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SYMPOSIUM PAPER

Streptomyces – from Basic Microbiology to Role as a Plant Pathogen

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Abstract Streptomycetes are spore-forming Gram-positive bacteria found in soil in large numbers world-wide. More than 600 *Streptomyces* species have been described. The complex developmental morphology and molecular genetics of *Streptomyces* is connected to production of a wealth of secondary products, including more than 60% of antibiotics in industrial and pharmaceutical use. Streptomycetes have important roles in soil ecology as decomposers, though specific roles in microbial community structure and plant health are poorly understood. Some species are used as biocontrol agents while others have specific associations with potatoes as endophytes, pathogens or as part of plant rhizosphere communities. Very few species are plant pathogenic (ca. 1%), causing common scab disease on underground tubers in potatoes and root diseases in a broad range of host plants. Several unique aspects of *Streptomyces* as a plant pathogen are that (a) there is a main dominant pathogenicity determinant (thaxtomin); (b) only the developing underground stems, stolons and tubers are susceptible to potato common scab (CS); (c) *Streptomyces* does not incite a plant defense response; and (d) CS is not easily managed. The best available control is the use of resistant potato cultivars and there is wide variation in resistance (tolerance) among potato cultivars, though none is completely resistant. New molecular genetic tools, including the complete genome sequences of a number of plant pathogenic *Streptomyces* species and association mapping using the potato genome sequence, promise greater understanding of the genetics of CS tolerance and of regulation of thaxtomin production and contributory pathogenicity factors for better management of potato CS.

Resumen Los Streptomycetos son bacterias que forman esporas, Gram-positivas, que se encuentran en gran número en el suelo en todo el mundo. Se han descrito más de 600 especies de streptomicetos. La compleja morfología de desarrollo y la genética molecular de los streptomicetos están conectadas a la producción de muchos productos secundarios, incluyendo más del 60% de antibióticos de uso industrial y farmacéutico. Los streptomicetos tienen un papel importante en la ecología del suelo como degradadores, a través de funciones específicas en la estructura de la comunidad microbiana y la sanidad de la planta es pobremente entendida. Algunas especies se usan como agentes de biocontrol mientras que otras tienen asociaciones específicas con las papas como endófitos, patógenos, o como parte de las comunidades de la rizosfera. Muy pocas especies son fitopatógenas (aprox. 1%), causando la enfermedad de la roña común en tubérculos bajo tierra en papas, y enfermedades de la raíz en una gran amplitud de plantas hospedantes. Varios aspectos únicos de *Streptomyces* como fitopatógeno son que (a) hay una determinante principal dominante de la patogenicidad (thaxtomin); (b) solo los tallos subterráneos en desarrollo, los estolones y los tubérculos son susceptibles a la roña común de la papa (CS); (c) *Sterptomyces* no incita a una respuesta de defensa de la planta; y (d) CS no es fácilmente manejable. El mejor control disponible es el uso de variedades resistentes de papa y hay una variación muy amplia en la resistencia (tolerancia) entre las variedades, aunque ninguna es completamente resistente. Nuevas herramientas de genética molecular, incluyendo las secuencias completas del genomio de un número de especies de *Streptomyces* fitopatógenas y el mapeo de la asociación

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Added as Dr. Wanner sadly passed away on 25 Dec 2014

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usando la secuencia genómica de la papa, prometen un mayor entendimiento de la genética de la tolerancia a CS y de la regulación de la producción de thaxtomin y de los factores que contribuyen a la patogenicidad para un mejor manejo de la CS de la papa.

Keywords Potato common scab · Pathogenicity determinant · Thaxtomin

Economic Significance of Common Scab

Soil-borne pathogens and pests cause about 90% of the major diseases of the most important US crops These diseases account for half of US crop losses - $4 billion annually- and limit yield potential. CS economic losses are primarily due to skin blemishes. For potato seed certification, CS falls under the category of skin defects; seed potatoes are rejected if more than 5% of the tubers have significant defects. Common scab reduces the quality and marketability of the potato crop. Although separate data on CS occurrence and severity are not kept, seed potato production, tablestock/fresh market, processing (French fries and potato chips (crisps) and dehydrated potato industries are all affected. There is evidence that CS also reduces yield in some cases (Hiltunen et al. 2009), and severely scabby greenhouse-grown tubers are always smaller than tubers grown in un-infected pots (Wanner, unpublished). For fresh market (ware), potatoes are rejected if defects substantially affect appearance. For processing, a potato lot is rejected if more than 5% of the potato weight must be removed by peeling. Although good records of economic losses due to potato CS are not kept, it was estimated that 82% of fields were affected by PCS in 2002, costing ca. $100/ha (Hill and Lazarovits 2005). Better estimates of losses due to CS would be valuable in targeting best scab management strategies.

