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SHORT COMMUNICATION

Lesson from the emergence, spread and decline of *Dickeya solani*, the virulent potato blackleg and soft rot bacterial pathogen in Finland

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Abstract

The threat of emerging plant diseases has become more frequent as global warming and international trade are increasing. Blackleg and soft rot of potatoes caused by the group of bacteria in the family Pectobacteriaceae and the genera *Dickeya* and *Pectobacterium* are important diseases causing economic losses globally. In the European Union, they are regulated non-quarantine pests. Five species are commonly known to cause blackleg symptoms on potatoes indistinguishable from each other. For decades, *P. atrosepticum* has been the classic seed potato bacterial pathogen in cool temperate climates of Europe and North America, causing blackleg disease. However, recently several new species, unknown in Northern Europe, have emerged as virulent pathogens. One of these species is *D. solani*. In Finland, *D. solani* was first found in 2004 and has been the cause of major outbreaks of blackleg in Finland for more than a decade. Currently, its incidence has declined significantly because of a stringent, concerted engagement strategy adopted to combat the pathogen that is described in detail in this article. This strategy implemented in Finland could serve as a model system to combat other emerging and re-emerging species of *Dickeya* and *Pectobacterium* and serve as useful support information for the formulation of a policy framework for the management of emerging plant health risks.

KEYWORDS
blackleg, *Dickeya solani*, emerging pathogens, Pectobacteriaceae, soft rot, zero-tolerance

1 | INTRODUCTION

Bacteria in the family Pectobacteriaceae and the genera *Dickeya* and *Pectobacterium* are identified as the causal agents of blackleg and soft rot on potatoes. The bacteria are listed among the 10 top economically important bacterial plant pathogens (Mansfield et al., 2002). To date five species, namely, *D. solani*, *P. atrosepticum*, *P. brasiliense*, *P. carotovorum* and *P. parmentieri* (formerly *P. wasabiae*) are commonly occurring on potatoes. The threat from these pathogens is constantly increasing because of the emergence and extension of new species towards the poles, as it is true for many other plant pathogens. Climate change and expanding international trade are considered the main drivers (Anderson et al., 2004; Bebber et al., 2013; Hickling et al., 2006).

Losses from blackleg and soft rot are going to increase in the changing climate since the emergence of new aggressive species difficult to control is becoming more frequent and widespread. The economic losses from blackleg and soft rot include direct yield

loss and losses from downgrading of seed lots. The global total loss from the disease is not well documented. However, a rough estimate of the annual loss in Europe is about 46 million euro (Dupuis et al., 2021). According to rough data from seed potato companies (personal communication), losses from downgrading seed potatoes to ware or food potatoes in Finland are approximately 3000 euro per hectare. Losses from blackleg and soft rot are forecasted to increase in the changing climate due to the emergence of new aggressive species difficult to control that are becoming more frequent and widespread. The bacteria are seed-borne and could stay latent in tubers until conditions favourable for infection prevail (Pérombelon & Kelman, 1980).

Dickeya solani, a species believed to have originated from the Netherlands (Toth et al., 2021, Tsror et al., 2009), was first found in Finland in Åland Islands (60.1785° N, 19.9156° E), an area where potato-processing industries are located. The emergence of *D. solani* changed the face of blackleg disease in Finland, from previous sporadic occurrence and mild losses caused by the endemic species, *P. atrosepticum*, to frequent and severe outbreaks and heavy losses in terms of direct yield reduction and downgrading of seed potato lots (Degefu et al., 2013; Paassilta, 2016). The emerging threat to potato production in Finland caused by *D. solani* prompted the development of a coordinated, multifaceted management strategy and catalysed collaborative actions by researchers, seed potato companies and potato growers in Finland which serve as a model system to combat similar emerging plant health risks.

Further threats of introduction and establishment of non-indigenous potato blackleg and tuber soft rot pathogens in Finland are still continuing. Just recently (Degefu, 2021), *P. brasiliense*, a species from Brazil (Duarte et al., 2004) and later introduced to South Africa (van der Merwe et al., 2010), was recorded as a prevalent blackleg bacteria in Europe (de Werra et al., 2015, 2021; van der Wolf et al., 2017). The species was first detected in Finland in 2013 on a potato variety imported from the Netherlands (Degefu, 2021). Since then, the prevalence of the species has been increasing rapidly (Figure 3) but its economic impact on potato production in Finland is not yet known. Another species of *Pectobacterium*, *P. parmenteiri* formerly known as *P. wasabiae* (Khayi et al., 2016) that has been present in Finland since the 1960s (Nykyri et al., 2012) has now emerged as a prevalent bacterial seed potato pathogen in Finland (Figure 3). Moreover, species not known before such as *Pectobacterium parvum* and *Pectobacterium polaris* from Finland and Norway, respectively, (Dees et al., 2017; Pasanen et al., 2021) are described but no detailed study has been conducted about the species and their economic impact on potatoes is unknown.

