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Airborne ascospores of *Didymella rabiei* as a major primary inoculum for Ascochyta blight epidemics in chickpea crops in southern Spain

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Abstract

The incidence and severity of Ascochyta blight in potted chickpea trap plants exposed for 1-wk periods near infested chickpea debris in Córdoba, Spain, or in chickpea trap crops at least 100 m from infested chickpea debris in several locations in southern Spain were correlated with pseudothecial maturity and ascospore production of *Didymella rabiei* from nearby chickpea debris. The period of ascospore availability varied from January to May and depended on rain and maturity of pseudothecia. The airborne concentration of ascospores of *D. rabiei* was also monitored in 1988. Ascospores were trapped mostly from the beginning of January to late February; this period coincided with that of maturity of pseudothecia on the chickpea debris. Most ascospores were trapped on rainy days during daylight and 70% were trapped between 12.00 and 18.00 h. Autumn-winter sowings of chickpea were exposed longer to ascospore inoculum than the more traditional spring sowings because the autumn-winter sowings were exposed to the entire period of ascospore production on infested chickpea debris lying on the soil surface.

Introduction

Ascochyta blight of chickpea (*Cicer arietinum* L.) caused by *Ascochyta rabiei* (Pass.) Labrousse, affects large areas of chickpea crops in Spain and the Mediterranean basin, Southwest Asia, and North America [Nene and Reddy, 1987; Trapero-Casas and Jiménez-Díaz, 1986]. Autumn-winter chickpea sowings have greatly increased yield because of reduced abiotic stresses and low incidence of other diseases, especially Fusarium wilt [Saxena and Singh, 1984; Trapero-Casas and Jiménez-Díaz, 1986], but chickpea blight has become the most important limiting factor of this agricultural practice. The symptoms of the disease develop on all aerial parts of the plant and consist of necrotic lesions which often cause breaking of stems and death of plant parts above the affected zone [Nene and Reddy, 1987]. *A. rabiei* forms the sexual or teleomorphic stage *Didymella rabiei* (Kovachevski) v. Arx (= *Mycosphaerella rabiei* Kovachevski) on chickpea crop residues that overwinter on the soil surface after harvest, in which the fungus develops saprophytically and forms abundant pycnidia and pseudothecia [Kovachevski, 1936; Navas-Cortés *et al.*, 1995; Trapero-Casas and Kaiser, 1992 b; Zachos *et al.*,1963]. In Spain, the teleomorph occurs widely in the main chickpea cultivation areas of southern and central Spain [Navas-Cortés *et al.*, 1990]. Pathogen dispersal within or between crops is usually attributed to conidia produced in pycnidia formed on infected seeds and harvest debris [Nene and Reddy, 1987]. However, ascospores produced in pseudothecia formed on infested debris are forcibly discharged into the air and may be carried great distances by winds [Kaiser, 1992; Trapero-Casas and Kaiser, 1992b] and may serve as primary inoculum for epidemics of Ascochyta blight.

The current work aimed to determine whether or not debris of chickpea plants infected by *D. rabiei* can be the source of primary inoculum for new epidemics of Ascochyta blight of chickpea in Spain, and was focused especially on the sexual stage of the fungus.

Data obtained would help to design strategies for an effective control of the disease.

Materials and methods

Potted trap plants

In October 1987 to 1991, pieces of stem debris 10–20 cm in length from the previous crop of chickpea cv. Blanco Lechoso with lesions of Ascochyta blight were placed on the soil surface in a plot 4×3 m at the 'Alameda del Obispo' research farm at Córdoba, Spain. The debris was collected in July each year and stored in sacks in a dry place at room temperature until used. The debris was held in place by a net attached to the soil to prevent dispersal of the stem pieces by wind during the experiment. From January to May each year, potted chickpea plants of cv. Blanco Lechoso were arranged close to and around the plot. The potted plants were grown from seeds in a non-sterile soil potting mixture in a greenhouse with a partially controlled environment. Cultivar Blanco Lechoso is highly susceptible to *D. rabiei* [Trapero-Casas and Jiménez-Díaz, 1986] and thereby potted plants served as a trap in the experiment to determine the infectivity of *D. rabiei* ascospores released into the air from the infested debris. Chickpea seeds used in this work were produced under blight-free conditions, and were subjected to a blotter-test to verify the absence of *D. rabiei* [Kaiser, 1987]. At weekly intervals during the study, three pots (three plants per pot) with trap plants at the flowering stage (approx. 6–7 weeks-old) were placed on each side of the rectangular debris-strewn plot and elevated some 40 cm above soil level. Each set of 12 pots was left exposed in the field for 1 week then arranged in trays containing a film of water in a hermetically-sealed black-plastic chamber with saturated moist air at 22 ± 5 °C for 48 h. The plants were then removed from the trays and kept in a greenhouse for the development of symptoms for 2 weeks after which the number of Ascochyta blight lesions was counted and plants rated for disease severity on a 1–10 scale. The scale values were transformed into percentage of affected tissue [Trapero-Casas and Kaiser, 1992a].

