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Factors influencing the airborne sporangia concentration of *Phytophthora infestans* and its relationship with potato disease severity

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ABSTRACT

Forecasting systems are widely used to predict the application of fungicides for managing late blight. However, airborne inoculum has rarely been included in these forecasting systems. Monitoring the sporangia in crop environments may offer an opportunity to improve late blight forecast systems by integrating pathogen pressure. Hence, this experiment aiming to analyze relationships between weather based risk systems and sporangia levels in the atmosphere of potato crops. The experiments were conducted during two growing seasons in a potato field. During the study, the concentration of *Phytophthora infestans* in the air, the weather conditions, the phenology of cultivars and r-AUPDC during the crop cycle were recorded. The weather-based risk of late blight was estimated using infection pressure (IP) and the daily risk value (DRV) based on hourly relative humidity (RH) and temperature (T). The effect of weather parameters on sporangia levels was analyzed. IP and DRV showed a strong positive correlation with sporangia concentration, standing out the pronounced effect of RH on the sporangia levels. Analysis of the hourly sporangia concentration within a day showed an increase in the sporangia concentration from 9 h to 18 h. This increase in sporangia was linked to an increase in T, spore release, and a decrease in RH. Our results identified a T of 10 °C and RH of 80% as the minimum threshold for significant sporangia concentration in the air. However, maximum sporangia level was found in the air at 88% (average relative humidity) and 17 °C (average temperature). Finally, the effect of weekly *P. infestans* sporangia was observed on cultivars with different susceptibility to late blight.

1. Introduction

Potato late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is one of the most destructive plant diseases. Despite decades of intensive breeding efforts, it remains a threat to potato production worldwide (Fry et al., 2015; Dey et al., 2018). In Galicia (NW Spain), the disease causes massive yield losses among potato growers due to the favorable weather conditions. Generally, the control of late blight in conventional potato production systems is often through weekly application of prophylactic fungicides during the growing season, with an average number of seven fungicidal sprays each crop season. This excessive use of fungicides is considered unsustainable, because increases production costs for the growers unnecessarily and degrades the environment. Concerns about fungicide resistance is also a major challenge arising from excessive usage of them. In agreement to this, the resistance to Fluazinam by some *P. infestans* genotypes has been reported (Schepers et al., 2018). Accordingly, there is a pressing demand by both local and regional policies for the reduction in the use of pesticides.

One way of regulating the use of fungicides to control late blight is using forecasting or decision support systems. Forecasting systems identify periods in the season with high risk for infection, and thus recommend the application of a fungicidal treatment. DSSs have been shown to reduce fungicides in several host-pathosystems, as documented for other fungal diseases in potatoes such as early blight (Abuley and Nielsen, 2017; Meno et al., 2020; 2021a). In the case of late blight, some forecasting systems such as: BlightManager (Abuley et al., 2020), IrishModel (Cucak et al., 2019) or SiMCAST (Grünwald et al., 2000) have been developed in different countries to predict outbreaks in potato crops.

A major shortcoming in most of these DSSs is the omission of the aerial sporangia concentration as part of the decision-making. Most models such as BlightManager, SIMCAST and Irish Models are premised on weather factors that influence infection, but not the aerial inoculum

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concentration of the pathogen, although this is important to achieve adequate control with minimal fungicide use (Jeger, 1990; Aylor et al., 2011; Escuredo et al., 2019a; González-Fernández et al., 2020; Meno et al., 2020). The weather is a dominant factor in the development of late blight epidemics, if there is concentration of inoculum in the environment of potato crop. Thus, the inclusion of airborne inoculum in disease forecasting is crucial (Aylor et al., 2011). When the disease is present, *P. infestans* is largely aerially dispersed during the crop season (Seijo-Rodríguez et al., 2018). So that, the monitoring of the airborne concentration of sporangia as well as the factors that influence their presence in the air, can be a useful to predict early attacks of pathogens to avoid secondary infections. Although aerobiology has existed for decades, recent advancement in the development of innovative technologies is contributing to an increase in the use of aerobiological data for several purposes such as the daily monitoring of aerial pathogens for disease forecasting (Escuredo et al., 2019b, 2019a; González-Fernández et al., 2020; Meno et al., 2020; Hjelkrem et al., 2021).

Forecasting the risk of infection by a pathogen in cultivars is indispensable for the management of agricultural crops (Escuredo et al., 2019a). In the case of potatoes many cultivars were breeding looking for a better agronomic yield, tuber quality and resistance. Albeit resistance can be short-lived due to the ability of the pathogen to defeat R-gene and thus render the R-gene ineffective (Ballvora et al., 2002), host resistance is a useful component in managing late blight (Abuley and Hansen, 2021). Currently, the cultivation of varieties considered to be more resistance to late blight in Galicia is scarcely practiced and effectiveness unknown. Thus, the evaluation of resistance of different potato cultivars is relevant. The objectives of this study were to: (1) monitor the airborne sporangia concentration of *P. infestans* under field conditions, (2) study the weather factors that influence sporangia concentration in the air and disease severity development; and (3) study the response of nine potato cultivars under pressure of late blight.

2. Material and methods

2.1. Experimental site and design

The study was conducted on an experimental plot located in the NW of Spain, in Betán (42° 14′ N, 7° 43′ W) for two growing seasons (2020 and 2021). Nine potato cultivars (Desiree, Frisia, Fontane, Agria, Red Pontiac, Kennebec and Fleur Bleue, Louisa and Daifla) were planted in each growing season. These cultivars were selected according to current market preferences as fresh (Kennebec, Red Pontiac, Frisia, Daifla and Desiree) and processing (Agria, Fleur Bleue, Louisa and Fontane). Certified seed tubers of each cultivar were planted in 10 m^2 plot on 11 April 2020 and 4 April 2021. Regarding maturity, the earliest cultivars were Frisia and Red Pontiac, Kennebec, Fontane and Daifla were medium maturity cultivars and Desiree, Fleur Bleue, Agria and Louisa had late maturity (Meno et al., 2021a). The potatoes were not treated with any late blight specific fungicide to allow for the natural development of late blight. Cultural practices and standard agronomic practices for potato production were performed as shown in Table S1 (Supplementary material).

2.2. Weather data monitoring

emperature (T) and relative humidity (RH) during each growing season were monitored with an iMetos 3.3 data logger by Pessl Instruments (Weiz, Austria) placed within the experimental plot. These data logger recorded the weather variables at 1.5-meter height and at an hourly interval.

2.3. Aerobiological sampling of airborne Phytophthora infestans sporangia

A 7-day Burkard recorder spore-trap (Manufacturing Co. Ltd., UK) located inside the experimental plot was used for sampling the aerial sporangia of *P. infestans*. The spore-trap contains a pump to suck the air of the environment and a removable drum which contains a melinex tape that is the impact surface. The movement of the drum is controlled by a clock lasting seven days. The melinex tape is impregnated with a 2% silicone solution allowing the adherence of the particles/biotic elements. Each week the drum was removed and the melinex tape replaced. In the laboratory, the tape was cut off in daily fragments and mounted on slides. Using a Nikon YS 100 microscope, the sporangia of *P. infestans* were quantified following the REA (Spanish Aerobiological Network) protocol proposed by Galán et al. (2007). The magnification used was 400X or 1000X, when necessary. Data were expressed such as sporangia/m^3.

