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THE 3RD INTERNATIONAL *SPONGOSPORA* WORKSHOP, OSLO, NORWAY, JULY 2024

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The 3rd International *Spongospora* Workshop was held on 6 July 2024 at the Scandic Fornebu Hotel in Oslo, Norway (www.spongospora.net/Oslo_2024), in association with the 22nd Triennial Conference of the European Association for Potato Research (EAPR).
The Workshop Organising Committee included Dr Ueli Merz (Convenor), Prof. Richard Falloon, Dr Iain Kirkwood (Potatoes New Zealand Inc.), Dr Alison Lees (James Hutton Institute, Scotland), and Prof. Calum Wilson (University of Tasmania, Australia). The Committee had collaborated for the previous 7 months, in association with the Organisers of the 22nd Triennial EAPR Conference, to develop the programme and finalise arrangements for the meeting.
The Workshop was attended by 37 participants from 14 countries, and 15 papers were presented on behalf of a total of 66 co-authors, indicating the extent and breadth of international research activity on diseases caused by *Spongospora*. The Workshop papers included: a knowledge review of diseases caused by *Spongospora subterranea* and prospects for their management; three papers on biology and detection of the pathogen, four papers on plant resistance to *S. subterranea*, six papers on aspects of control of these diseases, and a paper describing the recently established International Potato Research Partnership.

This report publishes abstracts of all the papers presented at the 3rd International *Spongospora* Workshop, to summarize recent knowledge advances publicized at the Workshop relating to this important potato pathogen and the diseases it causes.

KNOWLEDGE REVIEW

Spongospora diseases of potato; current knowledge and prospects for effective management

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Spongospora subterranea (*Plasmodiophorida, Protozoa*) was first described as a potato pathogen in 1842[a], although powdery scab of potatoes was probably known long before. This pathogen and its host most likely originated in northern South America, but *S. subterranea* has since disseminated to most potato-producing countries[b, c]. The pathogen causes potato root hair infections, root galls and tuber lesions, and vectors *Pomovirus solani*, all of which can harm crop productivity. Host resistance is the best strategy for *Spongospora* disease management. Other appropriate crop management practices can also reduce effects of the pathogen[c], including:
- pre-planting (long *Solanum*-free crop rotations, field choice, fertilizers, soilborne pathogen tests, potato processing effluent disposal, planting date);

- at planting (*Spongospora* resistant cultivars, disease-free seed tubers, soil and seed tuber pesticide treatments, organic amendments); and
- during crop growth (fertilizers, irrigation management).

Future research and technology transfer should involve[c]:
- implementing practical integrated disease management for potato producers;
- increasing knowledge of *Spongospora* genetics, and host/pathogen/environment interactions;
- identifying markers to assist potato breeding for *Spongospora* resistance;
- optimizing mass screening to identify resistant *Solanum* germplasm; and
- developing potato cultivars with resistance to *Spongospora* diseases.

[a] Wallroth RW (1842). Der Knollenbrand der Kartoffel. *Linnaea. Ein Journal für die Botanik in ihrem ganzen Umfang* 16: 332.

[b] Gau RD, U Merz, RE Falloon, PC Brunner (2013). Global genetics and invasion history of the potato powdery scab pathogen, *Spongospora subterranea* f. sp. *subterranea*. *PLoS ONE* 8(6): doi.org/10.1371/journal.pone.0067944

[c] Strydom RF, CR Wilson, RS Tegg, MA Balendres, JE van der Waals (2024). Advancements in *Spongospora subterranea*: current knowledge, management strategies, and research gaps. *Potato Research*: doi.org/10.1007/s11540-024-09701-8.

