain TK24, or noninoculated oatmeal broth (control) on shoot and root length (mm) of radish and alfalfa seedlings growing on water agar

	Radish		Alfalfa	
Inoculum	Shoot	Root	Shoot	Root
Control	54.7 a[z]	89.7 a	11.5 a	41.7 a
TK24	50.0 a	74.7 ab	10.7 ab	46.8 a
CS TK24	43.7 ab	70.0 ab	6.0 ab	47.5 a
84-34	7.5 c	10.7 c	6.5 ab	18.3 bc
CS 84-34	23.5 bc	51.0 b	6.7 ab	34.7 ab
87-22	7.0 c	6.8 c	4.2 b	7.3 c
CS 87-22	7.8 c	8.2 c	4.5 b	14.7 bc

[z] Shoot and root length are means of six replicates for one experiment. Means followed by the same letter within a column are not significantly different, using Tukey's studentized range test (experimentwise $P = 0.05$) for means separation.

Cross sections through swollen portions of radish shoots and roots treated with 10 µM thaxtomin A showed an increase in diameter of these structures. The average shoot radius of thaxtomin-treated shoots was 894 µm (SE = 83.6, n = 3) compared with 534 µm (SE = 27.5, n = 3) for untreated shoots. This increase in size was due to pronounced cell hypertrophy (Fig. 4). The average radius of the three largest cells on transects taken through cross

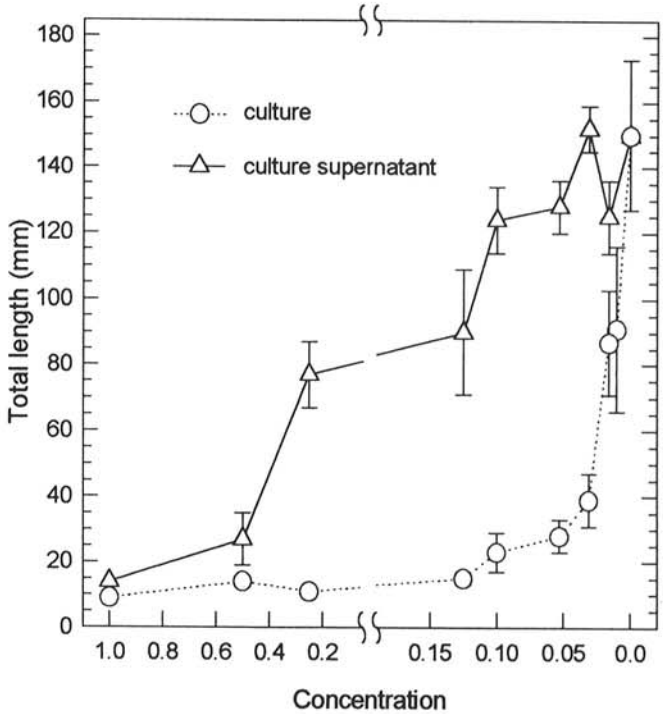

Fig. 1. Total length of radish seedlings treated with decreasing concentrations of an oatmeal broth culture of *Streptomyces scabies* strain 87-22 or culture supernatant of that strain.

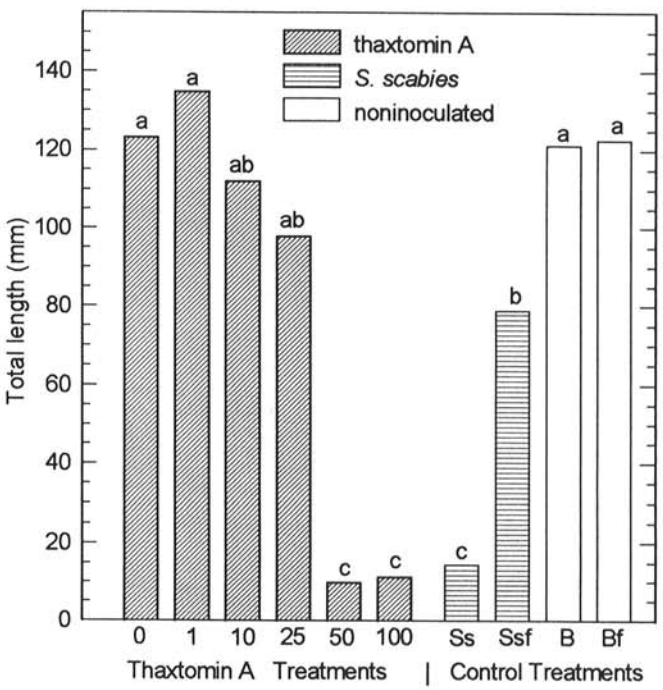

Fig. 2. Total length of radish seedlings treated with purified thaxtomin A at concentrations of 0, 1, 10, 25, 50, and 100 µM or control treatments of an oatmeal broth culture of *Streptomyces scabies* strain 87-22 (Ss), culture supernatant of that culture (Ssf), oatmeal broth (B), or filtered oatmeal broth (Bf).

sections of seedling shoots was 117.0 μm (SE = 10.8, n = 3) for thaxtomin-treated shoots and 56.0 μm (SE = 9.6, n = 2) for untreated shoots. Tissue expansion could not be attributed to an increase in cell numbers. The average cell number for thaxtomin-treated shoots, in transects from outside the endodermis to the epidermis, was 10.0 (SE = 1.0, n = 3) compared with 12.0 cells (SE = 0.0, n = 3) for untreated roots. Similar results were obtained with root cross sections.

