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Influence of Environmental Factors on Field Concentrations of *Alternaria solani* Conidia above a South African Potato Crop

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Trends in weather variables and concentrations of airborne conidia of *Alternaria solani* were monitored in a potato field in South Africa during three potato-growing seasons in 2001 and 2002. Distinct seasonal variation was noted, with a drop in spore numbers during winter. Peaks in spore concentration coincided with periods favorable for spore formation and dispersal; most notable was the effect of interrupted wetting periods. Diurnal periodicity of spore dispersal was also observed, with the peak of spore concentrations between 9h00 and 18h00. Few spores were sampled at night, when wind velocity and temperature are lowest and relative humidity is highest. Increased numbers of spores were sampled during days of harvesting or when other ground-operated farm equipment was used. The results obtained in this study will be useful in establishing decision support systems to control early blight on potatoes in southern Africa.

KEY WORDS: Early blight; epidemiology; *Solanum tuberosum*; spore dispersal.

INTRODUCTION

Potatoes are an important crop in South Africa, with production exceeding 1.6 million tons annually (25). The potato production areas in South Africa are divided into 14 main regions, namely, Limpopo (formerly Northern Province), North-West, Gauteng, Mpumalanga, Northern Cape, Western Free State, Eastern Free State, Kwazulu-Natal, Sandveld, Ceres, Southern Cape, South-Western Cape, Eastern Cape and North-Eastern Cape.

Early blight (causal agent *Alternaria solani* Sorauer) is one of the major foliar diseases of potatoes and causes premature defoliation of potato plants almost everywhere they are grown. In South Africa, early blight is also one of the most underestimated diseases on potatoes (22). Disease symptoms are characteristic dark brown to black lesions with concentric rings, which produce a 'target spot' effect. Symptoms are initially observed on older, senescing leaves.

The primary inoculum produces conidia in the spring, which are then splash- or wind-dispersed to the lower leaves of the plant, where they germinate and infect (33). Wind, rain and insects are the primary methods of dissemination of the pathogen (30). *A. solani* has typical dry-dispersed spores; the conidia have slightly rough surfaces with dark-colored

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walls and are produced away from the host surface on aerial conidiophores (12). Such dry-dispersed spores may be removed from the host by gusts of wind, by acceleration forces as leaves flap in the wind, and by rain or overhead irrigation splash, through puff or tap mechanisms (12,16). Pscheidt and Stevenson (29) have shown that on potato plants, sporulation occurs at temperatures of between 5 and 30°C, with the optimum around 20°C.

The objective of this study was to determine the relationship between weather variables and concentration of airborne conidia of *A. solani* above a potato crop. Although many authors have studied the dispersal of *A. solani* conidia (2-5,8,31), this is the first such study of *A. solani* on potatoes in southern Africa. It has previously been shown that, although correlations exist between sporulation and weather variables, the nature of conditions influencing these correlations depends on the characteristics of the specific region (33); hence the importance of conducting such a study in South Africa. The information will provide a better understanding of factors that affect *A. solani* spore production, liberation and dispersal, and will also provide a useful tool for early blight disease management in southern Africa.

MATERIALS AND METHODS

This study was conducted in the Gauteng region, at the Agricultural Research Council at Roodeplaat in Pretoria (25°35'S 28°21'E; alt. 1164 m). Weather conditions and concentrations of airborne conidia of *A. solani* were monitored in a potato plot at the Roodeplaat Agricultural Research Council, during the following growing seasons: March–May 2000, Nov. 2001–Jan. 2002, and Feb.–June 2002; the respective planting dates were 1 March 2000, 1 Oct. 2001 and 28 Feb. 2003. In each season the plot was planted with two different cultivars, one susceptible to early blight (BP1) and the other moderately resistant (Fianna) (41). The crops were naturally infected and no inoculum was added for disease development.

Weather parameters were monitored using an Adcon weather station (A730MD, Adcon Telemetry, Agrotop, Cape Town, South Africa) situated 1.5 m above soil level, and less than 10 m outside the trial plot. The recorded parameters were temperature, relative humidity, leaf wetness, precipitation, wind speed and radiation. Leaf wetness was measured with an electrical resistance-sensing grid that simulated leaf surfaces. Wind speed was measured approximately 2 m above the ground. The data logger scanned the installed sensors every 3 min and 15-min averages were downloaded remotely *via* a radio base-station linked to a personal computer.