Pathogens emerge without warning and are often detected after they have been established or started causing economic damage. The emergence of *D. solani* has led to an unprecedented outbreak of blackleg, never experienced in Finland before (Degefu et al., 2013; Paassilta, 2016) The bacterium was a game changer causing disease of epidemic proportion with sudden weather change from mild temperatures to hot days ≥25°C (hot according to Finnish weather classification) persisting for 5–7 days (Degefu, 2016).

Finland is one of the five countries in Europe (Germany, England, Ireland and the Azores Archipelago in Portugal) which are granted High-Grade status for seed potato production. The rationale of the High-Grade status is an obligation of applying stringent measures to keep the area clean from invasion by dangerous pests and pathogens of potatoes (Pohto, 2002). Some of these measures include the controlled importation of seed potatoes to these areas, the use of high-class certified seeds for potato production in the zone and reducing the number of food potato fields (area) in the designated High-Grade localities.

Although mandatory seed testing policy for *Dickeya* and *Pectobacterium* should be an integral component of the measures implemented, such policy guideline does not exist either in the European or Finnish Phytosanitary policy guidelines at the time of this writing. Although national-level expert discussions on the need for such a policy have been going on for several years, its formulation may still take time since decisions on policy matters in most cases are often dependent on social, economic and political factors. Thus, until such policies are in place, in addition to scientific research and knowledge production, raising the awareness of stakeholders and creating a shared understanding of blackleg disease management solutions are necessary for collective actions and plausible integrated management of emerging and re-emerging species of *Dickeya* and *Pectobacterium* for sustainable production of potato, a potential global food security crop (Wijesiha-Bettoni & Mouille, 2019). This short communication describes the concerted impact of research and stakeholders' engagement strategy which led to the decline of *D. solani*, the virulent species that emerged in Europe two decades ago, and to apply the lessons learnt to prevent the emergence of new variants or species in Finland and elsewhere in Europe.

2 | MATERIALS AND METHODS

The main components of this work have been firstly the development, standardization and validation of sensitive and specific molecular detection and characterization technology for the blackleg and soft rot Pectobacteriaceae. Secondly, the constant monitoring of the prevalence of the bacteria in the High-Grade and other potato production areas of Finland and thirdly, the dissemination of knowledge and technology to raise the awareness of stakeholders in the potato value chain for a cooperative multi-actor engagement in the management of emerging and re-emerging species of *Dickeya* and *Pectobacterium*.

Accordingly, the standardized species-specific PCR-based detection methods (endpoint and real Time) have been routinely used for research and service at the Natural Resources Institute Finland Molecular Biology Laboratory located in Oulu region (65.0121° N, 25.4651° E) just less than 50 km from the High-Grade municipalities of Tyrnävä and Liminka.

The detailed descriptions of the molecular detection, pre-PCR and PCR procedures as well as the primers and probes used in the study are clearly described by Degefu et al. (2009, 2013) and

Degefu (2021). The PCR detection targeted the bacteria latently present in the seed tuber and/or actively infective bacteria on symptomatic potato stem segments and soft rotten tubers collected from the the three regions highlighted in the map (Figure 1).

Parallel to the development of scientific knowledge, dissemination of information and raising awareness of stakeholders on problems blackleg and solutions were carried out based on knowledge generated and reported in the scientific articles published by the author (Degefu, 2015; Degefu, 2016, 2021; Degefu et al., 2009, 2013; Degefu & Virtanen, 2015), and dozens of short articles and notes in professional potato newsletters, potato bulletins and other media outlets have been used as an input in the outreach materials. In addition, information summary from Europe-wide potato research cooperation workshops and conferences such as the European Potato Research (EAPR) and annual meetings of the European Phytosanitary Research Coordination (Euphresco) *Dickeya* and *Pectobacterium* network were compiled and disseminated to reach local farmers and seed potato companies. A fair number of lectures have also been delivered in national and international workshops, annual potato meetings, conferences, field days and National Seed Potato Board meetings. This project involved up to 80 seed potato farmers in contract agreement with three major seed potato companies in Finland on a total production area of about 1200 hectares (the Seed Potato Strategy 2019–2023 Strategy document, https://perunasta.fi/uutiset_/2203-2/).

