Characterization of Streptomycetes Causing Russet Scab in Québec

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ABSTRACT

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Strains of actinomycetes causing russet scab on potato tubers were different from *Streptomyces scabies* and *S. acidiscabies*. The russet scab–inducing organisms were characterized by a bright yellow mycelium on yeast malt extract (YME) which turned brown with age, and by aerial mycelium forming flexuous spore chains which appeared as a gray mass on the colonies. The organisms utilized L-arabinose, D-fructose, D-glucose, D-mannitol, raffinose, rhamnose, sucrose, and D-xylose. They degraded xanthine and xylan, but did not produce melanin. The russet scab–inducing organisms should be placed in the genus *Streptomyces*, since they possessed the typical morphology, biosynthesized similar fatty acids, and produced LL-diaminopimelic acid in their cell walls, characteristic of *Streptomyces* species. A high level of similarity (78%) was found between the russet scab–inducing organisms and members of the cluster *S. aureofaciens*, indicating that both groups may be included in the same *Streptomyces* cluster.

Russet scab of potato (*Solanum tuberosum* L.) is a disease characterized by corky reticulations on the tuber surface. Infections are generally restricted to the skin. Potato quality being affected, the marketable value of infected tubers decreases. In Canada, russet scab does not significantly reduce domestic sales of potatoes. However, marketing of diseased tubers destined for export can be severely reduced.

Russet scab has been reported in the United States and Europe since 1902 (6); however, its cause remains obscure. Although russet scab was attributed to environmental conditions and was associated with *Rhizoctonia* infections (5,12), more recent works established that russet scab is caused by soilborne actinomycetes different from *Streptomyces scabies* (Thaxter) Waksman & Henrici (1,6). The causal organisms were not characterized sufficiently to permit identification as to species.

In this paper, we present a characterization of the streptomycetes causing russet scab in Québec. Strains were characterized using the diagnostic criteria proposed by Lambert and Loria (10,11) to identify two other plant pathogenic actinomycetes: *S. scabies* and *S. acidiscabies* Lambert & Loria. These last two species cause common scab and acid scab, respectively, on potato tubers. We compared the phenotypic traits of strains causing russet scab, common scab, and acid scab in Québec, and established the relationship between these pathogenic agents by numerical analysis of these traits.

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MATERIALS AND METHODS

Isolation of streptomycetes from russet scab-infected tubers. Potato tubers affected by russet scab were obtained from six potato-growing areas in Québec differing in soil type and climatic conditions. Actinomycetes were isolated from tubers belonging to the cultivars Kennebec, Superior, Atlantic, Norland, Shepody, and Belmont. The procedure used to isolate actinomycetes from tubers has been described previously (4). All isolates were maintained on yeast malt extract (YME) (13).

Pathogenicity tests. In this study, 15 strains were isolated and tested for pathogenicity. Pathogenicity tests were carried out according to Labruyère (9). Inoculum was prepared by growing test strains for two weeks at 30 C in 50-ml tubes containing sterilized vermiculite saturated with a modified Say-solution composed of 20 g of sucrose, 1.2 g of L-asparagine, 0.6 g of K_2HPO_4, and 10 g of yeast extract per liter of water (9). Russet scab-free whole tubers of *S. tuberosum* cv. Green Mountain obtained from the Centre de production de pommes de terre de semence Elite I de Manicouagan (Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec) were planted in 12.5-cm-diameter pots containing sterile sand mixed with 20 ml of inoculum. Plants were arranged in a growth chamber as a randomized complete block with five replicates. Uninoculated controls were included in the tests. Temperatures were maintained between 22 and 24 C with a 16-hr photoperiod. Plants were grown under Gro Lux wide-spectrum fluorescents with a quantum flux density of 175 $\mu E \cdot m^{-2} \cdot s^{-1}$. Soil was allowed to dry between waterings. A soluble fertilizer (20-20-20) was added twice a month. Potatoes were harvested after 13 wk, and progeny tubers were examined for russet scab symptoms.

