

Effects of meteorological factors on the levels of *Alternaria* spores on a potato crop

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Abstract *Alternaria solani* Soraeur produces early blight in *Solanum tuberosum* L., leading to significant agricultural losses. The current study was carried out on the extensive potato crop situated in north-western of Spain during 2007, 2008 and 2009. In this area potato crops are the most important source of income. In this work we used a Hirst-type volumetric spore-trap for the aerobiological monitoring of *Alternaria* spores. The highest spore concentrations were recorded during the 2009 cycle (10,555 spores), and the lowest concentrations were recorded during the 2008 cycle (5,471 spores). Over the 3 years of study, the highest concentrations were registered during the last stage of the crop. The aim of the study was to observe the influence of meteorological factors on the concentration of *Alternaria* spores, which can lead to serious infection and early blight. Prediction of the stages during which a crop is particularly vulnerable to infection allows for adjustment of the application of fungicide and is of environmental and agricultural importance. For this reason, we tested three models (P-Days, DD and IWP) to predict the first treatment and decrease the negative effect that these spores have on potato crops. The parameter that showed the most significant correlation with spore concentrations was minimum temperature. We used ARIMA (autoregressive integrated model of running mean) time-series models to determine the forecast. We considered weather data as predictor variables and the concentration of spores on the previous day as the fixed variable.

Keywords *Alternaria* · Potato crop · Meteorological factor · ARIMA

Introduction

The presence of *Alternaria* spores in the atmosphere and their impact on agriculture and human health have been studied by several authors (Angulo-Romero et al. 1999; Grinn-Gofroñ and Mika 2008; Munuera et al. 2001; Rizzi-Longo et al. 2009; Sabariego et al. 2000; Sánchez et al. 2009; Stennett and Beggs 2004).

Alternaria solani Soraeur can produce an early blight in potato crops. The only other disease that has a higher impact is the late blight caused by *Phytophthora infestans* Mont de Bary. Both pathogens can infect all aerial parts of solanaceous crops including tomato, potato, eggplant, and pepper, as well as potato tubers (Batista et al. 2006; Chaerani and Voorrips 2006).

The fungus infects the stems and leaves of potato plants and, to a lesser extent, the tubers, which can become infected through wounds made during harvest. The lesions appear as small spots between 1 and 2 mm and then become dark brown in colour. As new lesions form and old lesions expand, the leaves become necrotic and dry, but they remain on the plant (Alonso, 2008). The spores remain on the soil surface and on the leaves, and they can penetrate into the potato during harvest (Rouselle et al. 1999). The life cycle of *Alternaria solani* includes soil- as well as air-borne stages, making the pathogen difficult to control by means of rotation and sanitation (Chaerani and Voorrips 2006).

Early blight develops more rapidly during periods when environmental conditions alternate between humidity and drought. The attacks cause serious economic losses in potato crops (Bashi and Rotem 1975).

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In recent years, many studies have been carried out to examine the presence and dispersion of pathogenic fungal spores in crops (Burt et al. 1998; Davis and Main 1986; Rajasab and Chawda 1995; Uddin and Chakraverty 1996; Vittal and Krishnamoorthi 1981). Many authors have developed epidemiological models, in order to predict when the disease will occur and to improve the use of control measures (Bruhn and Fry 1981; Bugiani et al. 1996; Díaz et al. 1998; Fry 1998; Gudmestad 2003; Johnson et al. 1998; Shtienberg et al. 1989; Wiik 2002). Almost all these models are based on the use of meteorological parameters, especially relative humidity, temperature and rainfall. An accurate forecast of the spore concentrations in a geographical area allows for reductions in the use of fungicide treatments, preventing pollution of the atmosphere, crops and fields (Frenguelli 1998).

Moreover, *Alternaria* has been linked to the occurrence of severe allergic responses. Tilak (1991) estimated that between 2 and 30% of respiratory allergies are due to fungal spores and cited *Alternaria* and *Cladosporium* as the important genera (Pepeljnjak and Segvic 2003). These two taxa have been identified as the most abundant aeroallergens present on the Iberian Peninsula (Angulo-Romero et al. 1999; Fernández-González et al. 1998; González et al. 1994; Herrero et al. 1996; Infante et al. 1987; Munuera et al. 2001; Paredes et al. 1997; Sánchez et al. 2009; Sabariego et al. 2000, 2004) and in our geographic area (Aira et al. 2008; Méndez et al. 1997).

