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Influence of abiotic factors, inoculum source, and cultivar susceptibility on the potato tuber blemish diseases black dot (*Colletotrichum coccodes*) and silver scurf (*Helminthosporium solani*)

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Abstract

Black dot and silver scurf are potato blemish diseases whose economic impact has increased in recent years. Because their symptomatology on tubers is visually similar, disease assessment does not usually differentiate between the two pathogens, which share the same ecological niche. The epidemiology of black dot has been extensively studied, especially in the UK, but the factors that influence silver scurf have been less investigated. In this study, the influence of cultivar, source of inoculum, and environmental conditions on both diseases was studied in field trials over a three-year period (2016–2018) in Switzerland. Planting minitubers did not prevent either disease in daughter tubers, indicating the contribution of soil as an inoculum reservoir. An arbitrary threshold of *Colletotrichum coccodes* soil inoculum could be set to discriminate between low and high disease risk. For the first time, *Helminthosporium solani* DNA was detected in stolons, and infections appeared earlier in stolons than in tubers. *H. solani* stolon and tuber infections usually appeared later in the season than those of *C. coccodes*. Black dot severity correlated positively with precipitation, while silver scurf severity correlated positively with temperature. Table potato cultivars commonly grown in Switzerland exhibited significant differences in susceptibility to both diseases, and cultivars with low susceptibility to both silver scurf and black dot were identified. These results gave new insights into understanding the factors driving the epidemiology of potato blemish diseases and may contribute to building a risk assessment scheme to manage both diseases simultaneously.

KEYWORDS

disease severity, epidemiology, latent infection, pest management strategy, *Solanum tuberosum*, stolons

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1 | INTRODUCTION

Black dot (caused by *Colletotrichum coccodes*) and silver scurf (caused by *Helminthosporium solani*) are two potato blemish diseases that affect the quality of tubers and cause water losses during storage. Changes in the marketing of fresh tubers, particularly with respect to the increased demand for washed potatoes, have led to an increased economic impact of these two diseases once considered of minor importance. As tuber blemishes are more visible on washed potatoes than on unwashed ones, their negative impact on skin quality and price has increased.

Black dot is caused by *Colletotrichum coccodes*, a fungal pathogen that has numerous hosts, including tomato, onion, carrot, potatoes and other crop species, and in potatoes, infects all belowground organs as well as stems and leaves (Andrivon et al., 1998; Johnson, 1994). In potatoes, roots, stolons, and daughter tubers are quickly colonized by *C. coccodes*, showing symptoms of black dot soon after their emergence, while stems show disease symptoms only 7–10 weeks after inoculation (Andrivon et al., 1998). More black dot symptoms were observed at 22 °C than at 18 °C in greenhouse conditions, indicating that higher temperatures are conducive to the disease (Lees et al., 2010), and several studies have shown that irrigation results in higher disease levels (Brierley et al., 2015; Hide et al., 1994; Lees et al., 2010; Olanya et al., 2010). Long cultivation periods correlate with black dot disease severity, indicating that early harvest may be an efficient management strategy (Brierley et al., 2015). Fungicide application, the use of less susceptible cultivars, and short curing periods are other strategies to reduce the impact of black dot on potatoes (Andrivon et al., 1998; Brierley et al., 2015; Hide et al., 1994; Olanya et al., 2010; Read, 1991). Soil inoculum was found to be the primary source of *C. coccodes* inoculum and to be an important factor determining the incidence of black dot on progeny tubers (Denner et al., 1998; Lees et al., 2010; Nitzan et al., 2008). Crop rotation might help reduce soil inoculum, but attention has to be paid to the crops selected for rotation, because *C. coccodes* can infect other crops and weeds (Nitzan et al., 2006). Infected seed tubers planted in disease-free soils produce progeny tubers that can develop black dot symptoms (Denner et al., 1998), indicating that seed is also a source of inoculum.

Silver scurf is caused by *Helminthosporium solani* (Errampalli et al., 2001) and potato is its only known host. Planting infected seed tubers in the field is the primary origin of *H. solani* in the soil (Geary & Johnson, 2006). However, *H. solani* has been found in decaying material, which, together with volunteer potatoes, can be a source of inoculum (Mérida & Loria, 1994). A study using successive seed generations showed that silver scurf disease increases at each seed generation, and that using nuclear seed tubers generally results in disease control (Geary & Johnson, 2006). However, other authors have found that the use of nuclear seed tubers is not sufficient to prevent silver scurf symptoms in progeny tubers, especially in rotations of fewer than 3 years between potato crops (Bains et al., 1996; Mérida & Loria, 1994). Silver scurf does not usually cause any yield losses at harvest, but it does increase the permeability of the tuber's skin, which leads to water losses and shrinkage during storage, leading to weight losses reaching 17% (Read & Hide, 1984). Similar to black dot, this disease affects the quality of the tubers, leading to the downgrading or rejection of tuber stocks, especially in the fresh potato market (Errampalli et al., 2001; Lees & Hilton, 2003).

Black dot and silver scurf cause important losses in potato production, and their occurrence has been highlighted worldwide, including in Israel (Tsror [Lahkim] et al., 1999; Tsror [Lahkim] & Peretz-Alon, 2004), North America (Hunger & McIntyre, 1979; Rodriguez et al., 1996), Australia (Harrison, 1963), and especially in Europe (Andrivon et al., 1998; Brierley et al., 2015; Lees et al., 2010; Read & Hide, 1984, 1995). Although these diseases are caused by two unrelated phytopathogenic fungi with different host ranges and life cycles, their symptoms are very similar in appearance, and observation of their microscopic structures (microsclerotia for *C. coccodes* and conidiophores for *H. solani*) is needed to determine the pathogen causing the disease (Errampalli et al., 2001; Lees & Hilton, 2003). For commercial purposes, these pathogens are often scored together (as blemish diseases), and the level of acceptable incidence of these blemish diseases does not specify which fungus is responsible for the disease. Furthermore, both diseases often appear simultaneously not only in a tuber stock but also on the same tuber. Several studies have focused on the specific epidemiology or control measures of black dot in potato (Andrivon et al., 1998; Brierley et al., 2015; Lees et al., 2010) or silver scurf (Bains et al., 1996; Geary & Johnson, 2006; Hide & Read, 1991; Mérida & Loria, 1994; Mérida et al., 1994). However, there are no studies either on black dot and silver scurf joint infection or on the control measures and the conditions favouring these two blemish diseases in the same tuber stocks.