2.4. Daily risk value, infection pressure and sporangia released

The daily risk value (DRV) and the infection pressure (IP) for late blight during the crop seasons were calculated according to the methodology proposed by Abuley et al. (2020). The DRV was calculated considering the consecutive hours accomplishing a RH higher than 88% (humid hours) and temperature between 10 °C and 24 °C. The number of hours with these conditions are accumulated until a maximum of 33. Note that if the DRV is higher than 33, then the extra risk hours will be assigned to the next day. IP was calculated following the Danish late blight model (BlightManager) (Abuley et al., 2020) considering the DRV of previous and next few days, following Eq. (1):

$$\mathrm{IP} = \mathrm{DRV}_{-2} + \mathrm{DRV}_{-1} + \mathrm{DRV}_{0} + \mathrm{DRV}_{+1} + \mathrm{DRV}_{+2} \tag{1}$$

where DRV_0 is the risk hours for the present day, DRV_{-1} is the risk hours one day ago, DRV_{-2} is the risk hours two days ago, DRV_{+1} is the risk hours one day ahead, DRV_{+2} is the risk hours of two previous days.

Furthermore, the spore release (SR) was calculated according to Skelsey et al. (2009) basing on weather conditions as following in Eqs. (2a) and (2b):

$$\mathbf{SR} = \mathbf{0}\ \textbf{when RH} \geq \mathbf{88\%} \tag{2a}$$

$$\mathbf{SR} = \{(\mathbf{1} / (\mathbf{RH} - \mathbf{91})) + \mathbf{1}\ \}\textbf{when RH} < \mathbf{88\%} \tag{2b}$$

To unify the criteria of RH (relative humidity) with the BlightManager model (Abuley et al., 2020), 88% has been considered the lower limit instead of 90% proposed by Skelsey et al. (2009).

2.5. Disease severity assessment

The disease severity progression 5-7-day intervals were measured in three potato plants of each cultivar. The evaluation of severity was done from the plant emergence until senescence using the methodology proposed by Rahmatzai et al. (2017) with some modifications. The levels marked were:

1. 0%: No late blight lesions were observed.
2. 1%: when symptoms appeared
3. 10%, 25%, 50%, 75% when 10, 25, 50 and 75% of the leaves were attacked by late blight, respectively.
4. 100%, when leaves were completely dead/defoliated.

The disease severity data were used to calculate the area under the disease progress curve (AUDPC) using the mid-point method (Shaner and Finney, 1977). Subsequently, AUDPC values dividing by the duration of the epidemic were standardized to obtain the relative area under the disease progress curve (r-AUDPC) (Fry, 1978). The epidemic duration was defined as the days elapsed from onset of late blight until total defoliation or the end of the season. r-AUDPC is considered the better metric for comparing the cultivars due to their differential epidemic duration (Fry, 1978; Meno et al., 2021a).

2.6. *Plant phenology monitoring*

The phenological development of the cultivars were weekly monitored from emergence until crop senescence in each growing season. The phenological stages of BBCH scale (Hack et al., 1993) considered are summarized below:

1 Emergence: when 50% of the cultivars in each plot have emerged (09 in BBCH scale).
2 Foliar development: which is the period between emergence until 100% row closure (35 in BBCH scale).
3 Maturation: which is the period between foliar development and the beginning of senescence, i.e. when 25% of plants start to dry out and turn yellow (from 69 to 95 in BBCH scale).
4 Senescence: when more than 50% of the plants are yellowing or dead (95 in BBCH scale).

2.7. *Statistical analyses*

Statistical analyses and data handling were carried out with SPSS 21.0 software package for Windows (IBM, Somers, NY, USA). A non-parametric correlation analysis (Spearman correlation) was applied to determine relationships among meteorological variables and *P. infestans* sporangia concentration in air. The Spearman correlation coefficients were calculated using the sporangia concentration and weather variables for the same day and the 5 previous days. A similar statistical treatment was applied to identify significant relationships among *P. infestans* concentration in the air and the disease severity progression of each cultivar. The Spearman correlation coefficients were calculated for values of same week and the previous week. The established levels of *P. infestans* in the air (low, medium and high) were compared with weather parameters (temperature and relative humidity) to identify critical values on meteorological parameters, in which there are different concentrations of conidia. Similarities and differences between sporangia levels and weather conditions were checked throughout an ANOVA and the Bonferroni test for post hoc comparisons. The significance level was set at α=0.05.

3. Results

3.1. *Weather conditions*

Analyzing the weather trend during each crop season, the 2020 crop was warmer than 2021 crop. Daily temperatures were higher than 20.0 °C in most of days of 2020 crop season, recording an avgT of 17.0 °C, an average minT of 11.0 °C and an average maxT of 23.8 °C. If it is compared with 2021, the avgT was 14.4 °C, average minT of 8.8 °C and average maxT of 20.8 °C. In addition, RH was higher in 2020, with an avgRH of 84.7%, whereas 2021 had an average value of 75.4% (Fig. 1).

3.2. *Infection pressure and trapped sporangia*

The daily concentration of *P. infestans* sporangia was substantially higher in 2020 than in 2021 (Fig. 2). A total of 658 sporangia/m^3 were counted during the 2020 growing season, whereas 233 sporangia/m^3 were counted in 2021. Moreover, the maximum daily sporangia value was substantially higher in 2020 (40 sporangia/m^3) than in 2021 (20 sporangia/m^3). As evidenced by the higher infection pressure (IP), 2020 year was the most favorable for late blight outbreaks (Fig. 2). In this year, the first peak of IP was found 30 days after planting (DAP), whereas in 2021 season the first highest peak occurred after 80 DAP.

The period from the 31 of April (20 DAP) to the 10 of July (91 DAP) of 2020 the highest number of sporangia was recorded on 23 June (74 DAP) and 5 July (86 DAP), which coincided with a period of high and continuous infection pressure (Figs. 1a and 2a). However, after this critical period, the sporangia in the atmosphere of the crop decreased until the 1 of August (113 DAP) (Fig. 2a). This decline coincided with a period of increased T and decreased RH (Fig. 1a). During the first growing season (2020), the first peak was registered on 15 DAP (with daily concentration higher than 10 sporangia/m^3). In 2021 year, sporangia levels were lower, being the period with a higher concentration from the 1 of June (59 DAP) to the 31 of July (119 DAP). The first peak with daily concentration higher than 10 sporangia/m^3 appeared later than 2020 season (Fig. 2b).

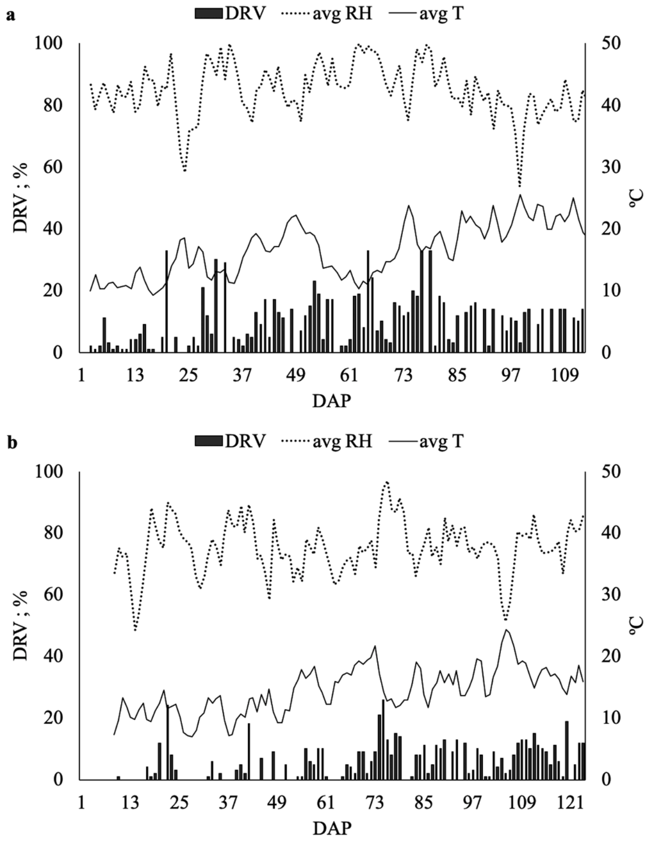

Fig. 1. Weather parameters and the accumulated daily risk value (DRV) for late bight for both crop seasons: 2020 (a) and 2021 (b). The weather parameters were daily average temperature (avgT) and relative humidity (avgRH). DAP is the number of days after planting. Planting dates were: (a) on 11 April 2020; (b) on 4 April 2021.