Morphology and pigmentation. Production of melanoid pigment was detected on a peptone-yeast extract–iron agar medium and on a tyrosine agar medium (16). Production of a diffusible pigment was tested on inorganic salts–glycerol agar medium (11). Colony and spore color were described after 10 days of growth at 30 C on YME.

To observe spore chain morphology, bacteria were inoculated and grown around round microscope slide cover slips obliquely inserted in YME plates. After bacterial sporulation, the slide covers were removed and the attached aerial mycelium and spore chains were observed under a light microscope with 100× total magnification.

Spore ornamentation was examined by scanning electron microscopy. Sporulating colonies were fixed in situ in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.3) for 2 hr at room temperature. After fixation, small pieces of agar containing two to three colonies were cut out with a razor blade. These pieces were postfixed in 2% osmium tetroxide in the same cacodylate buffer for 2 hr at room temperature. The pieces were then dehydrated in a graded ethanol series, critical point-dried using liquid CO_2, and evaporation-coated with gold–palladium at 10 mA and 4×10^{-6} Pa in an Edwards Sputter coater. The colonies were examined with a JEOL 840A scanning electron microscope.

Carbon and nitrogen source utilization. The mineral-base minimal medium used to test carbon source utilization contained the following: 2.64 g of $(NH_4)_2SO_4$, 2.38 g of KH_2PO_4, 5.65 g of $K_2HPO_4 \cdot 3H_2O$, 1.00 g of $MgSO_4 \cdot 7H_2O$, 6.4 mg of $CuSO_4 \cdot 5H_2O$, 1.1 mg

of $FeSO_4 \cdot 7H_2O$, 7.9 mg of $MnCl_2 \cdot H_2O$, and 1.5 g of $ZnSO_4 \cdot 7H_2O$ per liter (8). The mineral base was supplemented with Bacto agar (1.5% w/v) and with a sugar (1% w/v) as the sole carbon source (Table 1). The basal medium used to test nitrogen source utilization contained the following: 10 g of glucose, 5 g of $MgSO_4 \cdot 7H_2O$, 5 g of NaCl, 1 g of K_2HPO_4, 10 mg of $FeSO_4 \cdot 7H_2O$, and 15 g of Bacto agar per liter (8). An amino acid (1 g/L) was added to the basal medium as the sole nitrogen source (Table 1). Growth was scored after incubation for 7 days at 30 C.

Polymer degradation tests. Tests to evaluate the ability of strains to degrade xanthine, xylan, and arbutin were carried out as described by Lambert and Loria (11). Polygalacturonic acid degradation was observed on a medium containing 5 g of polygalacturonic acid, 6 g of Na_2HPO_4, 4 g of KH_2PO_4, 2 g of $(NH_4)_2SO_4$, 2 g of $MgSO_4 \cdot 7H_2O$, 1 g of yeast extract, 1 mg of $FeSO_4 \cdot 7H_2O$, 1 mg of $CaCl_2$, and 10 g of Bacto agar per liter.

Effects of different inhibitors and of pH on bacterial growth. The ability of the bacteria to grow between pH 4 and 6 at 0.5 unit intervals was tested on YME at 30 C. Chemical inhibitors (Table 1) were added to YME or to Bennett's medium modified as described by Williams et al (21). Inhibitors were used at the following concentrations: NaCl (4, 5, 6, 7, and 10% w/v), tellurite (10 and 100 μg/ml), thallium (10 and 100 μg/ml), oleandomycin (25 and 100 μg/ml), crystal violet (0.5 μg/ml), phenol (1 g/L), penicillin G (100 μg/ml), and streptomycin sulfate (20 μg/ml).

