Population Dynamics of *Streptomyces scabies* and Other Actinomycetes as Related to Common Scab of Potato

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ABSTRACT

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Effects of two potato cultivars on population dynamics of *Streptomyces scabies*, causal agent of common potato scab, and other actinomycetes were compared during 1985, 1986, and 1987. Population densities of total and melanin-producing actinomycetes were monitored in plots planted to the scab-susceptible cultivar Chippewa or the resistant cultivar Superior, and in fallow control plots. Colonies of *S. scabies* were identified by production of melanin, gray aerial mycelia, and spiral spore chains. Fewer than 6% of the isolates of *S. scabies* tested were pathogenic. Populations of actinomycetes in soils planted to potato, in potato rhizospheres, and on tuber surfaces generally increased during each growing season, but populations in fallow soil remained constant or decreased. Populations of total actinomycetes and *S. scabies* were greater on the surfaces of Chippewa than Superior tubers ($P \leq 0.05$), but populations in soil and the rhizosphere did not differ between cultivars. Scab severity was correlated with the population densities of total actinomycetes recovered from soil at 52 and 153 days after planting in 1986 and from the rhizosphere 88 days after planting in 1987, and with relative numbers of *S. scabies* on the tuber surfaces at harvest in 1987.

Common scab of potato (*Solanum tuberosum* L.) is induced by the actinomycete *Streptomyces scabies* (Thaxter) Waksman et Henrici. This disease is present in all potato-growing areas of North America and Europe. Although several other *Streptomyces* spp. can induce potato scab, *S. scabies* is the most important pathogen (4,12,16). Characteristics of *S. scabies* include production of melanoid pigments (often referred to as melanin), ash-gray aerial mycelia, and spiral chains of spores. These characteristics are based on descriptions of isolates from many locations (4,8,11,17,19,24). Combined with information on utilization of eight diagnostic carbon sources and spore-surface morphology, these characteristics distinguish *S. scabies* from other *Streptomyces* spp. (8,19,21). As pathogenicity is not a taxonomic criterion for prokaryotes at the species level (7,21), both pathogenic and nonpathogenic isolates have been included in the species *S. scabies* (25,26).

There is little information in the literature on the ecology of *S. scabies* or other actinomycetes in the potato rhizosphere or on tuber surfaces. *S. scabies* has been detected on the roots of potatoes grown in infested soil (25), but changes in the population density, relative to the nonrhizosphere population, were not reported. Actinomycetes colonize the lenticels of developing field-grown potato tubers (1). The density of actinomycetes in soil adhering to scabby potato tubers was 12–37 times greater than the population density in the surrounding soil (20). The population density of *S. scabies* was not determined in either study, however. Neither changes in the population of *S. scabies* in the rhizosphere or on the tuber surfaces during the growing season nor the role of a rhizosphere or tuber population of the pathogen in disease development has been examined.

As no selective method for isolating pathogenic *S. scabies* has been developed, it is difficult to monitor inoculum density. Labruyère (17) estimated inoculum density by isolating this species from field soil and testing the pathogenicity of isolates on greenhouse-grown potatoes. He found a positive relationship between inoculum density of *S. scabies* in the soil and scab incidence on potato cultivar Patrones.

It may be possible to use the population densities of total or melanin-producing actinomycetes, which are more easily measured, to predict incidence or severity of scab. In the Netherlands, numbers of melanin-producing actinomycetes were correlated weakly with scab incidence and severity on the susceptible cultivar Bintje in field experiments (17). In previous work in North America, the population density of total actinomycetes in soil had not been correlated with scab severity on the cultivars Bliss Triumph (10) or Cobbler (13). The effects of cultivar resistance on actinomycete populations have not been examined.

The objectives of this study were to monitor the changes in the population densities of *S. scabies* and other actinomycetes in soil, the rhizosphere, and on tuber surfaces during the potato growing season; to learn if host resistance to scab affects these populations; and to evaluate relationships between actinomycete

population densities and scab incidence and severity. A preliminary report has been published (15).

MATERIALS AND METHODS

Cultural conditions. Populations of *S. scabies* and other actinomycetes were monitored in field plots at Riverhead, NY, during three consecutive growing seasons. The soil was a Riverhaven sandy loam with the following characteristics (measured in 1985): a bulk density of 1.32 g/cc; organic matter, 2.6%; exchange acidity, 12.0 meq/100 g (pH 8.0); P, 28.4 μg/g; K, 121 μg/g; Mg, 64 μg/g; and C, 189 μg/g. In 1985, field plots were established on land that previously had been cropped to crucifers for 2 yr. In 1986 and 1987, plots were established on land that previously had been cropped to sweet corn for 2 yr. All areas had a rye cover crop during winter.