Concentrations of *A. solani* conidia present in the atmosphere were estimated by collecting spores using a volumetric spore sampler (Quest Developments, Brits, South Africa) – which was a modification of the Burkard Spore Sampler, and sampled 20 m^3 of air per min. The sampler was mounted on a tripod, with air intake at 0.5 m above ground level, and was powered by a 12 V DC battery that was charged from a solar panel. The spore sampler was situated less than 10 m outside the potato field on an open piece of land. Spores were collected on a monitoring disc coated with a Vaseline spray. The disc had an 8-day monitoring capability with 3-h resolution and interfaced with a light microscope. Spores on the disc were counted at 100 × magnification. Although *A. solani* spores are morphologically similar to those of *A. dauci* (Kühn) Groves & Skolko (19), there were no hosts (carrots) of *A. dauci* near the potato field. It was thus assumed that the number of *A. dauci* spores possibly collected and incorrectly identified as *A. solani,* was negligible.

Spores on the sampling disc were identified solely by morphological characteristics. A stepwise regression analysis was conducted on weather variables and spore data from 8 Feb. to 4 July 2002, from 09h00 to 18h00 daily, the period when most spores were released.

Early blight disease severity and amount of defoliation for both cultivars in an unsprayed plot of the Nov. 2001–Jan. 2002 trial was estimated visually every 7–10 days, using standard leaf area diagrams (18), starting with the first appearance of symptoms until plants began to senesce. Area Under the Disease Progress Curve (AUDPC) values were calculated from disease severity values for each cultivar, using Riemann Sums (11,39).

RESULTS

In all seasons, similar trends in spore concentrations were observed in relation to temperature, interrupted wetting periods (IWP) and harvesting. Throughout most of this study, wind speeds were above 2–3 m sec^{-1}, which has been shown to be the minimum speed required to release and disperse large numbers of spores of *Alternaria* species (37).

March – May 2000 Since this trial was not preceded by another potato or tomato crop, the initial inoculum levels of *A. solani* were low at the onset of the season, but during the season the levels slowly increased. A few distinct peaks in spore concentration were observed during the later part of the cycle (Fig. 1).

A spore count peak was recorded on 17 March. The 6 days preceding this date had pronounced IWPs. These IWPs were characterized by relative humidity of $>95\%$ for at least 6 h at night and $<80\%$ during the day. Leaf wetness showed similar trends to relative humidity, but was not used in the calculation of IWPs. The average temperatures recorded were 17°C at night and 25°C during the day. On 17 March between 6h00 and 12h00, when the greatest numbers of spores were recorded, wind speeds ranged from 6.67 to 8.00 m sec^{-1}.

Another spore count peak was recorded on 31 March, which could have been influenced by numerous factors. Among others, a neighboring potato field was harvested on that day, thus disturbing plants and soil. The maximum wind speed was 5.50 m sec^{-1}, which was lower than on 17 March. This date was preceded by a 5-day IWP. Maximum daily temperatures were lower and more rain was recorded when compared with mid-March.

Smaller peaks were recorded on 20, 21 and 28 April and these days were also preceded by IWPs of 3–5 days, with conditions similar to those recorded in mid-March.

November 2001 – January 2002 During this period, two fields were planted with potatoes, one commercial and one trial field. Both were planted immediately after another potato crop was harvested, which resulted in spore counts at the start of this season being higher than at the start of the March 2000 season. Plants in the commercial field were approximately 1 month old on 25 Oct., when the potatoes in the trial field had just started emerging. On 12 Nov. early blight lesions were observed in the commercial field. There was a marked increase in spores towards the end of the season (Fig. 2).

Early blight disease progress curves followed similar patterns for both cultivars, with Fianna showing the highest severity towards the end of the season (Fig. 3).

February 2002 – June 2002 Harvesting of the commercial field from 5–15 Feb., and the trial field on 15 March, once again resulted in disturbance of plants and soil and thus in an increase in spore counts (Fig. 4). A drop in spore concentrations was recorded for the period 1-14 April. Two nights with relative humidity $>95\%$ for at least 6 h resulted in an increase in spore concentrations on 14 and 15 April 2002 (Fig.4).

