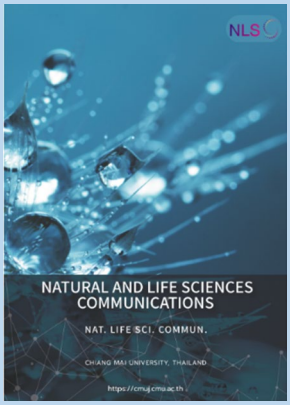
Research article



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Identification and Detection of a Virulence Gene of *Streptomyces scabies* Causing Potato Scab in Thailand

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ABSTRACT

Potato scab is caused by several pathogenic *Streptomyces* species which diminish crop quality, quantity and marketability. In the present study, a 16S rRNA gene sequence was used to detect *Streptomyces* species in potato tuber lesions harvested in Chiang Mai, Thailand and to evaluate a virulence gene as a reliable marker for the detection of pathogenic *Streptomyces* species by PCR assays. *Streptomyces* isolates were isolated from potato scab lesions, of which one isolate was pathogenic on potato tubers. The pathogenic isolate MJ21 was identified as *Streptomyces scabies* based on 16S rRNA gene sequence and morphological characteristics. Subsequently, isolate MJ21 produced PCR products from the tomA and txtAB genes, which are related to the production of tomatinase enzyme and thaxtomin A, respectively. Moreover, when grown on nutrient agar (NA) with MJ21, eggplant seedlings showed severe stunting of the roots and shoots, and failed to germinate; by comparison, seedlings/seeds grown on NA plates without MJ21 exhibited no symptoms. This study reports that *S. scabies* MJ21 has a toxigenic region (TR) that is associated with the tomA and txtAB genes.

Keywords: Pathogenicity tests, Potato scab, *Streptomyces scabies*, Toxigenic region, Virulence gene

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INTRODUCTION

Domestic demand for potato has increased in recent decades in Thailand. (Kittipadakul et al., 2016). Potato scab disease of *Solanum tuberosum* is caused by several *Streptomyces* strains and is widely distributed over all the potato-growing areas in the world. The disease is characterized by superficial corky tissue or deep corky lesions or erumpent lesions on surface potato tubers, depending on the environment and the *Streptomyces* strain; slightly raised lesions may also occur. Although these symptoms have little or no effect on gross total yield, but they result in reduced starch content and lowered market value (Takeuchi et al., 1996). The main causal agent of common scab widely distributed is *S. scabies*, followed by *S. turgidiscabies, S. luridiscabiei, S. acidiscabies* and *S. europaeiscabiei* (Lerat et al., 2009). Several *Streptomyces* strains have been presented to infect potato tubers in North America and *S. europaeiscabiei* was more common in the west and *S. scabies* was the most common from the mid-plains eastward (Wanner, 2007). Moreover, the studies of Bouchek-Mechiche et al. (2000) and Park et al. (2003) suggest that *Streptomyces* species may have different population profiles in different parts of the world that cause common scabs. *Streptomyces* strains can cause potato scab disease worldwide such as *S. scabiei, S. acidiscabies, S. europaeiscabiei, S. luridiscabiei, S. niveiscabiei, S. puniciscabiei, S. reticuliscabiei, S. stelliscabiei, S. turgidiscabies* and *S. ipomoeae* (St-Onge et al., 2008; Atiq et al., 2013; Wanner and Kirk, 2015). Yang et al., (2018) reported that 10 different species of *Streptomyces* (*S. scabies, S. turgidiscasies, S. acidiscabies, S. anulatus, S. europaeicabiei, S. enissocaesillies, S. luridiscaliei, S. caviscabies, S. aureofaciens*, and *S. griseus*) found on potato common scab in Yunnan, China. *Streptomyces* isolates in China identified isolates primarily as *S. scabies, S. acidiscabies, S. griseoflavus* based on morphologic, biochemical and molecular analysis. Among the *S. scabies* showed the highest scab index by exhibiting the scab-like lesions on potato tubers (Ismail et al., 2020). The present study isolated *Streptomyces* strain from scabby potatoes in China shared sequence similarity with *Streptomyces rhizophilus* (Wei et al., 2022).