DISCUSSION

S. scabies was pathogenic on seedlings of both monocot and dicot species. Macroscopic symptoms included reduction in length and thickening of shoots and roots and necrosis of these structures. These results confirmed and expanded on those of Hooker (5), who first documented seedling pathogenicity by *S. scabies* in 1949. Histological studies by Hooker (5) showed that *S. scabies* colonized cortical and epidermal cells of seedlings.

Hooker (5) demonstrated a correlation between pathogenicity of *Streptomyces* strains on potato tubers and seedlings, suggesting that there is a common mechanism of pathogenicity. Both of the *S. scabies* strains that we tested were pathogenic on both tubers (12) and seedlings of other plant species, although *S. lividans* was not pathogenic on any plant species. We also found differences in virulence between the two *S. scabies* strains on seedlings. Symptoms were usually more severe on seedlings treated with *S. scabies* strain 87-22 than on those treated with strain 84-34. We previously reported (12) that strain 87-22 is also more virulent on potato and produces approximately 25 times more thaxtomin A than does strain 84-34.

We observed differences among crops in the susceptibility of seedlings to *S. scabies*, based on seedling height. Shoot height of beet, buckwheat, and corn was not significantly reduced by either strain of *S. scabies*. However, root growth of these crops was visibly affected (data not shown). Hooker (5) reported a reduction in root growth of corn by *S. scabies,* though he found corn to be less susceptible than wheat. Hanson (4) also reported a reduction in root growth of corn inoculated with *S. scabies*. In this research, seedling height of cucumber was not reduced by *S. scabies* strain 84-34, but was reduced by the more virulent strain 87-22. Hooker (5) found that cucumber was resistant to *S. scabies*. In contrast, Hanson (4) found that fresh root weight of cucumber seedlings was reduced by inoculation with *S. scabies*. These data suggest that differences in results of previous studies may have been because of quantitative differences in thaxtomin production by the strains used. In general, reduction in seedling height by treatment with *S. scabies* was greater on small-seeded crops than on large-seeded crops in our study. These results may reflect the importance of roots in nutrient absorption in those species with little endosperm tissue.

Culture supernatants of *S. scabies* cultures reduced shoot and root lengths of seedlings. In the case of *S. scabies* strain 87-22, culture supernatant was as effective as whole culture in reducing plant growth. However, culture supernatant of strain 84-34 cultures reduced root length less than did whole culture. Differences in the effects of culture supernatants of these two strains may be because of the greater quantity of thaxtomin A produced by strain 87-22 than by strain 84-34 in OMB (12). When culture supernatant of strain 87-22 was diluted, the effects on radish seedlings diminished.

The symptoms produced by thaxtomin A on radish seedlings were not distinguishable from those produced by pathogenic strains of *S. scabies*. Seedlings were affected by thaxtomin A concentrations as low as 10 μM. At high concentrations, roots became necrotic and seedlings died quickly. Concentrations of 25 to 50 μM seemed to be necessary to produce cell death, as evidenced by necrosis. The concentration that resulted in cell death varied somewhat among experiments, possibly because of slight differences in the physiological maturity of the seedlings at the time the experiments were initiated. It appeared that 25 μM was near the threshold concentration necessary to cause cell death in this bioassay (Figs. 2 and 3), since the variability in seedling response occurred at this concentration, but not at 10 or 50 μM. Symptoms were more severe when radish seedlings were inoculated immediately after germination (radicle emergence), than if they were grown for an additional 1 to 2 days (data not shown). If seedlings did not have root hairs at the time they were treated with thaxtomin A, root hair formation was inhibited (Fig. 4). Hooker (5) also reported suppression of root hair development on seedlings by *S. scabies.*

Hooker (5) demonstrated increased growth of *S. scabies*, but not saprophytic *Streptomyces* strains, around seedling roots growing in agar. He hypothesized that *S. scabies* might be producing a toxin that injured roots and caused nutrients to be released into the medium. However, he could not demonstrate toxin production in aqueous extracts of potato dextrose agar cultures of *S. scabies*. We now know that thaxtomin A production is repressed by glucose (2), explaining Hooker's inability to demonstrate toxin production by *S. scabies.*

In 1984, Sakai et al. (13) reported that a toxin produced in cultures of pathogenic *Streptomyces* reduced root growth of rice seedlings. This toxin, which was extractable in ether, was said to produce hypertrophy of tuber cells. However, data documenting