SPONGOSPORA BIOLOGY AND DETECTION

Plant starch plays an important role in sporosorus formation by *Spongospora subterranea* f. sp. *subterranea*

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Powdery scab, caused by the soil-borne protist *Spongospora subterranea* f. sp. *subterranea* (*Sss*) (*Plasmodiophorales, Phytomyxea*), poses significant challenges to global potato production. Symptoms of this disease include skin blemishes and root galls. *Sss* produces resting spores in sporosori, characterized by robust cell walls that confer resistance to degradation and desiccation. Among the Plasmodiophorids, *Sss* produces the most elaborate sporosorus structures, which are sponge-like aggregations composed of many resting spores. Sporosorus formation within root galls was investigated, using scanning electron and light microscopy. Starch grains accumulated during sporosorus formation. Light microscopy of ultramicrotome sections showed presence of high-amylopectin starches enveloped by plasmodia as precursors to sporosori, indicating involvement of starch in sporosorus formation. Reduced total starch levels in galls and infected roots compared to healthy roots indicated that starch was consumed during gall maturation. Gene expression analysis revealed downregulation of starch-degrading enzymes and upregulation of starch synthesis-related genes in the infected roots, suggesting pathogen-mediated manipulation of starch homeostasis for sporosorus development. These results indicate that *Sss* manipulates starch homeostasis for sporosorus development within host root galls.

Complete genome sequence of *Spongospora subterranea* from North America

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Obtaining high-quality nucleic acids of *Spongospora subterranea* is difficult due to durability of the sporosori and the obligate nature of the pathogen. Root galls were collected from a potato plant ('Russet Burbank'), and Oxford Nanopore long-read sequencing was completed from sporosori in

the galls using genomic DNA. Illumina short-read sequencing was also completed using genomic DNA from sporosori collected from pustules on tubers from a single commercial potato field in the same region. Polishing long-reads with short-reads resulted in a 31.51 Mb high-quality genome with GC content of 45.7% assembled from 346 scaffolds. The genome was predicted to have 10,325 protein-coding genes, including 321 potential fungal effectors, 700 signal peptide proteins, 135 carbohydrate active enzymes, 1981 KEGG assigned genes, and 2660 COGs. This *S. subterranea* genome resource provides a basis for increased understanding of international populations of the pathogen, and knowledge to assist development of new management strategies for powdery scab and potato mop-top virus of potato.

Validation of methods/protocols for routine detection and quantification of *Spongospora subterranea* in field soils and in production and storage facilities

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Spongospora subterranean f. sp. s*ubterranea* (*Sss*) produces durable resting spores that can survive in soil for many years. Sporosori can also be transmitted on infected seed tubers, in infested growing substrates, and on contaminated farm equipment. Powdery scab is not a major disease in France, but occasional infections occur in potato plants grown in infested soils or substrates (mainly peat), so strict preventive measures are taken to avoid dissemination of *Sss*. A set of detection and quantification tools have been developed and used to monitor *Sss* in epidemiological studies. Reliability of these tools for routine preventative detection of *Sss* has been assessed for soils from regions where seed potatoes are grown in France, and from first generation seed potato production and storage operations. To assess reliability of field detection of *Sss*, eight soils with different textures were collected from seed potato fields in different geographical areas. For detection of *Sss* in greenhouses, dust was collected using a swab method. Different swabs and DNA extraction kits were used to optimize detection. Protocols for detection of *Sss* in water were also assessed, using different membranes and filters, and different DNA extraction kits. Detection sensitivity was compared for the different protocols using real-time PCR. The best protocols were selected and tested for the detection of *Sss* in samples collected from fields, greenhouses, or potato storage facilities. DNA extraction from soil was automated using a platform allowing DNA extraction from up to 380 samples. This is useful for routine detections, and this extraction system will be assessed for other substrates.