The pathogenicity island (PAI) is of importance for pathogenicity wherein the genes conferring pathogenicity are frequently clustered and appear to be responsible for the emergence of these more virulent strains or new pathogenic strains. These strains carry genes encoding virulence factors and four pathogenicities including a functional tomatinase (tomA) gene which virulence factor homologous to the gene encoding tomatinase, the biosynthetic pathway for thaxtomin (txt), a necrogenic protein (nec1) encodeing a protein that induces necrosis in plant tissue and a cytokinin biosynthetic pathway. These four virulence factors also exist in *S. scabies, S. acidiscabies, S. turgidiscabies* and some other *Streptomyces* strains, but are separated into two remote chromosomal regions, designated as the colonization region (CR) and the toxicogenic region (TR). Discovering the tomatinase homolog-encoding the tomA gene within the PAI of Streptomyces pathogens has led to speculation that this gene is also involved in virulence or pathogenicity in plant disease (Kers et al., 2005; Loria et al., 2006). In addition, the genes associated with thaxtomin production, such as the txtA and txtB genes called the 'toxicogenic region' are found in the first segment of the PAI. Whereas the virulence-related genes, nec1 and tomA, are located in the second segment, designated the 'colonization region' (Lerat et al., 2009).

The report in Thailand found that most *Streptomycetes* have characteristics as biocontrol and a few have characteristics as a plant pathogen. Shutsrirung et al. (2013) studied the diversity of endophytic actinomycetes in mandarin and their potential as plant growth promoters due to their ability to produce IAA. The isolates were classified into six genera including *Streptomyces, Nocardia*, *Nocardiopsis, Spirillospora, Microbispora* and *Micromonospora* based on spore chain morphology and 16S rRNA gene sequence. Whereas, Soe et al. (2010)

reported that *Streptomyces* and *Bradyrhizobia* showed negative effect on nitrogen fixation in soybean. Similar results that *Streptomyces* strain RM365 was showed highest activity to inhibit bacterial pustule disease in the soybean strain but showed negative effect on the growth of *Rhizobium*, symbiotic bacteria of soybean plants. The strain shared 99.28% similarity to *Streptomyces caeruleatus* GIMN4T. These findings point out importance of checking the growth inhibitory effect of actinomycetes against rhizobia before being selected for potential biocontrol for field trial (Mingma et al., 2014.).

Careful and thorough characterization of *Streptomyces* pathogens and virulence related genes and their pathogenicity is a prerequisite for the development of better management procedures for controlling potato scab disease. The objectives of this research were to identify *Streptomyces* species and to evaluate the virulence genes for the detection of pathogenic *Streptomyces* species on potato tubers.

MATERIALS AND METHODS

Bacterial isolates

The bacterial isolates were obtained from potato tubers cvs. Atlantic and Spunta collected from Jom Thong District (18.2659, 98.6189), Muang District (18.7668, 98.9282) and Chai Prakan District (19.7534, 99.1515), Chiang Mai Province. Scab lesions were excised by scalpel (ca. 5 × 5 mm) and immersed in sodium hypochlorite solution (NaOCl) 1% (w/v) for 1 min and washed with sterile distilled water. After that, the potato pieces were placed on nutrient agar (NA), water agar (WA) and NA mixed with 150 µl of carbendazim at a concentration of 500 ppm (for fungal growth inhibition), and incubated at 25°C for 7 days (Lehtonen et al., 2004), after which colonies characteristic of *Streptomyces* were transferred onto fresh NA.

Pathogenicity assay

Pathogenicity tests were conducted on mini-tubers. Potato seedlings, cv. Atlantic, were firstly transplanted in the field and routine cultivation processes were performed thereafter. When the potato plants were close to flowering, stem cuttings were prepared and were transferred to pots containing sterilized sand, to produce mini-tubers. The isolates were grown on NA plates at 25°C for 7 days. Bacterial suspensions were prepared with sterile distilled water by serial dilution (1×10^8 CFU/ml). Then, 50 µl of the bacterial suspensions were inoculated to the mini-tubers and the tubers were recovered with sterilized sand. Inoculated plants were incubated at 25°C for 50 days (Miyajima et al., 1998).