The correlation between weather and spore concentration has been recognised by many authors in different parts of the world (Bagni et al. 1977; Burch and Levetin 2002; Damialis and Gioulekas 2006; Katial et al. 1997; Mitakakis et al. 1997, 2001; Ricci et al. 1995; Rutherford et al. 1997; Stennett and Beggs 2004; Troutt and Levetin 2001). Atmospheric *Alternaria* spores, temperature and humidity are the factors that most closely correlate with the occurrence of this disease.

This paper presents an aerobiological study that was conducted with the aim of finding relationships between the *Alternaria* spore concentration and meteorological factors. We examined three crop cycles covering the years 2007, 2008 and 2009. We tried to develop an accurate model using autoregressive integrated model of running mean (ARIMA) time series analysis to forecast the *Alternaria* spore concentrations in the air. Our model takes into account the levels of this pathogen and the recorded values of the most influential weather variables in the preceding 3 days.

Materials and methods

The aerobiological survey was carried out for a period of three cycles on a potato crop. The study was conducted

from 15 May to 6 September (2007 cycle), from 16 June to 1 October (2008 cycle) and from 7 May to 10 September (2009 cycle). The studied potato crop area is situated in Ourense province in north-western Spain, with an average altitude of 640 m above sea level. It is one of the most well-defined territorial units in Galicia because it is basically formed by a depression filled with sediments, the central part being occupied in the past by Antela Lake. This lake, which was recently drained, is now intensively cultivated. Due to its geographic situation and altitude, the weather in this zone presents combined oceanic and Mediterranean characteristics, with a tendency for continental weather (Carballeira et al. 1983). The potato crop is the main economic source of income in this geographical region.

Daily counts of *Alternaria* were sampled using the volumetric VPPS 2000 Lanzoni pollen-spore trap (Hirst 1952). The sampler was situated 2 m above ground level, so that spore trapping would not be impeded by plant growth. The Lanzoni sampler is calibrated to handle a flow of 8 L air/min. Spores are impacted on a cylindrical drum covered by a melinex film coated with a 2% silicon solution as trapping surface. The drum was changed weekly and the exposed tape was cut into seven pieces that were mounted on separate glass slides. Spore identification was performed using a Nikon Optiphot II microscope equipped with a 40X/0.95 lens. Spore counts were made using the model proposed by the REA (Spanish Aerobiology Network), consisting of four continuous longitudinal traverses along the 24 h slide (Domínguez et al. 1992). Concentrations of the conidia type considered were expressed as the number of spores per cubic metre of air.

Meteorological data were obtained using a meteorological HOBO Pro Series, temp (°C), RH 1998 ONSET. This device recorded temperature and relative humidity data every hour throughout the period of study. The precipitation data were extracted from the website of Estación Fitopatológica de Areiro (<http://www.efa-dip.org/>), with a weather station available in this district.

We applied Spearman's rank correlation analysis in order to establish the influence of meteorological factors, as well as the maximum, minimum and mean temperatures (°C), the mean relative humidity (%) and the rainfall (mm), on *Alternaria* spore concentrations. Nonparametric statistical analysis was used, in this case, due to the nonexistence of normality in the data.

Weather conditions may affect spore production directly and may or may not stimulate fungal growth and spore production. Weather conditions may indirectly affect spore production through their effects on the substrates that support fungal development. Therefore, this study also determined the correlation between spore counts documented on a given day and the main weather parameter. The significance was calculated for $P < 0.01$, $P < 0.05$ and $P < 0.1$.

Different models use weather variables to predict the suitable conditions for the development of *Alternaria*. In this paper, three prediction models for this pathogen of the potato were analysed: the propitious days model (P-Days), the accumulation of disfavourable days model (DD) and the interrupted wet periods model (IWP). All of these models were based on temperature and relative humidity.

