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BACTERIAL AND PHYTOPLASMA DISEASES

Identification of potato scab-causing *Streptomyces* sp. occurring in strongly acidic soils in Saga Prefecture in Japan

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Abstract Acid scab of potatoes occurs frequently in strongly acidic soils at pH 3.9–5.2. On the basis of the phylogenetic relationships derived from 16S rDNA sequences and physiological characteristics, we identified the organism causing this disease in potatoes grown in the Uwaba district of Saga Prefecture, Kyushu Island, southwest Japan, as *Streptomyces acidiscabies*. Another pathogen that occurred more frequently in weakly acidic to neutral soils, rather than strongly acidic soils, was identified as *S. scabiei*. *Streptomyces acidiscabies* tended to produce superficial lesions, while *S. scabiei* mostly produced raised and/or erumpent lesions.

Keywords Acid scab · Phylogenetic analysis · Potato scab · *Streptomyces acidiscabies* · *Streptomyces scabiei*

Scab diseases of potatoes are caused by soil-inhabiting, gram-positive actinomyces of the genus *Streptomyces*. Although these diseases have little or no effect on total yield, the market value of the affected tubers is reduced, sometimes to the point that they can no longer be sold for table use or processing (Loria et al. 1997; Rich 1983). Damage due to scab diseases has recently become more severe in potato-producing areas of Japan (Tashiro et al. 1999).

Many reports have described *Streptomyces* species that cause scab diseases (Bouchek-Mechiche et al. 2000; Goyer et al. 1996; Loria et al. 1997; Miyajima et al. 1998; Park et al. 2003). Previously, we confirmed that scab diseases of potato in the Uwaba district of Saga Prefecture in Kyushu Island are caused by two genetically distinct *Streptomyces* spp. on the basis of DNA homology (Tashiro et al. 1990). This area of southwestern Japan has long been a potato-growing region. We showed that one of these pathogenic *Streptomyces* spp., which formed rectiflexible spore chains and did not possess melanoid pigment, was the causal organism for acid scab disease that occurs particularly in strongly acidic soils at pH 3.9–4.5 (Tashiro et al. 1999). However, at the time, we did not identify these pathogens at the species level.

Thus, the objective of this study was to identify these two *Streptomyces* species, i.e., the organism causing scab disease in strongly acidic soils and the organism that causes scab in weakly acidic to neutral soil.

Isolates and pathogenicity

Potato tubers in the Uwaba district of Saga Prefecture were more severely affected by scab disease in soil with a pH of 3.9–5.2. In these soils, the incidence of tubers with severe scab reached 96 %. Such severely diseased tubers were collected from 25 fields in the period 1979–1985. In these

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fields, scab tuber rates were over 30 %. One hundred fifty-one isolates of *Streptomyces* spp. were obtained from the scab lesions on collected potato tubers using previously described methods (Harrison 1962; Lawrence 1956). These isolates were divided into two distinct groups based on morphological characteristics. On a spore-forming medium (Matsumoto 1979), 126 isolates from soil with pH values of 3.9–5.2 produced well-developed white aerial mycelia and rectiflexible spore chains, and 25 isolates from soil with pH values of 5.1–5.2 produced well-developed gray aerial mycelia and spiral spore chains (Tashiro et al. 1999). The spore surface of all isolates was smooth (Fig. 1).

We examined the pathogenicity of these isolates in a greenhouse. Spore suspensions (200 mL, ca. 10^8 CFU/mL) were added to 30-cm-diameter pots containing sterilized (121 °C, 15 min) vermiculite, peat moss, and Kanuma-soil (1:1:1; v/v/v). The pH of the mixed soil was 5.5. Healthy seed potato tubers of scab-susceptible cv. Dejima were surface disinfected by dipping in ethanol (75 %) for 3 min, then rinsed in distilled water. Seed pieces were then planted at a depth of 5 cm. Potato plants were grown in the greenhouse from mid-September to mid-December. Progeny potato tubers were harvested and observed for scab symptoms.