HOST RESISTANCE TO *SPONGOSPORA SUBTERRANEA*

Salicylic acid-mediated defense against potato infection by *Spongospora subterranea*

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Powdery scab of potato is a soilborne disease caused by *Spongospora subterranea f. sp. subterranea* (*Sss*). The main symptoms caused by *Sss* are root galling and tuber blemishes. The pathogen also vectors potato mop-top virus (PMTV) that causes tuber necrosis. Both pathogens reduce the economic value of potato crops and impede foreign trade. Effective control methods are currently unavailable, emphasizing the need to investigate sources of host genetic resistance. Potato hairy roots were used to study gene expression responses to *Sss*, and to validate gene involvement using gene editing. Following *Sss* inoculations, differential expression of plant defense-related genes was observed in the hairy roots. Based on defense marker gene expression, a pivotal role was indicated of salicylic acid (SA)-mediated defense against *Sss*. This was further investigated by assessing the impact of SA-mediated defense on *Sss* infection. Transgenic hairy root lines were generated, including those overexpressing the SA receptor *SlNPR1* and those with knockdown of a second SA receptor, *StNPR3*, using CRISPR/Cas9-based gene editing. Reduced *Sss* propagation was observed in the *SlNPR1*-overexpressed lines and the *StNPR3*-knockdown lines. Consistent with these results, pretreatment of hairy roots with SA also reduced *Sss* propagation, supporting the role of SA-induced

defense mechanisms against *Sss*. Variations in susceptibility to *Sss* across potato cultivars have also been observed, suggesting a genetic basis for disease resistance. Transcriptomics using RNA-seq on hairy root samples from different cultivars after *Sss* infection has given insights into involvement of SA-mediated defense and other potential mechanisms for preventing *Sss* infections.

Comparative genomics of *Spongospora subterranea* f. sp. *subterranea* isolates for effector mining

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Breeding potato varieties resistant to *Spongospora subterranea* f. sp. *subterranea* (*Sss*) is impaired by phenotyping methods, which can give variable results due to environmental conditions, inoculum instability, and isolate-specific tolerance/resistance in host lines. Screening based on effector response ("effectoromics") could replace difficult phenotyping assays, and has been used to identify *R* genes in potato that confer resistance to *Phytophthora infestans* and *Synchytrium endobioticum*. Effectoromics relies on effectors identified in predicted secretomes, but no specific effector signatures are known for *Sss*. This study aimed to identify new effectors and corresponding signatures, and select secretome genes which could have resulted from previous *Solanum*/*Sss* interactions and are under diversified selection pressure. To capture the required genomic diversity for selection, *Sss* genomic DNA was prepared from sporosori from more than 20 different collections originating from 15 countries in five continents. These samples were assessed for *Sss* DNA proportions using Taqman-qPCR, and were subjected to Illumina paired-end sequencing. Initial comparison of the isolates showed at least two groups, one being very different from the current reference genome (SSUBK13), as indicated by regions that were either highly polymorphic or absent in this group when mapped to the reference. To help assemble polymorphic regions through *de novo* assemblies, two isolates representing the two groups were selected for long-read Nanopore sequencing. Characteristics of their assemblies were described, including insights into genome-wide diversity. There is potential to develop an *Sss* pangenome knowledge base as a resource for plant pathology and potato breeding research.

Development of a phytotron-based assay for potato resistance to *Spongospora subterranea* f. sp. *subterranea* root galls and tuber powdery scab

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S*pongospora subterranea* f. sp. *subterranea* (*Sss*) causes powdery scab on potato tubers and root galls. Tuber skin lesions adversely affect quality and marketability of fresh and seed tubers, and tubers for processing. Root galls impact plant health, reduce production and contribute to inoculum build-up in the soil. *Sss* is also the vector of potato mop-top virus (PMTV), which causes necrotic