To avoid the possibility that the position of the potted plants around the debris-strewn plot might influence the results, the experiment was designed as randomized complete blocks, each block comprising three pots placed on each side of the debris-strewn plot. Mean comparisons were made using Fisher's protected least significant difference at the 5% probability level [Steel and Torrie, 1985]. For each week during the 3-month period (January to March) of each year, linear correlations were determined between the percentage tissue infected or the number of blight lesions with rainfall, the number of days with rain, and the mean weekly temperature. The daily meteorological data were obtained from Córdoba airport, 3 km from the experimental plot.

Assessment of pseudothecial maturation

The infested chickpea stem debris was sampled to determine the stage of pseudothecial development in each 12-month period during the 5 yr study beginning October 1987. In each period, 12 pieces of debris were sampled at 15-day intervals during October-June and at 2-month intervals in the following months; the debris was washed under running tap water and dried on filter paper. The pseudothecial development was determined in at least 50 pseudothecia sampled from the debris by dissection, squashing in lactophenol-acid fuchsin and microscopic examination to determine the developmental stage on a 1–7 scale of pseudothecial-maturity-index (PMI) in which 1 = stromatic pseudothecial initial and 7 = empty pseudothecium with all ascospores discharged [Trapero-Casas and Kaiser, 1992b]. To estimate the discharge of ascospores from pseudothecia, several strips of stem tissue colonised by pseudothecia were chosen from each 15-day sampling interval and placed on a water agar (WA) block coverint an area of 4 cm^2; this was then attached to the inner surface of the lid of a Petri dish and the ascospores were allowed to discharge downwards onto 2% WA or into sterile water in the dark for 24 h at 20 °C.

Trapping of airborne ascospores

In 1988, the concentration of airborne ascospores of *D. rabiei* was monitored with a volumetric spore sampler (Burkard Manufacturing Co. Ltd., Rickmansworth, U.K.) located in the vicinity of the infested chickpea debris close to the trap plants, with the orifice at 1 m above ground level. Air was sampled at approximately 9 l/min and yielded a continuous record of ascospores in the air during the 6-month period from January to June. Ascospores were impacted onto tapes coated with a thin layer of an adhesive mixture of petroleum jelly and paraffin (9:1, w/w). The tape was mounted in a rotating cylinder operating at 2 mm/h and was changed weekly. The number of *D. rabiei*

ascospores deposited on the sampling surface was counted at ×500 with a microscope. Tapes removed weekly were cut into daily segments (48 mm), stained with lactophenol-acid fuchsin, and mounted on glass slides under 24 × 50 mm coverslips. Before mounting, tapes were marked at 4-mm intervals with a razor blade to indicate 2-h intervals. The number of ascospores collected for each 2-h period was determined by the ascospore deposit on a 0.34 mm traverse across the tape (diameter of the microscope field) centered on each 4-mm exposure. The average of the twelve 0.34-mm traverses for each 48-mm tape segment was used to estimate the daily concentration of ascospores. Spore counts were expressed as the number of ascospores per m^3 of air sampled [Aylor, 1993; McCartney and Lacey, 1990]. During the period of significant ascospore captures in January to February 1988, the relationship between the total number of ascospores trapped each day, and the occurrence of rain, rainfall in mm, and the mean temperature that day, were examined by correlation analysis. Homogeneity of correlation coefficients was also tested [Steel and Torrie, 1985].

Chickpea trap plots

In October of each of the 5 years of the study, stem debris of chickpea cv. Blanco Lechoso showing lesions of *D. rabiei* were placed on the soil surface of a 4 × 3 m plot at several sites. Chickpea stems were collected from fields at harvest time in the previous July and stored in a dry place at room temperature until used. The prevailing wind was taken into account at each site and in December of each year a 100 m^2 plot at least 100 m downwind from the debris was sown with *D. rabiei*-free seeds of cv. Blanco Lechoso. The healthy chickpea plants at these sites acted as traps to monitor the infectivity of the *D. rabiei* ascospores discharged from the nearby debris.