Pscheidt and Stevenson (1986) suggested that the P-Days model developed by Sands et al. (1979) could be used to predict potato development and early blight appearance. P-days are calculated taking in account the minimum and the maximum temperatures. The model is calculated by $P - Days = \{1/24[5P(T_{min}) + 8P(2T_{min}/3 + T_{max}/3) + 8P(2T_{max}/3 + T_{min}/3) + 3P(T_{max})]\}$, where $P(T) = 0$ if $T < 7^{\circ}\text{C}$, $P(T) = 10\left[1 - (T - 21)2 / (21 - 7)^2\right]$ if $7^{\circ}\text{C} \leq T \leq 21^{\circ}\text{C}$, and $P(T) = 10[1 - (T - 21)2 / (30 - 21)2]$ if $21^{\circ}\text{C} \leq T \leq 30^{\circ}\text{C}$ at the start of potato emergence. This model assumes 7°C as a minimum, 21°C as the optimum, and 30°C as the maximum temperature for potato plant development, as well as diurnal fluctuations (Gent and Schwartz 2003).

The accumulation of disfavourable days model was calculated by $DD = [(T_{max} - T_{min})/2] - 7.2^{\circ}\text{C}$ starting at planting (Franc et al. 1988).

The IWP model takes into consideration that relative humidity is fundamental for the development and dispersion of *Alternaria* spores. An IWP day occurs when this parameter is higher than 95% for 6 consecutive hours at night, and there are 6 h or less with a relative humidity less than 80% (Van der Waals et al. 2003).

Finally, we used the ARIMA model to predict *Alternaria* spore concentrations. The estimators for the model were weather variables with the highest positive correlation coefficients and spore concentrations for the previous days. We took the recorded values for the preceding 3 days. The time series in this model are a mixture of several components: T_t or the long trend value, E_t or the fluctuations of the series during periods of less than 1 year, C_t or fluctuations of the series in periods longer than 1 year, and finally, I_t or random or sporadic factors (Tobías et al. 2004). The equation followed by a time series is an additive model: $Y_t = T_t + C_t + E_t + I_t$.

A model is considered autoregressive if the values of the series depend on or are related to previous values of the variable. A multiple linear regression function can be established in which the dependent variable is observed in the " t " period and the independent variables are those of previous periods that are related to the dependent variable. In the model, the three ARIMA parameters autoregression, differentiation and the running mean were tested. Autoregression (p) is the number of autoregressive parameters

of the model; each parameter measures the independent effect of the values with a specified delay. Differentiation (d) is the number of times that a time series was transformed; this factor accounts for the differences between the values of the series and their predecessors. The running mean (q) is the order of the running mean of the process.

The SPSS 17.0 software package was used for all statistical analyses.

Results

Over the 3-year period during which this study was conducted, *Alternaria* spores were present throughout the entire cycle of potato growth, with a daily mean concentration from 52 to 83 spores/ m^3 . The 2009 cycle recorded the highest number of spores of this type with 10,555, followed by 6,029 and 5,471 spores in the 2007 and 2008 cycles, respectively.

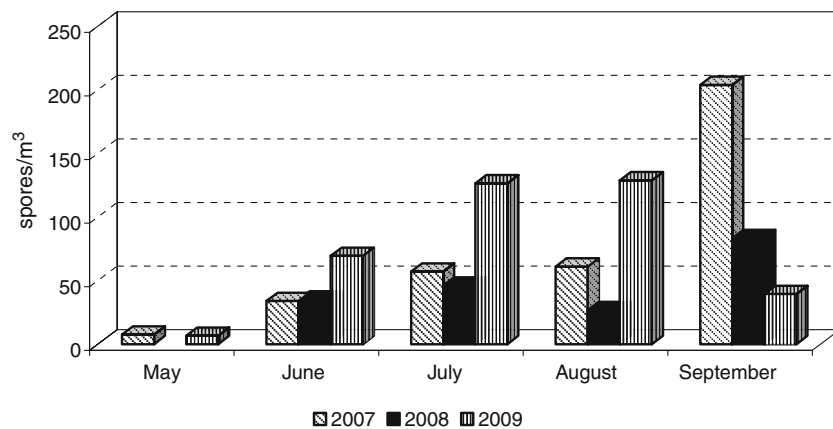
The distribution of conidia showed a clear monthly variation (Fig. 1). The maximum concentration appeared in September 2007 (204 spores/ m^3) and 2008 (83 spores/ m^3), and August 2009 (129 spores/ m^3) whereas the low concentrations occurred in May and June. The maximum concentrations were observed during periods of high mean temperature and low mean relative humidity (Table 1).