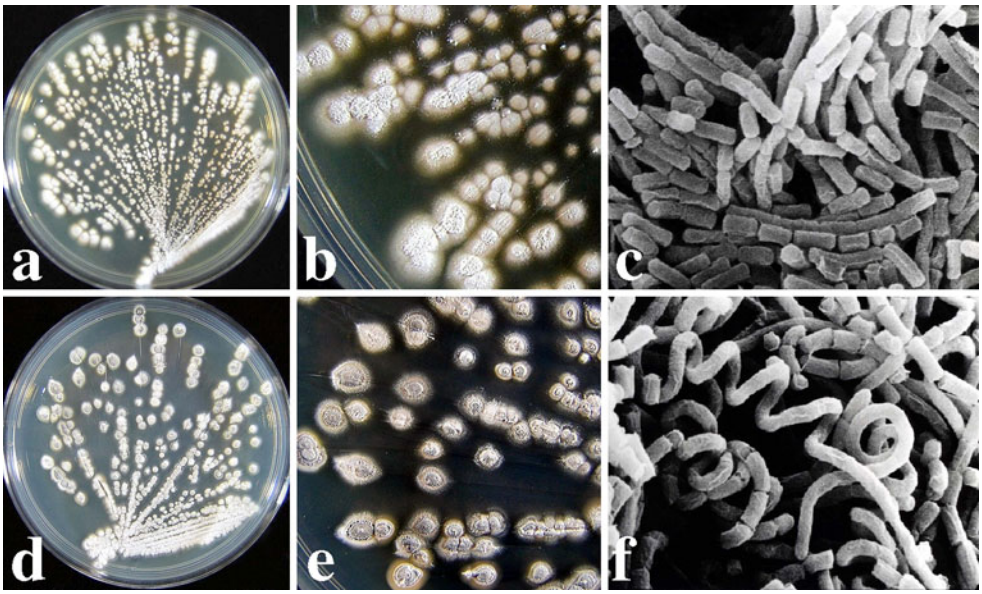

Fig. 1 Morphological properties of rectiflexible spore-chain-forming isolates, viz. *Streptomyces acidiscabies* (**a**–**c**), and spiral spore-chain-forming isolates, viz. *Streptomyces scabiei* (**d**–**f**), which cause potato scab disease. Colonies are shown in **a**, **b**, **d**, and **e**; spore chain morphology and ornamentation of spores are shown in **c** and **f**, respectively

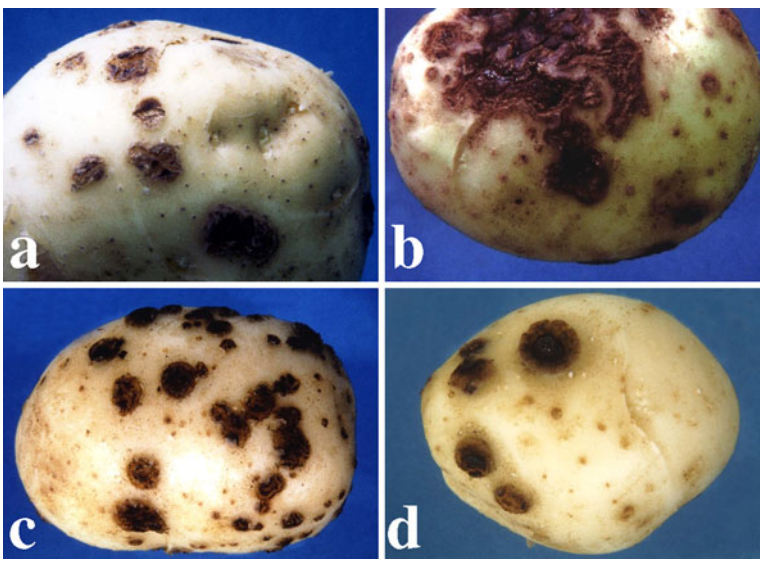

Fig. 2 Superficial lesions caused by rectiflexible spore-chain-forming isolates, viz. *Streptomyces acidiscabies* **a** isolate S-51, **b** S-173. Raised and/or erumpent lesions caused by spiral spore-chain-forming isolates, viz. *Streptomyces scabiei*, **c** isolate S-131, **d** S-851. In all figures, the potato cv. is Dejima