Host resistance is a widely used method to control diseases in agriculture. Differences in susceptibility to black dot have been observed in cultivars grown in the UK (Brierley et al., 2015; Read, 1991), in Israel (Tsror [Lahkim] et al., 1999), and in the USA (Hunger & McIntyre, 1979). Russet-type cultivars have been shown to be more resistant to black dot than thin-skin cultivars (Hunger & McIntyre, 1979) and early-maturing cultivars present more symptoms of black dot than late-maturing cultivars in field trials (Andrivon et al., 1998; Read, 1991). Susceptibility to silver scurf also differs among potato cultivars, but cultivars with high levels of resistance to silver scurf have not been identified (Joshi & Pepin, 1991; Sedláková et al., 2013). Wild tuber-bearing *Solanum* species present low disease severity, but introgression of their resistance traits into cultivated potato has not yielded resistant cultivars (Rodriguez et al., 1995). Furthermore, most silver scurf host resistance studies have been performed in the USA (Errampalli et al., 2001; Mérida et al., 1994; Rodriguez et al., 1996) and have not included cultivars commonly used in Europe. Little is known about the genetic basis of resistance to black dot and silver scurf, and information on the susceptibility of cultivars grown in Europe for fresh markets is also lacking.

In the present study, we evaluated the effects of the inoculum source on black dot and silver scurf severity in daughter tubers and studied whether the use of minitubers was sufficient to prevent either disease. We studied the climatic conditions that affect the development of both diseases in field trials, and we investigated the susceptibility of cultivars used in the fresh potato market in

Switzerland to both diseases. Finally, using molecular detection techniques, we monitored the development of both diseases on belowground organs sampled during plant growth under field conditions.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Three different experiments were carried out to elucidate the contribution of specific factors to disease development (Table 1). In experiment 1, three seed stocks were planted at different field sites to study the impact of soil inoculum, seed inoculum, and environmental conditions on fungal colonization and disease severity. Experiment 2 not only focused on cultivar susceptibility, but also generated data about source of inoculum and environmental conditions. Data on cultivar susceptibility from the randomized experiment 2 was added to by a wide-scale monitoring of commercial potato stocks in experiment 3.

2.2 | Disease assessment of seed and daughter tubers

Samples of 50 (experiment 2 and 3) or 100 (experiment 1) tubers of each seed stock were assessed for black dot and silver scurf before planting (seed tubers in experiments 1 and 2), or after a storage period of 3 (experiment 1) or 4 months (experiment 2 and 3) at 6 °C after a period of curing. The tubers were then washed and incubated for 2 weeks at room temperature and high relative humidity by placing them in closed plastic bags containing wet tissues to induce sporulation of fungal pathogens. Each tuber was individually observed under a binocular microscope for the presence of microsclerotia of *C. coccodes* (for black dot) or conidiophores of *H. solani* (for silver scurf). Depending on its affected tuber surface area, each tuber was then classified into one of the following classes: 0 (absence of the fungus), 1 (less than 15%), 2 (between 15% and 33%), 3 (between 34% and 66%), and 4 (more than 66%). Disease incidence was calculated as the percentage of tubers showing symptoms, and disease severity was calculated by multiplying the number of tubers in each class by the median value of the class (% affected area). For experiment 1, the commercially available seed tuber stocks always showed black dot and silver scurf symptoms, but the severity differed among stocks and years. Efforts were made to select a seed tuber stock showing low levels of black dot (below 15% disease severity) and silver scurf (below 25% disease severity) and a second seed tuber stock with relatively high levels of black dot (above 15% disease severity) and silver scurf (above 30% disease severity). As expected, the minituber seed stocks did not show either black dot or silver scurf symptoms.

2.3 | Seed stock

Certified seed tubers for use in experiments 1 and 2 were purchased in the autumn and maintained over winter in a cold chamber at 4–6 °C. No

TABLE 1 Overview of the three experiments carried out and the factors evaluated in each of them

	Experiment 1	Experiment 2	Experiment 3
Objective	Relationship between source of inoculum and meteorological conditions on disease severity and development of fungal colonization under field conditions	Cultivar susceptibility under field conditions	Wide-scale monitoring of black dot and silver scurf disease in commercial seed potato stocks
Factors investigated: 1) soil inoculum, 2) seed tuber inoculum, 3) environmental conditions, 4) cultivar susceptibility	1, 2, 3	1, 2, 3, 4	4
Seed stocks (per year)	3	16 (one per cultivar)	159–166 (7–15 per cultivar)
Years	2016, 2017, 2018	2016, 2017, 2018	2016, 2017, 2018
Cultivars	Charlotte	16 (see Materials and Methods)	12 (see Materials and Methods)
Field sites	6	Two conventional + one organic	>50
Soil sampling	2017, 2018	2016, 2017, 2018	
Plant sampling kinetic for disease incidence	10 plants/time point		
Assessed organs	Seed and progeny tubers (2016, 2017, 2018), roots and stolons (2017)	Seed and progeny tubers	Progeny tubers
Severity assessment before planting	✓	✓	
Severity assessment after storage	✓	✓	✓
Storage time before disease assessment	3 months	4 months	4 months

seed tubers were treated with fungicide. Four to six weeks before planting, tubers were placed in a chamber with permanent light to induce germination. Shoot cultures of all 16 potato cultivars were established in vitro and cultivar genotype was verified by microsatellite genotyping and comparison with information in the Agroscope database using previously published methods (Ghislain et al., 2009; Milbourne et al., 1998; Moisan-Thiery et al., 2005). Minitubers used in experiment 1 were produced in the greenhouse. DNA extraction and conventional nested PCR, as described below, was performed on minitubers to confirm the absence of fungal DNA of *H. solani* or *C. coccodes*.

2.4 | Experiment 1: Relationship between source of inoculum of *C. coccodes* and *H. solani* and environmental conditions on disease severity, and the extent of fungal colonization, under field conditions

Three potato seed tuber stocks of the widely grown cultivar Charlotte (two commercial seed stocks and a minituber seed stock) were selected each year and planted at six field sites in three consecutive years (2016–2018): Changins (46°23′52.9″N, 06°14′19.4″E), Goumoens (46°38′54.2″N, 06°35′46.8″E), Moudon (46°40′51.5″N, 06°49′16.3″E), Düdingen (46°50′22.8″N, 07°12′53.5″E), Zollikofen (46°59′29.5″N, 07°27′43.1″E), and Riedholz (47°13′15.9″N, 07°34′09.4″E). The specific field plot at each site differed every year to ensure a minimum of 4 years since the previous potato crop. Each seed tuber stock was planted in four rows of 25 plants with 75 cm between rows and 33 cm between plants on the same row, without replicates. The fields were cultivated according to standard agricultural practices for seed tuber production. To monitor the progression of the infections, daughter tubers were harvested every 2 weeks from the initiation of tuberization (which took place between 50 and 70 days after planting) until harvest (which took place between 123 and 135 days after planting) at the Changins field site (2016–2018). Additionally, in 2017, roots and stolons were harvested every 2 weeks from emergence (30 days after planting) until haulm destruction (118 days after planting) in the Changins field site. At each time point, samples from 10 plants of each seed tuber stock were analysed. DNA of *C. coccodes* or *H. solani* was detected by nested PCR as described below. Daughter tubers were harvested and disease severity assessed after 3 months of storage at 6 °C.