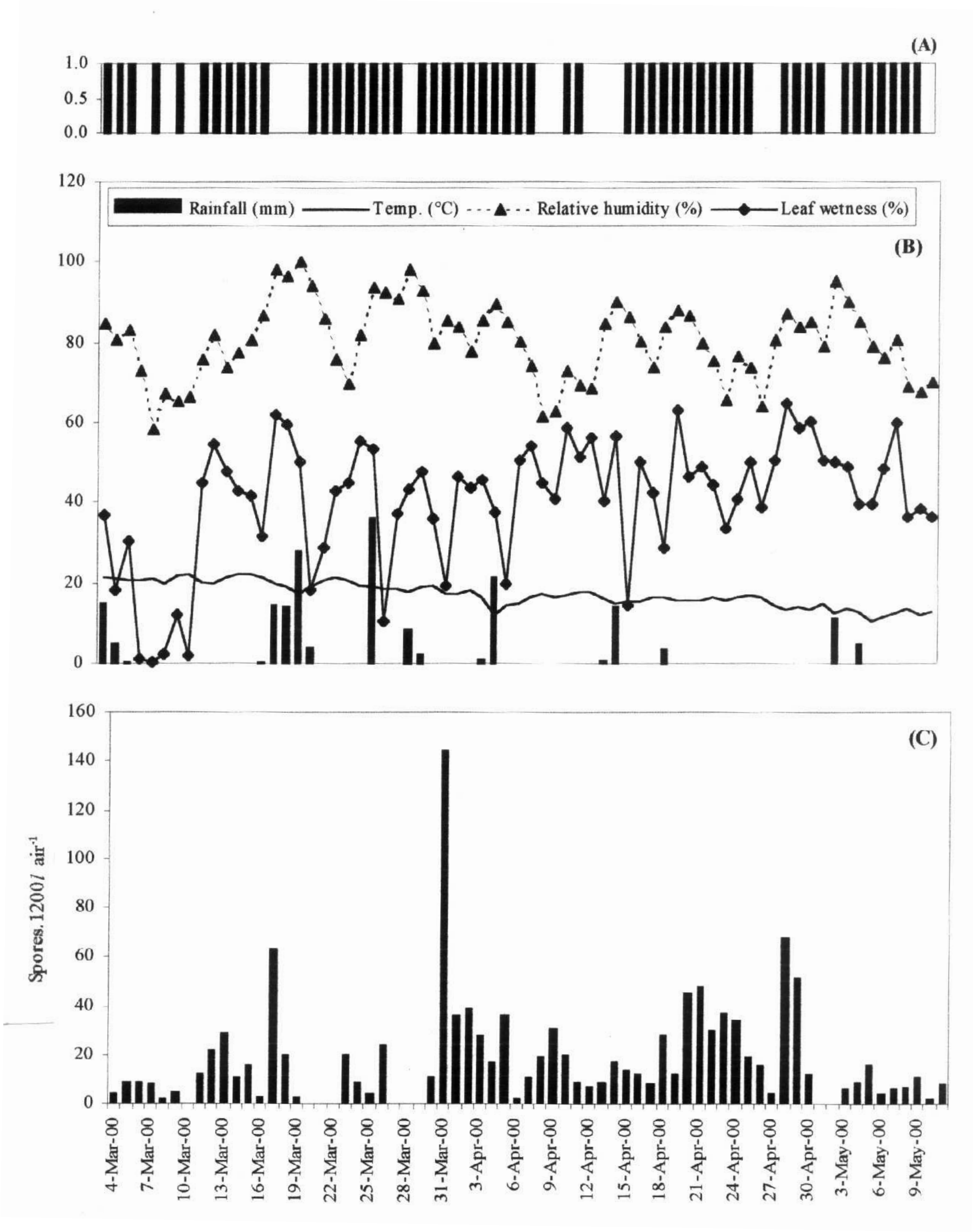

Fig. 1. Interrupted wetting periods (presence = 1 bar; absence = no bar) (A); daily weather variables (B); and *Alternaria solani* conidia concentration (C), for March – May 2000, at the Roodeplaat Agricultural Research Council, Pretoria, South Africa.