Figure 2 shows the daily changes in the meteorological parameters observed during the three crop cycles. The maximum temperature during the 2007 and 2009 cycles shows a similar pattern, reaching over 30°C in August and September. The relative humidity fluctuated widely between these 2 years with values from 45 to 95%, with a daily mean of about 70%. This affected the levels of *Alternaria* spores, which are favoured by high temperatures.

The 2008 crop cycle began a month later (13 June) due to the previous weather conditions. Heavy rainfall flooded the plot, delaying the planting of potatoes and subsequently the development of the green parts of the plants. In general, relative humidity was high, with mean values above to 79% (Table 1).

Spearman's rank correlation analysis was applied, taking into account the *Alternaria* spore counts and weather parameters recorded on the same day. Correlation coefficients (calculated using data for each year as well as data for the whole study period) were significant in most of cases (Table 2). In 2007, the weather parameters displaying the highest correlation coefficient were mean and maximum temperatures ($P < 0.01$), while in 2008, the highest values were found for mean relative humidity ($P < 0.05$). In 2009, the highest values were found for the mean and maximum temperatures ($P < 0.01$). The Spearman statistical test applied to the data for the whole study period (2007–

Fig. 1 Monthly mean of *Alternaria* spore concentrations



2008–2009), showed that *Alternaria* spores were highly and significantly correlated with the three parameters of temperature ($P < 0.01$).

There were differences in the weather patterns that occurred over the 3-year period of this study. The years 2007 and 2008 showed very low mean temperatures and high mean relative humidity. In 2009, the temperatures were higher than the other 2 years.

Due to the influence of meteorological factors on the development of early blight, they can be used to predict the appropriate time to initiate the application of fungicide. Three models have been tested to predict the levels of this potato pathogen and host susceptibility (Table 3): the P-Days, DD and IWP models.

The P-Days model predicted the first important *Alternaria* concentration in the field 6–8 days before it occurred in the period studied. In the 2007 cycle, the first important peak was recorded on 25 May, with 44 spores/m³ corresponding to 105 P-Days. On 19 May, the concentration exceeded 150 P-Days units. Therefore, we were able to predict this peak 6 days before it occurred. The same was true for the 2008 and 2009 cycles. The P-Days model predicted the first significant peak (95 spores/m³) 7–8 days before it occurred.

The DD model predicted only the first peak in the 2009 cycle, 8 days in advance. In the other two cycles, the model reached 30 DD units later than the first peaks. With the IWP model, there were 3 days with the indicated conditions just before the first peak in the 2007 cycle and 2 days in the 2009 cycle. During the 2008 cycle, it was not possible to record days with the conditions described by the IWP model.

Based on the correlation of the results, we evaluated the predictive capacity of each meteorological parameter and a combination of several parameters. We calculated the quantity of spores per day to obtain ARIMA time-series models and predict the *Alternaria* airborne spores on the potato crop. In this model, the minimum temperature 3 days earlier was an independent variable represented by an R^2 value of 0.849 (Table 4). Figure 3 shows the *Alternaria* spores observed and predicted by the adjusted model for each potato crop cycle studied.