In the one-year period 1987–88, the chickpea trap-plant plots were located in Córdoba, in Cañete de las Torres (Córdoba province), and in Jerez de la Frontera (Cádiz province). For the 1988–89 and 1989–90 periods, plots were located in Córdoba and Granada. In the 1990–91 and 1991–92 periods, the trap-plant plots were located only in Córdoba. In addition, in 1987, a plot without nearby *D. rabiei*-infested debris, but with similar characteristics to the others, was established in Carmona (Seville province). In each case, the plots with trap plants were located in areas where no chickpea crops had been cultivated for 2 yr previously. All the trap-plant crops were closely observed to study the development of symptoms of Ascochyta blight during the different phenological stages of the crop.

Results

Ascochyta blight severity in potted trap plants

The chickpea trap plants developed symptoms of Ascochyta blight when exposed from the middle of January in the 1988–90 period, and from the first 2 weeks of February 1991 and 1992, until the beginning of April each year. Disease development during May was slight. However, the severity and development of symptoms depended on the year studied (Fig.1).

In 1988, symptoms of Ascochyta blight were found mainly in the chickpea trap-plants exposed from the middle of January to the end of February. An average of 20% tissue was affected in this period. Maximum disease severity, 43%, occurred in the last week of January (Fig.1). In 1989, maximum disease severity, 40%, occurred at the end of February, while an average of 13% tissue was affected from the middle of March to the beginning of April and no disease occurred in the remaining weeks (Fig.1). In 1990 and 1992, average disease severity was similar to that found in 1988 and 1989, though blight in the trap plants occurred with higher variability. In 1990 and 1992, maximum values of affected tissue occurred in four weekly samples which, in 1990, ranged from 19–38%, and in 1992, between 10–43% and no disease for the remaining weekly intervals (Fig.1). In 1991, maximum disease severity occurred in the last week of February and the first week of March, and the percentages of tissue affected were 37 and 35%, respectively.

During the study, the mean disease severity in plants was significantly influenced ($P < 0.05$) by position around the infested debris in some of the weekly intervals of sampling. Although there were no definite trends in the years of the study, most frequently the highest severity values occurred in plants placed to the northeast, downwind from the prevalent wind direction.

Pseudothecial maturation

Differentiation of *D. rabiei* pseudothecia initials occurred within 2 weeks following placement of the infested debris on the soil surface. Differentiation of the asci and ascospores of the fungus (PMI=5) took place mainly in January 1988; in both January and February 1990; in February 1989 and 1991, and in