Inoculation of *Nicotiana tabacum* was also performed to assess the pathogenicity of *Streptomyces* species using the protocol of Fyans et al. (2016). Leaves of 6-week-old *N. tabacum* plants were examined for necrosis in the area of infiltration.

Pathogenicity assay on plant seeds

Germination of eggplant seeds with *Streptomyces* sp. on NA plates and NA plates without bacteria used as controls was examined. The appearance of the seedlings was recorded after growth with the bacteria. When the seedlings showed hypertrophy and abnormal growth, or if the seeds did not germinate, the *Streptomyces* sp. isolates were considered pathogenic. The entire experiment was performed twice (Dees et al., 2013).

Identification of putative pathogenic *Streptomyces* by PCR

DNA was extracted using the protocol of Cheng and Jiang (2006). The virulence-related genes was determined by PCR using specific primers and PCR

conditions for the tomatinase enzyme (tomA), thaxtomin A (txtAB) and the necrogenic protein (nec1) coding genes as previously described by Alejo et al. (2019). Primers and the expected sizes of the PCR products are indicated in Table 1. The PCR products were purified and directly sequenced. PCR products were sequenced and analyzed using a BLASTx algorithm-based program of MEGA10 and deposited in the GenBank database (Atiq et al., 2013).

Table 1. Primers used for PCR detection of virulence-related genes.

Gene	Primer pair	Product size (pb)
***nec*1**	Nf: 5′-ATGAGCGCGAACGGAAGCCCCGGA-3′	700
	Nr: 5′-GCAGGTCGTCACGAAGGATCG-3′	
***txt*AB**	TxtAB1: 5′-CCACCAGGACCTGCTCTTC-3′	385
	TxtAB2: 5′-TCGAGTGGACCTCACAGATG-3′	
***tom*A**	Tom3: 5′-GAGGCGTTGGTGGAGTTCTA-3′	392
	Tom4: 5′TTGGGGTTGTACTCCTCGTC-3′	

16S rRNA gene amplification

Amplification of the 16S rRNA gene sequence was performed using universal primers 16SF and 16SR for amplification of a 1,500 bp region of the 16S rRNA gene (Song et al., 2011). The PCR mixture was prepared in a total volume of 25 µl: containing 50-100 ng per µl of DNA, using Quick Taq HS DyeMix (TOYOBO CO., LTD.) and 20 µM of each primer. PCR conditions were as follows: 5 min at 94°C, followed by 30 cycles consisting of 30 sec at 94°C, 64°C for 30 sec, 72°C for 1.5 min and followed by a final extension at 72°C for 10 min (Lehtonen et al., 2004). The PCR products were purified and directly sequenced. The sequences of 16S rRNA genes determined in this study were aligned with the Clustal W program. An evolutionary tree was inferred using the neighbour-joining method of MEGA10 and assessed by performing bootstrap analysis on 1,000 resamplings (Song et al., 2004).

RESULTS

Bacterial isolates

In this study, four isolates of *Streptomyces* species were isolated from necrotic lesions of diseased potato tubers collected in Chiang Mai Province including Jom Thong District (MJ20 and MJ21), Muang District (MM03) and Chai Prakan District (PE04). On NA, *Streptomyces* spp. isolates MJ20, MJ21, and MM03 mycelia were sympodially branched and formed flexuous spore chains containing 20 or more spores which rarely curled at the tip as similarly report by Lambert and Loria (1989). The spores were smooth and cylindrical. The spores of all isolates were white (Figure 1a-c). In addition, the aerial mycelium of *Streptomyces* isolate PE04 was sympodially branched and formed spiral spore chains containing 20 or more spores which rarely curled at the tip. Spores were smooth and cylindrical. The spores of all isolates were white but turned to grey after 5 days (Figure 1d).