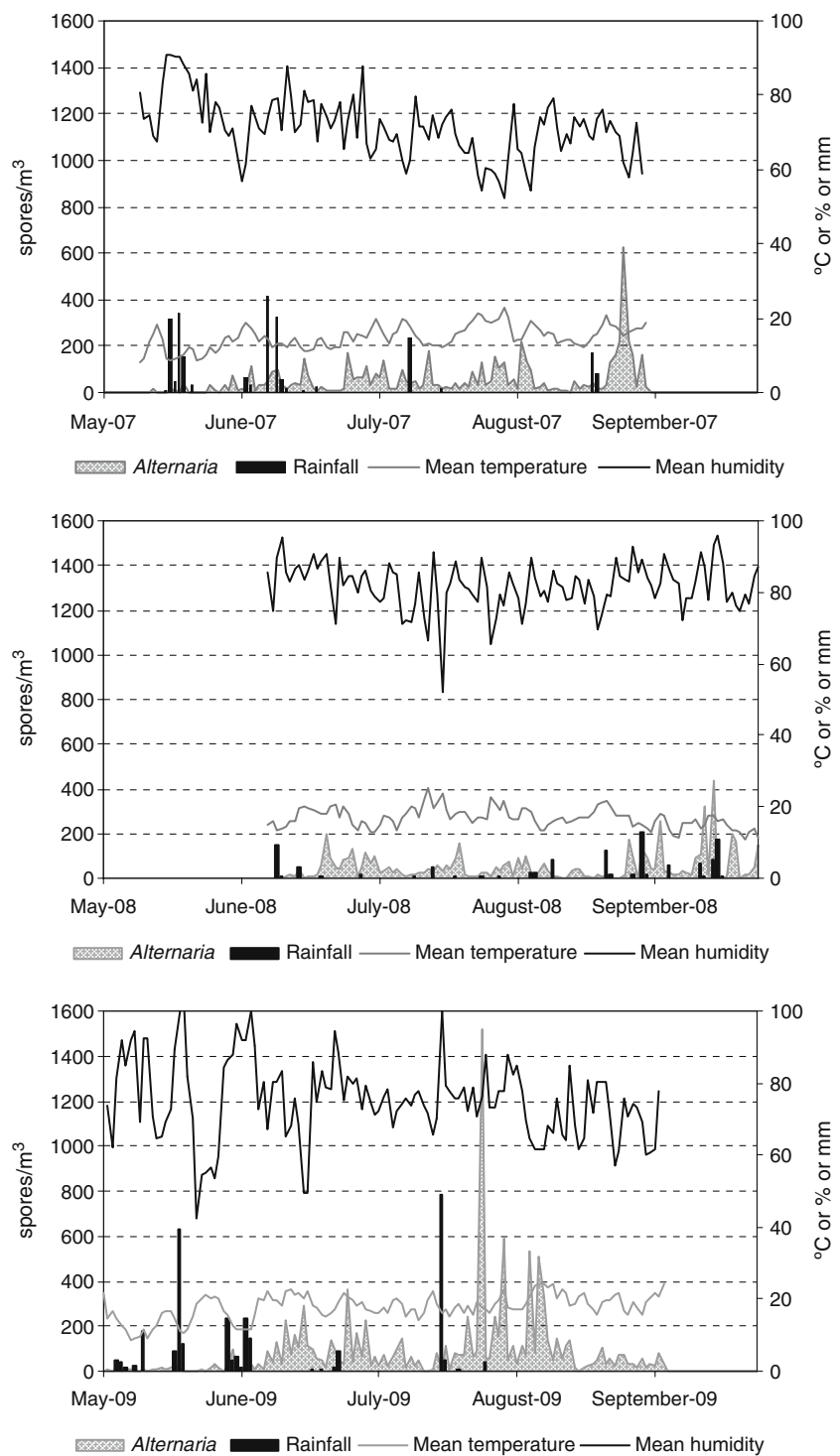
Discussion

The results indicate that *Alternaria* spores are present in the atmosphere during all the periods studied, but they

Table 1 Monthly meteorological factors during the 3-year study period. *T mean* Mean daily temperature, *T max* maximum daily temperature, *T min* minimum daily temperature, *H* mean relative humidity, *P* rainfall

	2007					2008				2009				
	May	June	July	August	September	June	July	August	September	May	June	July	August	September
T mean (°C)	11.2	13.8	16	16.5	17	17.6	18	17.8	14.8	14	18	18	19.9	19.1
T max (°C)	15.8	19.6	23	24.8	26.5	25.3	26	25.9	23	23	27.3	29	30.4	29.3
T min (°C)	7.1	7.7	8.5	8.4	7.6	10	9.7	9.8	7.9	5.6	9.6	7.4	9.9	8.1
H (%)	81.1	73.2	69.1	67.8	59	85.6	80	79.6	83.3	75	78.1	76	72.4	67.1
P (mm)	3.3	2	0.5	0.5	0	0.7	0.2	0.6	1.3	2.9	1.8	1.7	0.1	0

Fig. 2 Atmospheric *Alternaria* concentrations and mean temperature, mean relative humidity and rainfall during each crop cycle (2007, 2008 and 2009)



appeared in higher concentrations during the last stage of the crop. The same observation has been reported in several studies describing the levels of this conidia in other localities, where the highest levels appeared during the summer months (Larsen and Gravesen 1991; Hjelmoors 1993; Grinn-Gofroń and Rapiejko 2009). The spore

concentrations in the atmosphere when the crop emerge were very low. The development of the green parts of the potato plants allows a slow accumulation of the inoculum. This is due to the age-conditioned resistance of young plants and the time required for the development of the fungus. Spores are produced mainly on dead or dying