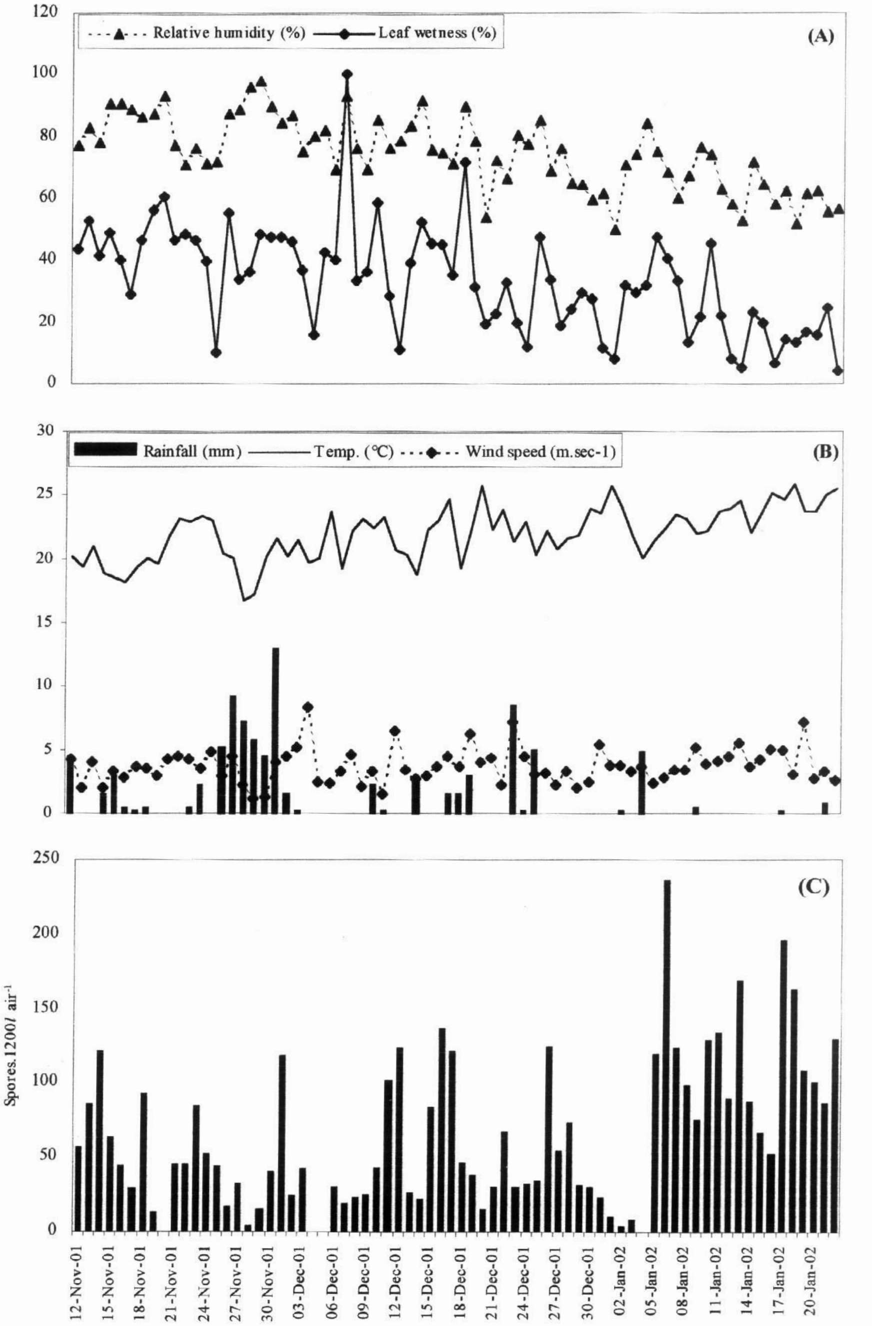

Fig. 2. Daily weather variables (A and B) and *Alternaria solani* conidia counts (C) for November 2001 – January 2002, at the Roodeplaat Agricultural Research Council, Pretoria, South Africa.