2.5 | Experiment 2: Cultivar susceptibility under field conditions

Sixteen cultivars commonly used for Swiss fresh market production (Agata, Amandine, Annabelle, Celtiane, Charlotte, Cheyenne, Ditta, Erika, Gourmandine, Gwenne, Jazzy, Lady Christl, Lady Felicia, Laura, Venezia, and Vitabella) were planted for three consecutive years (from 2016 to 2018) at three different field sites in Switzerland: Changins (46°23′52.9″N, 06°14′19.4″E) and Reckenholz (47°26′02.6″N, 08°30′47.6″E), where conventional practices were used, and Unterstammheim (47°38′35.8″N, 08°46′43.2″E), where organic practices were applied. The experiment followed a randomized complete block design with four repetitions. Daughter tubers were harvested and disease severity assessed after 4 months of storage at 6 °C.

2.6 | Experiment 3: Assessment of disease severity in tubers from a wide-scale monitoring of commercial potato stocks

Within the framework of the Swiss seed potato propagating programme, tubers received for certification as seed stock for the following season were assessed for black dot and silver scurf severity after 4 months of storage. Several stocks of the cultivars Agata, Amandine, Annabelle, Celtiane, Charlotte, Ditta, Erika, Gourmandine, Lady Christl, Lady Felicia, Laura, and Venezia, which had been grown in different field sites across the potato-growing regions of Switzerland, were used. The number of stocks assessed was 166 in 2016 (between 7 and 15 stocks per cultivar), 159 in 2017 (between 7 and 15 stocks per cultivar), and 166 in 2018 (between 10 and 15 stocks per cultivar).

2.7 | Plant and soil sampling and DNA purification

For microsatellite genotyping, DNA from in vitro plantlets was purified using a DNeasy Plant Mini Kit (Qiagen) according to the manufacturer's protocol. Soil samples were collected from each field plot before planting (experiment 1: 2017 and 2018; experiment 2: 2016, 2017, and 2018). The samples were taken from the top 20 cm of soil across the field site in a W-shape and processed according to a method previously described (Brierley et al., 2009). The method used for DNA precipitation and purification was that published by Cullen et al. (2001, 2002); however, the first steps of lysis and supernatant collection were modified according to the method described by Brierley et al. (2009) using a PM100 milling bowl (Retsch). Ten individual plants (experiment 1) were collected at each time point. The roots, stolons, and tubers were washed and maintained at 4 °C for a maximum of 24 hr. Roots and stolons were cut, flash frozen and then ground, after which they were maintained at −80 °C until DNA extraction. Similarly, whole tubers were peeled, pressed using a Pollähne press (Meku Erich Pollähne Gmbh) and 500 μl of the resulting juice was stored at −80 °C until DNA extraction. DNA extraction was performed using the CTAB method and DNA extracts were stored at −20 °C until PCR analysis.

2.8 | Quantification of pathogen DNA in soil

Inoculum of *C. coccodes* and *H. solani* was quantified according to previously published real-time PCR methods (Cullen et al., 2001, 2002). Three quantitative PCR (qPCR) repetitions were carried out for each of the four subsamples (60 g soil), and the mean of the 12 values was calculated. Aberrant values of the nonexponential qPCR amplification curve were eliminated from the analysis.

2.9 | Detection of *C. coccodes* and *H. solani* in plant organs

Detection of *C. coccodes* and *H. solani* in plant organs was carried out by conventional nested PCR on undiluted (for *H. solani*) or diluted (1/10 for *H. solani* and *C. coccodes* and 1/100 for *C. coccodes*) DNA extracts as described previously (Cullen et al., 2001, 2002). The PCR products were separated on a 1% agarose gel stained with ethidium bromide and viewed under UV light. The samples were considered positive if at least one of the dilutions resulted in amplified PCR products.

2.10 | Statistical analysis

Data on disease severity expressed as a percentage were transformed (arc sine or Johnson's transformations) to meet the assumptions of normality and heteroscedasticity. A three-way analysis of variance (ANOVA) was performed on the overall transformed data with two (experiment 1)- or three (experiment 2)-level interactions. The post hoc Tukey's range test was used for multiple pairwise comparisons. Furthermore, two-way ANOVA with (experiment 2) or without (experiment 1) interactions was carried out for year. In experiment 1, the field site Moudon was not included in the ANOVA because harvest did not take place in this field site in 2017 because of technical problems. Meteorological data from the field sites were downloaded from the publicly available site Agrometeo (https://www.agrometeo.ch/meteorologie). Mean temperature and relative humidity data and total precipitation (including irrigation) data were calculated per month or for 2-week periods. Principal component analysis (PCA) and Pearson's correlation coefficients were analysed between meteorological parameters and severity data. Linear, logarithmic, and polynomial regressions were calculated. All the data were analysed using XLSTAT software.

3 | RESULTS

3.1 | Impact of inoculum source on black dot disease severity at harvest

Soil samples from field trials (experiments 1 and 2, Table 1) exhibited levels of *C. coccodes* inoculum that ranged from undetectable (below the limit of detection of 1 pg DNA/g soil) to 948 pg/g DNA soil (Figure 1). Half of the soil samples contained less than 100 pg DNA/g soil and 80% of the samples less than 250 pg DNA/g soil. Regression analysis showed no correlation between soil inoculum level and disease incidence, severity, or percentage of unmarketable tubers. However, black dot severity at harvest was lower than 10% in all but two field sites with less than 50 pg DNA/g soil, which could become an arbitrary threshold for disease risk.

Black dot incidence on seed tubers did not correlate with black dot severity in daughter tubers (Figure 2a). No significant differences in black dot severity at harvest were observed between the seed tuber stocks with low or high infection levels used in experiment 1 (Figure 2b). However, the use of minitubers resulted in daughter tubers with 35% lower disease severity than using commercial seed tubers (Figure 2b), making the effect of the seed tuber statistically significant (Table 2).