Table 2 Correlation coefficients and significance levels between the number of spores and meteorological factors applying Spearman's test

	2007	2008	2009	2007– 2009
Mean temperature	0.467***	−0.070	0.439***	0.337***
Minimum temperature	0.156*	0.212**	0.342***	0.244***
Maximum temperature	0.444***	−0.187*	0.413***	0.312***
Mean relative humidity	−0.354***	0.246**	−0.049	−0.066
Rainfall	−0.143	0.180*	−0.203**	−0.078

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$

leaves (Rotem 1994). Therefore, in the final phase (senescence), when the leaves start to dry, there were major peaks of spore concentrations (Fig. 2).

The formation of conidiophores and the spore content in the atmosphere are influenced by changes in atmospheric conditions. A strong positive correlation was found between spore concentration and temperature. The spore content in the atmosphere increases when the mean, maximum and minimum temperatures increases, making *Alternaria* a temperature-dependent fungus. *Alternaria* is a saprophytic genus with an optimal development shown to occur in the temperature ranges of 22–28°C (Hjelmroos 1993). This can explain the differences in the obtained correlations between the three periods studied.

In the city of Córdoba, Angulo-Romero et al. (1999) found that the most conidia appear in the atmosphere when minimum temperatures are over 10°C, maximum temperatures are under 30°C and mean temperatures are between 20 and 25°C. The highest *Alternaria* spore concentrations recorded in our studied area occurred under these conditions.

Some authors (Burch and Levetin 2002; González et al. 1994; Infante et al. 1987; Marchisio and Airaudi 2001; Méndez et al. 1997; Munuera and Carrión 1995; Ricci et al.

1995; Stennett and Beggs 2004) have suggested that temperature and relative humidity play a major role in the dispersion of *Alternaria*. A negative correlation is observed with rainfall and humidity (Sabariego et al. 2000).

Considering the correlation of the weather parameters and the levels of spores the pattern observed during the three periods of study appears to be similar, but our results highlight the differences among them. These differences are thought to be present during every period. The year 2009 was the warmest year and had a large thermal amplitude that induced important variations in the values of the relative humidity. These factors are favourable for the development of *Alternaria* and, as a result, the level of the spores was the highest. However, during the 2007 and 2008 the temperature was lower and the values of daily thermal oscillation were small.

It is necessary to control *Alternaria* in order to prevent crop losses. Farmers use models to predict the 1st day of fungicide application. This disease treatment can and must be adjusted to the particular conditions of each geographical area in order to minimise the environmental impact and optimise the use of fungicides for late blight and early blight (Campbell and Madden 1990; Shtienberg and Fry 1990).

Several authors (Batista et al. 2006; Johnson et al. 1998) have analysed different statistical models in an attempt to adjust the 1st day of treatment based only on the recorded meteorological factors. The values derived from some of these models for the location observed in the present study are shown in Table 3.

Aerobiological studies are an important tool for prediction of the risk of disease because they allow determination of the levels of inoculum. In this context, Munuera et al. (2001) defined a classification of *Alternaria* spore concentrations in air. They set these concentrations in five classes or levels: very low (0–15 spores/m³), low (16–30 spores/m³), medium (31–70 spores/m³), high (71–120 spores/m³) and very high (>121 spores/m³). We used this classification

Table 3 Relationship between *Alternaria* first peak and the models used to predict host susceptibility. *P-Days* Propitious days model, *DD* accumulation of disfavoured days model, *IWP* interrupted wet periods model

Year	First peak					Host susceptibility ^c			
	Date	Concentration spores/m ³	Accrued P-Days ^a	Accrued DD ^a	IWP days ^b	150 <i>P-Days</i> date	<i>P-Days</i> forecast lead time (days)	30 DD date	DD Forecast lead time (days)
2007	25 May	44	105	3	3	19 May	6	15 July	−50
2008	25 June	61	221	21	0	19 June	7	29 June	−3
2009	5 June	95	89	69	2	28 May	8	28 May	8

^a Results of each model for date of the first peak

^b Number of days IWP just before the first peak

^c Risk of infection according the model (dates and days forecast)

Table 4 Time series autoregressive integrated model of running mean (ARIMA) model proposed

	ARIMA (2,0,2), adjusted R ² =0.849			
	B ^d	ET ^c	t	P
AR ₁ ^a	1.672	0.345	4.848	0.000
AR ₂ ^a	-0.726	0.263	-2.763	0.006
MA ₁ ^b	1.463	0.342	4.273	0.000
MA ₂ ^b	-0.560	0.191	-2.923	0.004
Minimum T-3 ^c	-2.145	0.984	-2.178	0.030

^a Autoregressive value^b Running mean value^c Minimum temperature of 3 days before^d Standardized coefficients of the model^e Typical error

to reflect the first significant *Alternaria* levels and then applied three meteorological models to determine the influence of the weather on the concentrations of these spores.