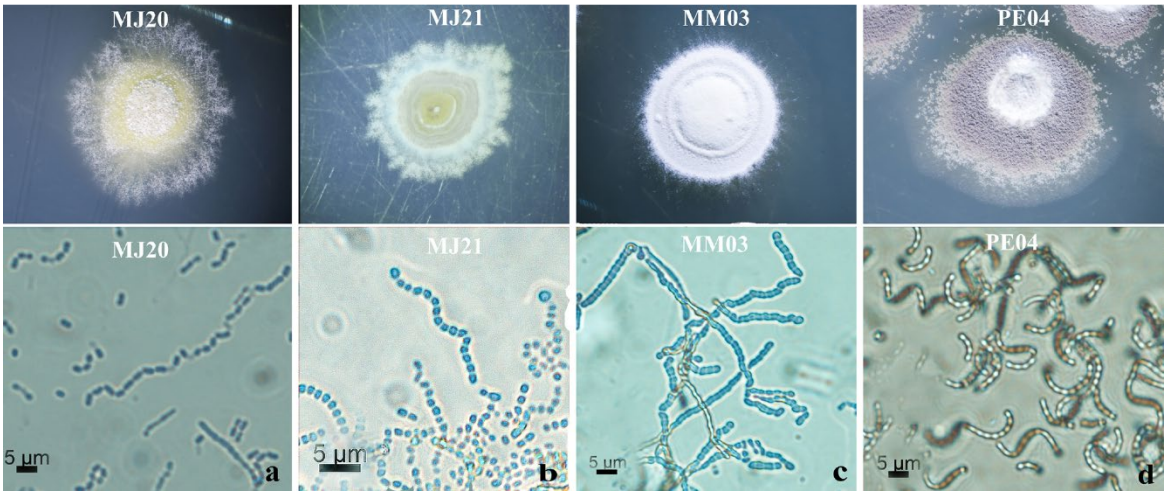

Figure 1. Cultural and micro-morphological characteristics of *Streptomyces* isolates: Colonies in nutrient agar at 28°C (top). Micromorphology of aerial growth appears as white hyphae under light microscope 100x (below) (Bar = 5 µm), (a) *Streptomyces* isolate MJ20, (b) *Streptomyces* isolate MJ21, (c) *Streptomyces* isolate MM03, (d) *Streptomyces* isolate PE04.

Pathogenicity assay

In pathogenicity tests, *Streptomyces* sp. isolate MJ21 induced raised or deeply-pitted corky lesions when compared with control under incubator conditions (Figure 2). Similar to scab lesions on field-grown tubers; but isolates MJ20, MM30 and PE04 did not produce lesions during the mini-tuber assay. In addition, a *N. tabacum* leaf infiltration assay showed that only isolate MJ21 could induce rapid necrosis in the area of infiltration. This later observation is of particular interest as it suggests that another virulence factor besides a phytotoxin. The isolate MJ21 is responsible for the observed tissue necrosis.