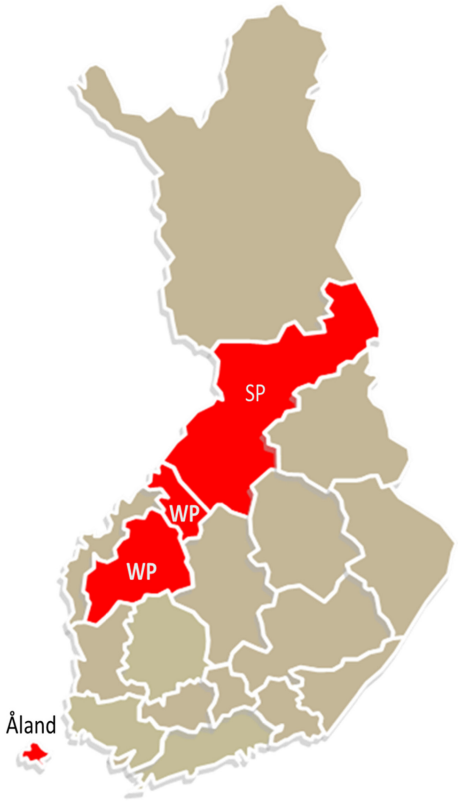

FIGURE 1 Regions of Finland where *Dickeya* and *Pectobacterium* pathogens monitoring and diseased potato plants sampling were carried out (red). The seed potato (SP) High-Grade zone, the north Osterbothnia. The major food or ware potato (WP) production localities in the central and Southern Osterbothnia and the Åland islands where potato processing industries are located. All the seed potatoes in Finland are produced in the High-Grade zone and cover a total area of about 1200 hectares and about 80 seed potato farmers are engaged in the business in the country. All are contract farmers for three major seed potato companies operating in the High-Grade zone. A total of one hundred diseased plant samples were randomly picked from those collected from the three regions during annual disease surveys and tuber samples submitted by seed companies for routine seed certification purposes were analysed annually for *Dickeya* and *Pectobacterium* species using diagnostic PCR.

3 | RESULTS

The in-house availability standardized and validated the molecular detection and diagnostic methods, and qualified research and laboratory technical staff facilitated the constant annual monitoring and documentation of the prevalence of the blackleg and soft rot. Pectobacteriaceae including the follow-up of the changing faces of these group of pathogens in Finland for two decades (Figures 2 and 3). In addition, the research on the ecology and epidemiology of the bacteria has resulted in relevant knowledge and understanding of the problems of blackleg and soft rot that served as an input for a strategy for integrated management of the disease highlighted in this short communication.

The well-coordinated networking, dissemination of knowledge and stakeholders' engagement that played instrumental role in the creation of shared understanding of management solutions among players in the potato production chain led to the adoption of crucial and impactful decisions and implementation of measures such as zero tolerance to the emerging *D. solani* and voluntarily self-imposed mandatory seed testing despite the absence of national or European policy guidelines related to these particular measures. As a result (Figure 2), *D. solani* is practically not detected in seed potatoes produced in Finland. On the other hand, the prevalence of the recently emerged *P. brasiliense*, the re-emerging *P. parmenteiri* and the endemic *P. atrosepticum* been increasing in Finland in recent years (Figure 3) since the zero-tolerance principle has not yet applied against these species.

4 | DISCUSSION

Protecting the High-Grade zone and other potato production regions of Europe (van der Wolf et al., 2021) from dangerous pests and diseases is important for future food security in Finland and the rest of Europe. Finland is one of the five countries in Europe with the High-Grade status for seed potato production granted by the European Union (Pohto, 2002). Safeguarding the status is the responsibility of the countries holding the status. According to Pohto (2002) maintaining the High-Grade status costs about 80,000 euro annually to the Finnish Government. This cost is related to the applications of