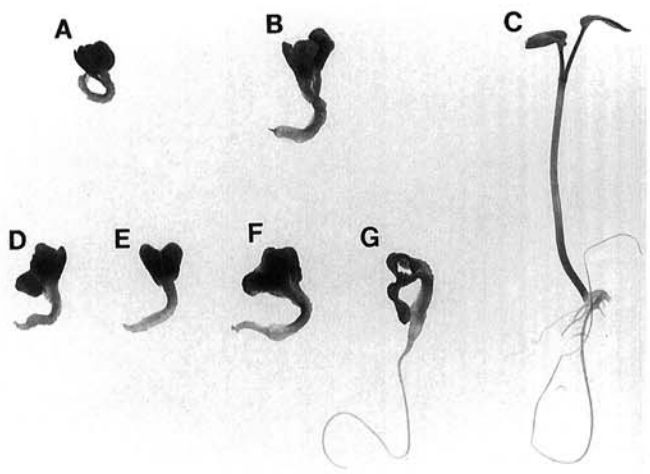

Fig. 3. Symptoms produced on radish seedlings treated with **A,** an oatmeal broth culture of *Streptomyces scabies* strain 87-22; **B,** culture supernatant; or purified thaxtomin A at concentrations of **C,** 0; **D,** 100; **E,** 50; **F,** 25; or **G,** 10 μM.

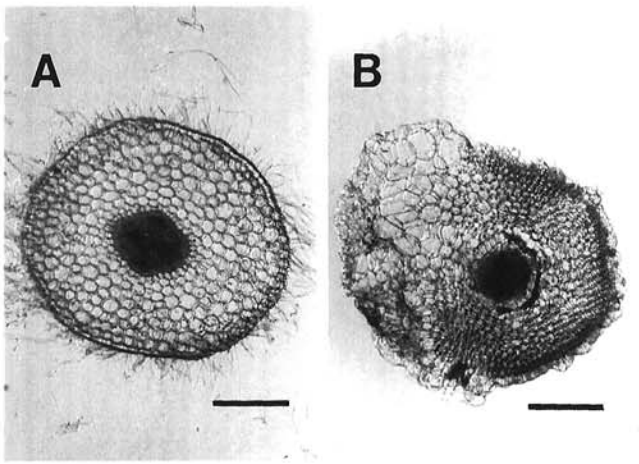

Fig. 4. Cross sections of roots of radish seedlings treated with thaxtomin A at concentrations of **A,** 0 or **B,** 10 μM. Scale bar is **A,** 500 μm and **B,** 450 μm.

this effect were not included in the manuscript. This toxin was never identified or characterized, but thaxtomins are soluble in nonpolar solvents such as ether.

Lesions produced by *S. scabies* on potato tubers range from erumpent (slightly raised) to deeply pitted. We believe that lesion type may be partially determined by the concentration of thaxtomin A, and probably other members of the thaxtomin family (8), at the infection site. Lawrence et al. (11) reported that thaxtomin A at concentrations of 10^{-5} to 10^{-6} M produced tissue expansion on potato minitubers, suggesting that erumpent lesions may be produced when the tubers are exposed to low concentrations of the toxin. Cell death, ultimately resulting in a pitted lesion, may be the result of high concentrations of thaxtomin A at the infection site. *S. scabies* strain 87-22, which was isolated from a pitted lesion, produces more toxin and more necrosis of minitubers than does strain 84-34, which was isolated from an erumpent lesion (12). We have observed cell necrosis and collapse, as well as cell hypertrophy, around infection sites of *S. scabies* on young, rapidly expanding tubers (R. Loria and R. Bukhalid, *unpublished data*).

Although reduction in the marketability of potato tubers is the major economic impact of common scab, *S. scabies* appears to have broader pathogenic capabilities. We assessed the virulence of *S. scabies* on seedlings growing in culture media. However, Hooker and Kent (6) reported that radish seedlings were unable to survive in peat soil infested with *S. scabies*, indicating virulence in a soil environment. Furthermore, unidentified species of *Streptomyces*, reported to cause russet (netted) scab of potato, also reduced growth of fibrous roots of potato (14). *S. ipomoeae* produces thaxtomins (8) and infects both fibrous and tap roots of sweet potato. Although other species of *Streptomyces* have not been widely reported as root pathogens, actinomycete species may have a role in apple replant disease (16). Such evidence suggests that pathogenicity on roots may be present in other actinomycete species.

The identification of thaxtomin A and other members of this family of phytotoxins was a breakthrough in our understanding of plant pathogenicity in the genus *Streptomyces*. Correlation of toxin production and pathogenicity (8,9) suggests, but does not prove, that thaxtomin production is required for pathogenicity on potato. Based on data presented here, it appears that thaxtomin A is a nonspecific phytotoxin that is involved in disease development on seedlings of many plant species. These data also suggest that thaxtomins may interact with a universal target in plant cells. Specifically, the symptom of cell hypertrophy is consistent with a direct or indirect effect on the plant cytoskeleton.

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