Plots were established on 23 May 1985, 25 April 1986, and 11 May 1987, and planted to the potato cultivars Chippewa (susceptible to common scab) and Superior (resistant to scab) or left fallow. Whole seed tubers (average weight 42.5 g) were sorted, and those with scab lesions were discarded. Remaining tubers were washed, surface-disinfested with 0.5% sodium hypochlorite for 15 min, and dusted with mancozeb (8% dust formulation) to preclude introducing *S. scabies* on the tubers. Seed tubers were planted 23 cm apart in rows spaced 86 cm apart. A randomized complete block design with eight replications was used. Plots were 7.5 m long and 10 rows wide, with 1.5 and 3.4 m between individual plots at ends of rows and parallel to rows, respectively. Cultural practices were consistent with commercial practices on Long Island, except that irrigation was reduced to promote scab development. Irrigation (2.5 cm/ha) was applied only in 1987, on 22 June and 22 July. Fallow plots received herbicide, and rows were hilled as in the potato plots, but no fertilizer or insecticide was applied. Ground limestone was applied before planting in 1985 and 1986 (6.7 and 2.2 t/ha, respectively); hydrated lime (9.0 t/ha) was used in 1987. Soil pH (measured in 0.01 M $CaCl_2$ and adjusted by adding 0.6 pH unit) was 5.5 in 1985, 4.8 in 1986, and 7.0 in 1987. Potato vines were killed 2 wk before all tubers >3.5 cm in diameter were harvested from the center 4.5 m of one of the center two rows of each potato plot. Tubers were washed and scab severity was assessed visually by estimating the percentage (0 to 100, inclusive) of the surface covered by scab lesions. Incidence (percentage of tubers scabbed) was determined after rating.

Sampling. Soil samples were collected from plots 0, 28, 42, 63, 82, and 119 days after planting in 1985; harvest was on 18 September, 118 days after planting. In 1986, soil samples were collected 0, 52, 74, 98, 118, 136 (8 September, harvest), and 153 days after planting. Soil was sampled on 0, 70, and 117 days after planting in 1987; plots were harvested on 15 September, 127 days after planting. Thirty soil cores (2 × 15 cm) were collected from the center six rows of each plot (five cores per row), 10 cm from the stems of plants in the potato plots. Composite soil samples (about 3 kg) were screened through 8-mm mesh, mixed, and divided in half three times. The remaining soil (one-eighth of the original volume) was screened through 2-mm mesh. Four plants in each plot were dug and roots were collected 52, 74, 98, and 118 days after planting in 1986, and 26, 88, and 112 days after planting in 1987. Second-order roots were selected from each of the four plants to form one representative sample (10 g fresh weight) for each plot. A total of 10 progeny tubers was collected from four plants in each plot at 52, 74, 98, 118, and 136 days after planting in 1986, and at 50, 70, 88, and 127 days after planting in 1987. Soil and all plant materials were dried at room temperature for about 12 hr before assaying to reduce the numbers of bacterial contaminants on the dilution plates (28).

Population densities of actinomycetes were estimated by dilution-plating techniques. One sample of soil, roots, or tubers was assayed per plot. Soil (100 g) was blended in 1 L of sterile distilled water for 2 min (17). Serial tenfold dilutions were made, and 0.5 or 1.0 ml of the 10^{-4} and 10^{-5} dilutions was added to 15 ml of molten (55 C) agar medium. Six plates of glycerol-asparagine agar (21), with 0.5% tyrosine (17) and 100 mg/L of nystatin, 100 mg/L of cycloheximide, 10 mg/L of polymixin B sulfate, and 1 mg/L of penicillin (sodium salt) (6) were prepared per sample. For rhizosphere assays, roots were washed in 100 ml of phosphate buffer (pH 7.2) for 30 min on a wrist-action shaker. Serial tenfold dilutions were made, and aliquots (0.5 or 1.0 ml) of the 10^{-3}, 10^{-4}, or 10^{-5} dilution of the wash were plated. For tuber-surface assays, one disk (1 cm diameter) was cut from a randomly selected area of each of 10 tubers to form one composite sample. The 10 disks were washed 30 min in phosphate buffer (50 ml). Aliquots (0.5 or 1.0 ml) of the 10^{-2} and 10^{-3} dilution were plated. All plates were held at 28 C.

To determine if *S. scabies* and other actinomycetes were more abundant in the corky tissue of the scab lesions than on the healthy periderm, population densities on Chippewa tubers were estimated. One disk (1 cm diameter) was cut from a healthy area (i.e., no visible lesions) of each of 10 tubers, and one disk was cut from a diseased area on the same tubers. Disks in the scabby sample averaged 50% scab severity. Populations were assayed as described for the tuber surface.

Identification of streptomycetes. *S. scabies* produces melanoid pigments on agar media containing tyrosine (4,8,11,17). After 4–5 days of growth, colonies producing melanoid pigments, i.e., those that were tyrosinase-positive, were counted; after 9–10 days, total actinomycetes were counted. Melanoid pigment production was used as a preliminary criterion for selecting streptomycetes for study. In 1986 and 1987, ≤30 melanin-producing colonies were selected from the dilution plates for each plot and transferred to inorganic salts-starch agar (ISP Medium 4, Difco Laboratories, Detroit, MI). After 14 days' growth at 30 C, the number of ash-gray colonies with spiral spore chains characteristic of *S. scabies* was determined. Representative isolates were maintained on slants of yeast extract-malt extract agar (ISP2) (ISP Medium 2, Difco).