Numerical taxonomy. Numerical analysis was carried out as described by Lambert and Loria (11) to compare russet scab–inducing strains to strains of the different clusters described by Williams et al (21) and to *S. scabies* and *S. acidiscabies* strains. Strain characteristics existing in one of two mutually exclusive states were scored either plus (100) or minus (0). For qualitative multistate characteristics (spore color, spore chain morphology, spore ornamentation, and colony color), chosen properties were given a value of 100 (+), and any alternative was given a value of 0 (−). These values were averaged by trait to form group composites for 10 *S. scabies* strains (EF5, EF35, EF46, EF49, EF54, EF58, EF63, EF64, EF68, and EF84) isolated from Québec by Faucher et al (4), four *S. acidiscabies* strains (EF9, EF12, EF81, and ATCC 49003), and 15 russet scab–inducing strains. To determine the level of similarity between two groups of strains, differences in the values for each trait were added and then divided by the number of traits examined. The resulting number was subtracted from 100 to obtain the percentage of similarity. The three groups were compared with each other and also with the major and minor cluster groups of Williams et al (21) by examining 52 traits common to both studies.

Thin-layer chromatography of isomers of diaminopimelic acid. The procedure of Becker et al (2) was followed for the hydrolysis of whole cells preceding diaminopimelic acid analysis. Isomers were separated by thin-layer chromatography according to Staneck and Roberts (17).

Fatty acid analysis. Fatty acid analysis of three russet scab–inducing strains (EF38, EF69, and EF115) was performed on midlog phase cultures grown in fatty acid free Difco trypticase soy broth at 30 C. Cultures were passed through cellulosic 0.45 μm pore filters to eliminate the culture medium. Approximately 40 mg wet weight of growth were transferred to 13 × 100 mm glass test tubes with Teflon-lined caps, for fatty acid extraction. Cellular fatty acids were extracted and derivatized to their methyl esters as previously described (14). Fatty acid methyl esters were analyzed by the MIDI Microbial Identification system. Fatty acid patterns were analyzed using the MIDI Library version, TSBA 3.50, and Library Generation System software, version 3.30. Extraction of strain EF38 was performed twice to assess reproducibility of the extraction technique and the MIDI gas chromatographic system.

Table 1. Characteristics of strains inducing russet scab, *Streptomyces scabies* and *S. acidiscabies*

Characteristics	Russet scab–inducing bacteria	*S. scabies*	*S. acidiscabies*
Spore color	Gray	Gray	White
Chain spore morphology	Flexuous	Spiral	Flexuous
Spore ornamentation	Smooth	Smooth	Smooth
Colony color on YME[a]	Bright yellow	Tan to brown	Gold
Melanin on tyrosine agar	0/15[b]	10/10	0/4
Melanin on PYI[c]	0/15	10/10	0/4
Diffusible pigment	0/15	0/10	4/4
Utilization			
L-Arabinose	15/15	10/10	4/4
D-Fructose	15/15	10/10	4/4
D-Glucose	14/15	10/10	4/4
D-Mannitol	15/15	9/10	3/4
Raffinose	15/15	7/10	2/4
Rhamnose	15/15	7/10	4/4
Sucrose	15/15	7/10	4/4
D-Xylose	15/15	7/10	4/4
meso-Inositol	15/15	8/10	3/4
L-Hydroxyproline	14/15	10/10	4/4
L-Methionine	15/15	7/10	4/4
Degradation			
Arbutin	7/15	2/10	0/4
Polygalacturonate	0/15	2/10	0/4
Xanthine	15/15	4/10	0/4
Xylan	12/15	7/10	4/4
Growth			
4% NaCl	14/15	4/10	3/4
5% NaCl	13/15	2/10	0/4
6% NaCl	8/15	1/10	0/4
7% NaCl	1/15	0/10	0/4
10% NaCl	0/15	0/10	0/4
Tellurite (10 μg/ml)	15/15	9/10	4/4
Tellurite (100 μg/ml)	11/15	0/10	2/4
Thallium (10 μg/ml)	0/15	0/10	1/4
Thallium (100 μg/ml)	0/15	0/10	0/4
Crystal violet (0.5 μg/ml)	0/15	7/10	3/4
Phenol (0.1%)	11/15	9/10	1/4
Penicillin (10 μg/ml)	15/15	10/10	4/4
Oleandomycin (25 μg/ml)	15/15	3/10	2/4
Oleandomycin (100 μg/ml)	8/15	2/10	0/4
Streptomycin (20 μg/ml)	0/15	0/10	4/4
Growth at pH 4.5	0/15	0/10	4/4