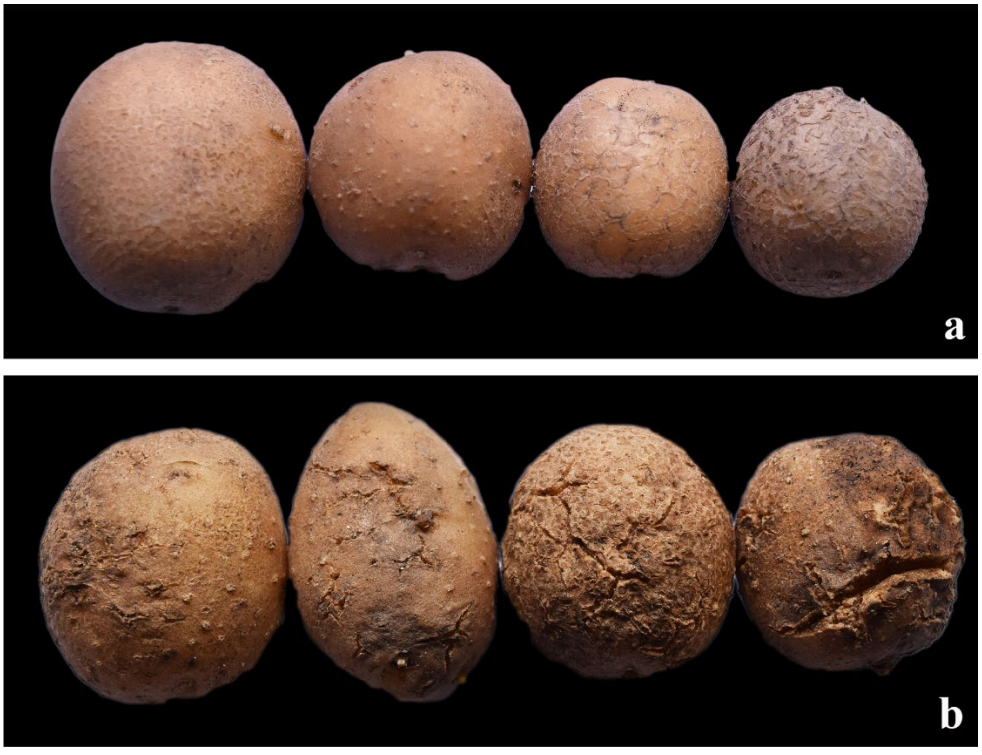

Figure 2. Pathogenicity of *Streptomyces* isolate MJ21on potato, (a) control, (b) symptoms on infected potato mini-tubers.

Pathogenicity assay on plant seeds

In pathogenicity tests, one of the putative pathogenic *Streptomyces* isolate MJ21 was tested on eggplant seeds. The abilities of isolate MJ21 to inhibit eggplant seeds germination were consistent with the presence of the phytotoxin, the pathogenicity determinant. The eggplant seeds grown with MJ21 failed to germinate. Although, the seeds grown on NA plates without bacteria germinated normally (Figure 3). Therefore, MJ21 can produce a phytotoxic secondary metabolite that inhibited the growth of roots and shoots of plant seedlings.

Figure 3. Appearance of plant seedlings 5 days after seeds were grown in a petri dish containing a 5-day-old culture of *Streptomyces* isolate MJ21 in comparison with the seeds grown on nutrient agar (NA) without bacteria.

Identification of putative pathogenic *Streptomyces* by PCR

The set of primers Nf and Nr was designed to amplifiy a 700-bp fragment of the nec1 intergenic region, 385 bp of the txtAB intergenic region and 392 bp of the tomA intergenic region. Isolate MJ21 produced a PCR product for two of the three pathogenic gene sets of primers tested. The *Streptomyces* isolate MJ21 only yielded PCR products for the tomA and txtAB set of primers, which are related to the production of a tomatinase enzyme and thaxtomin A. Isolate MJ27, MM03 and PE04 did not yield the three expected PCR gene size products (Table 2). When the sequences were deposited, the tomatinase gene clustered at 98.90-100% with the tomA gene of *Streptomyces* sp. strain st101 (accession number AIX97194.1) and *S. scabies* (accession number ACJ682220.1), and thaxomin synthetase A clustered at 96.15-100% with txtAB gene of *S. scabies* (accession number ACJ74085.1), *S. acidiscabies* (accession number AFK93859.1) and *S. turgidiscabies* (accession number ACJ74077.1). Furthermore, the *Streptomyces* isolate MJ21 has a toxigenic region that is associated with the tomA and txtAB genes (accession number OK064161 and OK064162, respectively).

Table 2. Detection of the virulence-related genes of Streptomyces from potato tubers by PCR.

***Streptomyces* isolates**	**Virulence-related genes**		
	Nec1 gene	txtAB gene	tomA gene
MJ20	-	-	-
MJ21	-	+	+
MM03	-	-	-
PE4	-	-	-

(+) presence; (-) absence

16S rRNA gene amplification

The sequence was compared with those in the GenBank (Table 3). The neighbour-joining dendrogram confirmed that MJ21 is a member of the genus *Streptomyces*, dendogram most closely related to *S. scabies* ATCC 49173 (accession number NR116531) and *S. scabies* RL-34 (accession number NR025865) with a sequence similarity of 99.93 – 100.00 %. Therefore, the bacterial isolate MJ21 was identified as *Streptomyces scabies* (accession number MW683488) (Figure 4).

Table 3. List of Sequences and GenBank accession numbers of *Streptomyces* species used in phylogenetic analyses.