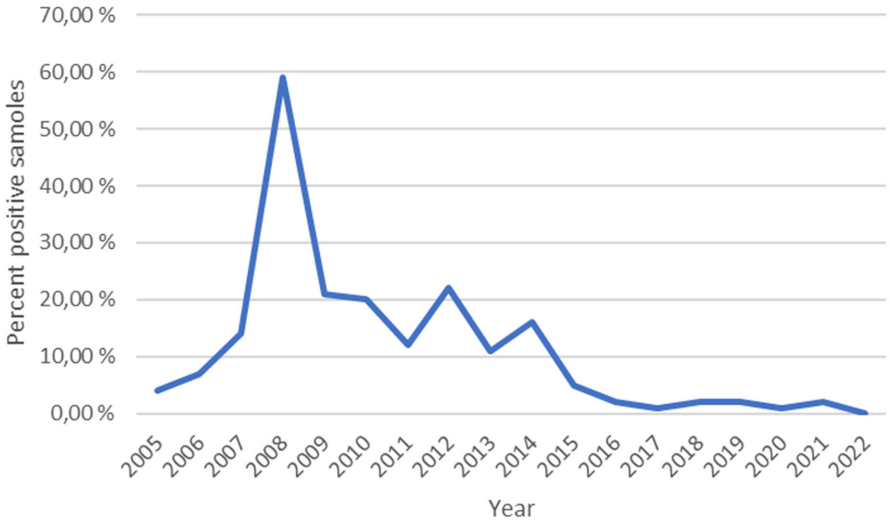

FIGURE 2 Incidence of *Dickeya solani* on potatoes in Finland. A total of one hundred potato plants with typical blackleg symptoms were analysed for *D. solani* and *Pectobacterium* species from samples collected from representative seed potato and ware potato-producing regions of Finland using conventional and real-time quantitative PCR detection systems. The names and sequences of the specific primers and probes used in the PCR are presented by Degefu (2021). The percentages of samples positive for the different species are recorded.

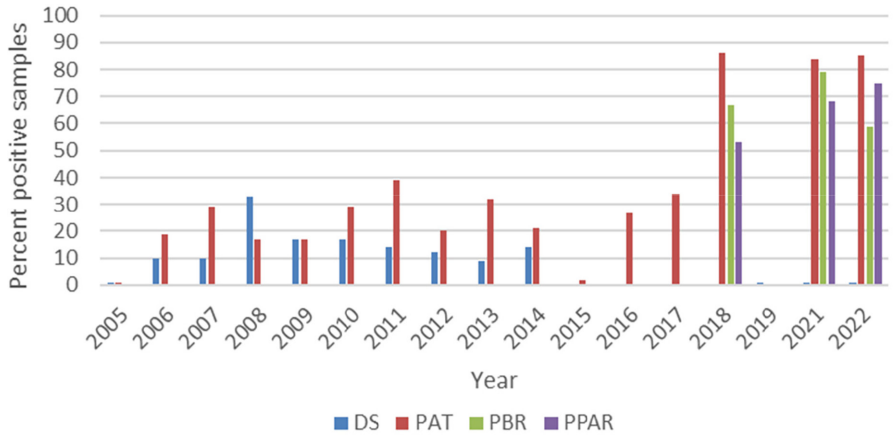

FIGURE 3 Prevalence of *Dickeya* and *Pectobacterium* species in Finland. Survey data from High-Grade seed potato production municipalities of Tyrnävä and Liminka and the ware potato growing regions of central and Southern Ostrobothnia in Finland in 2021 growing season. PCR detection results from one hundred potato plant segments showing typical blackleg symptoms indicating the decline of *D. solani* (DS) and increasing incidence of particularly the recently emerged and re-emerged species of *P. brasiliense* (PBR) and *P. parmenteiri* (PPAR). The incidence of the endemic species, *P. atrosepticum* (PAT) has been consistent throughout the study period.

stringent measures such as the use of only certified seeds for planting by seed potato producers in the High-Grade localities of Tyrnävä and Liminka and restricting the area for food potato production to a maximum of 500 hectares. Despite the stringent obligations and costs involved, the High-Grade status offers potential economic benefits to the countries holding the status.

However, the safety of the High-Grade status in Finland has been under constant threat because of the emergence and poleward/northward extension of new aggressive blackleg and soft rot Pectobacteriaceae as commonly observed with many other plant pathogens (Bebber et al., 2013; Hickling et al., 2006) with climate change and increasing international trade as main drivers.