A subsample of isolates of *S. scabies* was tested in the greenhouse to identify the proportion of isolates that were pathogenic. To produce inoculum, cultures were grown on ISP2 slants at 30 C for 2 wk. Spores and mycelia were gently scraped from the agar surface and suspended in 200 ml of sterile distilled water. Infection of tubers produced on stem cuttings of the scab-susceptible potato cultivar Chippewa was used as the criterion for pathogenicity (18). Stem cuttings were taken from stock plants that had been induced to form tubers by maintaining them under a 10-hr photoperiod for 1 wk. Both rooted and nonrooted cuttings with tubers were planted in steamed quartz sand in Cone-tainers (Ray Leach Cone-tainer Nursery, Canby, OR) and inoculated with 15 ml of a spore suspension with $>10^4$ cfu/ml. Five or six replicates were used per isolate. An isolate of *S. scabies* known to be pathogenic was used as the positive control in all tests, and cuttings inoculated with sterile distilled water served as negative controls. Cuttings were fertilized with Hoagland's solution weekly. In two tests, sprouted, greenhouse-grown Chippewa tubers were inoculated at planting with 30 ml of spore suspension. Tubers on cuttings were rated for scab severity 3 wk after inoculation; tubers produced by whole plants were rated 8–10 wk after inoculation.

ISP procedures (21) were used to test a subsample of isolates of *S. scabies* for carbon utilization (7). Briefly, isolates were grown in tryptone-yeast extract broth (ISP Medium 1, Difco) for 48 hr. Mycelia were washed twice by centrifugation at 4,600 *g* and resuspended in sterile distilled water; 0.05 ml of the suspension was plated on carbon-utilization media. Carbon sources tested included L-arabinose, D-fructose, D-mannitol, raffinose, rhamnose, sucrose, and D-xylose; D-glucose and no carbon served as positive and negative controls, respectively. Plates were held at 28 C for 10 days, and growth was rated according to the degree of carbon utlilization: strongly positive, positive, doubtful, or negative.

Data analysis. Because the same plots were sampled throughout the growing season, a repeated measures analysis was used to examine changes in the populations over time. PROC GLM of SAS (Statistical Analysis System, SAS Institute, Inc., Cary, NC),

with the Repeated Option, was used to construct orthogonal polynomials for the sampling dates (expressed as days after planting) and for analysis of variance. Single-degree-of-freedom orthogonal contrasts were used to compare treatments. To stabilize the variance, all counts (except those of total actinomycetes in the soil in 1985) were transformed by computing the base ten logarithm. Scab incidence and average scab severity for each plot were regressed against the population densities from the different environments with PROC GLM to determine inoculum density-disease relationships. Regressions with scab incidence were weighted according to the inverse of the numbers of tubers examined in each plot (23). The arcsin-square root transformation was used for the disease data and for the proportions of *S. scabies* among the melanin-producing colonies examined for each plot. Use of the base ten logarithm of counts of *S. scabies* per gram of soil or square centimeter tuber in analyses of variance produced nonrandom patterns of residuals. Main effects of treatments and interactions were judged significant at $P \leq 0.05$ and $P \leq 0.10$, respectively, unless indicated otherwise.

RESULTS

Population dynamics of *S. scabies*. Population densities of *S. scabies*, as a proportion of the melanin-producing actinomycetes, did not change in the soil (1.9 ± 0.4% [SE]) or on tuber surfaces (3.0 ± 1.1%) in 1986, but increased in the rhizosphere (Fig. 1). In 1987, the proportion of *S. scabies* in the soil was significantly lower at 70 days after planting (4.3 ± 1.8%) than at planting (7.6 ± 1.8%) or harvest (7.8 ± 2.3%). The proportions changed linearly ($P \leq 0.05$) on the tuber surfaces (Fig. 1), but did not change significantly in the rhizosphere (29.0 ± 4.5%). In 1986, the proportion of *S. scabies* among all melanin-producing actinomycetes was significantly greater in the rhizosphere than in soil or on tuber surfaces between 74 and 118 days after planting. The number of colonies of *S. scabies* increased almost sixfold in 1987 over 1986, with the greatest proportion recovered from the tuber surfaces.

Evaluation of isolates of *S. scabies*. Isolates of *S. scabies* collected in 1986 (28% of the total number of colonies observed) were tested in the greenhouse for pathogenicity to potato. Only two of the 61 isolates tested were pathogenic. Both pathogenic isolates had been recovered at 118 days after planting: one from the rhizosphere and one from a tuber surface. A total of 69 isolates collected in 1987 (5.5% of the total number of colonies) were tested for pathogenicity: four isolates (of 25) from the tuber surfaces were pathogenic. All four were recovered at 88 days after planting. Isolates that did not resemble *S. scabies* were not tested.