With respect to the IWP model, the spores of some pathogenic fungi are able to develop despite the prolonged lack of humidity. Several authors claim that this happens to several *Alternaria* species when short periods of humidity (usually at night) are interrupted by intervals of low humidity during the day. These conditions favour the production of seven times more conidia (Bashi and Rotem 1975; Everts and Lacy 1990; Rotem et al. 1978). This is because the immature and mature conidiophores formed during the night are able to withstand the unfavourable dry conditions the next day and continue to develop in the humid conditions on the following night. A study made by Rotem (1994) confirms that sporulation in the field requires at least 2 days with alternating high and low humidity, and a minimum of 6 h of consecutive periods of humidity. These minimum humidity requirements occurred in the 2007 and 2009 cycles before of the appearance of the spores in the air, as shown in the column of IWP days of the Table 3 for the first peaks proposed.

Van der Waals et al. (2003) applied the IWP model to a South African potato crop. The weather in this geographic area is very different from ours, with very high temperatures recorded during the growing season and large temperature differences between day and night, which affect the humidity. In our studied area, the weather is frequently drier and colder.

The same is true for the other two models (P-Days and DD model), which were validated in Colorado (Gent and Schwartz 2003). This is an area with high temperatures and high precipitation, especially in the months of

the potato crop. The meteorological conditions during the 2009 cycle in our study were similar to the conditions in Colorado, so these models were more accurate during this year.

The P-Days model also determined a temperature range suitable for the development of *Alternaria*. These ranges allow us to select the conditions most influential in the development of this potato pathogen and to establish a more accurate prediction of *Alternaria*. Of the three models tested, this model was the best predictor of initial *Alternaria* spore concentrations. Pscheidt and Stevenson (1986) in Wisconsin observed the first symptom of the early blight when they had accumulated values of P-Days above 300 units. Gent and Schwartz (2003) state that the P-days model is a good predictor of *Alternaria* infection, but it is necessary to take into account the climatic and geographical conditions of the area. Iglesias et al. (2007) indicate that the P-Days model is the best predictor of the occurrence of *Alternaria* spores in our area when the model reaches 150–175 units (accumulated P-Days). Considering this range in the area studied here, the first treatment in the 2007 cycle should have been applied on 19 May to slow the development of early blight disease. It should have been applied on 19 June during the 2008 cycle and on 28 May during the 2009 cycle.