[a] YME = yeast malt extract.
[b] Proportion of strains giving a positive reaction.
[c] PYI = peptone yeast extract–iron agar.

RESULTS

Pathogenicity tests. In a previous study carried out to identify the species causing common scab of potato in Québec (4), we also isolated some strains which induced russet scab symptoms on tubers. These strains were characterized by the formation of yellow colonies on YME and gray spores borne in flexuous chains. One purpose of this work was to confirm that these strains were effectively the causal agent of russet scab. Consequently, we isolated other actinomycetes exhibiting this particular

phenotype from tubers with russet scab symptoms. Fifteen such strains were isolated from 20 different tubers, and all strains induced russet scab on tubers. In fact, all tubers grown in infested soil showed evident russet scab reticulations (Fig. 1). In contrast, only one of 14 tubers grown in uninoculated pots showed symptoms. Koch's postulates were successfully completed for all 15 strains.

Phenotypic characterization of russet scab-inducing bacteria. Russet scab-inducing organisms differed morphologically and physiologically from *S. scabies* and *S. acidiscabies* (Table 1). Actinomycetes causing russet scab were characterized by a bright yellow mycelium on YME which turned brown after about 2 wk. The aerial mycelium formed flexuous spore chains which appeared as a gray mass on the colonies. The spores were cylindrical and smooth, and measured 0.5–0.6 μm in diameter by 0.7–0.9 μm in length (Table 1 and Fig. 2).

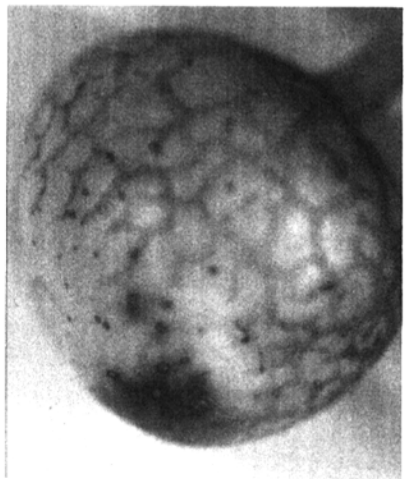

Fig. 1. Russet scab symptoms on a young potato tuber cv. Green Mountain infected by strain EF69.

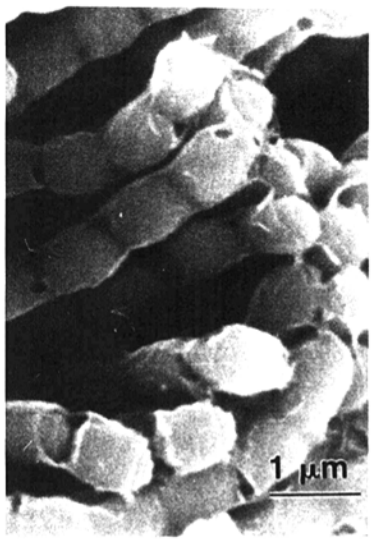

Fig. 2. Scanning electron micrograph of smooth spores of strain EF69. Bar = 1 μm.

These strains did not produce melanin, but all degraded xanthine and xylan. Most of the strains utilized L-arabinose, D-fructose, D-glucose, D-mannitol, raffinose, rhamnose, sucrose and D-xylose. Most grew in the presence of NaCl (5%), tellurite (100 μg/ml), penicillin (100 μg/ml), phenol (0.1%), and oleandomycin (25 μg/ml); but their growth was inhibited by thallium (10 μg/ml) and streptomycin sulfate (20 μg/ml).