Potato common scab is a saprophyte that may over-winter either in soil or on the surface of tubers, thereby serving as next year's inoculum source. The inoculum is spread by water; wind, on seed tubers and farm equipment with leftover soil residue. Once present in the soil, *S. scabies* may survive indefinitely since it finds refuge in organic matter (disease cycle in Kirk and Wharton 2014).

Formation of CS Lesions

Only the developing underground parts of stems, as well as stolons and tubers are susceptible to (potato) CS. Roots and aboveground plant parts are not susceptible nor are tubers with fully mature skin (lignified). Common scab lesion symptoms are highly variable in both form (superficial, raised or warty, and pitted lesions) and in extent of coverage of underground tuber skin (Rosenzweig 2014). Plant pathogenic *Streptomyces* initially infect the developing tuber epidermis (periderm). As epidermal layers are infected, the periderm breaks and the addition of new corky repair layers form a scabby lesion. No wound is required for lesion initiation, though scab symptoms are often seen in wound areas. The pathogenic bacteria may enter through lenticels but lenticels are not a prerequisite for infection. Once the mature periderm is formed (suberized) tubers are no longer susceptible to pathogenic *Streptomyces* and there is no further increase in scab lesion size in long-term storage. Types of scab lesions formed are apparently dependent on cultivar, timing of infection, virulence of the infecting strain and environmental conditions, and may depend on additional virulence factors.

Morphology, Biology and Genomes of *Streptomyces*

Streptomyces are Gram-positive, filamentous spore-forming bacteria that are commonly found in soils, although they have also been isolated from marine organisms and infrequently in plants or animals (Seipke et al. 2012). Agricultural soils contain about 10^6-10^7 CFU per gram of soil (Janssen 2006). Though these numbers are large, this is only a tiny proportion of the estimated agricultural soil microbial population of 10^9 CFU per gram. At least 600 *Streptomyces* species have been described (Labeda 2010) but only a small fraction (about a dozen) of these are known to be plant pathogens (St-Onge et al. 2008; Hao et al. 2009; Wanner 2009). They are largely decomposers of plant or other biological materials. They have been isolated from bulk soil, plant rhizospheres and as endophytes. Although little is known about their distribution and activities in soil, some species may be specifically associated with certain plant genera/species (Manter et al. 2010; Weinert et al. 2011).

Streptomyces have linear genomes capped by long terminal inverted repeats, which serve to protect them from degradation by abundant soil nucleases. The complete genome sequences of more than 20 *Streptomyces* species are now available, including both industrially useful and plant pathogenic species. *Streptomyces* genomes are relatively large, ranging from ca. 8 Mb to 12 Mb (as compared to *E. coli* at 4.6 Mb, or *Bacillus cereus* at 5.4 Mb). The central 4.5–6 Mb appears to contain the housekeeping genes necessary for growth and metabolism (Chater et al. 2010), while multiple gene cassettes/operons encoding a wide variety of secondary metabolites are found largely in the 2–3 Mb at each chromosome end. Many of these are demarcated by having small inverted repeats, insertion sequence elements or phage integration sites on both sides of the secondary metabolite-encoding cassettes, suggesting that they have been horizontally transferred into and between *Streptomyces* genomes.

Genomes of five plant pathogenic *Streptomyces* species have been sequenced, *Streptomyces scabies* RL 87- 22 (10.15 Mb) DDBJ/EMBL/GenBank accession number NC_013929; *Streptomyces acidiscabies* 84-104 (~11 Mb), accession number AHBF01000000 (Huguet-Tapia and Loria 2012); *Streptomyces ipomoea,* the cause of scab in sweet potato, accession number AEJC00000000.1, and two whole genome sequences from *Streptomyces stelliscabiei* NY02-03A and from *Streptomyces sp*. ID01-12c (Wanner, unpublished). These five genomes have not yet been fully characterized and aligned.