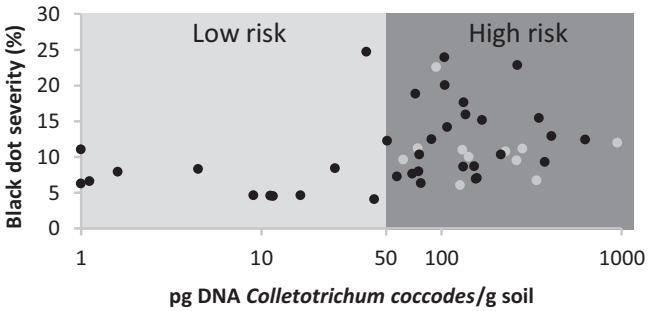

FIGURE 1 Relationship between concentration of soilborne inoculum (pg DNA/g soil on log scale) and black dot severity (percentage of surface area with symptoms) on potato tubers from experiments 1 (grey dots) and 2 (black dots). The threshold separating low and high risk was fixed at 50 pg DNA/g soil

3.2 | Impact of environmental conditions on black dot severity at harvest

In experiment 1, ANOVA revealed that the main effect "year" was more important than the main effect "field site" in influencing black dot severity, the latter not being statistically significant (Table 2). Furthermore, the interaction between these two main effects was not statistically significant ($p = .057$). Meteorological data recorded in the different field sites were used to study the effects of temperature, precipitation, and relative humidity on black dot severity (Table S1). By the use of data from 2-week intervals, PCA showed that climatic conditions differed more between years than between field sites (Figure 3). PCA suggested that black dot severity was positively correlated with relative humidity and negatively correlated with temperature. Pearson's correlation analysis confirmed a negative trend between black dot severity and season-average temperature, especially in the samples collected during the period from 76 to 120 days after planting (dap) (Table S1). Similarly, a positive trend between black dot severity and season-average precipitation and relative humidity was observed. Positive correlations between precipitation and disease severity were observed between 31 and 75 dap, and relative humidity was positively correlated with black dot severity from 46 to 105 dap (Table S1). Temperature, precipitation, and relative humidity between 0 and 15 dap (from planting to emergence) were significantly correlated with black dot severity.

3.3 | Monitoring of *C. coccodes* infections during plant growth

All belowground tissues (roots, stolons, and tubers) were colonized by *C. coccodes*. Infections of *C. coccodes* in the roots and stolons

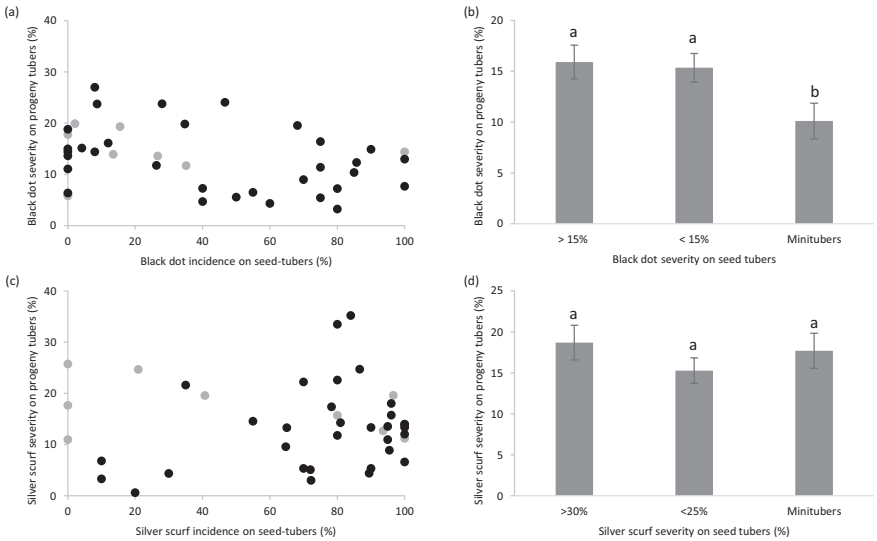

FIGURE 2 Relationship between inoculum on potato seed tuber and disease severity of black dot or silver scurf on tubers at harvest. (a) Relationship between black dot incidence on seed tubers and black dot severity on daughter tubers (experiment 1, grey dots, and experiment 2, black dots); (b) black dot disease severity of progeny tubers from highly infected seed tubers (>15% disease severity), mildly infected seed tubers (<15% disease severity), and minitubers (experiment 1); (c) relationship between silver scurf incidence in seed tubers and silver scurf severity in progeny tubers (experiment 1, grey dots, and experiment 2, black dots); and (d) silver scurf disease severity of progeny tubers from highly infected seed tubers (>30% disease severity), mildly infected seed tubers (<25% disease severity), and minitubers (experiment 1). Values in (b) and (d) are means of 17 observations. Vertical bars represent standard error of means. Different letters indicate statistically significant differences ($p < .01$, Tukey's test)

TABLE 2 Three-way analysis of variance (experiment 1) of the main effects of seed tuber stock, field site, and year (and their interactions) on disease severity of black dot and silver scurf of potato

		Black dot				Silver scurf			
Source	***df***	**MS**	***F***	***p***	**Effect size, η^2**	**MS**	***F***	***p***	**Effect size, η^2**
Main effects									
Seed-tuber lot (A)	2	202.63	11.46	<.001***	0.23	27.54	2.91	.084	0.02
Field site (B)	4	37.89	2.14	.122	0.09	106.02	11.19	<.001***	0.15
Year (C)	2	153.90	8.71	.003**	0.18	660.03	69.69	<.001***	0.46
Interaction									
A × B	8	7.34	0.42	.895	0.03	16.46	1.74	.165	0.05
A × C	4	43.27	2.45	.089	0.10	7.24	0.76	.563	0.01
B × C	8	44.20	2.50	.057	0.20	91.02	9.61	<.001***	0.26
Model	28	51.79	2.93	.014*	0.84	96.00	10.14	<.001***	0.95
Residuals	16	17.68				9.47			

*$p < .05$
**$p < .01$
***$p < .001$.

appeared very early in the season and their incidence remained stable throughout the growing season (Figure 4a,b). Five days after emergence (34 dap), incidence of infection on roots was 70%, and subsequently it was between 63% and 100%. In stolons, incidence of infection was 76% at the first observation (47 dap), and thereafter was between 76% and 93%. Daughter tubers were infected with *C. coccodes* soon after tuberization, with at least 40% of the tubers infected at 70 dap and between 60% and 80% at 100 dap and thereafter (Figure 4c).