The cell walls of the organisms contained the LL-diaminopimelic acid isomer. Fatty acid profiles of three russet scab-inducing organisms consisted of 12–18 acids, most of which were branched iso- and anteiso acids. Unsaturated fatty acids were not prevalent, accounting for less than 4% of the total fatty acid profile (Table 2). These bacteria were characterized by the predominance in their profiles of the 15:0 anteiso acid (more than 26% of the total profile) and of the 16:0 acid (16–19% of the total fatty acid profile). The three strains clustered within a Euclidian distance of 4.5, indicating that the strains were likely to be in the same species.

Taxonomy. The levels of similarity between organisms causing russet scab, common scab, and acid scab, and between these plant pathogenic organisms and the cluster groups of Williams et al (21) are shown in Table 3. The russet scab-inducing group showed the highest similarity level (78%) with Williams' cluster group 14, *Streptomyces aureofaciens,* suggesting that these plant pathogenic bacteria may belong in this cluster group. *S. scabies* and *S. acidiscabies* are, respectively, 70 and 68% similar to members of cluster 14, which is closely related to the levels of similarity found between those two species and the russet scab-inducing organisms (73% for *S. scabies* and 67% for *S. acidiscabies*).

In this study, the levels of similarity among organisms causing russet scab, common scab, and acid scab were about 70%. We found 67% similarity between *S. scabies* and *S. acidiscabies.* Lambert and Loria (10) found 64% similarity between these two plant pathogenic species. This slight disparity might be explained by the fact that strains isolated from Québec differed phenotypically from strains isolated in the United States. *S. scabies* showed high similarity with cluster groups 18, 19, and 23 (*Streptomyces cyaneus, S. diastaticus,* and *S. microflavus*). This is similar to the results reported by Lambert and Loria (11).

Table 2. Fatty acid composition of three russet scab-inducing strains

	Proportion of fatty acid (%)[a]		
Fatty acids	**Strain EF38**	**Strain EF69**	**Strain EF115**
14:0 Iso	2.38[b]	2.85	1.26
14:0	0.79	1.68	0.00
15:0 Iso	15.65	14.84	10.18
15:0 Anteiso	30.69	28.27	26.97
15:0	2.23	2.36	0.00
16:0 Iso	7.38	8.75	7.32
16:0 Anteiso	0.00	0.00	4.06
16:1 *cis* 9	2.49	1.72	0.00
16:0	16.36	19.02	18.58
17:1 Iso F	1.31	1.00	0.00
17:0 Iso	8.71	7.49	4.78
17:0 Anteiso	9.58	8.41	10.26
17:1 *cis* 10	0.00	0.00	3.86

[a] Fatty acids accounting for less than 1% in all strains have been omitted from table.
[b] Mean of two different extractions.

Table 3. Levels of similarity of phytopathogenic *Streptomyces* groups with selected cluster groups of Williams et al

	Similarity (%)[a]		
Species or cluster group	**Russet scab-inducing bacteria**	***S. scabies***	***S. acidiscabies***
Russet scab-inducing bacteria	90	73	66
S. scabies	73	86	67
S. acidiscabies	66	67	92
Cluster group 2 *S. olivoverticillatum*	72	59	61
Cluster group 14 *S. aureofaciens*	78	70	68
Cluster group 18 *S. cyaneus*	65	79	55
Cluster group 19 *S. diastaticus*	68	75	60
Cluster group 21 *S. griseoruber*	65	70	55
Cluster group 23 *S. microflavus*	63	78	55
Cluster group 24 *S. flaveolus*	72	69	58

[a] The table includes cluster groups which exhibit at least 70% similarity with species we investigated.