The first frost in this trial was recorded on 6 May, after which there was a noticeable drop in spore numbers sampled daily.

The regression analysis of weather variables and spore data from 8 Feb. to 4 July 2002 between 09h00 and 18h00 showed that temperature accounted for 40.4% of the variation in (log) spore count ($P<0.001$), relative humidity accounted for another 12.1% ($P<0.001$), and the interaction between leaf wetness and time of day for another 5% ($P=0.008$). Thus, the combination of these factors accounted for 60% of the variation in spore counts.

Diurnal dispersal of spores The highest spore counts were found between 09h00 and 18h00 daily, with a peak around 15h00 (Fig. 5), showing diurnal periodicity.

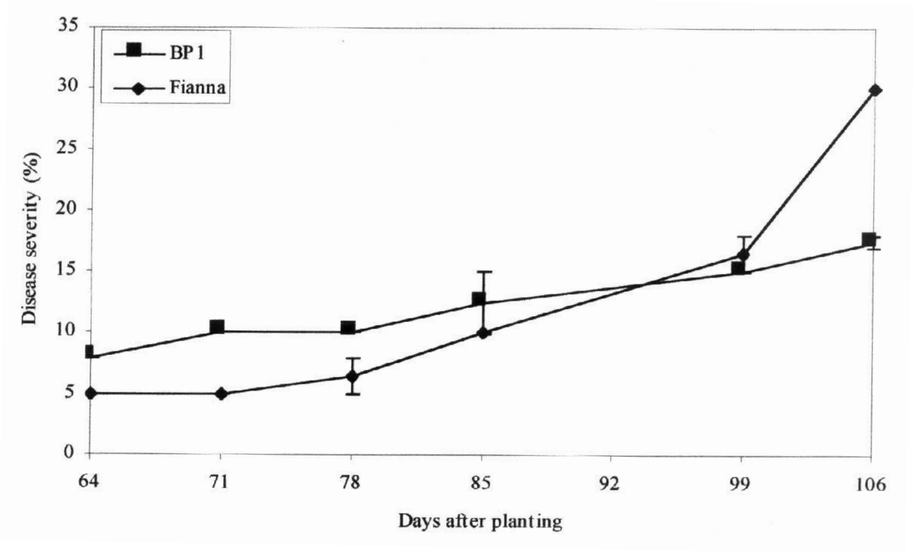

Fig. 3. Early blight disease progress curves on potato cultivars BP1 and Fianna during December 2001 – January 2002, at the Roodeplaat Agricultural Research Council, Pretoria, South Africa. The planting date was 1 October 2002. Error bars are S.E. values; those not shown were negligible.

DISCUSSION

The temperature and moisture requirements for spore dispersal of *A. solani* in potatoes observed in this study are in line with those reported previously (2-5,8,31). The present data also resemble the requirements of other *Alternaria* species, such as *A. alternata* (Fr: Fr.) Keissl. (40), *A. dauci* (19,37), *A. porri* (Ellis) Cif. (9,10), *A. brassicae* (Berk.) Sacc. and *A. brassicicola* (Schwein.) Wiltsh. (17). However, this study showed that, for *A. solani*, IWPs are more important than high leaf wetness in spore formation and dispersal, contrary to that found with *A. dauci* (37). Since the stepwise regression analysis of weather variables and spore data could account for only 60% of the variation in spore counts, the use of other statistical analyses may be necessary to augment the results and explain the remaining 40% of the variation.

Integrated effects of host and environment on number of airborne spores The number of *A. solani* conidia in the atmosphere dropped drastically from summer to autumn,