Of the *S. scabies* that were tested for carbon utilization in 1986, eight of 13 soil isolates, nine of 13 rhizosphere isolates, and all six isolates from tuber surfaces utilized all seven carbon sources, a pattern characteristic of *S. scabies* (8,19). Both pathogenic isolates had complete carbon-utilization patterns. Isolates with incomplete carbon-utilization patterns were unable to utilize mannitol, or utilized xylose or both mannitol and xylose poorly. Eight of these nine isolates were tested for pathogenicity; all were nonpathogenic. The number of isolates with incomplete carbon-utilization patterns did not differ significantly between the soil and the rhizosphere (chi-square analysis, $P \geq 0.10$). All isolates tested for carbon utilization in 1987 (five soil, seven rhizosphere, and 26 tuber-surface isolates) utilized all seven carbon sources.

Effects of potato production and host resistance on actinomycetes. Population densities of total actinomycetes in soil from the potato plots were significantly greater than those from fallow plots in all 3 yr (Figs. 2–4). The difference between densities of melanin-producing actinomycetes from potato plots and fallow plots was highly significant in 1985 ($P < 0.0001$) (Fig. 2), significant in 1986 ($P \leq 0.05$) (Fig. 3), and not significant in 1987 ($P > 0.10$)

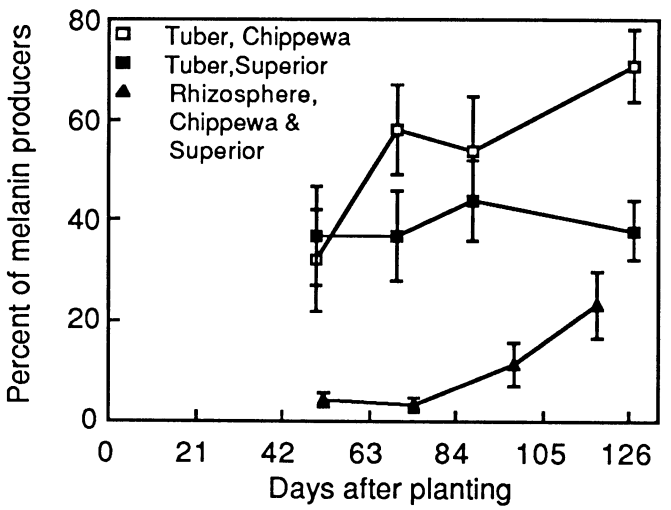

Fig. 1. Population densities of *Streptomyces scabies* as percent of melanin-producing actinomycetes recovered from the rhizospheres of Chippewa and Superior potatoes in field plots during 1986 and from the tuber surfaces during 1987. Colonies of *S. scabies* were identified by ash-gray aerial mycelia and spiral spore chains. Vertical bars give standard errors of mean proportions.

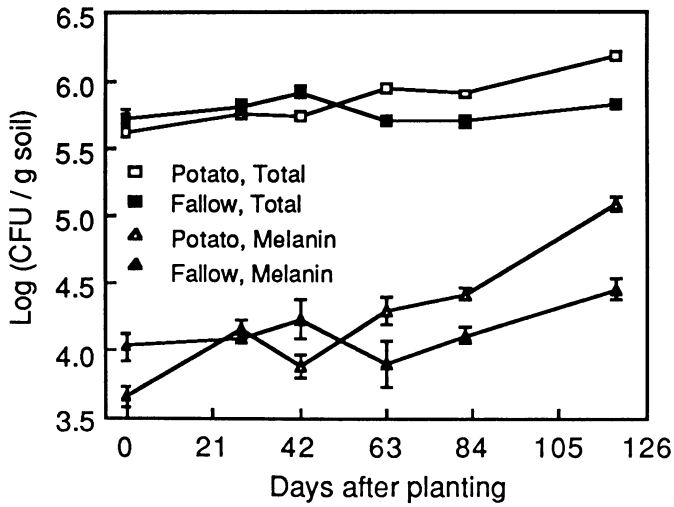

Fig. 2. Population densities of total and melanin-producing actinomycetes recovered from soil in field plots planted to potatoes or in fallow plots during 1985. Vertical bars give standard errors of $\log_{10}$-transformed mean counts.

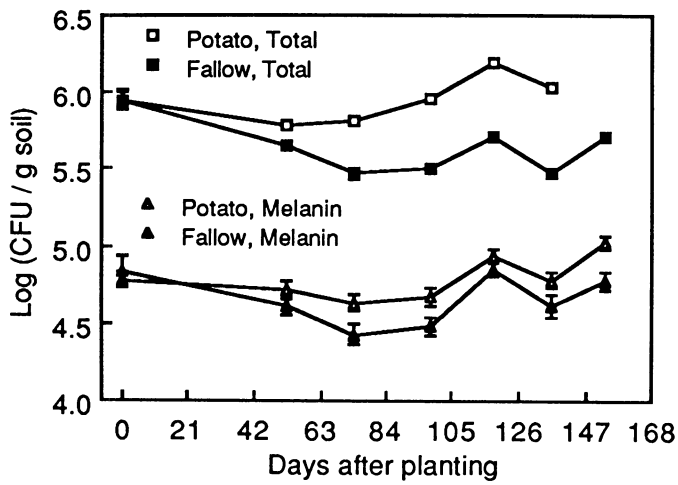

Fig. 3. Population densities of total and melanin-producing actinomycetes recovered from soil in field plots planted to potatoes or in fallow plots during 1986. Vertical bars give standard errors of $\log_{10}$-transformed mean counts.