DISCUSSION

Since the work of Harrison (6), it is generally accepted that russet scab is caused by actinomycetes different from *S. scabies.* However, the organisms isolated by Harrison were not characterized in detail, and consequently, the taxonomic identity of the organisms inducing russet scab remains obscure. More recent works on russet scab of potato were conducted in Europe (1,15,18), but the russet scab occurring in North America differs from the European disease with respect to several characteristics (cultivar susceptibility, root attack, and optimum soil temperature). Scholte and Labruyère (15) proposed that the American russet scab and the European russet scab were two different diseases, and named the European disease "netted scab."

In this work, we confirmed that actinomycetes are the causal agents of russet scab. Moreover, we propose that the russet scab–inducing organisms should be placed in the genus *Streptomyces,* based upon colony morphology, fatty acid profiles (especially the branched iso- and anteiso fatty acids) (19), and the presence of LL-diaminopimelic acid in their cell walls (2). As Harrison (6), we conclude that organisms causing russet scab are different from *S. scabies,* since they produce a pigmented mycelium, flexuous spore chains, and no melanin. They also differ from *S. acidiscabies* with respect to mass spore color and the inability to grow at pH 4.5. Lack of growth at pH 4.5 corresponds to field observations since russet scab in Québec has not been reported to occur in fields below pH 5.0.

Strains described in this study appeared to be different from the russet scab–inducing strains isolated by Harrison (6), which produced sparse aerial mycelia lacking a distinct yellow color. This suggests that a taxonomic diversity exists among russet scab–inducing bacteria, as well as for common scab–inducing bacteria (3,4,7). Taylor and Decker (20) also reported that superficial russeting of the surface of the tubers was associated with inoculation by streptomycetes of widely different types. This suggests that streptomycetes might cause russeting at the high densities used in pathogenicity tests. In a previous study (4), we observed that saprophytic streptomycetes could on rare occasions induce slight and diffuse russeting of tubers. However, strains described in this study consistently induce characteristic russet scab symptoms.

In a study on the numerical classification of *Streptomyces,* Williams et al (21) divided the members of that genus into 19 major and 40 minor clusters. Based upon 52 criteria, we compared the causal agents of russet scab, common scab, and acid scab with the major and minor clusters of Williams et al (21). The most probable identification for the russet scab–inducing streptomycetes is *S. aureofaciens,* since the level of homology (78%) between the two groups was the highest. Williams et al (21) considered that two strains showing a level of homology of 77.5% should be included in the same cluster.

S. aureofaciens and our strains causing russet scab shared numerous morphological and physiological characteristics. Both groups produce gray spores in flexuous chains, and their mycelium contains a yellow pigment. They do not produce melanin or diffusible pigments, and all strains degrade xanthine. Most strains can grow in the presence of tellurite (0.1%), penicillin (100 μg/ml), and phenol (0.1%); but their growth is inhibited by thallium (10 μg/ml) and streptomycin sulfate (20 μg/ml).

The level of homology among organisms causing common scab, acid scab, and russet scab is about 70%. This level of similarity is considered by Williams et al (21) to be low enough to permit recognition as different species; however, the similarity is higher than with most other *Streptomyces* clusters. Thus, physiological traits common to the three species pathogenic to potato might be of significant importance in the successful colonization of potato tubers. Little has been published on the mechanisms of virulence of russet scab–inducing bacteria. The recent work of King et al (8) indicated a positive correlation between production of a phytotoxin, Thaxtomin A, and pathogenicity in *S. scabies* and *S. acidiscabies.* Studies are in progress to determine whether Thaxtomin A is also associated with russet scab lesions.