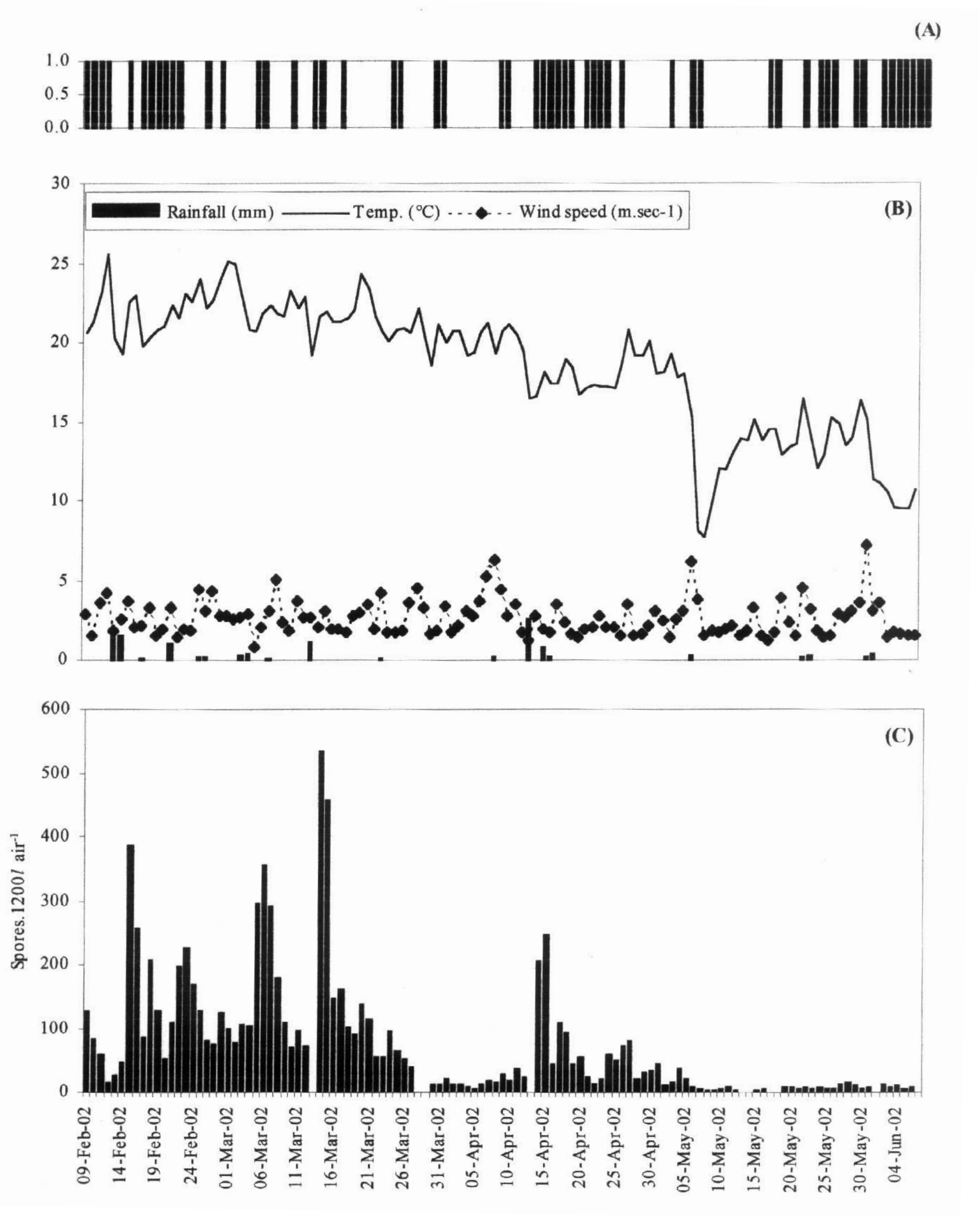

Fig. 4. Interrupted wetting periods (presence = 1 bar; absence = no bar) (A); daily weather variables (B); and *Alternaria solani* conidia concentration (C), for February – June 2002, at the Roodeplaat Agricultural Research Council, Pretoria, South Africa.

with very few spores collected during the winter months. The drop in spore concentrations after the first frost in May 2002 can be attributed to the fact that night temperatures fell to well below 8°C, which has been shown to be the minimum temperature for spore production by *A. solani* (13). This reduced sporulation capacity of *A. solani* during periods