3.3. *Determining the periods of aerobiological risk during the crop season*

The DRV units accumulated per month of each growing season had considerable differences (Fig. 3). However, even though the year 2020 had the highest levels of *P. infestans*, the upward trend of April, May and June were similar for both years, registering the highest value of DRV in June. In July, the DRV are similar in both years, despite the value was lower in comparison with the previous months for 2020 and higher when comparing with those months of 2021 season. It should be noted that the concentration of sporangia showed the same trend than the risk units.

3.4. *Determining the intra-daily pattern distribution of sporangia*

The results of the aerobiological sampling allowed to detect maximum values of the total sporangia trapped in the central hours of the day (between 9 h and 18 h) compared with values trapped at other hours of the day (Fig. 4). The period comprised between 8 h and 10 h showed significant trend changes in all considered parameters. The maximum of accumulated sporangia occurred at 13 h, registering an avgT of 18.5 °C and an avgRH of 72.4%. The highest avgT was recorded

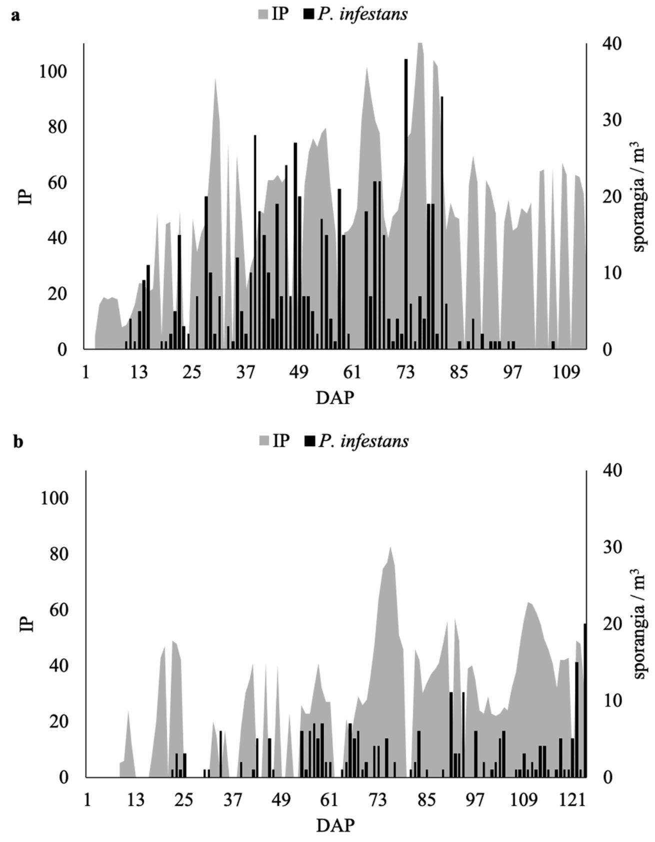

Fig. 2. Infection pressure (IP) and daily sporangia concentration of *P. infestans* registered during each crop season: 2020 (a) and 2021 (b). DAP is the number of days after planting. Planting dates were: (a) on 11 April 2020; (b) on 4 April 2021.

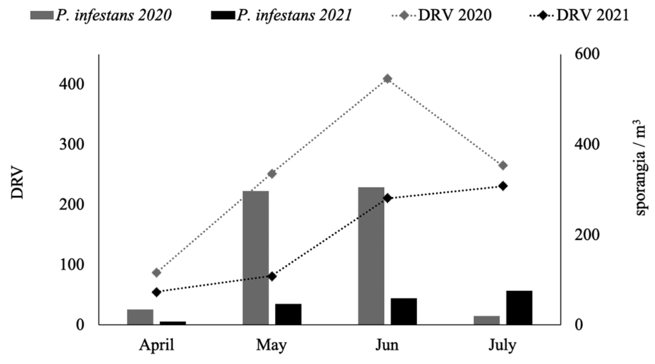

Fig. 3. Monthly sporangia concentration of *P. infestans* and daily risk value (DRV) in 2020 and 2021.

between 17 h and 18 h (22.1 °C), coinciding with the lowest avgRH (57%). Then, the number of accumulated sporangia was declining from 18 h to 9 h.

3.5. Relationships between weather variables and trapped sporangia

The influence of the weather conditions up to five previous days was considered (Table 1). Each period (2020 and 2021) in a separate way was analyzed, due to the highest levels of sporangia found in each growing cycle. In some cases, high correlation coefficients were obtained, which can be useful for predictive models.

In the case of 2020 season, the temperature (average, minimum and maximum) had significant negative correlation coefficients with sporangia concentration, except for minT the same day (0d) and the previous day (-1d) (Table 1). The higher correlation coefficient was found on -3d for all the temperature parameters. Furthermore, avgRH and minRH (for all considered days) had significant positive correlation coefficient with sporangia concentration. However, the highest correlation coefficient was on -1d (avgRH) and -3d (minRH). DRV on -2d and IP on 0d and -2d were positively correlated with sporangia levels. In 2021, T variables were positively significant correlated with the sporangia, except for -5d (avgT), -2d, -4d and -5d (minT) (Table 1). Respect to RH, only maxRH on 0d was positively significant correlated with sporangia levels. Finally, DRV and IP were positive correlated with sporangia concentration on -1d (DRV and IP) and -4d (DRV).

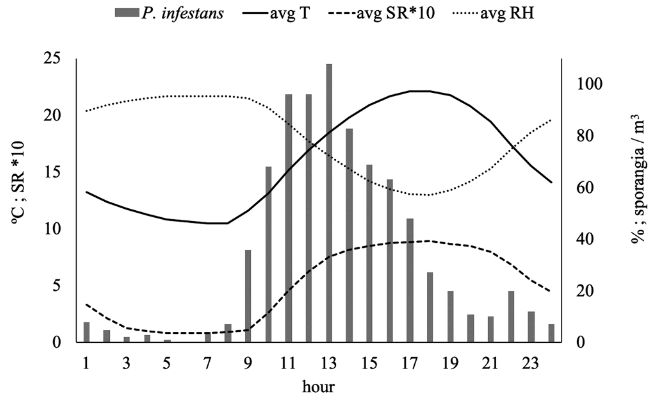

Fig. 4. Hourly accumulated sporangia concentration and the average values of temperature (avgT), the average relative humidity (avgRH), the average sporangia released (avgSR*10) in both years. In X axis are represented the hours of the day.

The daily concentration of sporangia in the atmosphere of the crop is variable. The sporangia during several days of the studied period were not detected, and values below 15 sporangia/m^3 many days were counted, while values over 15 sporangia/m^3 occasionally appeared. Hence, three levels based on the values of sporangia in the air: 1 (0 sporangia/m^3), 2 (1-15 sporangia/m^3), and 3 (>15 sporangia/m^3) were defined to evaluate the influence of weather parameters and infection pressure in them (Table 2).

Significant differences found between the avgRH and minRH in each of the period, coinciding with the sporangia levels, between the level 1 and 3 (Table 2). On the contrary, the temperature did not show significant differences when comparing the levels, despite T (avg, min and max) was higher when the number of spores increased. Thus, the level 3 was associated with the highest values of minT, maxT, avgT, avgRH, maxRH and minRH, and level 1 was associated with the lower values of T and RH. In the case of risk infection parameters (DRV and IP), significant differences between the three levels were found. At the same time, the sporangia levels increased with DRV and IP variables. The highest sporangia level (level 3) responded to the higher values of IP and DRV, whereas the lowest sporangia level (level 1) had the lower values. Therefore, high sporangia levels were associated with higher values of T and RH, and higher value of DRV and IP.