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LITERATURE CITED

1. Bång, H. 1979. Studies on potato russet scab. I. A characterization of different isolates from northern Sweden. Acta Agric. Scand. 29:145-150.
2. Becker, B., Lechevalier, M. P., Gordon, R. E., and Lechevalier, H. A. 1964. Rapid differentiation between *Nocardia* and *Streptomyces* by paper chromatography of whole-cell hydrolysates. Appl. Microbiol. 12:421-423.
3. Doering-Saad, C., Kämpfer, P., Shulamit, M., Kritzman, G., Schneider, J., Zakrzewska-Czerwinska, J., Schrempf, H., and Barash, I. 1992. Diversity among *Streptomyces* strains causing potato scab. Appl. Environ. Microbiol. 58:3932-3940.
4. Faucher, E., Savard, T., and Beaulieu, C. 1992. Characterization of actinomycetes isolated from common scab lesions on potato tubers. Can. J. Plant Pathol. 14:197-202.
5. Frank, J. A. 1981. Rhizoctonia canker (Black scurf). Pages 52-54 in: Compendium of Potato Diseases. W. J. Hooker, ed. American Phytopathological Society, St. Paul.
6. Harrison, M. D. 1962. Potato russet scab, its cause and factors affecting its development. Am. Potato J. 39:368-387.
7. Healy, P. G., and Lambert, D. H. 1991. Relationship among *Streptomyces* spp. causing potato scab. Int. J. Syst. Bacteriol. 41:479-482.
8. King, R. R., Lawrence, C. H., and Clark, M. C. 1991. Correlation of phytotoxin production with pathogenicity of *Streptomyces scabies* isolates from scab infected potato tubers. Am. Potato J. 68:675-680.
9. Labruyère, R. E. 1971. Common scab and its control in seed-potato crops. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands.
10. Lambert, D. H., and Loria, R. 1989. *Streptomyces acidiscabies* sp. nov. Int. J. Syst. Bacteriol. 39:393-396.
11. Lambert, D. H., and Loria, R. 1989. *Streptomyces scabies* sp. nov., nom. rev. Int. J. Syst. Bacteriol. 39:387-392.
12. Morse, W. J., and Shapovalov, M. 1914. The rhizoctonia disease of potatoes. Maine Agric. Exp. Stn. Bull. 230.
13. Pridham, T. G., Anderson, P., Foley, C., Lindenfelser, L. A., Hessetine, C. W., and Benedict, R. G. 1956-57. A selection of media for maintenance and taxonomic study of streptomycetes. Antibiot. Annu. 1956-57:947-953.
14. Sasser, M. 1990. Identification of bacteria through fatty acid analysis. Pages 199-204 in: Methods in Phytobacteriology. Z. Klement, K. Rudolph, and D. Sands, eds. Akademiai Kiado, Budapest.
15. Scholte, K., and Labruyère, R. E. 1985. Netted scab: a new name for an old disease in Europe. Potato Res. 28:443-448.
16. Shirling, E. B., and Gottlieb, D. 1966. Methods for characterization of *Streptomyces* species. Int. J. Syst. Bacteriol. 16:313-340.
17. Staneck, J. L., and Roberts, G. D. 1974. Simplified approach to identification of aerobic actinomycetes by thin-layer chromatography. Appl. Microbiol. 28:226-231.
18. Sundheim, L. 1968. A *Streptomyces* sp. causing russet scab of potatoes in Norway. Eur. Potato J. 11:194.
19. Suzuki, K. 1988. Cellular fatty acid analysis in actinomycete taxonomy. Pages 251-256 in: Biology of Actinomycetes '88. Y. Okami, T. Beppu, and H. Ogawara, eds. Japan Scientific Press, Tokyo.
20. Taylor, C. F., and Decker, P. 1947. A correlation between pathogenicity and cultural characteristics in the genus *Actinomyces.* Phytopathology 37:49-58.
21. Williams, S. T., Goodfellow, M., Alderson, G., Wellington, E. M. H., Sneath, P. H. A., and Sackin, M. J. 1983. Numerical classification of *Streptomyces* and related genera. J. Gen. Microbiol. 129:1743-1813.