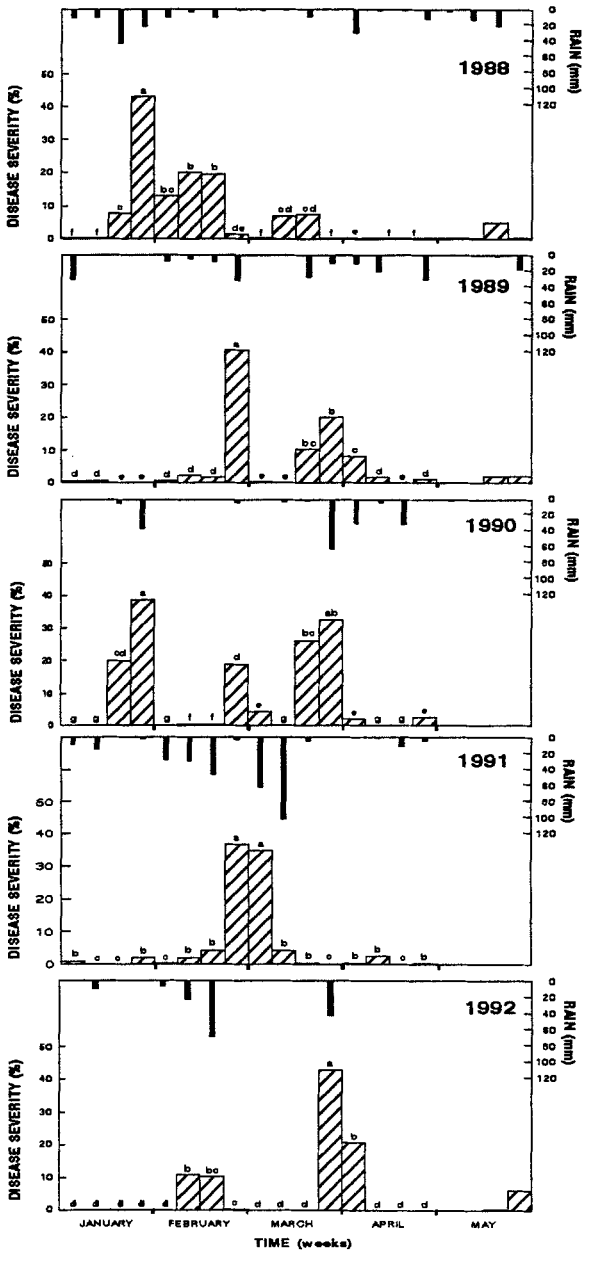

Fig. 1. Weekly precipitation, and mean Ascochyta blight disease severity in chickpea trap plants exposed to airborne ascospores of *Didymella rabiei* for weekly intervals during January-May 1988, 1989, 1990, 1991 and 1992 near *D. rabiei*-infested chickpea debris in a plot at the 'Alameda del Obispo' research farm in Córdoba, Spain. Each bar in the histogram represents the mean severity in 12 pots (3 plants/pot). For each year, mean severities with a letter in common do not differ significantly ($P < 0.05$) according to Fisher's protected LSD test.

March and April 1992 (Fig.2A). Under controlled conditions, ascospore discharge from stem debris suspended over WA or water took place from the beginning of January to April or May, although the most important discharges occurred between the end of January and the beginning of February 1988 and 1990; between February and March 1989 and 1991, and during April and May 1992 (Fig.2B). Except in 1992, ascospore discharge markedly decreased from the middle of March and all the pseudothecia on the debris were found empty. In 1992, ascospore discharge was prolonged until the beginning of June (Fig 2B). None of the empty pseudothecia developed new asci. No new pseudothecia formed on the debris during the following autumn-winter period.

Concentrations of airborne Didymella rabiei *ascospores*

The sampling of airborne ascospores of *D. rabiei* from January to June 1988 revealed that the concentration of ascospores (Fig. 3) was significant during January and February. Maximum concentrations of 918, 551, and 125 ascospores/m^3 respectively, occurred at the end of January, at the middle of February and end of February (Fig. 3). The hourly distribution of ascospore counts for the sampling period (Fig. 4) revealed a diurnal periodicity. Of the total daily number of ascospores collected, 82.7% were found in day-time samples (from 08.00 to 20.00 h); and 69.5% were found between 12.00 and 18.00 h (Fig. 4).

Relationships between Ascochyta blight severity, number of airborne ascospores, and meteorological factors

Both the percentage of trap-plant tissue affected (PTA) and number of lesions (NL) showed a significant correlation ($P < 0.05$) with the number of days with rain during weekly periods (Table 1). No significant differences ($P \geq 0.05$) were observed between correlation coefficients for number of rainy days and PTA or NL in the different experimental periods. In all the experimental periods of the present work, weekly temperatures did not correlate significantly with the incidence of Ascochyta blight.

During the sampling period of January-February 1988, when there was a significant concentration of airborne ascospores of *D. rabiei*, 94% of all ascospores were trapped within the 12 days in which rain was recorded. Nevertheless, the remaining 6% of the total ascospore count for the period was collected on two