Pathogens emerge without warning and in most cases, they are detected after they have been introduced and started causing economic losses. *D. solani*, a bacterium that was assumed to have been transferred from the ornamental plant *Hyacenthus orientalis* to potato, emerged as a virulent blackleg pathogen first in the Netherlands and spread to the rest of Europe within a short time. The bacterium exhibited unique features of high aggressiveness including causing heavy infections from low inoculum levels and the ability to overtake the other endemic blackleg Pectobacteriaceae (Toth et al., 2011). In Finland since its appearance in 2004, *D. solani* has become very prevalent causing major blackleg outbreaks (Degefu et al., 2013) that have led to more rejections of seed lots that were costly to seed producers (Paassilta, 2016) for more than a decade (Figure 3). The lesson learnt from these observations is pathogen emergence is very complex that the emerging pathogen in many respects is not familiar to the researchers and new encounter to the plant itself. It is, therefore, reasonable to assume that the crop may not have the least resistance against the alien pathogen to slow down its spread in the new environment. This is consistent with the experiences during the early years of introduction of *D. solani* into Finland and the rest of Europe (Degefu et al., 2013; Golanowska & Lojkowska, 2016; Toth et al., 2011; Toth et al., 2021; Tsror et al., 2009).

The effective network and cooperation established between the Finnish seed potato importing and producing companies and those

abroad exporting seed varieties to Finland played a vital regulatory system that helped to prevent the further spread of *D. solani* in Finland (Paassilta, 2016) since generally free trade (import/export) is the main route of introduction of the blackleg Pectobacteriaceae to new territory.

These multifaceted approaches that involved monitoring, surveillance and the practice of zero tolerance through the active engagement of the actors in the potato production chain have successfully excluded *D. solani* from the seed system resulting in a marked decline in the prevalence of the pathogen (Figure 2). This model mechanism of intervention could be applied to the recently emerged and widely spreading species of *P. brasieliense* and *P. parmenteiri* (Figure 3). *Pectobacterium brasieliense* is currently known as very virulent on potatoes in several countries of Europe. In Finland, both species are increasing in prevalence. The management of emerging pathogens is very complex and the economic impact could be overwhelming. In the case of *D. solani*, the disease prevalence and the extent of losses during the first 10 years of its emergence were considerable (Degefu et al., 2013; Paassilta, 2016; Toth et al., 2011).

The increase in the prevalence of the emerging species *P. brasiliense* and the re-emerging *P. parmentieri* (Figure 3) particularly after the decline of *D. solani* is very interesting. One might speculate that the decline or removal of the competitive *D. solani* from the system might have led to the increased prevalence of the *Pectobacterium* species. Although it is difficult to draw valid conclusion on this subject, it is worth noting three findings of competition among the blackleg Pectobacteriaceae especially the dominance of *D. solani* over the other species. First, the report of almost no co-occurrence of *D. solani* and *P. atrosepticum in tubers and infected plants* (Degefu, 2021). Second, findings of the genomic study (Motyka-Pomagruk et al., 2021) revealed some peculiar gene pools specific to *D. solani*, which might contribute to the occupation of an isolated ecological niche. Third, the preliminary results of a study (Garlant et al., 2013) suggest the involvement of toxic secondary metabolites that may confer adaptation to the new environment and its ability of spreading very fast in the potato ecosystem. Therefore, further investigation is required to verify the impact of these possible selection mechanisms on the cycle of emergence and re-emergence of this group of pathogens.

5 | CONCLUSIONS AND PROSPECTS

Recent decades have seen repeated emergence of plant pathogens and the phenomenon has become one of the major food security challenges. Pathogen emergence or re-emergence is a very complex incident that advances in Plant Pathology alone may not bring long-lasting sustainable solutions (Almeida, 2018). Alternative ways should be devised. Several review articles have recently been published which strongly justify the need for integrating strategies such as stakeholder involvement (Shackleton et al., 2019), use of media and digital technology (Thomas et al., 2011), Social and Citizen Sciences (Brown et al., 2020; Ryan et al., 2018) in the plant disease management. The growing number of multi-actor EU-funded projects: under the main theme scientists and farmers creating solutions together (2020) (https://ec.europa.eu/eip/agriculture/en/about/multi-actor-projects-scientists-and-farmers) (Accessed on 13.8.2023) and the proposal for integrating natural and social science perspectives (Mills et al., 2011) are some examples of steps towards a paradigm shift in the plant disease management approaches.

Furthermore, the requirement for inclusion of Citizen Science as part of the Horizon 2022 PestRisk project call is one of the notable examples of steps towards the promotion of multi-actor projects in plant disease research and control strategy. In the global challenges facing Plant Pathology, such multidisciplinary approaches could enable it to meet food security and environmental challenges (Jeger et al., 2021; Murray-Watson et al., 2022). The strategies reported in this short communication are consistent with these lines of thought and future prospects worth pursuing.

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CONFLICT OF INTEREST STATEMENT

The author declares that there is no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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