lines and rings in potato tubers. Presence of *Sss* and PMTV in soils in several countries is increasing. Germplasm screening for resistance/tolerance to *Sss* has been mostly based on field trials which are labour intensive, costly, time-consuming, and require the use of infected tubers for planting. These factors result in resistance selection processes that can take up to 4−5 years, which is unsuitable for early-generation selection in plant breeding programmes. Powdery scab and PMTV are also dependent on climatic conditions, which affect repeatability, reproduction and reliability of individual trails. The main focus of field trails is on powdery scab skin lesions, because root gall field assessment is complex. An assay was therefore developed to assess susceptibility of germplasm to *Sss* at an early stage and under controlled environment conditions, which would assist resistance breeding. Effects on disease expression of temperature, humidity, LED light spectra, growth substrate, time of inoculation, and inoculum origin and concentration, have been assessed. Experiments conducted in a phytotron using *in vitro* cultured plantlets of several varieties have shown grades of tolerance to *Sss* root galling and tuber skin lesions.

***Spongospora subterranea* f. sp. *subterranea* affects plant susceptibility to subsequent pathogen infections under controlled environment conditions**

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Effects of *Spongospora subterranea* f. sp. *subterranea* (*Sss*) on potato susceptibilities to subsequent infections by above ground pathogens have not been previously reported. Effects were assessed of *Sss* on disease susceptibility to, and symptom development from, subsequent pathogen infections, on six potato cultivars of economic importance in the USA. Tubers of 'Lamoka' and 'Snowden' were the most susceptible to powdery scab, but 50 to 92% of asymptomatic tubers (depending on cultivar) across the six cultivars tested positive for *Sss* DNA. No correlations were detected between frequency of *Sss* on asymptomatic tubers and *Sss* biomass on these tubers, nor across the six cultivars between root colonization and root gall formation. Through detached leaf assays for leaves from *Sss*-infected and non-infected potato plants at 12 weeks post-inoculation, *Sss*-infected 'Silverton' plants were more susceptible to hemibiotrophic late blight, and less susceptible to necrotrophic white mold, than non-*Sss* infected plants, and *Sss* infection increased susceptibility of the leaves of 'Goldrush' and 'Atlantic' plants to white mold. These results highlight the complexity of *Sss*-host interactions, and emphasize that lack of disease expression does not necessarily indicate resistance of a potato cultivar to *Sss*.

MANAGEMENT OF SPONGOSPORA DISEASES

Potassium to magnesium ratios affect expression of *Spongospora subterranea* in compacted clay soils

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Spongospora subterranea (*Ss*) causes galls on potato roots and powdery scab on tubers. Although, this pathogen can survive in the soil for > 10 years, knowledge is lacking on how soil physical and chemical factors affect diseases caused by *Ss*. Potassium (K) and magnesium (Mg) in soils have an antagonistic relationship, and K to Mg ratio should be 0.3 for best plant nutrient uptake, while an imbalance from this inhibits root growth. This study evaluated influences of different responses to K/Mg ratios

on development of *Ss* in three *Ss*-susceptible potato cultivars ('Red Lady', 'Asterix,' 'Rosara'). The cultivars were established in a field experiment in irrigated soil naturally infested with *Ss*. The soil was a red clay with subsoil compaction. Experimental treatments included K/Mg ratios of 0.1, 0.3, 0.4 or 0.6, combined with either nil fungicide (-F) or application of fungicide (+F; 3 L ha^{-1} of Shirlan® 500 SC), with four replicates in the experimental design. At each of three host plant phenological stages (emergence, tuber initiation, flowering), five plants were harvested from each treatment and each replicate. The roots were washed and examined for presence of root galls. Compared with 0.3 K/Mg ratio, treatments of 0.4 and 0.6 K/Mg without Shirlan® increased the presence of root galls by, respectively, 54% and 51%, while 0.6 K/Mg ratio plus Shirlan® with fumigation increased the presence of root galls by 40%. These results show that Mg deficient and high K soils can favour expression of *Ss* on potato crops, but disease expression can be reduced with Shirlan® applications. Soils with optimum K/Mg balance decrease *Ss* diseases. Use of pesticide management of *Ss* diseases will also be discussed.