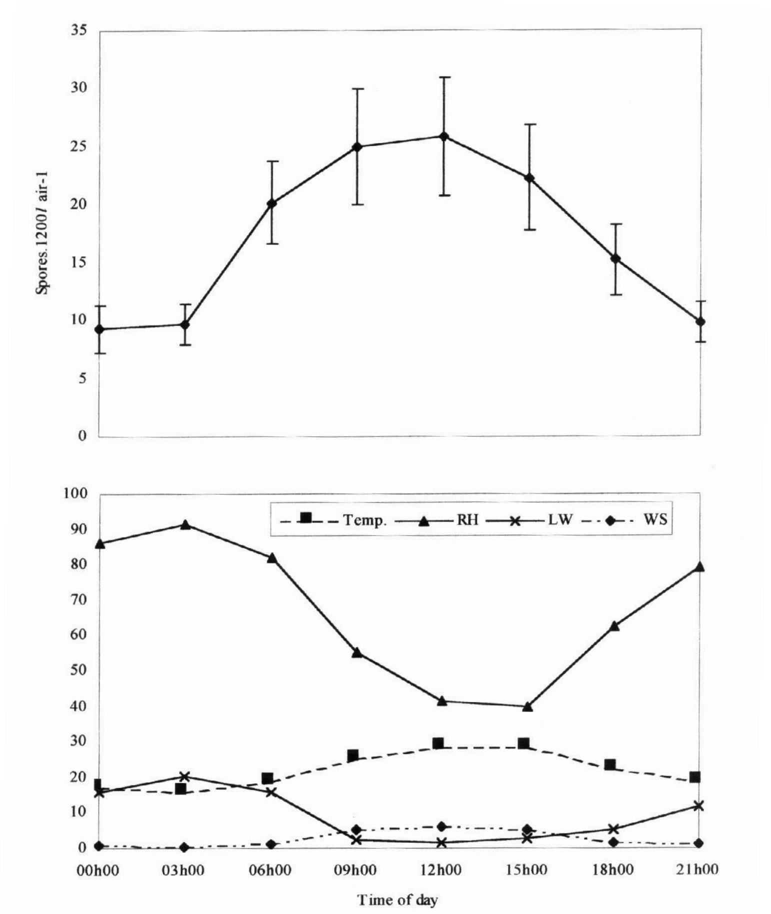

Fig. 5. Mean daily circadian trends of *Alternaria solani* spores, air temperature (°C), relative humidity (RH, %), leaf wetness (LW, %), and wind speed (WS, m.sec^{-1}). Values are averages of data for February – March 2002. Y-axis error-bars are S.E. values.

of low temperatures, even when relative humidity is high, is of epidemiological importance in reducing the spread of disease during winter, especially in growing areas with winter temperatures below 8°C at night. Although low temperatures did not stop the production of spores, the rate of spore production was reduced. Reduced conidial dispersal during periods with low temperatures has also been noted to be the case with *Alternaria brassicicola* in the UK (17). Temperature can thus be used in decision support systems (DSS), as it gives an indication of expected spore abundance.

In fields planted after winter or a fallow season, initial spore concentrations are low and the build-up of inoculum is slow. This is due to the age-conditioned resistance of young plants; the fact that spores are produced mainly on dead or dying leaves (33); and the low number of spores produced during winter months. Various authors have noted this trend in spore concentrations of *A. solani* (8,14,21,29). In a study of *A. solani* on tomatoes in Israel, Rotem (31) showed that maximum spore dispersal occurred 2 weeks after death of the tomato plants and continued for a further 2 weeks. However, in this study there was a drop in spore concentrations at the beginning of April 2002, towards the end of the season. This can be explained by the fact that this was a dry period with no rain, and relative humidity seldom exceeding 88%. It could also be that, in spite of an increase in tiny early blight lesions late in the season, very few spores are produced per lesion (27). It was also noted that spore concentrations did not drop drastically between consecutive potato or tomato cropping seasons, as shown by the fact that initial spore counts were higher in Nov. 2001 than they were in March 2000.

Controlled environment studies on tomato plants have shown that early blight severity is directly proportional to inoculum concentration (7,42). This has also been shown to be the case with other *Alternaria* pathogens (42; I. Vloutoglou, Ph.D. thesis, 1994). Results from the present study confirmed this correlation. Disease progress curves showed only a slight increase in disease severity from 13 Dec. to 10 Jan. (71–99 days after planting) for BP1; and from 3 to 20 Dec. (64–78 days after planting) for Fianna. During these times, there was also no significant increase in spore counts, although occasional peaks were observed. Disease severity on Fianna increased markedly towards the end of the season, whereas on BP1 there was a more gradual increase. For both cultivars, this correlated with the increase in spore counts recorded after 5 Jan. Although the final disease severity on the moderately resistant cultivar, Fianna, was higher than that on the susceptible cultivar, BP1, the AUDPC value for BP1 was significantly higher than that for Fianna. AUDPC is a more accurate measurement of disease, as it measures the development of disease over the whole epidemic (20).