3.4 | Susceptibility of potato cultivars to black dot

In the field trials conducted to assess cultivar susceptibility (experiment 2), disease severity ranged from 4.5% (Changins in 2018) to 23% (Reckenholz in 2016) (Figure S1). Significant differences in cultivar susceptibility to black dot were observed, and the main effect "cultivar" accounted for 26% of the total variance (Table 3). The mean black dot disease severity ranged from 5% in the most resistant cultivar Erika to 19% in the most susceptible cultivar Celtiane (Figure 5a). The main

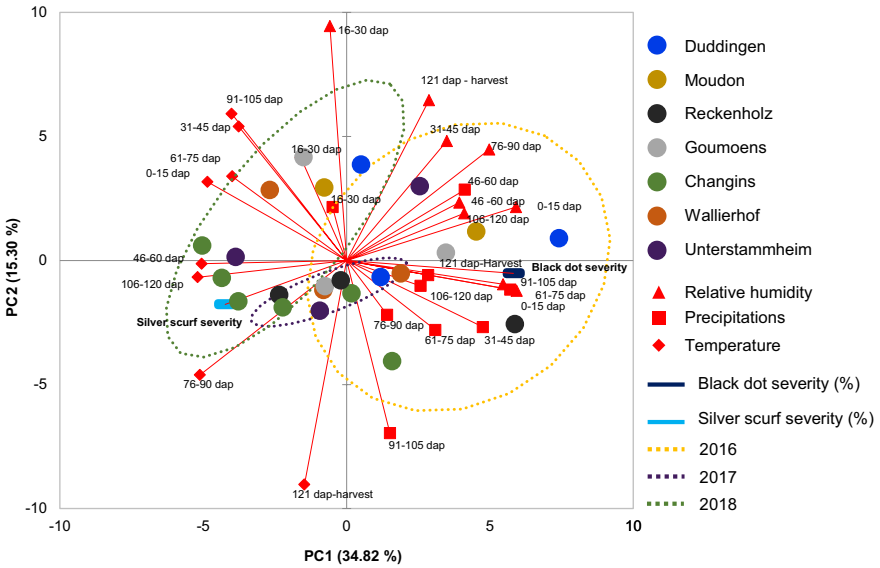

FIGURE 3 Biplot of the principal component analysis (PCA) for meteorological data and the severity of black dot and silver scurf diseases (experiments 1 and 2) on potato tubers at the different field sites. The two first components (PC1 and PC2) explained 50.12% of the total variation. Coloured circles represent observations (field sites), dotted ellipses indicate 95% of confidence of each year's observations (yellow for 2016, violet for 2017, green for 2018), red lines indicate variables (meteorological parameters and disease severity), with data recorded at 2-week intervals from emergence to harvest (dap, days after planting)

effect "year" contributed to 25% of the variance observed and the main effect "field site" contributed to 8% of the variance (Table 3). Interactions between the main effects were statistically significant, but their contribution to the total variance was always less than 6%. The interaction between the factors "cultivar" and "year" could be mainly explained by a single potato cultivar (Ditta), which showed heterogenous behaviour for susceptibility in the three years (Table S2). For the other cultivars, the relative disease severity remained stable in the different field sites (data not shown) and years.

In experiment 3, the overall average black dot severity was 1.5%. Disease severity varied among cultivars, and a correlation between data from the randomized field experiment (experiment 2) and the commercial seed potato stocks (experiment 3) was observed for the incidence (data not shown) and the severity of black dot ($r^2 = .44$, $p < .05$; Figure 6a). However, the cultivar Celtiane showed low susceptibility to black dot in experiment 3 and high susceptibility in experiment 2 (Figure 6a, grey dot). After removal of this cultivar from the analysis, the relationship between black dot severity in both trials (experiment 2 and experiment 3) for the remaining 11 cultivars improved ($r^2 = .72$, $p < .001$; Figure 6a). Black dot severity did not correlate with maturity class, dormancy, or starch content of the cultivars, suggesting that these physiological parameters do not influence black dot severity (Table S3) and the year of registration did not significantly correlate with disease severity, indicating that recently developed cultivars are not more resistant than older potato cultivars. It is worth noting that the cultivars were not genealogically closely related (data not shown).

3.5 | Impact of inoculum source on silver scurf disease severity at harvest

H. solani soil inoculum was not detected at any field site for either experiment (1 or 2, Table 1). However, due to technical reasons, the limit of detection of *H. solani* DNA in soil samples was 500 pg DNA/g soil. Silver scurf disease severity on seed tubers did not correlate with disease severity at harvest (Figure 2c). In experiment 1, planting minitubers did not prevent the emergence of disease symptoms in daughter tubers, and no differences in silver scurf severity between the various seed tuber stocks were observed (Figure 2d).

3.6 | Impact of environmental conditions on silver scurf severity at harvest

In experiment 1, the main effect "year" presented the highest contribution to the total variability (46%), the main effect "field site" contributed to 15%, and the interaction between them explained 26% of the total variability, all of them being statistically significant (Table 2). In experiment 2, the main effect "year" contributed to 18% of the total variability, while the main effect "field site" and their interaction explained 4% and 8% of the total variability, respectively, all being statistically significant (Table 3). PCA of the meteorological data indicated a positive trend between silver scurf severity and temperature (Figure 3). However, the correlation between temperature and disease severity was found to be significant only between 31 and 60 dap and between 106 and 120 dap (Table S1). Furthermore, a negative trend between precipitation (or relative humidity) and silver scurf severity was observed in the PCA (Figure 3). Precipitation was negatively correlated ($p < .05$) with disease severity at the beginning of the season (0–30 dap and 46–60 dap), while relative humidity was negatively correlated ($p < .05$) with silver scurf symptoms at 0–15 dap and at 76–120 dap (Table S1).

3.7 | Monitoring of *H. solani* infections during plant growth

DNA of *H. solani* was found in fewer than 20% of root samples throughout the season (Figure 4a). Fewer than 10% of stolons