(Fig. 4). No differences between the two potato cultivars were detected for actinomycete populations in the soil or the rhizosphere.

In 1986, population densities of total actinomycetes on Chippewa tubers consistently were greater than those on Superior tubers (Fig. 5); the time linear × cultivar interaction was significant ($P \leq 0.05$). Population densities of melanin-producing actinomycetes also were greater on Chippewa than on Superior at two of the five samplings (Fig. 5). The average proportion of *S. scabies* was significantly greater for Chippewa (0.061) than for Superior (0.029) tubers. Averaged over the 1987 season, population densities of total actinomycetes on Chippewa tubers were again significantly greater than those on Superior tubers (Fig. 6). The time linear × cultivar interaction was significant for population densities of melanin-producing actinomycetes (Fig. 6) and *S. scabies* (Fig. 1). More total actinomycetes were associated with scabby tissue (9.2 [±2.2] × 10^4 cfu/cm^2 tuber) than with healthy tissue (2.4 [±0.4] × 10^4) on Chippewa tubers ($P \leq 0.0001$). There also were ×10 as many melanin-producing actinomycetes on scabby tissue, and *S. scabies* accounted for 97% (±1.3) of the melanin-producing colonies recovered from scabby tissue, but only 48% (±7.9) of those from healthy periderm.

Population dynamics of actinomycetes. Approximately 10% of the total actinomycetes in soil, the rhizosphere, and on tuber surfaces produced melanin. Population densities of both total and melanin-producing actinomycetes in the soil (Fig. 4) and in the rhizosphere (Fig. 7) were greater in 1987 than in 1985 (Fig. 2) and 1986 (Fig. 3). Densities on the tuber surfaces were greater in 1987 (Fig. 6) compared with 1986 (Fig. 5) only at the final sampling date.

Population densities of total and melanin-producing actinomycetes in the nonrhizosphere, nontuber surface soil in potato plots increased during all 3 yr. In the soil during 1987, densities of total actinomycetes increased in the potato plots but decreased in the fallow plots (Fig. 4). In general, total and melanin-producing actinomycetes increased in the rhizosphere (Fig. 7) and on the tuber surfaces (Figs. 5 and 6) in both years. Densities of both populations increased on tuber surfaces until 98 days after planting in 1986 (Fig. 5); thereafter, densities decreased. In 1987, there were large increases in the densities of both total and melanin-producing actinomycetes on the tuber surfaces during the growing season (Fig. 6).

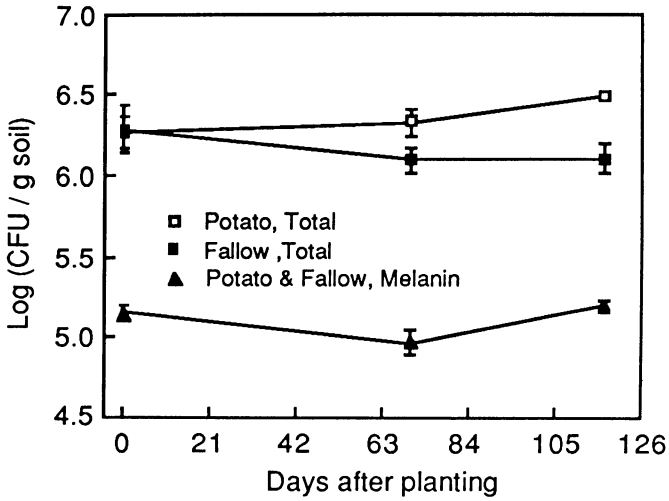

Fig. 4. Population densities of total and melanin-producing actinomycetes recovered from soil in field plots planted to potatoes or in fallow plots during 1987. Vertical bars give standard errors of $\log_{10}$-transformed mean counts.

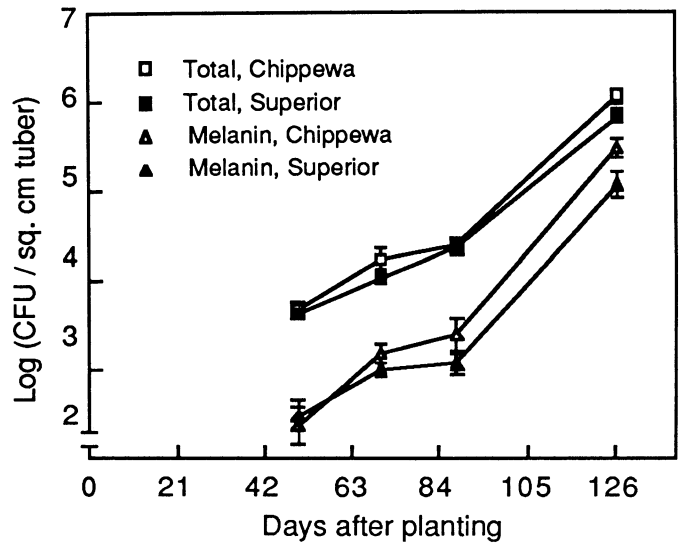

Fig. 6. Population densities of total and melanin-producing actinomycetes recovered from the tuber surfaces of Chippewa and Superior potatoes grown in field plots during 1987. Vertical bars give standard errors of $\log_{10}$-transformed mean counts.