Increased numbers of spores were sampled during days of harvesting or when other ground-operated farm equipment was used, indicating that spores may have been dislodged from leaves. The observation in this study that spore concentrations also increased when a fallow field – previously planted to potatoes – was plowed, supports the conclusion that the life cycle of *A. solani* includes a soilborne stage during which conidia and mycelia overwinter in infected potato debris buried in the soil (6,23,24,26,30,32).

Interrupted wetting periods *Alternaria solani* and various other *Alternaria* species are among the few pathogens that are able to sporulate, despite a lack of prolonged humidity, by using several short wet periods (usually at night) interrupted by dry intervals during the day, otherwise known as interrupted wetting periods (5,9,34). *A. solani* is able to produce seven times more conidia under IWP than under a continuous wetting period of the same duration in darkness (5). This is because mature and immature conidiophores formed at night, are able to withstand unfavorable dry conditions the following day and continue to develop during the humid conditions of the subsequent night. This adaptation allows *A. solani* to thrive equally well in areas with continuous humidity and in areas with alternating wet–dry conditions. This study has confirmed the observation of Rotem (33) that sporulation in the field requires at least 2 days of IWPs, with minimum wetting periods of 6 h. This is an important consideration in the development of DSS, especially in areas where these types of conditions are evident. The climate of most South African potato-growing regions manifests these conditions.

Diurnal periodicity The release of many dry-dispersed spores, including those of *A. solani*, *A. dauci* and *A. porri*, shows diurnal periodicity, with the majority of spores being collected during midday when temperature, wind speed and level of turbulence near the ground are highest, and relative humidity lowest (1,8,9,15,17,31,36). The dispersal of *A. solani* conidia in this study also clearly displayed this diurnal periodicity. However, this study showed that spores were also dispersed at night, contrary to the findings of Strandberg (37), who did not collect any *A. dauci* spores at night.

Control strategies for early blight cannot depend on the use of resistance, as no true resistance to early blight exists in commercial cultivars (33). Therefore, growers must rely on good cultural control practices and a protective fungicidal spray program in order to manage the disease adequately. In growing areas where potato crops are planted in succession, early blight has the potential to become a serious threat to potato production, due to a continued increase in inoculum levels. The danger of cross-infection by airborne inoculum to new potato plantings can be reduced by removal of plant debris, crop rotation with non-hosts, or increasing the time that fields lie fallow between successive potato crops.

Some disadvantages of using a volumetric spore sampler to assess amounts of inoculum present in the air, as done in this study, are that it is time consuming, and the concentration of spores in a unit volume of air is determined, rather than the number of spores actually produced and released during a certain time period. One is not able to determine the epidemic potential of spores, as this depends not only on the number of spores sampled but also on the factors that affect their dispersal, viability, infectivity and ability to survive until the time of infection (34). However, it may be assumed that, given a susceptible host at the right time in an environment favorable for disease development, the pathogen is able to induce disease (34,38). These findings, and those of similar studies in other countries (2-5,13,27,28,31,37), show thus that early blight on potatoes has the epidemic potential to be a highly destructive disease in many growing regions of southern Africa: only a relatively short incubation period is required, especially in older or more susceptible plants (27,35); spore formation and dispersal are promoted by IWPs as opposed to a continuous wetting period; growth (28), sporulation and dispersal are possible over a range of temperatures and wind speeds; and inoculum pressure increases during the growing season due to premature shedding of leaves and increasing necrotic tissue on which sporulation is possible.

The aim of this particular study was to relate spore production and dispersal to environmental factors. It is, however, possible to make disease management decisions based on assumed or actual detection of inoculum (38). Continuation of this study, with attention to the relation of plant age and threshold inoculum levels to epidemic development, could aid in the development or improvement of early blight disease forecasters and DSS for South Africa.

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