***Streptomyces* species**	**Strain**	**Source**	**Origin**
Bacterial strain			
	MJ21	*Solanum tuberosum*	Thailand
Reference strains			
Streptomyces scabiei	RL-34	*Solanum tuberosum*	-
Streptomyces scabiei	ATCC 49173	*Solanum tuberosum*	Canada
Streptomyces europaeiscabiei	KACC 20186	*Solanum tuberosum*	-
Streptomyces europaeiscabiei	CFBP 4497	*Solanum tuberosum*	-
Streptomyces bottropensis	ATCC 25435	*Solanum tuberosum*	-
Streptomyces stelliscabiei	CFBP 4521	*Solanum tuberosum*	France
Streptomyces turgidiscabiei	ATCC 700248	*Solanum tuberosum*	-
Streptomyces turgidiscabiei	266	*Solanum tuberosum*	-
Streptomyces puniciscabiei	S77	*Solanum tuberosum*	Korea
Streptomyces acidiscabies	RL-110	*Solanum tuberosum*	-
Streptomyces acidiscabies	-	*Solanum tuberosum*	Mexico
Streptomyces tendae	175	Brown semidesert soil	Mongolia

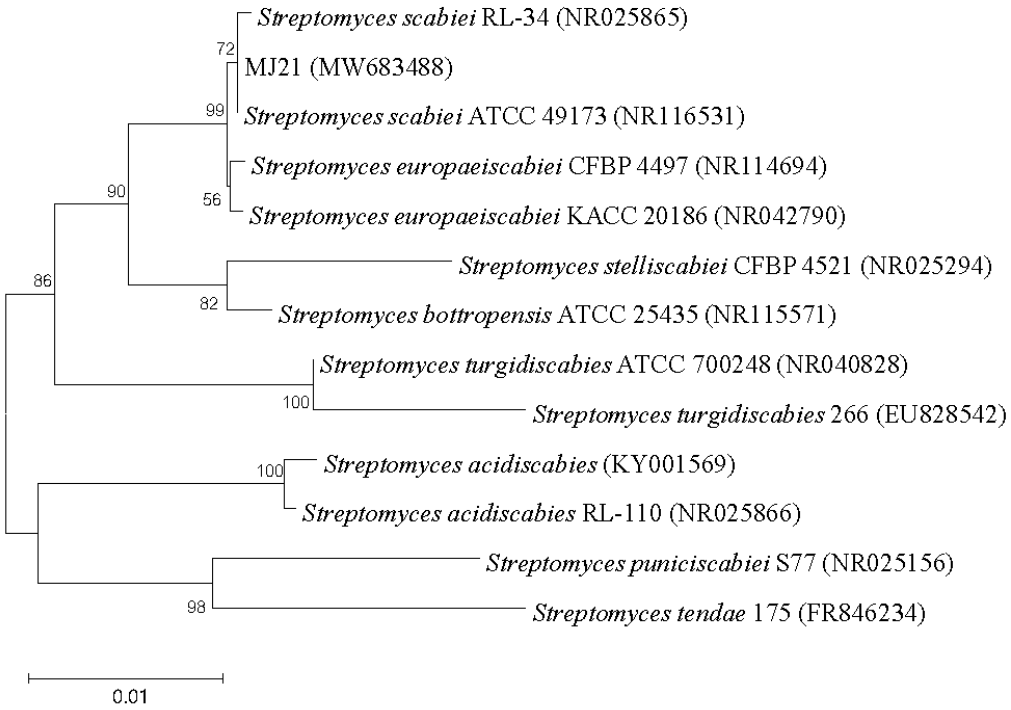

Figure 4. Phylogenetic tree of *Streptomyces* isolate MJ21 based on the 16S rRNA gene sequences obtained by the Neighbor-Joining method. The numbers at the branching points are the percentages of occurrence in 1000 bootstrapped trees.