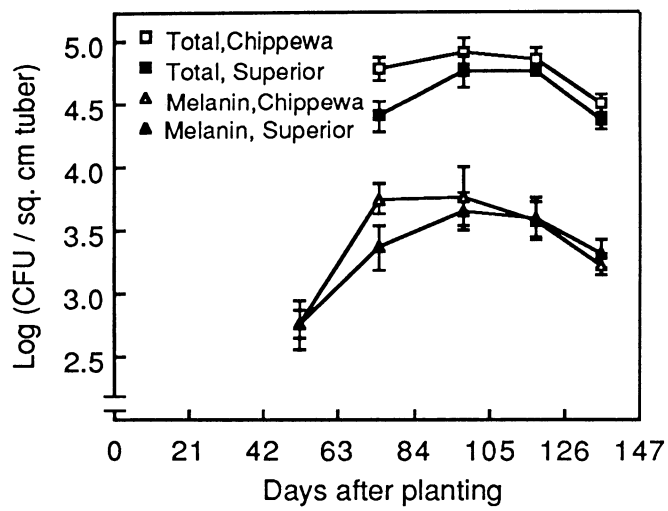

Fig. 5. Population densities of total and melanin-producing actinomycetes recovered from tuber surfaces of Chippewa and Superior potatoes grown in field plots during 1986. Vertical bars give standard errors of $\log_{10}$-transformed mean counts.

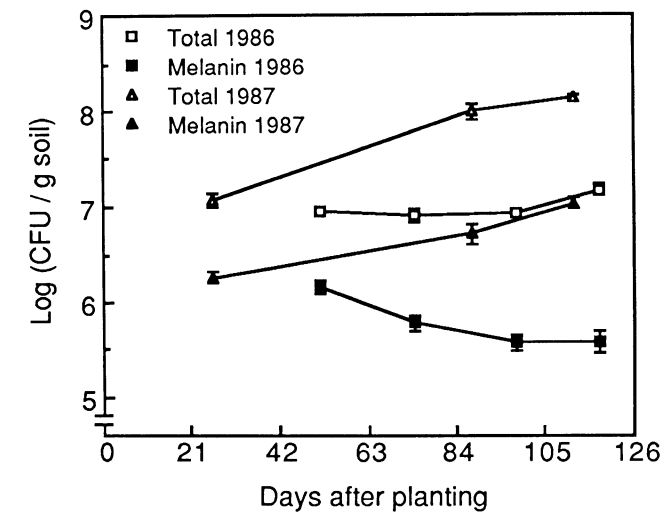

Fig. 7. Population densities of total and melanin-producing actinomycetes recovered from the rhizospheres of potatoes grown in field plots during 1986 and 1987. Vertical bars give standard errors of $\log_{10}$-transformed mean counts.

Changes in population densities of actinomycetes in the soil, in the rhizosphere, and on tuber surfaces were relatively independent of each other. In general, population densities in the rhizosphere and on the tuber surfaces were not correlated with those in the soil at the same sampling time or with those at planting; neither were population densities on tuber surfaces correlated with those in the rhizosphere at the same sampling. The only exception was a highly significant correlation ($P \leq 0.01$) between the population densities of total actinomycetes in the rhizosphere at 88 days after planting and those in the soil at planting in 1987.

Disease incidence and severity. Scab incidence in 1985 for cultivar Superior averaged 0.5% (±0.3), whereas 70% (±5.1) of the Chippewa tubers were scabbed. In 1986, scab incidence was 12% (±5.0) for Superior, and 57% (±8.9) for Chippewa. In 1987, scab incidence was 3% (±1.2) for Superior and 53% (±7.0) for Chippewa. Average scab severity was low in all 3 yr. In 1985 it was 0.1% (±0.1) for Superior and 2% (±0.3) for Chippewa; in 1986 it was 0.3% (±0.2) for Superior and 2.7% (±0.8) for Chippewa; in 1987 it was 0.03% (±0.01) for Superior and 1.8% (±0.4) for Chippewa. There were no significant differences among years for either scab severity or incidence. Average soil pH within the range 4.7–7.5 had no significant effect on disease, based on analysis of variance.

Linear regressions of scab incidence and severity on population density were calculated separately for 73 population determinations: six from 1985, 37 from 1986, and 30 from 1987. Nine population densities were significantly correlated with incidence or severity (Table 1), with the model sequence block|cultivar|population parameter|cultivar × population ($P \leq 0.02$ for overall model sums of squares, $R^2 \geq 0.90$). Significant effects of cultivar indicated separate intercepts were necessary for the two cultivars. The population × cultivar interaction was significant in the models with rhizosphere and tuber-surface populations in 1987. For these regressions, separate intercepts and slopes were necessary for the two cultivars.