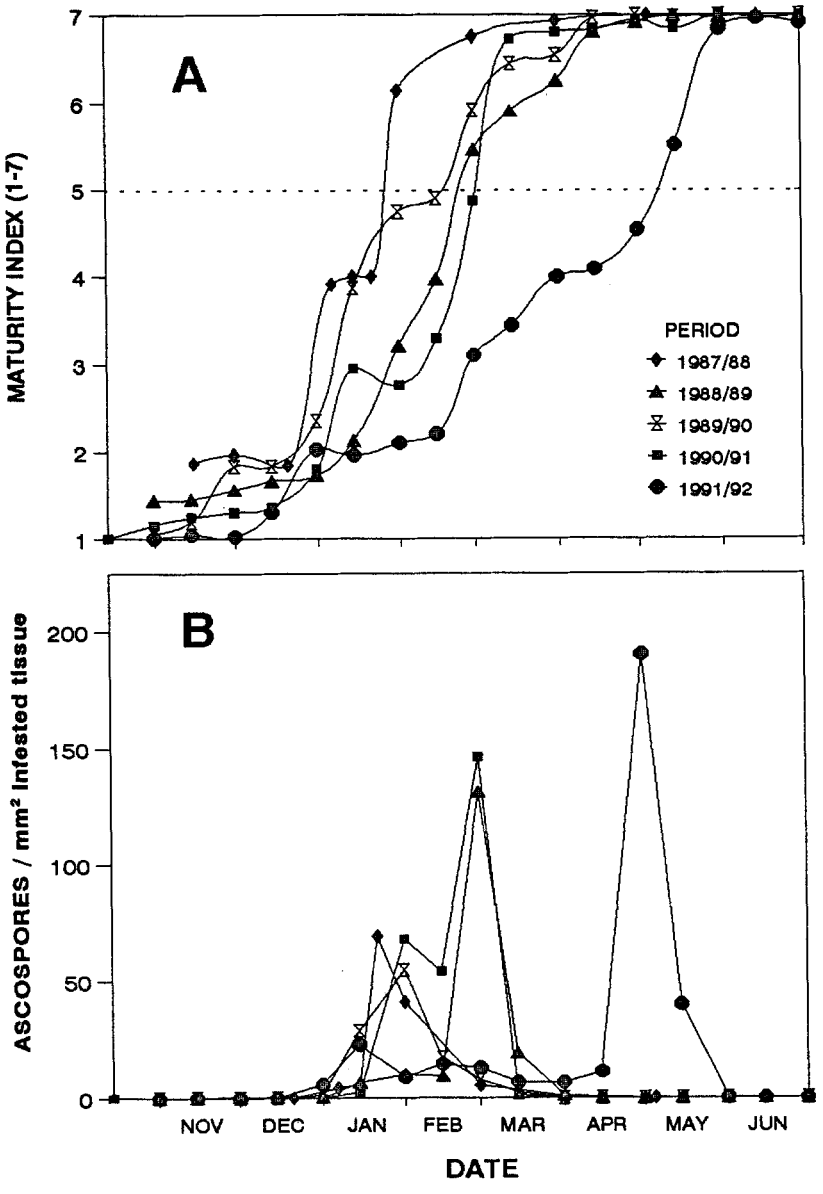

Fig. 2. Development of *Didymella rabiei* on chickpea stem debris placed on the soil surface of a plot at the 'Alameda del Obispo' research farm in Córdoba, Spain. A, Increase of pseudothecia maturity index over time (Broken line=pseudothecia with mature ascospores fully developed). For each sampling date and year, at least 60 pseudothecia were removed from the debris and observed to estimate the pseudothecial maturity index. B, Ascospore discharge from debris sampled from the plot and incubated under controlled conditions suitable for ascospore liberation. For each sampling date and year, 4 cm^2 of highly infested tissue were used to determine the number of discharged ascospores.

days (Fig. 3). Total number of ascospores trapped each day was positively and significantly correlated ($P < 0.05$) with each daily rainfall in mm, the occurrence of rain, and the mean daily temperature (°C) during the period of sampling (Table 2). The level of correlation increased when multiple linear correlations were calculated between either the daily rainfall or the occurrence of rain, and the mean temperature (Table 2). However, no significant differences were observed between correlation coefficients of variables considered in simple or multiple linear correlation analyses.

In the 1988 January to February period, the presence of airborne *D. rabiei* ascospores (Fig. 3) was coincident with the period of maturity of the pseudothecia on the debris (Fig. 2) and was correlated with the incidence of blight on the chickpea trap-plants.