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Advances in development of integrated management of powdery scab (caused by *Spongospora subterranea* f. sp. *subterranea*) in potato crops in Chile

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Potato is an important crop in Chile, where 45,000 ha are cultivated annually, with production of 1,300,000 tons. Climate change and decreased rainfall make irrigation important for maintaining crop yields. Lack of experience and information for irrigation decision-making have generated problems of efficiency and crop health, and there has been a 30% increase in the incidence of disease caused by *Spongospora subterranea* f. sp. *subterranean* (*Sss*), which causes losses in yields, quality and profitability. The present study aimed to develop integrated *Sss* disease management, through early detection of the pathogen, efficient irrigation and manipulation of soil factors, and validating and implementing disease control based on a risk assessment support tool. This considers seed tuber quality, varietal resistance, chemical and biological control, efficient irrigation management, and detection and quantification of *Sss* soil inoculum using qPCR. The PLAS Satellite Agricultural Platform (https://www.agrisatwebgis.com/app/es/agrisat/map?group=Plas#spUsrMapSidebarLayersTab) has been validated on three farms, to define efficient irrigation use, with physical and chemical soil characterization, showing reduction in *Sss* diseases in potato roots and tubers, depending on soil compaction and nutritional balance, especially K:Mg ratios. Susceptibility to *Sss* has been evaluated for 14 potato cultivars, and chemical control results show 30% efficacy. Soil quantification of *Sss* has been validated and standardized with two markers, using soils with powdery scab histories.

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***Spongospora subterranea* spread, and development of disease management in the United States of America**

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Potato mop-top virus (PMTV), which is vectored by *Spongospora subterranea*, was detected in 2000−2001 in seed potatoes from Maine that were exported to Canada. A survey was therefore undertaken of all seed potato producing regions of the USA in 2002, and PMTV was only detected in Maine. Subsequently, PMTV has been reported in most major potato-producing regions in the USA, and PMTV and *S. subterranea* are causing increasing concerns. Because of a powdery scab outbreak at a mini-tuber production facility, commercial potting mixes were tested, and *S. subterranea* was shown to be present, but the sources of the pathogen are unknown. This discovery caused changes in how minitubers are produced, with some growers now using hydroponics systems, or routinely testing peat-based potting mixes for *S. subterranea.* Because of the prevalence of *S. subterranea* and PMTV in some regions, potato varieties, rotation crops, and two chemical management methods were assessed to provide disease management recommendations. Potato varieties vary in susceptibility, and amount of inoculum increase in soil, and the chemicals growers were using to manage powdery scab were ineffective. Roles are currently being assessed of soil type, moisture, temperature, potato variety, and soil microbiomes for *S. subterranea* inoculum increase, PMTV incidence, and in development of spraing and powdery scab, in an experiment that spans four potato production regions in the USA.

Fifteen years' experience with soil diagnostic testing for *Spongospora subterranea* in Scotland, and its contribution to reducing powdery scab in potato crops

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The Scottish Agricultural College developed a soil test for *Spongospora subterranea* (*Ss*) (Brierley *et al.*, 2008)[a], and this was launched in 2009/10. High incidence of powdery scab in potato crops in 2010 indicated that seed and ware potato growers would both use the test, but seed potato producers have been the prime users, mainly to assess *Ss* soil infestations on rented land. The test uses a single soil sample per field, made up of 100 10 g core samples from a representative 4 ha block in the assessed field. The test results categorise risk of powdery scab as 'low' (*Ss* undetected), 'medium' (trace to 9.9 sporosori g^{-1} soil), or 'high' (> 10 sporosori g^{-1}). There have been more fields in the low risk category and fewer fields with high risk than was expected. Feedback on the test indicates that growers find the results meaningful, and reflect subsequent levels of powdery scab in a field. Many growers submit samples annually. Powdery scab has declined as a problem in potato production in Scotland since the test was introduced, which could be due to climate change (consistent warm and dry spring conditions), and use of potato cultivars with reduced powdery scab susceptibility. However, the test has provided increased confidence to grow susceptible varieties in low risk fields, and decision support for necessity for fluazinam soil incorporation. Availability of off-label fluazinam soil treatments has probably been the most important factor in reduction of powdery scab over the last 15 years. Whether this pesticide will continue to be approved for use in the United Kingdom is uncertain.