3.6. Disease development and monitoring of crop phenology of potato cultivars

The late blight severity and the main phenological stages of the cultivars are summarized in Fig. 5. Favorable conditions (high IP and high sporangia concentration) for late blight development occurred early in 2020 than in 2021. For this crop season, the period between emergence and senescence of plants was longer, occurring favorable conditions when senescence stage started. Accordingly, the onset of late blight was markedly delayed in 2021 (99 DAP) compared to 2020 (43 DAP). In 2021, the late-maturing cultivars such as Agria, Fleur Bleue and

Table 1
Spearman correlation coefficients between sporangia concentration and weather parameters until 5 days before recorded in both crop seasons (2020 and 2021): average temperature (avgT), minimum temperature (minT) and maximum temperature (maxT), average relative humidity (avgRH), maximum relative humidity (maxRH), minimum relative humidity (minRH), daily risk value (DRV) and infection pressure (IP).

	Previous days	avgT	maxT	mint	avgRH	maxRH	minRH	DRV	IP
Pooled data	0d	0.193**	0.144*	0.136*	0.289**	0.351**	0.219**	0.258**	0.270**
	- 1d	0.159*	0.098	0.192**	0.325**	0.284**	0.266**	0.253**	0.280**
	- 2d	0.097	0.058	0.070	0.239**	0.238**	0.214**	0.246**	0.255**
	- 3d	0.058	0.011	0.056	0.255**	0.236**	0.241**	0.130	0.173*
	- 4d	0.047	0.032	0.035	0.183**	0.196**	0.132	0.146*	0.215**
	- 5d	-0.008	-0.014	-0.051	0.219**	0.228**	0.170*	0.130	0.205**
2020	0d	-0.222*	-0.265**	-0.177	0.309**	0.064	0.313**	0.191	0.203*
	- 1d	-0.268**	-0.303**	-0.132	0.342**	0.040	0.343**	0.113	0.173
	- 2d	-0.291**	-0.309**	-0.215*	0.266**	-0.010	0.303**	0.291**	0.218*
	- 3d	-0.331**	-0.332**	-0.270**	0.321**	0.044	0.350**	0.101	0.138
	- 4d	-0.316**	-0.328**	-0.252*	0.240*	0.018	0.262**	0.025	0.170
	- 5d	-0.293**	-0.296**	-0.267**	0.280**	0.067	0.255*	0.042	0.149
2021	0d	0.452**	0.417**	0.285**	0.033	0.395**	-0.064	0.178	0.174
	- 1d	0.445**	0.377**	0.363**	0.094	0.180	0.043	0.282**	0.250**
	- 2d	0.331**	0.325**	0.179	-0.053	0.100	-0.036	0.125	0.170
	- 3d	0.302**	0.232*	0.246**	-0.080	0.092	-0.010	0.017	0.025
	- 4d	0.293**	0.308**	0.183	-0.139	0.030	-0.186	0.187*	0.128
	- 5d	0.172	0.199*	0.046	-0.052	0.129	-0.119	0.096	0.089

[*] $P < 0.05$

[**] $P < 0.01$.

Table 2
Average data of weather parameters calculated by level of *P. infestans* considering both crop season (2020 and 2021). Average temperature (avgT), minimum temperature (minT) and maximum temperature (maxT), average relative humidity (avgRH), maximum relative humidity (maxRH), minimum relative humidity (minRH) and sum of hours with RH>88% (sumRH>88%), daily risk value (DRV) and infection pressure (IP) for late blight.

	Sporangia levels		
	1	2	3
avgT (°C)	15.0a	16.1a	17.2a
maxT (°C)	21.5a	22.9a	23.7a
minT (°C)	9.3a	10.0a	11.3a
avgRH (%)	77.5a	80.5a	88.6b
maxRH (%)	97.0a	98.3a	99.9a
minRH (%)	51.2a	53.9a	67.7b
DRV	5.3a	8.5b	12.6c
IP	29.6a	41.1b	55.0c

Different letters show significant differences between sporangia levels according to the Bonferroni test ($P < 0.05$). Sporangia levels: 1 (0 sporangia/m^3); 2 (1-15 sporangia/m^3); 3 (> 15 sporangia/m^3).

Desiree completed their growing cycle after the onset of favorable late blight conditions. However, for early and medium-maturing cultivars such as Frisia and Kennebec, the first late blight attack was in the senescence stage, thus the effect was lower, and the disease progression did not reach 100% severity. In Red Pontiac, the late blight attack was more severe, accounting for the highest percentages of severity in both years of crop (Fig. 5). Anyway, the late blight severity was higher in 2020 than in 2021.

3.7. Relationships between airborne sporangia and disease severity

The relationships between late blight severity progression of the different cultivars and the weekly sporangia level were statistically estimated using a Spearman correlation analysis (Table 3). Significant positive correlation coefficients between sporangia concentration and late blight severity by cultivar were found for most of them. It should be mentioned Kennebec and Frisia did not shown symptoms of disease in 2021, so both cultivars were only included for 2020 season (Fig. 5; Table 3). The obtained correlation coefficients were slightly higher considering the data of the previous week (Week-1) for all the cultivars excepting Frisia and Kennebec.

3.8. Susceptibility ranking of the cultivars

Generally, r-AUDPC values of studied cultivars were higher in 2020 than in 2021 (Fig. 6). In 2020, Louisa had the lowest r-AUDPC, followed by Desiree and Fleur Bleue, whereas Red Pontiac had the highest r-AUDPC (Fig. 6a). In 2021, we did not consider Kennebec and Frisia because both cultivars had reached senescence before the onset of late blight. Louisa, Desiree, and Fleur Bleue also had the lowest values of r-AUDPC. Again, Red Pontiac was the cultivar with the highest value of r-AUDPC in 2021 (Fig. 6b).

Based on the results of the Bonferroni test applied to r-AUDPC, Red Pontiac was significantly different in two crop seasons respect to other cultivars (Fig. 6). On the contrary, the cultivars with significantly lower values of r-AUDPC were Louisa, Fleur Bleue and Desiree. Thus, three groups of susceptibility to late blight can be established: susceptible (Red Pontiac), moderate (Kennebec, Agria, Daifla, Frisia and Fontane) and resistant (Louisa, Fleur Bleue and Desiree). These cultivar groups showed the same significant differences in each growing season. Despite the different conditions of the two crop cycles studied, the response behavior to the disease by cultivar seems to be similar.

4. Discussion

The use of forecasting systems to predict and time the application of fungicides for managing late blight is widely known (Beaumont, 1947; Smith, 1956; Wallin, 1962; Ullrich and Schrodter, 1966; Krause et al., 1975; Fry et al., 1983; Winstel, 1993; Hansen et al., 1995; Taylor et al., 2003; Singh and Sharma, 2013). These are based mainly on weather factors that influence infection, but not the aerial inoculum concentration of the pathogen. However, information regarding the aerial dispersal and sporangia released are relevant for the accurate prediction of late blight outcomes and to achieve adequate control with minimal fungicide use (Jeger, 1990; Aylor et al, 2011; Seijo-Rodríguez et al., 2018; González-Fernández et al., 2020; Supriya et al., 2020). Several studies have emphasized that understanding the factors underpinning the aerial dispersal of *P. infestans* is crucial for the correct prediction of late blight epidemics (Aylor et al., 2001; Skelsey et al., 2009; Seijo-Rodríguez et al., 2018). Our study is one of the few that have aimed at quantifying airborne sporangia and the weather factors influencing the airborne sporangia concentration of *P. infestans*. While several factors (e.g., wind, temperature, solar radiation, rain) to forecast the outbreak of late blight could be used (Beaumont, 1947; Smith, 1956; Ullrich and