High genomic complexity in both housekeeping genes (Doroghazi and Buckley 2010; Labeda 2010) and in genomic islands found at the ends of the chromosome is connected to the ability of *Streptomyces* species to produce large numbers of secondary compounds (Chater et al. 2010). Various *Streptomyces* species have been the source of more than 60% of medically important bioactive anti- or pro-microbials, including antibiotics (e.g., erythromycin, neomycin, streptomycin, tetracycline, vancomycin, rifamycin, chloramphenicol), anti-fungal agents (e.g., nystatin and amphotericin B), and immunosuppressive agents and anticancer compounds (e.g., microstatin). Streptomycetes also produce enzymes widely used in industry, which include pigments, enzymes (proteinases, glucosyl hydrolases), and plant growth regulators (Chater et al. 2010). Several *Streptomyces* strains have been developed [and marketed] as biocontrol agents against fungal and nematode pathogens and pests. At least two species have been formulated into microbial products, (Mycostop® from *Streptomyces griseoviridis* strain K61and Actinovate® from *S. lydicus* WYEC 108) (Minuto et al. 2006; Zeng et al. 2012).

***Streptomycetes* as Plant Pathogens**

A combination of factors is needed for the inception and progression of plant disease, including a susceptible plant host, a virulent pathogen and numerous environmental factors such as soil characteristics, climate and weather, cultivation practices, and the agricultural soil microbial community. Plant pathogenic *Streptomyces sp*. cause underground tuber and root diseases known as common scab. Only about a dozen species of *Streptomyces* are known to include pathogenic isolates, and nearly all of these fall into one narrow segment of the *Streptomyces* phylogenic tree. Plant pathogenic *Streptomyces* species are broad host range pathogens, and cause a wide range of scabs, wart or pit symptoms (Rosenzweig 2014). Large numbers of isolates have been obtained from potato scabby lesions, clean potato skins and potato rhizosphere soil. They differ in phenotypic characteristics, such as color of the substrate mycelium and spores, and utilization and secretion of a wide variety of secreted enzymes and secondary products (Rosenzweig 2014). The most important host is potato but underground root and tuber crop hosts, including sugar beet, radish, turnip, carrot, and even peanut, are all apparently susceptible (Goyer and Beaulieu 1997; Loria et al. 1997). A few other poorly characterized diseases are associated with pathogenic *Streptomyces sp.*, such as root tumor of melon (Loria et al. 1997). The basis of pathogenicity in the plant pathogenic streptomycetes is production of a family of toxins called thaxtomins. Thaxtomin has phytotoxic effects and can also function as an herbicide, causing necrosis and seedling wilting (King et al. 1991; King et al. 2001; King and Calhoun 2009).

To date, 13 species or strains of plant pathogenic *Streptomyces* have been found in North America, based on the traditional bacterial criterion of the sequence of the bacterial 16S ribosomal RNA gene (St-Onge et al. 2008; Hao et al. 2009; Wanner 2009). The distribution of *Streptomyces* species and pathotypes that have been associated with potato CS in North America is patchy. *S. scabies* seems to be most abundant from the mid-plains eastward, with *S. europaeiscabiei* and *S. IdX* (Wanner 2007) more common in the west (Wanner 2009). Another widespread and abundant plant pathogenic species is *S. stelliscabiei*; again found sporadically in the upper Midwest and northeast. In addition, a number of infrequently identified strains/ribotypes have been found. *S. acidiscabies*, described as a prevalent species causing ‘acid scab’ because of its ability to tolerate soil pH below 5.0 in the 1950–1960 era, is no longer prevalent in isolates from Maine and New Brunswick (only 10 isolates out of a few thousand), though *S. acidiscabies* has been identified in Japan, China and Korea (Dees and Wanner 2012). A species found rarely in Wisconsin, *S. turgidiscabies*, is apparently prevalent in Scandinavia, the UK, Korea, China and Japan (Dees and Wanner 2012). Of the 13 North American ribotypes, 6 include isolates that have been tested and confirmed as pathogens on potato and/or radish (Wanner 2009; Wanner, unpublished). Both non-pathogenic and pathogenic isolates of all of these species/strains have been identified on potato tubers or in the soil surrounding potato plants (Wanner, unpublished).