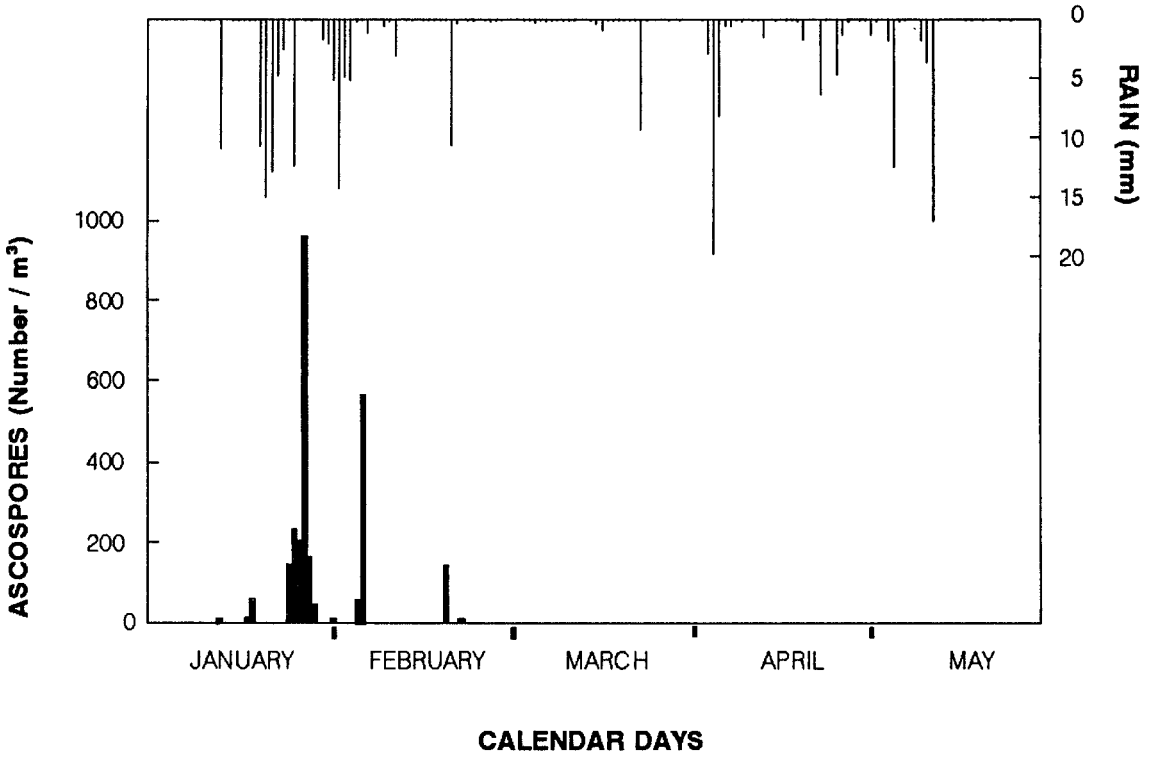

Fig. 3. Daily precipitation and average concentration of airborne ascospores of *Didymella rabiei* (number per m^3) trapped by means of a Burkard spore-trap installed near *D. rabiei*-infested debris in a plot at the 'Alameda del Obispo' research farm in Córdoba, Spain, during January-May, 1988.

The total number of airborne ascospores trapped in the 7 days of plant exposure to the air gave a positive and highly significant correlation ($P < 0.001$) with the mean number of blight lesions (NL), or with the percentage of tissue affected by the disease (PTA), but the simple linear correlation coefficient for number of lesions ($r = 0.857$) was significantly lower ($P < 0.001$) than that given by the percentage of tissue affected ($r = 0.932$).

Occurrence of Ascochyta blight in trap plots

In the 1987–88 experimental period, patches of plants affected by Ascochyta blight were found in the autumn-sown trapplots at the beginning of January and the beginning of March at Córdoba and Cañete de las Torres, respectively. At both sites the disease spread rapidly until most of the plants was affected. No symptoms of blight were found in the trap-plants in Jerez de la Frontera and Carmona.

In the 1988–90 experimental periods, the first blight symptoms were detected at the beginning of January in Córdoba and in the middle of February in Granada. Similar to the 1987–88 period, blight affected all plots by the time of harvest. In the 1990–92 periods, chickpea trap plots were located only in Córdoba. In both periods, the first blight symptoms were observed in February, but subsequent development of the disease was limited. Nevertheless, in 1992 at the end of the growing season in June, blight spread rapidly to all of the trap plot.