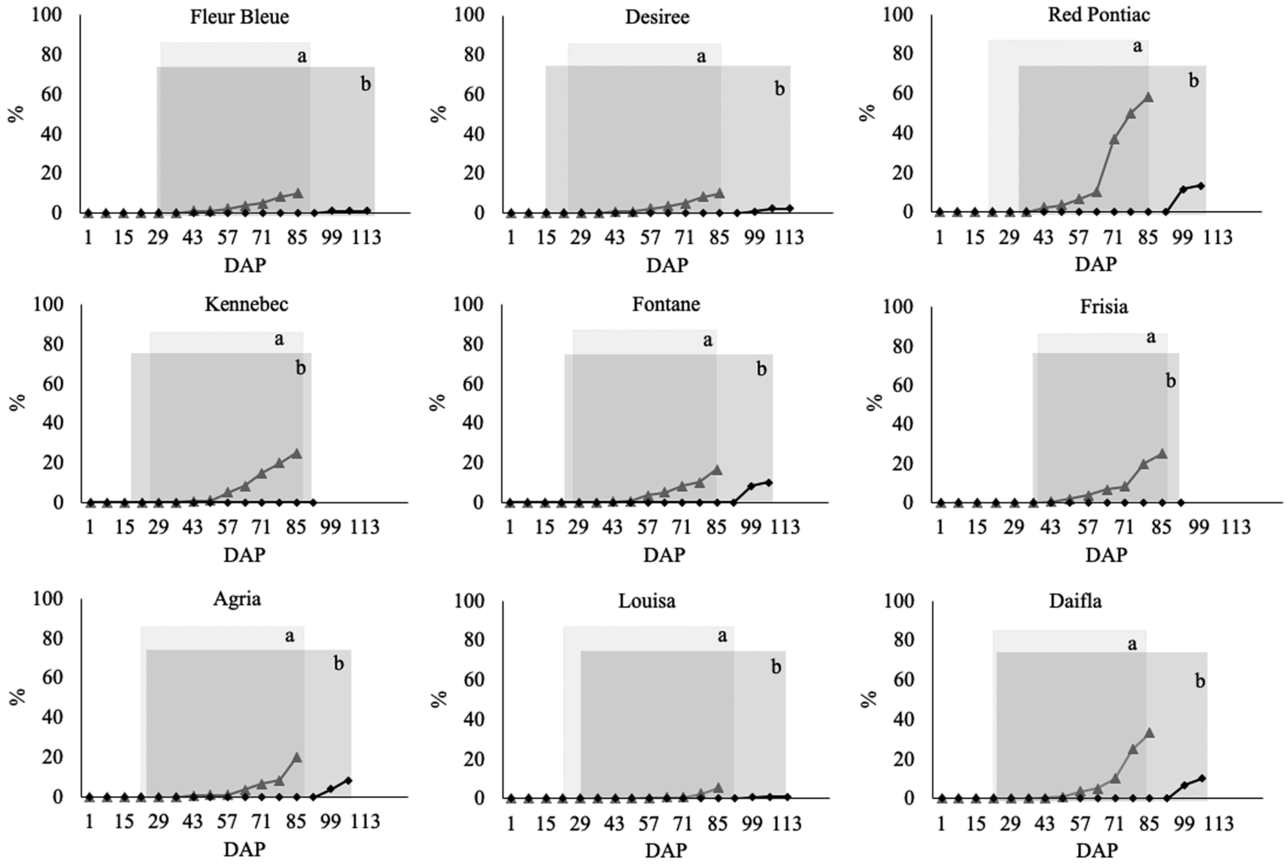

Fig. 5. Severity progression curves after planting day of 9 potato cultivars during the two crop seasons are represented. DAP is the number of days after planting. Planting dates were: (a) on 11 April 2020; (b) on 4 April 2021. Gray shading on the chart shows the phenological stage of foliar development (period between 50% of emergence to start of maturating stage) of crop seasons 2020 (a) and 2021 (b).

Table 3

Spearman correlation coefficients between total weekly sporangia concentration and disease severity for each cultivar.

Avg. sporangia	% Severity Desiree	Fleur Bleue	Red Pontiac	Kennebec	Fontane	Frisia	Agria	Louisa	Daifla
Week-0	0.587**	0.635**	0.617**	0.625*	0.617**	0.625*	0.620**	0.336	0.611**
Week-1	0.645**	0.677**	0.651**	0.622	0.651**	0.622	0.660**	0.446*	0.648**

[*] $P < 0.05$

[**] $P < 0.01$. Week-0: the average sporangia value of current week. Week-1: the average sporangia value of previous week.

Schrodter, 1966; Fry, 1983), this study focused on the main weather factors (T and RH) that affect in sporangia dispersal and easy to control for disease forecasting (Figs. 1 and 2). Therefore, the results of this study have a quick and easy practical application for the agricultural sector.

The pooled data of different crop seasons (Table 1) is very useful when applying prediction models, as this reflects the average conditions of the disease development. However, it is equally crucial to understand the yearly variation in the factors affecting the disease development, especially in the face of the rapidly changing climate (Meno et al., 2021b). Indeed, the results showed marked differences between the years for sporangia level concentration, disease severity as well as the factors that the factors that combine T and RH as DRV. Hence, particular conditions of each year influenced early or late outbreaks of late blight, being this situation crucial to develop robust disease-forecasting models. An important component of late blight forecasting system is the field inspection for primary infection lesions. The combination of observations in field of the disease and the optimal conditions for its development accompany the satisfactory results of decision support systems. An example is the Danish decision support system for the control of potato late blight known as NegFry (Hansen et al., 1995). This model gives the forecast of primary attack (initial spray) and recommend subsequent times of fungicide applications during the season enabling to use optimal number of fungicide applications for crop protection against late blight. The weather conditions and the IP were key factors that differentiated 2020 and 2021 for the total sporangia counted. High sporangia in 2020 than in 2021 can be linked to the high IP in 2021. It is also noteworthy that the highest sporangia counted in each year occurred after an episode of high IP or high RH. This evidence that high values of sporangia in the air are coupled to potato late blight episodes (Olanya et al., 2016; Seijo-Rodríguez et al., 2018).

Sporangia concentrations were higher in May and June than in April, due to favorable phenological stage as foliar development (where plants are greener) as well as favorable weather conditions (e.g. high RH and IP) during these months (Fig. 3). In addition, *P. infestans* like other pathogens (as occurs with *Plasmopara viticola*) need carbohydrates to support sporulation. These carbohydrates are taken from green tissues when the plants are photosynthetically active (Caffi et al., 2012).