Plant pathogenicity depends on thaxtomins, a phytotoxic group of very closely related cyclic dipeptides, first discovered and characterized by Russell King and colleagues in New Brunswick (Lawrence et al. 1990; King et al. 1991). Thaxtomins are the only known pathogenicity determinants for CS disease. Pure thaxtomin A applied to potato tissue causes necrosis (is phytotoxic) in potato tuber slices and has herbicidal activity in growing sprouts of virtually all plants species. A small gene cluster contains all necessary genes for a non-ribosomally-encoded peptide synthase and genes responsible for modification of thaxtomin (Kers et al. 2005; Bignell et al. 2010). This gene cluster functions as a PAI (Pathogenicity Island), and has shown it can be horizontally transferred from pathogenic to certain closely-related nonpathogenic *Streptomyces* species (Kers et al. 2005). Thaxtomin apparently disrupts cellulose biosynthesis or deposition, weakening the plant cell wall and leading to wound deposition of additional layers of periderm that accumulate to form a scab lesion (Khatri et al. 2011). One of the mysteries of CS is the variation in symptoms, ranging from relatively superficial individual 'freckles' or scabs to raised warty or callus-like lesions to deep pitted lesions, all of which may occur as few discrete lesions, or they may coalesce to cover large areas of the tuber surface.

Although there is an influx of Ca^{++} and H^{+} ions, which are typical early signals for plant defense (Tegg et al. 2005; Errakhi et al. 2008), there is currently no evidence of a classic defense response in potato tubers after infection with plant pathogenic *Streptomyces* (Flinn et al. 2005). Rather, the ion influx appears to be related to a thaxtomin-triggered necrotic or hypersensitive response leading to cell death in seedlings and other tissues, like cut potato tuber slices.

Accessory factors leading to these complex CS phenotypes are not well-understood, and may not be directly attributable to the *Streptomyces* genomic sequence, as the type and frequency of lesions in the same cultivar and inoculated with the same *Streptomyces* strain can develop different amounts and types of CS in different fields or different years (Wanner et al. 2014). Though tryptophan is a substrate for thaxtomin, high tryptophan levels as well as high auxin levels have been shown to down-regulate the expression of genes in the biosynthetic gene cluster (Lerat et al. 2010; Legault et al. 2011).

Worldwide, occurrence and distribution of plant pathogenic *Streptomyces* species seems to be somewhat patchy as well. In Europe, the prevalent species seems to be *S. europaeiscabiei*, while *S. turgidiscabies* has been found in China, Japan, Korea, North America (rare), and the UK. Since *S. scabies* and *S. europaeiscabiei* cannot be distinguished by 16S rDNA sequence, there is some doubt whether species that have been called *S. scabies* are all *S. scabies*. The two species can be separated by the sequence of the bacterial ribosomal intergenic spacer (Flores-González et al. 2008), but this has often not been done.

Scab Management Practices and their Effectiveness

Control of *Streptomyces*-caused CS is inadequate and the disease is not easily managed. There are currently no consistently reliable control measures, except the use of resistant potato cultivars (Table 1).

There is no complete resistance/tolerance in commercially grown potato cultivars, though there is large variation in CS susceptibility. Progress is being made in developing more CS-resistant cultivars, and there are now several lines now have lines with substantially better resistance to CS (Michigan State University and University of Wisconsin potato breeding programs, personal communications). Testing of varieties for CS in field trials is an on-going activity (Haynes et al. 2010).