DISCUSSION

The percentage of pathogenic *S. scabies* among the actinomycetes morphologically and physiologically resembling *S. scabies* was relatively low (3.3–5.8%). Low percentages of pathogenic isolates have been reported previously. The percentage of pathogenic *S. scabies* among soil isolates resembling *S. scabies* based on the ISP criteria ranged from 0 to 33% in the Netherlands (25). Between 4 and 22% of the melanin-producing actinomycetes from soil in potato plots were pathogenic *S. scabies* (17). In Hungary, *S. scabies* comprised 1.6% (3/190) of the streptomycete isolates recovered from soil previously cropped to potato (9).

Use of the ISP criteria, either in their original form (21) or modified according to the method of Elesawy and Szabó (9), was impractical for the identification of *S. scabies* in an ecological study involving many samplings and isolates. The identification method of Williams, Davies, and Hall (27), involving colors of spores, colony underside, and any pigment produced in the medium, and production of melanin, was not sensitive enough for detection of *S. scabies*. This method was modified by excluding the colors of the colony underside (which is not distinctive [22] for *S. scabies*) and pigment other than melanoid pigment (none is produced), and substituting spore-chain type. A distinction was made between spiral spore chains characteristic of *S. scabies* and other types of spiral chains, e.g., tightly coiled spirals. The resultant population of streptomycetes was relatively uniform for utilization of the seven diagnostic carbon sources tested. Nevertheless, only two of 61 isolates tested in 1986 and four of 69 tested in 1987 were pathogenic to potato. The only ISP criterion not examined was spore surface, which is smooth for *S. scabies*. However, Elesawy and Szabó (9) found that only one isolate from the group of those resembling *S. scabies* (based on color of sporulating aerial mycelia, melanin production, spore chain morphology, and carbon utilization) had nonsmooth spores, indicating that spore surface is not a useful criterion in distinguishing *S. scabies* from streptomycetes that are morphologically and physiologically similar.

Although actinomycetes have been studied since the early 1900s (5), there have been few reports on population dynamics of these organisms. Most studies have focused on actinomycete populations present at one or a few times during the sampling period. The densities of most actinomycete populations associated with potatoes increased during the growing season in this study. In previous studies conducted in the Netherlands, seasonal increases in the population densities of total or melanin-producing actinomycetes in soils cropped to potato also were observed (17,25).

The maximum density of total actinomycetes recovered from soil planted to potato in New York was 1.6×10^6 colony-forming units (cfu)/g of soil in 1985 and 1986 at an average soil pH of 5.1. In 1987, when the soil pH was 7.0, the maximum population density was 4×10^6 cfu/g of soil. These values agree with the maximum population densities for total actinomycetes from potato soils reported in previous studies: 2.5 (17) and 7.5 (25) $\times 10^6$ and 1.4×10^7 (13) cfu/g of soil. Population densities of $1\text{–}5 \times 10^6$ cfu/g of soil were observed for total actinomycetes in fallow soil (14). In New York, the population density in the fallow plots ranged from 5×10^5 in 1986 to 2.6×10^6 cfu/g of soil in 1987.

Rhizosphere population densities of total actinomycetes increased during both seasons. Densities of melanin-producing actinomycetes also increased in 1987. In Idaho, the population density of total actinomycetes decreased on roots between 50 and 85 days after planting (2). In a subsequent year, there was no consistent trend between 29 and 97 days after planting (3). In the Idaho studies, rhizosphere soil was sampled differently than in our study, which could account for the different trends observed.

Differences between the susceptible and resistant potato cultivars clearly were reflected in actinomycete population densities on the tuber surfaces. Population densities, especially of total actinomycetes, were greater for Chippewa than Superior. In England, larger numbers of actinomycetes were isolated more frequently from the periderm of the scab-susceptible cultivar Maris Piper than from the moderately resistant cultivar Pentland Crown in 1 of 2 yr (1). In a greenhouse study, the treatment with the lowest scab incidence also had the lowest density of actinomycetes in the soil adhering to the tubers (20). The increase observed on Chippewa tubers partially was due to reproduction of the actinomycetes in the corky tissue of the scab lesions, since more actinomycetes were recovered from scab lesions on Chippewa than from healthy periderm. The increase of *S. scabies* as a proportion of the melanin-producing population on Chippewa compared with Superior during the 1987 growing season (Fig. 1) may reflect the additional corky tissue present as the lesions expanded over time. Because pathogenic isolates first were recovered from tuber surfaces at 88 days after planting in 1987, they may have originated in lesions on the tubers.

The population densities of total actinomycetes in soil at 52 days after planting in 1986 were correlated positively with both scab incidence and severity (Table 1). The density of total actinomycetes may be an indication of a favorable environment for actinomycete development. The correlation of disease with soil populations early in the growing season could be useful in a predictive model for scab incidence or severity, but additional work is necessary to test this relationship.