Table 1 Potato scab-causing *Streptomyces* isolates used in this study

Isolates	Geographic origin	Year isolated	References
Rectiflexible spore-chain-forming isolates (RFIs)			
S-51, S-173, S-411	Uwaba district in Saga Prefecture	1980	Tashiro et al. 1990
S-52, S-111, S-132, S-212, S-243, S-311, S-324, S-415, S-852, S-2422, S-2423, S-2426, S-3121, S-3122, S-3221, S-3228, S-4012	Uwaba district in Saga Prefecture	1985	This study; Tashiro et al. 1990, 1999
Spiral spore-chain-forming isolates (SIs)			
S-18, S-151	Uwaba district in Saga Prefecture	1980	Tashiro et al. 1990
S-11, S-23, S-81, S-82, S-112, S-121, S-131, S-211, S-241, S-312, S-412, S-851, S-1111, S-1112, S-3321, S-3326, S-3668, S-4056	Uwaba district in Saga Prefecture	1985	This study; Tashiro et al. 1990, 1999

One hundred thirty-two isolates caused scab disease. Rectiflexible spore-chain-forming isolates (RFIs) produced superficial lesions, including small lesions (less than 5 mm diameter). In spiral spore-chain-forming isolates (SIs), small lesions were superficial; however, lesions larger than 5 mm were raised and/or erumpent (Fig. 2). In addition, the spore color and morphology of pathogens reisolated from scabbed tubers were identical to those of the inocula.

The representative isolates of the potato scab-causing *Streptomyces* used in this study are listed in Table 1.

Molecular phylogenetic analysis

Two representatives of the RFIs, S-51 and S-173, and one representative of the SIs, S-851, were subjected to 16S rDNA sequence analysis. DNA samples from these isolates were prepared using the method of Marmur (1961). Primers 27f [5′-AGATTTGATC(CA)TGGCTCAG-3′] and 1522r [5′-TACGG(CT)TACCTTGTTACGACTT-3′] (Lane 1991) were used to amplify a portion of the 16S rRNA gene. The conditions for amplification were as follows: initial denaturation at 98 °C for 3 min, denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 30 s, and final extension at 72 °C for 2 min. Polymerase chain reaction (PCR) products were purified using a GENECLEAN II kit (Qbiogene, Carlsbad, CA, USA). The amplified products were then directly sequenced.

Table 2 List of potato scab-causing *Streptomyces* species and other *Streptomyces* species used in the molecular phylogenetic analysis

Streptomyces species	Isolates	Accession[a]	References
Streptomyces sp. RFI	S-51	AB258461	This study
Streptomyces sp. RFI	S-173	AB688917	This study
Streptomyces sp. SI	S-851	AB258460	This study
Scab-causing *Streptomyces*			
S. acidiscabies	ATCC49003^T	D63865	Takeuchi et al. (1996)
S. acidiscabies	NB05-2F	FJ546739	Wanner (2009)
S. scabiei	ATCC49173^T	D63862	Takeuchi et al. (1996)
S. scabiei	KACC20192	AY207603	
S. turgidiscabies	ATCC700248^T	D63866	Takeuchi et al. (1996)
S. turgidiscabies	NBRC16079	AB301483	Tagawa et al. (2008)
S. caviscabies	ATCC51928^T	AF112160	
S. europaeiscabiei	CFBP4497^T	FJ007406	St-Onge et al. (2008)
S. reticuliscabiei	CFBP4531^T	AJ007428	Bouchek-Mechiche et al. (2000)
S. stelliscabiei	CFBP4521^T	FJ007385	St-Onge et al. (2008)
S. luridiscabiei	KACC20252^T	AF361784	Park et al. (2003)
S. puniciscabiei	KACC20253^T	AF361785	Park et al. (2003)
S. niveiscabiei	KACC20254^T	AF361786	Park et al. (2003)
Other *Streptomyces*			
S. bottropensis	ATCC25435^T	D63868	Takeuchi et al. (1996)
S. coelicolor	A3(2)	Y00411	Baylis and Bibb (1988)
S. diastatochromogenes	ATCC12309^T	D63867	Takeuchi et al. (1996)
S. griseus subsp. *griseus*	KCTC9080	M76388	Kim et al. (1993)
S. ipomoeae	NBRC13050^T	AB184857	Tagawa et al. (2008)
S. lydicus	ATCC25470^T	Y15507	Kreuze et al. (1999)