[a] Brierley, J. et al. (June 2008). Improving decision making for the management of potato diseases using realtime diagnostics. Potato Council Project Report 2008/6.

A novel rhizosphere bacterium for management of powdery scab and associated root disease

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Management of root and tuber diseases of potato caused by *Spongospora subterranea* infections is challenging and often ineffective. There is need for new management options that can augment current systems, to increase disease control and mitigate against the impacts of these diseases. Selection and testing of a bacterium as a potential biocontrol agent were described. When applied as a seed tuber dressing, the organism resided in resulting potato plant rhizospheres. There it interfered with natural chemical signalling processes in the soil, reducing capacity for *S. subterranea* to detect potato host plants, for resting spores to germinate, and for zoospores to chemotactically locate host

roots. This resulted in reduced root and tuber disease caused by the pathogen. The bacterium also has plant growth promoting ability, and its establishment within potato rhizospheres resulted in increased plant root mass and tuber yields. This dual activity assisted disease management and mitigation of the impacts of infections on potato plant productivity and yield.

Management of powdery scab: novel approaches and critical knowledge gaps

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The importance of root and tuber diseases of potato, caused by the biotrophic protozoan pathogen *Spongospora subterranea*, is recognised wherever potato is grown. Management of these diseases is difficult and often ineffective. This is because of the pathogen's ability to form resistant and long-lived resting spores that persist in cropping soils, it's propensity to transmit as seed tuber-borne inoculum, the lack of effective registered pesticides that target the pathogen, rapid and polycyclic infection cycles by the pathogen within potato roots, and scarcity of potato cultivars with tolerance or resistance to *S. subterranea*. Long rotations between potato crops, seed tuber and soil health, pesticide treatments, and cultivar choice provide only partial disease control solutions. Therefore, novel approaches are required for management of *Spongospora* diseases, which can integrate with and augment these current disease management methods to provide improved control. This paper described new approaches targeting soil-borne inoculum, infection, and disease development, which are being assessed to improve management of *S. subterranea* diseases. Critical relevant knowledge gaps were highlighted, and areas for future research were suggested.

INTERNATIONAL COLLABORATION

The International Potato Research Partnership and collaborative framework

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Development of an International Potato Research Partnership is an initiative of several participating countries (see below). Conception and development of the Partnership have resulted from recognition of, and response to, short and longer-term changes that are occurring in the potato industry globally, particularly in relation to achieving the United Nations (UN) sustainability goals (ref A/RES/70/1. UN General Assembly, Transforming Our World: the 2030 Agenda for Sustainable Development, 21 October 2015), and the Paris Agreement to the United Nations Framework Convention on Climate Change, Dec. 12, 2015, T.I.A.S. No. 16-1104. The partnership addresses the need to adopt an integrated approach, deploying research funding available on a global level. This will provide investors with a coordinated series of research activities, ensuring the highest probability of success. It also addresses the need to build collaboration and teamwork between researchers internationally, and hence improve efficiency in research resource use. This initiative is a template for the future, is mission driven and industry guided, and is a broadly collaborative co-investment in potato research. The participating partners have committed to build relationships that aim to develop international collaboration. The proposed partnership will initially involve relationships between researchers in Australia, New Zealand, the United Kingdom, South Africa, Germany, the Netherlands, and the African Potato Coalition, and other countries and organisations have expressed interest in joining the association. This collaboration is important and will help achieve rapid progress towards the UN sustainability development goals, as well improve partner's research capability through scientific exchange and collaboration.