The correlation between scab and the total actinomycete population density in soil after harvest in 1986 (153 days after planting) may reflect reproduction by actinomycetes on the tubers. A similar correlation was observed with the proportion of *S. scabies* on tuber surfaces in 1987 at harvest (Fig. 8A). The tuber surface population density-disease relationship most likely is due to reproduction of the actinomycetes in the scab lesions, as discussed previously. Lower densities of actinomycetes on tuber surfaces of the resistant cultivar Superior may help to limit the increase in the soil inoculum density. However, population densities at these two samplings at the end of the season were not correlated with scab severity, suggesting that reproduction

TABLE 1. Correlation of actinomycete population densities with scab severity or incidence

Year	Source	Population	Days after planting	$P > F$-value[a]	
				Severity	Incidence
1986	Soil	Total	52	0.02	0.01
		Total	153	0.05	0.01
	Rhizosphere	Total	52	0.01	ns[c]
		Melanin	52	0.004	ns
		Spiral	74	ns	0.03
		Total	98	ns	0.05
1987	Rhizosphere	Total	26	ns	0.03
		Total	88	0.001[b]	0.003[b]
	Tuber surfaces	Spiral	127	0.06[b]	ns

[a]Probability of a greater F-value for correlations of the specific population density with scab severity or incidence, measured at harvest.
[b]The population density × cultivar interaction was significant for these correlations.
[c]Not significant ($P \geq 0.05$).

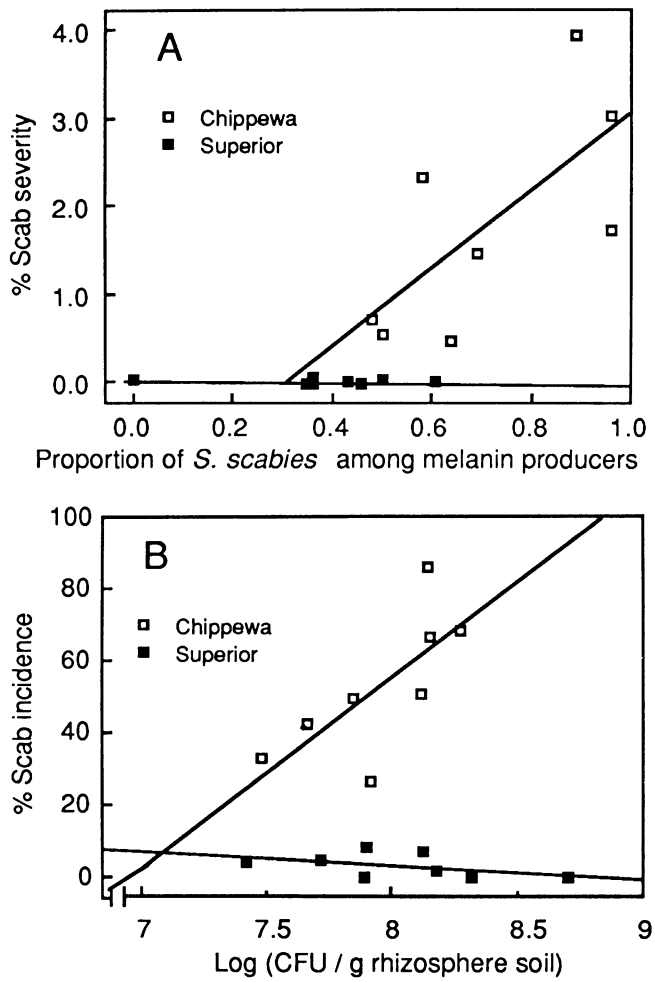

Fig. 8. Relationship between the proportion of *Streptomyces scabies* among melanin-producing actinomycete colonies and scab on Chippewa and Superior tubers from field plots in 1987. **A,** Actinomycetes were recovered from the tuber surfaces at harvest, 127 days after planting. **B,** Actinomycetes were recovered from the rhizosphere at 88 days after planting.

on healthy tuber periderm also contributed to the population increase.

A strong positive correlation between disease and the population density of total actinomycetes in the rhizosphere at 88 days after planting in 1987 was observed with the scab-susceptible cultivar Chippewa, whereas there was no significant change in disease with the resistant cultivar Superior (Fig. 8B). If the pathogen were included in the total actinomycete population in the rhizosphere, this correlation would suggest two epidemiological consequences: Scab resistance of Superior may involve a greater tolerance to higher pathogen population densities than that of a more susceptible cultivar; and a rhizosphere population of the pathogen could serve as inoculum, since roots are often in contact with tubers.

This study has demonstrated that actinomycete populations respond to the production of roots and tubers by the potato plant. Population densities increased in soil, the rhizosphere, and on tuber surfaces during the growing seasons. Pathogenic isolates of *S. scabies* were recovered from the rhizosphere and the tuber surfaces after disease developed, although little selective stimulation of the pathogen by either the susceptible or resistant potato host was evident before infection. As a result, the population densities of *S. scabies* and other actinomycetes producing melanin were not better predictors of disease than was the total actinomycete population. A lack of selective isolation techniques currently limits the amount of information that can be obtained about this pathogen. Serological or molecular approaches to identification of pathogenic *S. scabies* are being considered.

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