The weather had a pronounced effect on the sporangia concentration each year. This differential response of the weather variables and sporangia concentration reflects the general challenges in predicting the

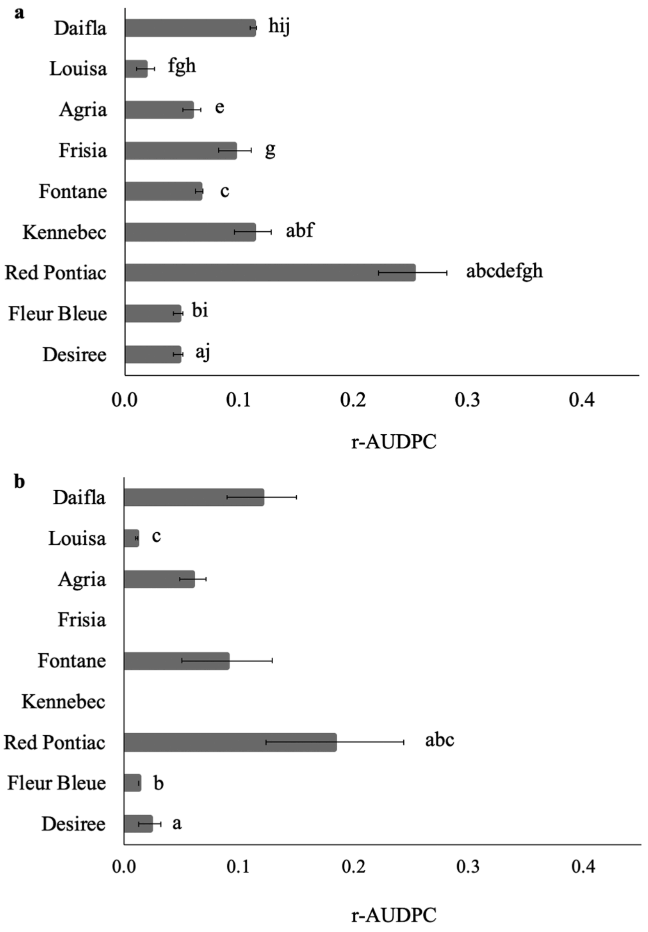

Fig. 6. r-AUDPC of 9 potato cultivars during both crop seasons: 2020 (a) and 2021 (b). Same letters show significant differences between the potato cultivars for each growing season according to the Bonferroni test ($P < 0.05$). Standard error is represented on the top of each bar, and it represents the standard deviation among plants per cultivar.

airborne sporangia concentration under field conditions. The crop season of 2020 was wetter than 2021 in May and June and hotter than 2021 in July and August of the cropping season. This fact could explain the negative correlation coefficients between sporangia and temperature shown in 2020, and the positive correlation coefficients between sporangia and temperature in 2021 (Table 1). Despite slight differences between crop seasons (2020 was hotter than 2021), there were some similarities in terms of the relevance of some weather factors that favor sporangia dispersal. The results of the study showed significant relationships between sporangia and avgT and maxT for all the days analyzed (Table 1). Therefore, these weather factors are important for predicting the sporangia concentration of *P. infestans* as other researchers reported (Mizubuti et al., 2000; Sunseri et al., 2002).

In contrast to other parameters analyzed, IP and DRV were consistently positively correlated with sporangia concentration. This consistent relation observed between IP/DRV and sporangia is expected, because IP and DRV integrate the weather factors T and RH, and thus reflect a better metric for measuring the suitability of the weather to late blight. The results also suggest the suitability of IP and DRV for predicting the sporulation potential of a given day for timing the application of fungicides. The statistical analyses of the factors on the levels of sporangia identified IP/DRV as the most influential parameter (Table 2). Moreover, the relation between the sporangia levels and *T* values was not significant, suggesting *T* is a less sensitive or robust parameter affecting late blight, as was reported before by Harrison and Lowe (1989).

The results suggested the dispersal of sporangia during the night and early morning hours (from 23 h to 8 h) was lower, whiles the riskiest time of the day for sporangia dispersal was from 9 h to 18 h (Fig. 4). These periods establish the low and high risks of sporangia dispersal. A striking difference between the low and high-risk periods are their marked differences for weather conditions. For example, the low-risk period coincided with low T and high RH, whereas the high-risk period coincided with higher T and lower RH. Therefore, these differences suggest that the spore dispersal generally favored by dryness, which occurs during the high-risk period (9 h–18 h). Lynch and Poole (1984) also found that the weather was the key determinant for the dispersal of *Botrytis cinerea* and *Chrysonilia sitophila*.

Establishing critical spore levels in the air are key to decision-making for disease control (Meno et al., 2021b). The quantification of the pathogen inoculum in the potato crop atmosphere combined with specific thresholds of the weather parameters would improve the prediction. If there are no sporangia in the environment, then there will be no risk to the crop even if favorable conditions exist. Similar levels of other pathogens were used for warning against their presence in urban and agricultural environments (Munuera et al., 2001; Escuredo et al., 2019b; Meno et al., 2020). The three established *P. infestans* levels in this study can be integrated into disease management and forecasting. Despite not finding significant differences between daily temperature values based on three sporangia levels, it was found that a minimum daily temperature greater than 10 °C favored the presence of *P. infestans* in the environment.

Late blight has been described as a moisture-driven disease, which increases its severity under continuous moisture (Fry et al., 2015; Olanya et al., 2016; Seijo-Rodríguez et al., 2018). Our findings showed that the sporangia concentration increased with RH. Sporangia in the environment crop were not found with values of avgRH below 80%. However, with values higher than 88%, daily concentrations reached the maximum level of sporangia. The results confirm the validity of the 88% RH threshold in the Danish late blight model (Abuley and Nielsen, 2017). However, the 88% RH threshold is useful for predicting high sporangia levels, but due to moderate sporangia levels occur at 80%, using such high RH thresholds might result in missing several moderate sporangia levels, which might influence the disease epidemic. Other studies have also shown that lower RH threshold will be more appropriate to accurately predict late blight infections (Harrison and Low 1989; Lehsten et al., 2017).

The consistently strong correlation between of IP/DRV and sporangia is noteworthy. This also suggest the importance of these variables for predicting the sporulation potential of *P. infestans* during the season. Sporangia were found in crop environments with values of 8.5 and 41.1 for DRV and IP, respectively. Currently, IP and DRV are used to successfully schedule fungicide application and forecast late blight in Denmark, considering a minimum IP threshold of 10 for timing fungicide application (Abuley and Hansen, 2020). This difference could be due to the different climatic conditions between the geographical areas and *P. infestans* population in Spain and Denmark. Further studies are required to ascertain the validity of the observed thresholds in this study.

The strong effect of sporangia on late blight severity on all tested cultivars re-emphasizes the need to consider sporangia concentration in the forecasting of late blight outbreaks (Fig. 5). The phenology of the crop was key to determining the severity of late blight stated (Seijo-Rodríguez et al., 2018). The onset of late blight during the later stage of the crop's life (e.g., senescence) mattered less compared to earlier epidemic onset (e.g., foliar development). Moreover, such late epidemics have an inconsequential effect on the yield (Fig. S1).

The variability in the susceptibility ranking of the cultivars reflects the instability of resistance/susceptibility classification of potato cultivars to late blight as in other studies (Runno-Paurson et al., 2019; Abuley et al., 2020). Cultivar resistance to late blight is a more promising way to control late blight disease with minimum use of pesticides.

There are potato cultivars with partial resistance to late blight (Forbes, 2012), but they have not been sufficiently exploited by conventional producers. In Europe, the resistant cultivars are not grown on a large scale because other commercially important characteristics such as quality, yield, and earliness are not usually present in late blight resistant cultivars (Cooke et al., 2011). The crop phenology, the sporangia concentration, and the weather conditions were the factors that caused these differences. In 2021, cultivars such as Kennebec and Frisia escaped late blight attack because they reached senescence earlier. Thus, the observed resistance due to the low r-AUDPC was unreal.

Although sporangia concentration had an impact on late blight severity, the most noticeable effect of sporangia was the accumulated sporangia of the previous week. Indeed, late blight has an incubation period of 3–5 days under field conditions (Fernández et al., 2020), thus reflecting a greater influence of the previous week's sporangia on late blight severity in the current week. This result is useful for predicting the appearance of symptoms in plants with aerobiological and meteorological data from a week before.

5. Conclusions

The present study identified weather parameters such as RH, IP and DRV as the most influential in the concentration of sporangia. Values of avgRH of 80% were required for at least a moderate sporangia level in the field. Moreover, high values of sporangia were found in certain hours of the day (9 h and 18 h), coinciding with low RH and high T. The results also showed that sporangia concentration in air is a key determinant of the late blight severity. Susceptibility to late blight varies also depending on the potato cultivar. Of the cultivars analyzed, Desiree showed fewer lesions and Red Pontiac were the most susceptible plants. Finally, the results of present study are relevant for the development and/or adjustment of disease forecasting models for potato late blight. In future, the inclusion of more growing seasons will probably improve the adjustment of the weather thresholds looking for a better forecast of late blight in the field betting on sustainable agriculture.