Discussion

The present work focused mainly on the rôle of ascospores of *D. rabiei* from infested chickpea debris. Results from 5 years of experiments provided clear evidence that ascospores of this fungus are a major primary inoculum for epidemics of Ascochyta blight in southern Spain. Maximum disease severity in the chickpea trap plants occurred in periods when the numbers of ascospores discharged from the infested debris were highest (Figs. 1, 2). In 1988, maximum disease also coincided with the highest concentration of ascospores in the air (Fig. 3). A significant positive correlation was found with the number of lesions

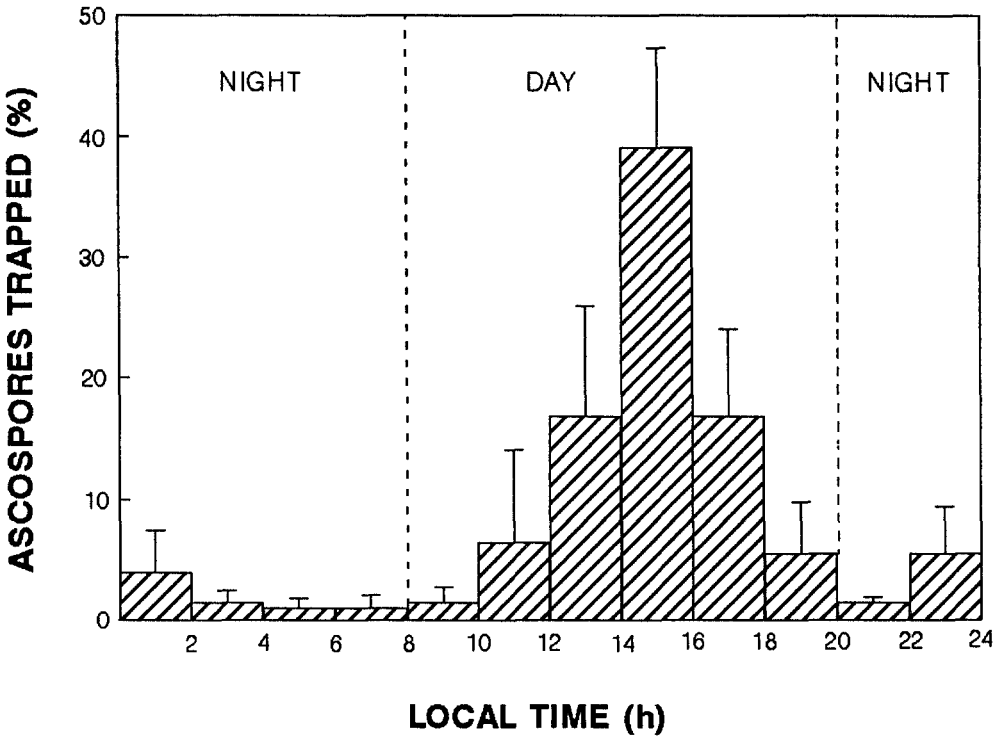

Fig. 4. Mean percentage of airborne ascospores of *Didymella rabiei* trapped at 2 h intervals with a Burkard spore-trap installed near *D. rabiei*-infested chickpea debris in a plot at the 'Alameda del Obispo' research farm in Córdoba, Spain, during January-February, 1988. Vertical bars represent standard error of the mean.

or the percentage of tissue affected in chickpea plants exposed in the field during ascospore release. These data suggest measurements of exposure to airborne ascospores could be useful for assessing the development potential of Ascochyta blight or for designing control strategies, as has been indicated for other diseases [Aylor and Kiyomoto, 1993; McCartney and Lacey, 1990; Rotem, 1988].

Disease severity was closely correlated with the occurrence of rain which is an important environmental factor for pseudothecia maturation and ascospore discharge [Navas-Cortés, 1992], as well as for the infection process [Trapero-Casas and Kaiser, 1992a]. There were four instances during the 5 yr study in which very little disease developed in the absence of rain; these occurred when the pseudothecia of *D. rabiei* contained higher percentages of mature ascospores. Low disease levels could be caused by slight discharges of ascospores brought about through moistening of the pseudothecia by frequent and heavy dew, or night-time or early-morning frost common in these months. However, slight infection occurred in May (Fig.1), when the pseudothecia had discharged all their ascospores. These outbreaks were always associated with heavy rains accompanied by strong winds. In these conditions, the impact of raindrops on the infested debris near the chickpea trap-plants would release the conidia formed in pycnidia which would then be transferred in wind-blown droplets and by splash contamination from the ground to the trap-plants, as suggested by Meredith [1973]. Our results confirm the prime importance of rain in stimulating *D. rabiei* ascospore release since 94% of airborne ascospores were captured during days in which rain was recorded. Moreover in the present work, ascospore discharge depended more on the occurrence of rain than on its amount (Fig. 3; Table 2). Our results support the field observations in Genesee, Idaho, and Pullman, Washington, U.S.A., where airborne ascopores of *D. rabiei* showed close association with rain, and discharge appeared to start very shortly after the initial wetting of infested debris [Kaiser, 1992].