DISCUSSION

Potato scab is a worldwide disease caused by different *Streptomyces* species. The pathogenicity test on potato revealed that *Streptomyces* isolate MJ21 induced damage to the general skin and caused symptoms in a larger proportion of the surface of the tubers. The current study showed that *Streptomyces* MJ21 causing potato scab disease can be classified as *Streptomyces scabies*. The *S. scabies* MJ21 formed flexuous spore chains, which are sympodially branched and rarely curled at the tip as similarly reported by Lambert and Loria (1989). The number of *Streptomyces* species is increasing as cited by literature listing more than 10 *Streptomyces* species which have been described as the causal agents of the potato scab complex disease in different geographical regions worldwide.

S. scabies MJ21 produced PCR products for the tomA and txtAB sets of primers, which are related to the production of a tomatinase enzyme and thaxtomin A, respectively. The characteristic PAI, also a saponinase like gene (tomA), apparently lies outside of nec1, more distant from txtAB. Nevertheless, some species typically have a different composition of PAI genes. Wanner (2007) reported that *Streptomyces* sp. Idaho X nearly always had tomA but not nec1. The tomA gene from the *Streptomyces* PAI has led to speculation as to virulence in potato diseases or its involvement in pathogenicity (Bouarab et al., 2002; Kers et al., 2005; Wanner, 2006). Flores-Gonzalez et al. (2008) and Wanner (2009) reported that different pathogenic *Streptomyces* species lack nec1 or tomA. Actually, most researchers suggested that nec1 and tomA genes are associated with pathogenicity but they weren't the primary determinants. Some pathogen strains lacking one or two of these genes were reported by Wanner (2009), Dees et al. (2013) and Leminger et al. (2013). According to Karagöz and Kotan (2017),

many researchers have formed a consensus that scab-causing strains most often produce thaxtomin but this may not be already operative. In Korea, *Streptomyces scabiei, S. acidiscabies* and *S. turgidiscabies* were pathogenic on progeny tuber and determined by the production of thaxtominA and homologs of nec gene (Park et al 2003). *Streptomyces scabiei* appeared more frequently in weakly acidic to neutral soils rather than strongly acid soil (Tashiro et al., 2012). Moreover, the existence of nec1 and tomA genes were also reported in non-pathogenic strains. On the other hand, Loria et al. (2006), Flores-Gonzalez et al. (2008) and Wanner et al. (2004) investigated some scab-causing *Streptomyces* species that may not have txtAB. Lapaz et al., (2017) Obtained *Streptomyces* isolates from potato-producing regions in Uruguay that found *Streptomyces scabiei, S. acidiscabies*, and *S. europaeiscabiei*. These isolates carried the txtA, txtB, tomA and nec1 genes, commonly associated with pathogenicity in Streptomyces and characteristic of PAI. However, as previously reported by Gartemann et al. (2003) potato also produces saponins, which could be the substrate for the putative tomatinase in the PAI. Further characterization of the identified Streptomyces strain and the phytotoxic substance of plants produced is currently progressing to better understand how the substance can cause disease. A particularly interesting finding of this study was that *Streptomyces scabies* MJ21 displayed a severe pathogenic phenotype against different plant hosts exhibited as inhibition of plant seed germination presumably by production of a novel secreted phytotoxic substance. As previously reported by Cao et al. (2012), a *Streptomyces* strain causing deeply-pitted lesions on potato tubers produced an 18-membered macrolide called borelidin, inhibited the growth of shoots and roots of radish seedlings and induced necrosis of potato tuber slices. The tomA and nec1 genes are also present in a wide range of potato common scab - inducing *Streptomyces* strains (Seipke and Loria, 2008).

CONCLUSION

Streptomyces isolate MJ21 causing potato scab disease is *Streptomyces scabies*. This is identifying and detecting a virulence gene of *S. scabies* in Chiang Mai, Thailand. The current research extends the knowledge of the presence of this microorganism in this area. Thorough characterization of bacterial pathogens of the potato common scab will deepen our cognition of the pathogenicity and this has important implications for the development of long-term control strategies that can be effective for the management of disease in potato growing regions.

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AUTHOR CONTRIBUTIONS

Conceptualization: Angsana Akarapisan, Methodology: Athidtaya Kumvinit, Supaporn Falert, Writing-review and editing: Angsana Akarapisan, Athidtaya Kumvinit, Supaporn Falert, Wichai Kositratana, All authors have read and agreed to the published version of the manuscript.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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