Table 2 continued

Streptomyces species	Isolates	Accession[a]	References
S. neyagawaensis	ATCC27449^T	D63869	Takeuchi et al. (1996)
S. sampsonii	ATCC25495^T	D63871	Takeuchi et al. (1996)

[a] DDBJ/GenBank/EMBL nucleotide sequence accession numbers

The determined 16S rDNA nucleotide sequences were deposited in the DNA Databank of Japan. The accession numbers are AB258461 for S-51, AB688917 for S-173, and AB258460 for S-851. Homology searches using BLAST (Altschul et al. 1990) revealed that the sequences for S-51and S-173 were 100 % and 99.93 % identical, respectively, to that of *S. acidiscabies* ATCC 49003^T (Lambert and Loria 1989b), while the sequence of S-851 was 99.93 % identical to that of *S. scabiei* ATCC 49173^T (Lambert and Loria 1989a).

The aligned sequences were analyzed by the neighbor-joining method with a *p*-distance substitution model, using MEGA 5.05 software (Tamura et al. 2011). Potato scab-causing *Streptomyces* spp. and other *Streptomyces* spp. used in the molecular phylogenetic analysis are listed in Table 2. Branch support for the tree was evaluated using 1000 bootstrap replications (Felsenstein 1985). In phylogenetic trees (Fig. 3), the grouping of S-51 and S-173 in the *S. acidiscabies* clade exhibited 100 % bootstrap support, while the grouping of S-851 in the *S. scabiei* clade was supported with 77.8 % bootstrap support.

Physiological characterization

The formation of melanin pigments and utilization of carbon compounds (Pridham and Gottlieb 1948) by the isolates were previously determined (Tashiro et al. 1990). The pH value that allowed growth was determined by the method of Tashiro et al. (1999). Additionally, the effects of antibiotics and toxic compounds, selected from those used by Williams et al. (1983), were tested using their protocol.

Rectiflexible spore-chain-forming isolates could grow at pH 4.0 or pH 3.5, like *S. puniciscabiei* and *S. niveiscabiei* (Park et al. 2003). RFIs grew in the presence of 5 % NaCl, thallium (10 μg/mL), crystal violet (0.5 μg/mL), penicillin (10 IU/mL), oleandomycin (25 μg/mL), and streptomycin (20 μg/mL) (Table 3). In contrast, *S. puniciscabiei* was unable to grow in the presence of thallium (10 μg/mL) or streptomycin (20 μg/mL), and *S. niveiscabiei* did not grow in the presence of 5 % NaCl, thallium (10 μg/mL), crystal violet (0.5 μg/mL), oleandomycin (25 μg/mL), or streptomycin (20 μg/mL) (Park et al. 2003).