The concentration of airborne *D. rabiei* ascospores shows a well-defined diurnal periodicity. The highest ascospore counts occurred in daylight in the 6 h from 12.00 to 18.00 h with a pronounced peak in the 2 h

Table 1. Simple linear correlation of the number of necrotic lesions (NL) and percentage tissue affected (PTA) on chickpea trap plants exposed weekly to ascospore inoculum of Ascochyta blight and the number of rainy days during the period of January-March over five years[z]

Year	Dependent variable	Correlation	
		r	*P*
1988	NL	0.556	0.076
	PTA	0.621	0.041
1989	NL	0.659	0.002
	PTA	0.641	0.025
1990	NL	0.924	<0.001
	PTA	0.923	<0.001
1991	NL	0.661	0.019
	PTA	0.623	0.030
1992	NL	0.612	0.045
	PTA	0.605	0.048

[z] For each week, NL and PTA were assessed on twelve pots with three plants per pot.

Table 2. Simple and multiple linear correlation of the total number of airborne ascospores of *Didymella rabiei* trapped per day and daily precipitation and mean temperature[y]

Independent variable[z]	Correlation	
	r	*P*
P_1	0.388	0.002
P_2	0.364	0.004
T	0.286	0.027
$P_1 + T$	0.462	<0.001
$P_2 + T$	0.405	0.001

[y] Airborne ascospores were trapped by means of a Burkard spore-trap installed near *D. rabiei*-infested chickpea debris in a plot at the 'Alameda del Obispo' research farm in Córdoba, Spain, during January-February, 1988.
[z] P_1 = daily precipitation (mm); P_2 = occurrence or absence of rain; T = mean daily temperature (°C).

between 14.00 and 16.00 h (Fig. 4). The diurnal periodicity could be due to the combined effect of a number of different environmental factors such as rain, light intensity and wavelength composition, temperature and wind-speed but none of these alone determines its occurrence [Fitt and McCartney, 1986; Hirst, 1953; Meredith, 1973]. The diurnal periodicity of discharge of *D. rabiei* ascospores could be an important factor in the epidemiology of Ascochyta blight since the highest concentrations of airborne ascospores are recorded before the meteorological dew point and in the night hours and early morning when the moist surfaces of the plant foliage and mild temperatures favour infection [Trapero-Casas and Kaiser, 1992a; Zachos *et al.*, 1963].

Ascochyta blight spread extensively in plots located at sites where there was considerable production of airborne ascospores by pseudothecia in nearby infested chickpea debris (Córdoba, Cañete de las Torres, and Granada). The incidence and severity of the disease in the chickpea trap plots closely correlated with the maturity and discharge of *D. rabiei* ascospores from the infested chickpea debris [Navas-Cortés *et al.*, 1990]. However, no disease symptoms were found when the development of *D. rabiei* in the debris was very slight and only small numbers of ascospores were produced (Jerez de la Frontera), or where there was no nearby infested chickpea debris (Carmona).

For all locations and years of this study, the outbreaks of Ascochyta blight in the chickpea trap-plots and in the potted trap-plants in Córdoba (Fig.1) occurred a little earlier than mid March, the usual chickpea sowing period in southern Spain [Trapero-Casas and Jiménez-Díaz, 1986]. Sowing at this time or slightly later is recommended to escape environmental conditions favourable for Ascochyta blight [Saxena and Singh, 1984; Trapero-Casas and Jiménez-Díaz, 1986]. Furthermore, late sowings ensure that the growing crop is not exposed in the period of maximum abundance of airborne ascospores of the pathogen. Nevertheless, in all 5 yr of this study there were episodes of late discharge of ascospores that coincided with the early-growth stages of spring crops. Therefore, airborne ascospores of *D. rabiei* might serve as primary inoculum for an outbreak of Ascochyta blight in spring crops. Early discharge of *D. rabiei* ascospores at the end of winter and beginning of spring is of particular concern for outbreaks of the disease in autumn-winter-sown chickpeas. The favourable meteorological conditions for infection at this time and the long growth season greatly increase the risk of exposure in winter crops to *D. rabiei* ascospores, so that large-scale outbreaks of Ascochyta blight can occur if winter-sown cultivars lack resistance to the disease [Nene and Reddy, 1987; Saxena and Singh, 1984; Trapero-Casas and Jiménez-Díaz, 1986].

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