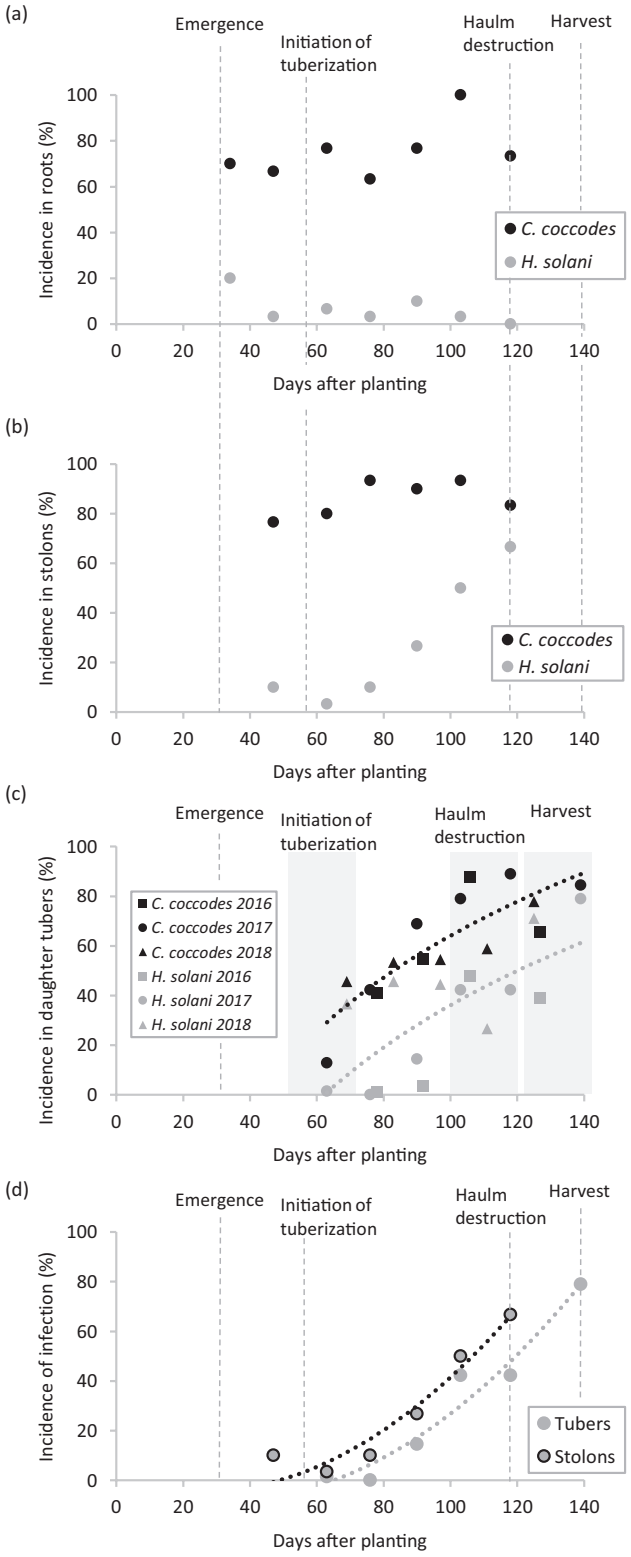

FIGURE 4 Colonization of potato belowground organs by the fungal pathogens *Colletotrichum coccodes* and *Helminthosporium solani* (experiment 1). Incidence of *C. coccodes* (black) and *H. solani* (grey) infections in (a) roots, (b) stolons, and (c) progeny tubers, recorded at 2-week intervals from emergence to harvest in the field site Changins in 2017 (roots and stolons; $n = 30$ per time point) or 2016–2018 (daughter tubers; $n = 90$ per time point). (d) Comparison of infection incidence in stolons and progeny tubers in 2017; lines fitted by polynomial regression ($p < .1$). Incidence was calculated as the percentage of infected samples (detected by PCR) from the total number of samples analysed at each time point

showed infection until 76 dap. Afterwards, a linear increase in *H. solani*-infected stolons was observed, with 27% of stolons infected at 90 dap, 50% at 103 dap, and 67% at haulm destruction (118 dap; Figure 4b). Similarly, fewer than 15% of the tubers were infected with *H. solani* before 92 dap in 2016 and 2017, but this percentage increased to 40% at 100 dap, reaching between 40% and 80% of the tubers infected at harvest (Figure 4c). Early contamination of daughter tubers with *H. solani* occurred in 2018, with more than 35% of the tubers infected at 69 dap. During all 3 years, the number of tubers infected remained below 50% until haulm destruction and increased to 71% at harvest (Figure 4c). In 2017, at each time point, infection incidence was higher in stolons than in tubers, and regression analysis suggested that infection appeared earlier in stolons than in tubers, with an average delay of about 10 days (Figure 4d).

3.8 | Susceptibility of potato cultivars to silver scurf

In experiment 2, conducted to assess cultivar susceptibility, silver scurf disease severity ranged from 8% (Reckenholz in 2017) to 33% (Unterstammheim in 2018) (Figure S1). The main effect "cultivar" explained 48% of the total variance, whereas the factors "year" and "field site" explained only 18% and 4% of the total variance, respectively, all factors being statistically significant (Table 3). Lady Christl was the most susceptible cultivar with an average of 40% of the tuber surface exhibiting symptoms of the disease (Figure 5b). The cultivar Lady Felicia also showed high susceptibility to silver scurf, with an average of 29% disease severity. Five cultivars showed an average disease severity between 20% and 23%, and seven other cultivars between 10% and 15%. The least susceptible cultivars, Gwenne and Cheyenne, showed less than 5% disease severity. The interactions between the main effects "cultivar" and "field site" or "year" were statistically significant but accounted for only 1% and 7% of the total variance observed, respectively (Table 3). Indeed, the relative severity of silver scurf was found to be stable throughout the years for most cultivars, although two cultivars (Annabelle and Ditta) showed very low susceptibility to silver scurf only in 2017 (Table S2). In experiment 3, silver scurf severity on commercial seed stocks was between 1% and 7% in the different cultivars, and there was a strong correlation with cultivar disease severity from experiment 2 ($r^2 = .76$, $p < .001$; Figure 6b). There was no relationship between cultivar susceptibility to silver scurf and that to black dot, but the cultivars Gwenne and Laura showed low susceptibility to both diseases. A negative correlation between maturity classes and silver scurf disease severity on daughter tubers was observed, suggesting that early-maturing cultivars are more susceptible to silver scurf than are late-maturing cultivars (Table S3). On the other hand, silver scurf severity did not

TABLE 3 Three-way analysis of variance (experiment 2) of the main effects of cultivar, field site, and year (and their interactions) on disease severity of black dot and silver scurf of potato

		Black dot				Silver scurf			
Source	*df*	MS	*F*	*p*	Effect size, η^2	MS	*F*	*p*	Effect size, η^2
Main effects									
Cultivar (A)	15	10.03	29.19	<.001***	0.26	21.15	127.77	<.001***	0.48
Field site (B)	2	24.29	70.68	<.001***	0.08	14.77	89.25	<.001***	0.04
Year (C)	2	72.66	211.44	<.001***	0.25	59.13	357.30	<.001***	0.18
Interaction									
A × B	30	0.79	2.31	<.001***	0.04	0.30	1.80	.007**	0.01
A × C	30	0.79	2.30	<.001***	0.04	1.50	9.03	<.001***	0.07
B × C	4	7.50	21.84	<.001***	0.05	13.25	80.06	<.001***	0.08
A × B × C	60	0.53	1.54	.008**	0.06	0.26	1.56	.007**	0.02
Model	143	3.17	9.23	<.001***	0.79	4.11	24.81	<.001***	0.89
Residuals	432	0.34				0.17			