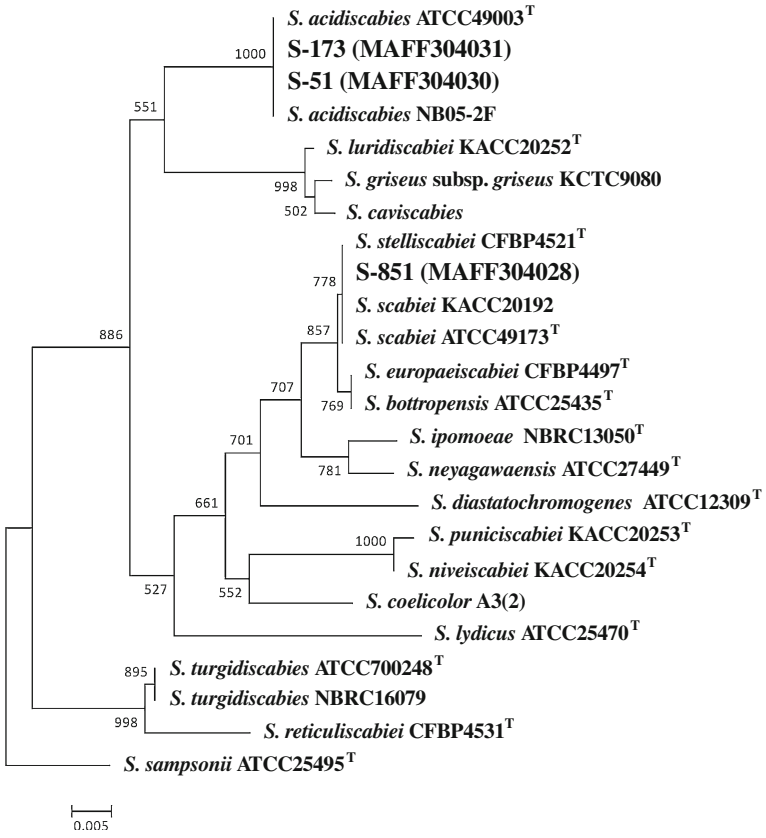

Fig. 3 Phylogenetic tree compiled from 16S rDNA sequence data using a neighbor-joining bootstrap method. *Streptomyces sampsonii* ATCC25495T was used as the outgroup. The *bar* represents a phylogenetic distance of 0.005. The 16S rDNA sequences, excluding those of the isolates S-51 (MAFF304030), S-173 (MAFF304031), and S-851 (MAFF304028), were acquired from the DDBJ database

Table 3 Comparison of morphological characteristics and physiological properties of potato scab-causing *Streptomyces* spp.

Characteristics	RFIs	*S. acid*	*S. luri*	*S. cav*	SIs	*S. scab*	*S. stel*	*S. euro*	*S. puni*	*S. nivei*	*S. turg*	*S. reti*
Spore mass color	W	W	YW	W	G	G	G	G	PO	W	G	LG
Spore chain morphology	Rf	Rf	Rf	Rf	Sp	Sp	Sp	Sp	Rf	Rf	Rf	Rf
Melanin on PYIA (ISP No.6)	−	−	+	−	+	+	+	+	−	−	−	−
Carbon source usage												
L-Arabinose	+	+	+	−	+	+	+	+	+	+	+	+
D-Fructose	+	+	+	−	+	+	+	+	+	+	+	+
D-Mannitol	+	+	+	−	+	+	+	+	+	+	+	+
Raffinose	V	−	−	+	+	+	+	+	+	+	+	+
Rhamnose	+	+	+	−	+	+	+	+	+	+	+	+
Sucrose	+	+	+	−	+	+	+	+	+	+	+	+
D-Xylose	+	+	+	−	+	+	+	+	+	+	+	+
Growth at low pH												
3.5–4.0	+	+	−	ND	−	−	ND	ND	+	+	−	ND
4.5	+	+	+	−	−	−	ND	ND	+	+	+	ND
5.0	+	+	+	ND	V	+	ND	ND	+	+	+	ND
Growth in the presence of												
5 % NaCl	+	ND	−	ND	+	+	−	ND	+	−	−	−
Thallium (10 μg/mL)	+	+	+	+	−	−	ND	ND	−	−	−	ND
Crystal violet (0.5 μg/mL)	+	+	+	V	+	−	−	−	+	−	−	−
Penicillin (10 IU/mL)	+	+	+	+	V	−	+	+	+	+	+	+
Oleandomycin (25 μg/mL)	+	+	−	ND	V	+	+	+	+	−	+	+
Streptomycin (20 μg/mL)	+	+	−	+	V	−	−	−	−	−	−	−

The morphological characteristics and physiological properties of *S. acidiscabies* (*S. acid*), *S. luridiscabiei* (*S. luri*), *S. caviscabies* (*S. cavi*), *S. scabiei* (*S. scab*), *S. stelliscabiei* (*S. stel*), *S. europaeiscabiei* (*S. euro*), *S. puniciscabiei* (*S. puni*), *S. niveiscabiei* (*S. nive*), *S. turgidiscabies* (*S. turg*), *S. reticuliscabiei* (*S. reti*) from references Bouchek-Mechiche et al. (2000); Goyer et al. (1996); Lambert and Loria (1989a), b; Miyajima et al. (1998); Park et al. (2003)