The microbial community in and on developing potato tubers is a poorly understood factor in the inception and development potato CS disease symptoms. The soil endophyte microbial community has been shown to differ between potato cultivars (Mendes et al. 2011) and potato fields (Kinkel et al. 2012). Microbial soils in potato fields differ as well under different tillage practices (Krechel et al. 2002; Peters et al. 2004; Sessitsch et al. 2004; Sturz et al. 2005; Wiggins and Kinkel 2005; Berg and Smalla 2009; Larkin et al. 2010; 2011). Specific *Streptomyces* strains have been connected to fields suppressive for CS (Lorang et al. 1995; Neeno-Eckwall et al. 2001). Future research directed toward characterization of rhizosphere/endophyte microbial communities in and on

Table 1 Control measures for common scab and their effectiveness

Control measure	Effectiveness
Clean seed potatoes	Insufficient; *Streptomyces* is endemic, ubiquitous, soil-borne
Seed treatment with chemicals	Results erratic
Lower soil pH to<5.2	Limits rotation crops; can fail
High soil moisture (near field capacity for 4–5 weeks beginning at tuber initiation)	Often fails
Soil amendments: mulches, plant residues; organic amendments (liquid swine manure) potential elicitors, e.g., chitosan (crab shells), BTH (ActiGard); green clay	Results variable, inconsistent; often fail
Chemical fumigation (PCNB, chloropicrin)	Works for a season; expensive
Rotation crops or long rotations	Ineffective
Sulfur fertilizers	Reduces scab severity in some locations
Resistant plant varieties	Most reliable, cost effective control method, but no known complete resistance
Biocontrol	Needs testing and validation

Table adapted from (Dees and Wanner 2012) developing tubers may correlate with CS susceptibility/resistance, providing further avenues for enhancing control of CS.

A new resource for studies of plant pathogenic *Streptomyces* species is the curated research collection at the Agricultural Research Service in Beltsville, MD (Wanner, unpublished). Isolates mainly form America but also some from Africa are available on request from the author for anyone to use. This is an active and growing research collection consisting of more than 2500 isolates. Most were derived from scabby potato lesions, clean potato skins, and potato rhizosphere or field soils. This collection is envisioned as a useful tool for comparative genomics, population biology and epidemiology, soil ecology, sources of mobile elements, sources of biocontrol strains, and more. A preliminary description is found in Wanner 2009 (Wanner 2009).

Summary and Outlook

Traditional CS control measures are insufficient and often fail. Factors that have hampered effective CS management and development of more CS-resistant potato cultivars include the wide variability in CS incidence and severity from year to year and location to location, variable effects of environmental conditions and genetic variation in pathogen populations. Knowledge gaps limit efforts to devise better strategies for control of CS. Current knowledge gaps include a thorough understanding of the plant genetics of CS tolerance, the mechanisms of *Streptomyces* bacterial infection of plants, and the dynamics of the soil and potato microbial flora. Recent research on the Gram-positive soil *Streptomyces species* causing (potato) CS has focused on two areas that may help in controlling CS: developing rational, research-based measures based on understanding the pathogen, characterizing pathogen variation, distribution and phylogenetic relationships in order to better define what circumstances lead to disease, and development of reliable disease-resistant potato cultivars. Future research will be aimed at the dynamics of the rhizosphere microbial flora/potato/pathogen interaction during disease development. We recently began studies of the soil microbial flora that will hopefully shed additional light on CS disease etiology and strategies to minimize or eliminate the disease.

Research is needed to understand the plant/pathogen/(microbial) environment interaction and use this knowledge to understand what is a healthy soil or rhizosphere microbial flora, and to improve control of CS diseases. Further progress in developing integrated management strategies for controlling CS is likely to come from

1. Physiological studies exploring what potato plants produce in response to *Streptomyces*/thaxtomin, and if plants produce and exude molecules that induce thaxtomin production by the bacteria.
2. Studies of rhizosphere and endophyte biology.
3. Mapping of genes connected to CS resistance or susceptibility for use in breeding programs.
4. Identification of better sources of CS resistant potato lines by traditional breeding utilizing resistant germplasm (potentially from wild species) or by creating transgenic lines using new knowledge of potato and pathogen genomics to examine the epidemiology of CS, search for pathogenicity factors in various *Streptomyces* species and strains, and search for susceptibility/resistance factors to CS in potatoes.

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Sadly, Dr. Wanner passed away on 25 December 2014. The potato community will miss Leslie. She contributed greatly to our knowledge of Common Scab and Streptomycetes.

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