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CRediT authorship contribution statement

L. Meno: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **I.K. Abuley:** Formal analysis, Conceptualization, Investigation, Data curation, Writing – review & editing, Writing – original draft. **O. Escuredo:** Conceptualization, Formal analysis, Writing – review & editing. **M.C. Seijo:** Conceptualization, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

Data Availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2022.111520.

References

Abuley, I.K., Hansen, H.H., 2020. Control of late blight (*Phytophthora infestans*) and early blight (*Alternaria solani*) in potatoes. In: Jørgensen, L.N., Heick, T.M., Abuley, I.K., Mathiassen, S.K., Jensen, P.K., Kristjansen, H.S., Hartvig, P. (Eds.), Applied Crop Protection 2020. Aarhus University, DCA - Danish Centre for Food and Agriculture, p. 114. DCA report. https://pure.au.dk/ws/files/151969419/05_Control_of_late_blight.pdf.

Abuley, I.K., Hansen, J.G., Hansen, H.H., 2020. IX Controlling late blight in susceptible and resistant potato cultivars with BlightManager. eds.. In: Jørgensen, L.N., Heick, T. M., Abuley, I.K., Jensen, P.K., Kristjansen, H.S., Hansen, A. (Eds.), *Applied Crop Protection 2020* (pp. 92-96). Aarhus Universitet - DCA - Danish Centre for Food and Agriculture, p. 114. DCA report.

Abuley, I.K., Nielsen, B.J., 2017. Evaluation of models to control potato early blight (*Alternaria solani)* in Denmark. Crop Prot. 102, 118–128. https://doi.org/10.1016/j.cropro.2017.08.012.

Abuley, I.K., Hansen, J.G., 2021. An epidemiological analysis of the dilemma of plant age and late blight (*Phytophthora infestans*) susceptibility in potatoes. Eur. J. Plant Pathol. 161 (3), 645–663. https://doi.org/10.1007/s10658-021-02350-4.

Aylor, D.E., Fry, W.E., Mayton, H., Andrade-Piedra, J.L., 2001. Quantifying the rate of release and escape of *Phytophthora infestans* sporangia from a potato canopy. Phytopathology 91 (12), 1189–1196. https://doi.org/10.1094/PHYTO.2001.91.12.1189.

Aylor, D.E., Schmale, D.G., Shields, E.J., Newcomb, M., Nappo, C.J., 2011. Tracking the potato late blight pathogen in the atmosphere using unmanned aerial vehicles and lagrangian modeling. Agric. For. Meteorol. 151 (2), 251–260. https://doi.org/10.1016/j.agrformet.2010.10.013.

Ballvora, A., Ercolano, M.R., Weiß, J., Meksem, K., Bormann, C.A., Oberhagemann, P., Gebhardt, C.M., 2002. The R1 gene for potato resistance to late blight (*Phytophthora infestans*) belongs to the leucine zipper/NBS/LRR class of plant resistance genes. Plant J. 30 (3), 361–371. https://doi.org/10.1046/j.1365-313x.2001.01292.x.

Beaumont, A., 1947. The dependence on the weather of the dates of outbreak of potato blight epidemics. Trans. Brit. Mycol. Soc. 31 (1–2), 45–53. https://doi.org/10.1016/S0007-1536(47)80005-1.

Caffi, T., Gilardi, G., Monchiero, M., Rossi, V., 2012. Production and release of asexual sporangia in *Plasmopara viticola*. Phytopathology 103 (1), 64–73. https://doi.org/10.1094/PHYTO-04-12-0082-R.

Cooke, L.R., Schepers, H.T.A.M., Hermansen, A., Bain, R.A., Bradshaw, N.J., Ritchie, F., Nielsen, B.J., 2011. Epidemiology and integrated control of potato late blight in Europe. Potato Res. 54 (2), 183–222. https://doi.org/10.1007/s11540-011-9187-0.

Cucak, M., Sparks, A., Moral, R.D.A., Kildea, S., Lambkin, K., Fealy, R., 2019. Evaluation of the 'Irish rules': the potato late blight forecasting model and its operational use in the Republic of Ireland. Agronomy 9 (9), 515. https://doi.org/10.3390/agronomy9090515.

Dey, T., Saville, A., Myers, K., Tewari, S., Cooke, D.E., Tripathy, S., Roy, S.G., 2018. Large sub–clonal variation in *Phytophthora infestans* from recent severe late blight epidemics in India. Sci. Rep. 8 (1), 1–12. https://doi.org/10.1038/s41598-018-22192-1.

Escuredo, O., Seijo-Rodríguez, A., Rodríguez-Flores, M.S., Seijo, M.C., 2019a. Decision support systems for detecting aerial potato Phytophthora infestans sporangia in Northwestern Spain. Agron. J. 111 (1), 354–361. https://doi.org/10.2134/agronj2018.02.0124.

Escuredo, O., Seijo-Rodríguez, A., Meno, L., Rodríguez-Flores, M.S., Seijo, M.C., 2019b. Seasonal dynamics of *Alternaria* during the potato growing cycle and the influence of weather on the early blight disease in North-West Spain. Am. Potato J. 96 (6), 532–540. https://doi.org/10.1007/s12230-019-09739-2.

Fernández, C.I., Leblon, B., Haddadi, A., Wang, K., Wang, J., 2020. Potato late blight detection at the leaf and canopy levels based in the red and red-edge spectral regions. Remote Sens. 12 (8), 1292. https://doi.org/10.3390/rs12081292.

Forbes, G.A., 2012. Using host resistance to manage potato late blight with particular reference to developing countries. Potato Res. 55 (3–4), 205–216. https://doi.org/10.1007/s11540-012-9222-9.

Fry, W.E., 1978. Quantification of general resistance of potato cultivars and fungicide effects for integrated control of potato late blight. Phytopathology 68, 1650–1655. https://doi.org/10.1094/Phyto-68-1650.

Fry, W.E., Apple, A.E., Bruhn, J.A., 1983. Evaluation of potato late blight forecasts modified to incorporate host resistance and fungicide weathering. Phytopathology 73 (7), 1054–1059. https://doi.org/10.1094/Phyto-73-1054.

Fry, W.E., Birch, P.R.J., Judelson, H.S., Grünwald, N.J., Danies, G., Everts, K.L., Smart, C. D., 2015. Five reasons to consider *Phytophthora infestans* a reemerging pathogen. Phytopathology 105 (7), 966–981. https://doi.org/10.1094/PHYTO-01-15-0005-FI.

Galán, C., Cariñanos, P., Alcázar, P., Domínguez, E., 2007. Spanish Aerobiology Network (REA): Management and Quality Manual, 2007. University of Córdoba, Publication Service, Córdoba, Spain, p. 61 pp.

González-Fernández, E., Piña-Rey, A., Fernández-González, M., Aira, M.J., Rodríguez-Rajo, F.J., 2020. Identification and evaluation of the main risk periods of *Botrytis cinerea* infection on grapevine based on phenology, weather conditions and airborne conidia. J. Agric. Sci. 158, 88–98. https://doi.org/10.1017/S0021859620000362.

Grünwald, N.J., Rubio-Covarrubias, O.A., Fry, W.E., 2000. Potato late-blight management in the Toluca valley: forecasts and resistant cultivars. Plant Dis. 84 (4), 410–416. https://doi.org/10.1094/PDIS.2000.84.4.410.