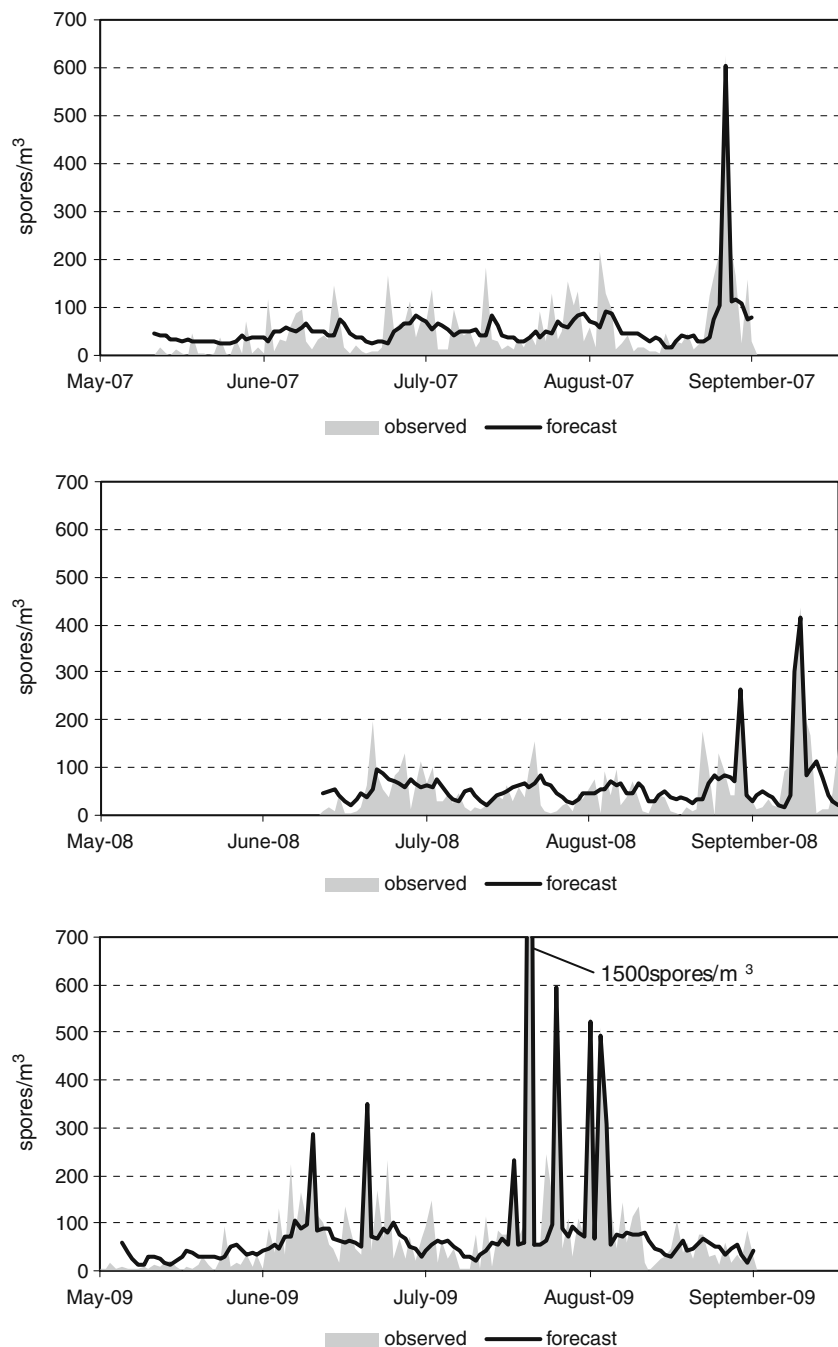
Only the meteorological conditions in the year 2009 allowed for appropriate adjustment of the three tested models for prediction of the first treatment (28 May).

A combination of these models, based on minimum and maximum temperatures and humidity, with statistical models that take into account the spore concentration in the air on the previous days, allows for improved forecasting of the risk of an *Alternaria* infection. Therefore, to complete the study, we constructed an ARIMA time-series model. This model takes *Alternaria* spore counts over the previous days as an autoregressive parameter.

Aerobiological studies generally use linear logistic models to predict spore concentrations (Rodríguez-Rajo et al. 2002). These linear regression models, using only weather variables for prediction, yield results showing a low predictive capacity. The ARIMA time-series model presents a high accuracy in the forecasting of the spore or pollen counts (Cotos-Yañez et al. 2004).

The best adjusted ARIMA time-series model for forecasting was an ARIMA (2,0,2). The meteorological factor include in this model was the minimum temperature recorded 3 days earlier, taking into account the *Alternaria* concentration recorded 1 and 2 days earlier (Table 4). In conclusion, as stated throughout the entire work, the temperature is the factor that most affects the development of *Alternaria* spores. A higher minimum temperature produced an increase in spore concentration.

Fig. 3 Daily mean *Alternaria* spore concentrations observed and predicted during the 3 years of crop testing using the proposed *ARIMA* model



The influence of meteorological parameters on the release and air transport of propagules of *Alternaria* is manifested in the observed differences in seasonal and monthly patterns in different biogeographical and climatic areas (Ricci et al. 1995). Furthermore, our study confirms the importance of collection of climate information in the area of the crop for the prevention and prediction of development of plant pathology (Paredes et al. 1997).

Therefore, we believe that it is important not only to take into account the meteorological variables recorded on the

same day or the days prior to the appearance of fungal spores, but also to know the inoculum concentration of conidia in the air. The results of models based on meteorological factors must be complete statistical models that incorporate variable spore concentrations and adjust for the factors that most affect spore development.

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