**$p < .01$
***$p < .001$.

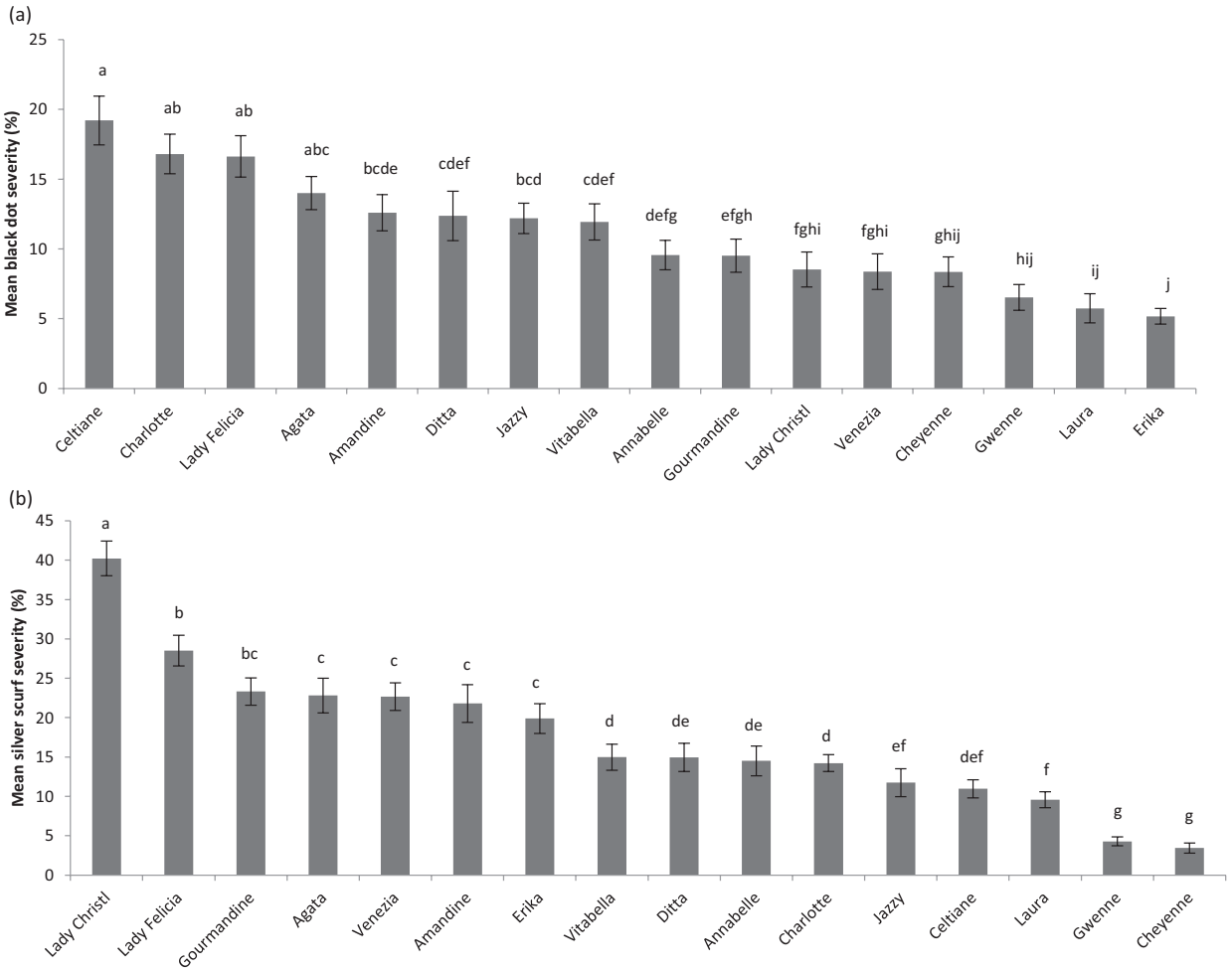

FIGURE 5 Disease severity of (a) black dot and (b) silver scurf among 16 potato cultivars (experiment 2). Values are means of the three years' field trials at three sites in randomized plots ($n = 36$). Vertical bars represent standard error of means. Different letters indicate statistically significant differences ($p < .01$, Tukey's test)

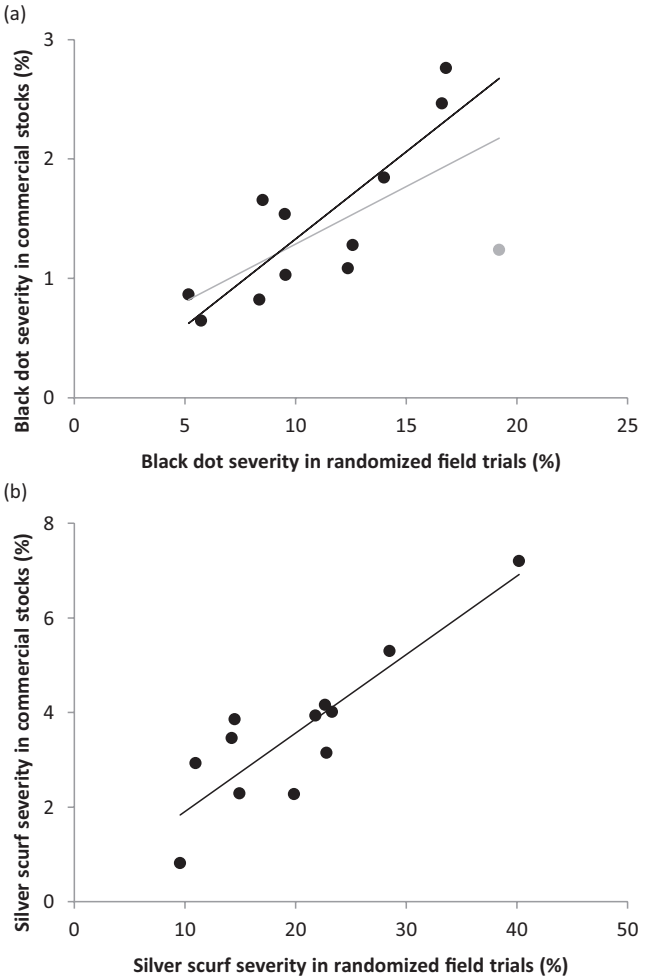

FIGURE 6 Correlation between (a) black dot severity and (b) silver scurf severity for 12 potato cultivars from the randomized field trial (experiment 2) and the wide-scale monitoring of commercial seed stocks (experiment 3). In (a), the grey dot is the potato cultivar Celtiane, the grey line is linear correlation between all cultivars, and the black line indicates the correlation between all cultivars except Celtiane. Variance accounted for is 44% and 72% (for all cultivars and all cultivars except Celtiane, respectively) for black dot and 76% for silver scurf

correlate with dormancy or starch content, and disease severity of recently developed cultivars did not differ from that of older cultivars.

4 | DISCUSSION

Black dot and silver scurf are tuber blemish diseases of potato with similar visible symptoms. Even though the pathogens causing these diseases are fungi with quite different characteristics, they share the same ecological niche: the potato periderm. Because, in a commercial context, symptoms of these diseases are often scored together, an efficient pest management strategy should include both of them. This study presents new insights into epidemiological factors that drive the development of each disease.