Hack, H., Gall, H., Klemke, T.H., Klose, R., Meier, U., Stauss, R., Witzenberger, A., 1993. The BBCH-scale for phenological growth stages of potato (*Solanum tuberosum* L.). In: Proceedings of the 12th Annual Congress of the European Association for Potato Research, pp. 153–154.

Hansen, J.G., Andersson, B., Hermansen, A., 1995. NegFry-a system for scheduling chemical control of late blight in potatoes. Phytophthora Infestans 150, 201–208.

Harrison, J.G., Lowe, R., 1989. Effects of humidity and air speed on sporulation of *Phytophthora infestans* on potato leaves. Plant Pathol. 38 (4), 585–591. https://doi.org/10.1111/j.1365-3059.1989.tb01455.x.

Hjelkrem, A.G.R., Eikemo, H., Le, V.H., Hermansen, A., Nærstad, R., 2021. A process-based model to forecast risk of potato late blight in Norway (The Nærstad model): model development, sensitivity analysis and Bayesian calibration. Ecol. Model. Risk Assess. 450, 109565 https://doi.org/10.1016/j.ecolmodel.2021.109565.

Jeger, M.J., 1990. Mathematical analysis and modelling of spatial aspects of plant disease epidemics. ed.. In: Kranz, J. (Ed.), Epidemics of Plant Disease. Springer, Berlin, pp. 53–95.

Krause, R.A., Massie, L.B., Hyre, R.A., 1975. Blitecast: a computerized forecast of potato late blight. Plant Dis. Rep. 59 (2), 95–98.

Lehsten, V., Wiik, L., Hannukkala, A., Andreasson, E., Chen, D., Ou, T., Grenville–Briggs, L., 2017. Earlier occurrence and increased explanatory power of climate for the first incidence of potato late blight caused by *Phytophthora infestans* in Fennoscandia. PLoS One 12 (5). https://doi.org/10.1371/journal.pone.0177580.

Lynch, J.M., Poole, N.J., 1984. Aerial dispersal and the development of microbial communities. eds. In: Lynch, J.M., Poole, N.J. (Eds.), Microbial ecology: A Conceptual Approach. Blackwell, Oxford, pp. 140–170.

Meno, L., Escuredo, O., Rodríguez-Flores, M.S., Seijo, M.C., 2021a. Looking for a sustainable potato crop. Field assessment of early blight management. Agric. For. Meteorol. 308, 108617 https://doi.org/10.1016/j.agrformet.2021.108617.

Meno, L., Seijo, M.C., Rodríguez-Flores, M.S., Escuredo, O., Villa, P.M, 2021b. Impact of climate change on potato early and late blight occurrence in A Limia (NW Spain). In: The Potato Crop: Management, Production and Food Security. Nova Science Publishers Inc., New York https://doi.org/10.52305/RHLO1469.

Meno, L., Escuredo, O., Rodríguez-Flores, M.S., Seijo, M.C., 2020. Modification of the TOMCAST model with aerobiological data for management of potato early blight. Agronomy 10 (12), 1872. https://doi.org/10.3390/agronomy10121872.

Mizubuti, E.S.G., Aylor, D.E., Fry, W.E., 2000. Survival of *Phytophthora infestans* sporangia exposed to solar radiation. Phytopathology 90 (1), 78–84. https://doi.org/10.1094/PHYTO.2000.90.1.78.

Munuera, M., Carrión, J.S., Navarro, C., 2001. Airborne *Alternaria* spores in SE Spain (1993–98): Occurrence patterns, relationship with weather variables and prediction models. Grana 40, 111–118.

Olanya, M., Anwar, M., He, Z., Larkin, R.P., Honeycutt, C.W., 2016. Survival potential of *Phytophthora infestans* sporangia in relation to environmental factors and late blight occurrence. J. Plant Prot. Res. 56 (1), 73–81. https://doi.org/10.1515/jppr-2016-0011.

Rahmatzai, N., Zaitoun, A.A., Madkour, M.H., Ahmady, A., Hazim, Z., Mousa, M.A., 2017. *In vitro* and *in vivo* antifungal activity of botanical oils against *Alternaria solani* causing early blight of tomato. Int. J. Biosci. 10 (1), 91–99. https://doi.org/10.12692/ijb/10.1.91-99.

Runno-Paurson, E., Hansen, M., Kotkas, K., Williams, I.H., Niinemets, Ü., Einola, A., 2019. Evaluation of late blight foliar resistance of potato cultivars in northern Baltic conditions. Liet. Zemdirbystes 106 (1), 45. https://doi.org/10.13080/z-a.2019.106.006. Mokslinio Tyrimo Inst. Darb.

Schepers, H.T.A.M., Kessel, G.J.T., Lucca, F., Förch, M.G., Van Den Bosch, G.B.M., Topper, C.G., Evenhuis, A., 2018. Reduced efficacy of fluazinam against *Phytophthora infestans* in the Netherlands. Eur. J. Plant Pathol. 151 (4), 947–960. https://doi.org/10.1007/s10658-018-1430-y.

Seijo-Rodríguez, A., Escuredo, O., Rodríguez-Flores, M.S., Seijo, M.C., 2018. Improving the use of aerobiological and phenoclimatological data to forecast the risk of late blight in a potato crop. Aerobiologia 34 (3), 315–324. https://doi.org/10.1007/s10453-018-9515-9.

Shaner, G., Finney, R.E., 1977. The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. Phytopathology 67 (8), 1051–1056. https://doi.org/10.1094/Phyto-67-1051.

Singh, B.P., Sharma, S., 2013. Forecasting of potato late blight. Int. J. Innov. Hortic. 2 (1), 1–11.

Skelsey, P., Kessel, G.J.T., Holtslag, A.A.M., Moene, A.F., Van Der Werf, W., 2009. Regional spore dispersal as a factor in disease risk warnings for potato late blight: a proof of concept. Agric. For. Meteorol. 149 (3–4), 419–430. https://doi.org/10.1016/j.agrformet.2008.09.005.

Smith, L.P., 1956. Potato blight forecasting by 90 per cent humidity criteria. Plant Pathol. 5 (3), 83–87. https://doi.org/10.1111/j.1365-3059.1956.tb00093.x.

Sunseri, M.A., Johnson, D.A., Dasgupta, N., 2002. Survival of detached sporangia of *Phytophthora infestans* exposed to ambient, relatively dry atmospheric conditions. Am. J. Potato Res. 79 (6), 443–450. https://doi.org/10.1007/BF02871689.

Supriya, H.N., Nagaraj, M.S., Sudarshan, G.K., 2020. Studies on aerobiology and management of late blight disease of potato. Int. J. Curr. Microbiol. App. Sci. 9 (10), 2592–2600. https://doi.org/10.20546/ijcmas.2020.910.312.

Taylor, M.C., Hardwick, N.V., Bradshaw, N.J., Hall, A.M., 2003. Relative performance of five forecasting schemes for potato late blight (*Phytophthora infestans*) I. Accuracy of infection warnings and reduction of unnecessary, theoretical, fungicide applications. J. Crop Prot. 22 (2), 275–283. https://doi.org/10.1016/S0261-2194(02)00148-5.

Ullrich, J., Schrödter, H., 1966. Das problem der vorhersage des auftretens der kartoffelkrautfäule (*Phytophthora infestans*) und die möglichkeit seiner lösung durch eine "negativprognose. Nachrichtenblatt Deutsch. Pflanzenschutzdienst 18, 33–40. Braunschweig.

Wallin, J.R., 1962. Summary of recent progress in predicting late blight epidemics in United States and Canada. Am. Potato J. 39 (8), 306–312. https://doi.org/10.1007/BF02862155.

Winstel, K., 1993. Kraut-und knollenfaule der kartoffeleineeeueprognosemoglichkeit–sowiebekampfunggrategien. Med. Fac. Landbouww Uni. Gent 58(3b), 1477–1483.