G gray, *W* white, *YW* yellowish white, *PO* pale orange, *LG* light gray, *S* spiral, *Rf* rectiflexible, *PYIA* peptone-yeast extract iron agar, *ND* not determined

+, positive reaction; −, negative reaction; V, reaction varied according to isolate

Other scab-causing *Streptomyces* spp., with similar spore-chain morphology and identical carbon-source usage to the RFIs, *S. reticuliscabiei* and *S. turgidiscabies*, did not grow in the presence of 5 % NaCl, crystal violet (0.5 μg/mL), or streptomycin (20 μg/mL) (Bouchek-Mechiche et al. 2000; Miyajima et al. 1998). *Streptomyces luridiscabiei* did not grow in the presence of 5 % NaCl, oleandomycin (25 μg/mL), or streptomycin (20 μg/mL) (Park et al. 2003). *Streptomyces caviscabies* differed in its ability to catabolize carbon sources and growth at pH 4.5 (Goyer et al. 1996).

Rectiflexible spore-chain-forming isolates that were grouped into the *S. acidiscabies* clade by molecular phylogenetic analysis were found to be similar to *S. acidiscabies* in their physiological characteristics (Lambert and Loria 1989b) except for raffinose utilization. From these results, we identified them as *S. acidiscabies*.

These results indicate that characters of growth at pH 4.0, in the presence of 5 % NaCl, thallium (10 μg/mL), crystal violet (0.5 μg/mL), oleandomycin (25 μg/mL), or streptomycin (20 μg/mL) seemed to be useful in distinguishing scab-causing *Streptomyces* spp. having rectus-flexibilis sporophores.

On the other hand, SIs grouped into the *S. scabiei* clade by molecular phylogenetic analysis were similar to *S. scabiei* in physiological characteristics (Lambert and Loria 1989a), except for sensitivity to crystal violet (0.5 μg/mL), penicillin (10 IU/mL), oleandomycin (25 μg/mL), and streptomycin (20 μg/mL). Because these physiological characteristics, except sensitivity to crystal violet, of the SIs varied according to the isolates, we identified them as *S. scabiei*.

Sensitivity to antibiotics and toxic compounds of scab-causing *Streptomyces* spp. having spiral sporophores, e.g., *S. scabiei*, *S. stelliscabiei*, and *S. europaeiscabiei* were similar. Thus, it is difficult to distinguish the species using the antibiotics and toxic compounds tested in this study.

Conclusion

On the basis of the phylogenetic relationships derived from 16S rDNA sequences and the physiological characteristics, we identified the RFIs as *S. acidiscabies*. RFIs S-51 and S-173 were deposited in the National Institute of Agrobiological Sciences Genebank, with accession numbers MAFF 304030 and MAFF 304031. The SIs were identified as *S. scabiei*. S-851 was also deposited, with accession number MAFF 304028.

We determined that the causal organism of potato scab disease that occurred in the strongly acidic soils in the Uwaba district of Saga Prefecture was *S. acidiscabies*. Moreover, in this study, we found that the lesions caused by *S. acidiscabies* and *S. scabiei* were different. This result supported previous studies (Thwaites et al. 2010; Zhao et al. 2010), indicating that differences in lesion types on the tubers may be useful for deducing the identity of the causal pathogens. We also observed differences in lesion types on cv. May Queen inoculated with *S. acidiscabies* or *S. scabiei*, but it will be necessary to examine additional potato varieties in future.

In this study, we did not isolate *S. turgidiscabies* (Miyajima et al. 1998), which is another causal pathogen of potato scab that is widely distributed throughout Hokkaido, northern Japan. However, Nishi et al. (2007) found *S. turgidiscabies* in Kagoshima Prefecture in Kyushu Island, southern Japan. Because potato scab spreads via diseased seed tubers (Hooker 1981; Rich 1983; Tashiro and Matsuo 1986), it will be necessary to monitor the geographic expansion of these pathogens by examining numerous strains isolated throughout Japan. Such measures will facilitate appropriate preventive measures against potato scab diseases that are caused by each of the different pathogenic *Streptomyces* species.

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