The level of *C. coccodes* soil inoculum has previously been shown to be related to black dot disease severity (Lees et al., 2010). In the field trials presented here, no such correlation was found. However, a threshold was defined of 50 pg DNA/g soil, above which the risk of high disease severity increased. The existence of a threshold but no correlation between subsequent increases in soil inoculum level and disease severity suggests that the presence of soil inoculum in sufficient quantity is a prerequisite for disease development, but that other factors determine final disease severity. Assuming that tubers with more than 10% black dot severity may be unmarketable, the choice of fields with soil inocula below this threshold would have reduced the share of unmarketable tubers from 24% to 16% in the experiments presented. In contrast, *H. solani* inoculum was not detected in any of the soils analysed, but because the detection limit of *H. solani* in the soil was relatively high in these tests, its presence cannot be excluded. Planting minitubers in some of these soils resulted in diseased progeny tubers, suggesting that *H. solani* inoculum was indeed present in these fields. Studies conducted in Canada (Bains et al., 1996) showed that disease-free seed tubers produce diseased progeny tubers even in fields without a known history of potato cultivation. However, other authors have found that the use of clean minitubers results mostly in healthy progeny tubers (Geary & Johnson, 2006; Miller et al., 2015). *H. solani* inoculum has been shown to not survive for more than one season in the soil (Mérida & Loria, 1994). However, volunteer potatoes often grow in fields where potato crops have been cultivated previously. Furthermore, *H. solani* has been shown to be saprophytic to a number of crop species such as maize and wheat (Mérida & Loria, 1994), which are cultivated in rotation with potatoes in Switzerland.

Disease severity on seed tubers did not influence disease severity at harvest for either disease, as found elsewhere (Denner et al., 1998; Dung et al., 2012; Firman & Allen, 1995; Read & Hide, 1984). Compared to commercial seed stocks, minitubers did not reduce silver scurf severity at harvest, but did produce progeny tubers with significantly fewer black dot symptoms (35% reduction). For *C. coccodes*, similar results were observed in South African trials (Denner et al., 1998), although other studies showed that the use of clean minitubers did not reduce disease severity at harvest (Dung et al., 2012). The effect of inoculum sources has been suggested to be cultivar specific (Nitzan et al., 2005), which may explain these different observations. Furthermore, in the present study, plants originating from minitubers were generally smaller in the field, mostly with a single main stem, and tuberization occurred slightly later in the season. This is probably due to the physiological age of the seed tubers, which were harvested in July for the commercial seed tuber stocks and in late autumn for the minitubers. The delay in tuberization in plants originating from minitubers might explain the lower disease severity, because it has been shown that disease severity is positively correlated with the length of time the tubers are in infested soil (Hide & Boorer, 1991; Hide et al., 1994).

Environmental conditions had a significant impact on the development of both diseases. In general, warm and dry conditions were associated with increased silver scurf severity. This data is in

accordance with the growth rate of *H. solani* mycelium increasing along a temperature gradient from 6 to 30 °C (authors' unpublished data) and optimal conditions for conidial formation and maturation being at 20–25 °C (Hunger & McIntyre, 1979). Potato plants grown during humid seasons were more prone to black dot, which is in line with other reports that showed that this disease is favoured by irrigation (Brierley et al., 2015; Hide et al., 1994; Lees et al., 2010; Olanya et al., 2010).

The monitoring of fungal infections in the field revealed that *C. coccodes* is able to infect all belowground organs of potato plants at early stages, which is in accordance with previous studies (Andrivon et al., 1998; Lees et al., 2010). *H. solani* DNA was detected on progeny tubers and, for the first time, in stolons, but rarely in roots. Previous work has shown that roots, stolons, and stems do not show silver scurf symptoms (Fahn, 1982), but molecular biology techniques have not previously been used to detect latent *H. solani* infections in belowground organs. The demonstration that this fungus is able to infect potato stolons, and the observation of a delay between stolon and tuber infection, is in accordance with a previous report showing that silver scurf lesions appear first at the stolon end of the tuber (Jellis & Taylor, 1977). This time sequence of infections suggests that the pathogen progresses from the seed tuber to the progeny tubers through the stolons. Alternatively, *H. solani* mycelia or conidia present in the soil may infect the potato organs as they develop, as stolons appear about 10 days before tubers. The results presented here also showed that infections of potato belowground organs by *H. solani* occurred later in the season and progressed more slowly than those of *C. coccodes*. Because warm temperatures usually occur during the second half of potato production in Switzerland, *H. solani* may be more active during that period of the season. Higher temperatures at the beginning of the season were recorded in 2018, which correlated with relatively early infections of daughter tubers with *H. solani*.

All potato cultivars studied showed symptoms of black dot and silver scurf, confirming the absence of full resistance in commercial potato cultivars, as found in other studies (Brierley et al., 2015; Joshi & Pepin, 1991; Sedláková et al., 2013). However, cultivar had a strong impact on disease severity, especially for silver scurf. Cultivar susceptibility data from the randomized field trials was validated by the wide-scale monitoring of commercial seed potato stocks over a broad range of environmental conditions representative of the Swiss potato-growing regions. Silver scurf severity was higher in the early-maturing cultivars than in the late-maturing cultivars. Similarly, cultivar maturity has been suggested to be involved in susceptibility to black dot (Andrivon et al., 1998), but this was not confirmed here. Instead, other genetic characteristics may be more important in determining cultivar susceptibility to black dot, and recent studies suggest that resistance may include several mechanisms (Massana-Codina et al., 2020). Taken together, the results presented here contribute to a better understanding of the epidemiology of black dot and silver scurf and can help reduce the risk of both diseases.

Planting disease-free seed tubers was not an effective measure to control these blemish diseases, although it could prevent the introduction of the pathogens in uninfested soils. Instead, the focus should rather be on reducing soil inoculum, which could be achieved by cultural methods, such as long rotations without alternative hosts of *C. coccodes* and the management of volunteer potatoes. *C. coccodes* soil inoculum could be quantified to determine the risk of tubers developing severe black dot symptoms. Through this work, potato cultivars for the fresh market with different degrees of susceptibility to black dot and silver scurf have now been identified, including cultivars with low levels of susceptibility to both diseases. Furthermore, cultivar was shown to be a major determinant of black dot severity, and even more so for silver scurf severity, and therefore cultivar choice could reduce the risk of severe disease impact. Monitoring meteorological conditions may help predict the risk of disease development. Altogether, the factors of soil inoculum, weather conditions, and cultivar susceptibility could be used in a risk assessment scheme. Because black dot and silver scurf may progress during storage (Hide et al., 1994; Peters et al., 2016; Rodriguez et al., 1996), the early distribution of tuber stocks with high risk should be prioritized.

The present work is part of a Swiss collaborative project including several approaches (disease severity monitoring from planting to distribution, *C. coccodes* host range, chemical and biological treatments during planting and postharvest) aimed at the development of an integrated management strategy to control both diseases.

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DATA AVAILABILITY STATEMENT

The meteorological data that support the findings of this study are derived from the resources available in the public domain Agrometeo at https://www.agrometeo.ch/meteorologie. The additional data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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