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Studies on the epidemiology of the tar spot disease complex of maize in Mexico

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During the period 1986–1988 field studies were conducted on the epidemiology of the tar spot disease complex (TDC) of maize (*Zea mays*) caused by *Phyllachora maydis*, *Monographella maydis* and *Coniothyrium phyllachorae*. Under field conditions we found that *P. maydis* symptoms always appeared first, followed by symptoms of either *M. maydis* or *C. phyllachorae*. *M. maydis* causes leaf necrosis and has the most devastating effect. The primary symptoms covered about 12% of the leaf area below the ear leaf, whereas the total necrotic leaf area amounted to 30–60%, here considered as a secondary effect. Maximum TDC severity occurred during the winter season of 1988, which was characterized by a temperature range of 17–22°C, a mean RH > 75%, and > 7 h of leaf wetness per night. The highest numbers of windborne ascospores of *P. maydis* were trapped at an RH > 85% and at temperatures of 17 to 23°C in the winter of 1987 and 1988, although large numbers were also caught at temperatures of > 23°C and RH < 70%. Spore release was strongly influenced by light conditions and followed a similar diurnal curve throughout three seasons, reaching a maximum at 17.00–21.00 hours. The spread of *P. maydis* within the field was very homogeneous. The incubation period of *P. maydis* was 12 to 15 days, and most of the ascospores were released within 3 weeks after formation of the ascostromata. *M. maydis* inoculum in plant debris was reduced by 90% within 3 to 4 months.

INTRODUCTION

The tar spot disease complex (TDC) of maize (*Zea mays*) is caused by *Phyllachora maydis* Maubl., *Monographella maydis* Müller & Samuels, and *Coniothyrium phyllachorae* Maubl. *P. maydis* and *C. phyllachorae* have been known to occur on maize in Mexico since 1904 (Maublanc, 1904), and were originally considered to be pathogen and hyperparasite, respectively. Müller & Samuels (1984) identified and described in Mexico the second pathogen involved in the 'fisheye' symptom as *M. maydis*. Under field conditions, symptoms of *P. maydis* always appeared first. Subsequently, *M. maydis* surrounds the tar spot with a necrotic halo, thus giving rise to the fisheye symptom (Hock *et al.*, 1992). Müller & Samuels (1984) discussed the possible endophytic nature of *M. maydis*. The symptoms of the TDC are tar spots with surrounding necrotic tissue which may eventually lead to entirely necrotic leaves. These typical symptoms have been described or shown previously (Schieber, 1968; Castaño, 1969; Malaguti & Subero, 1972; Liu, 1973; Shurtleff, 1980), which suggests that this disease complex has occurred for at least 20 years in several Latin American countries. The only countries from which reports are lacking are Brazil, Surinam, Paraguay, Argentina and Chile (Hock *et al.*, 1989). All previous studies have attributed leaf necrosis and yield loss to *P. maydis*. Both warm but undefined temperature conditions in Puerto Rico (Liu, 1973) and cool tropical mountainous regions in Venezuela (Malaguti & Subero, 1972) are considered favourable for the development of the disease. We here describe the epidemiology of TDC based on holistic field experiments conducted over a period of 3 years, which involved the study of disease development, ascospore catches and diurnal dispersal of *P. maydis* in relation to weather conditions in the lowland tropics. We also present information about the relationships between the three fungi involved, the TDC incubation period, disease spread,

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Table 1. Class ranges for nine-class standard diagrams for *Phyllachora maydis* and *Monographella maydis*

Class	*P. maydis*[a] (number of lesions)	*M. maydis* (percentage diseased leaf area)
1	1–30	0–1
2	31–60	1–2
3	61–110	2–3
4	111–200	3–4·5
5	201–400	4·5–7
6	401–750	7–11
7	751–1500	11–17
8	1501–2700	17–25
9	2701–4000	25–40

[a] Disease severities for the trial were converted to percentage of diseased leaf area based on measured leaf area. *M. maydis* severity was estimated as a percentage.

survival of inoculum and the possible colateral hosts in Mexico.

MATERIALS AND METHODS

Field experiments

Field experiments were carried out in 1986, 1987 and 1988 at the CIMMYT experimental station near Poza Rica (20° N, altitude 60 m) The climate is characterized by an annual mean temperature of 24°C (1975–1987) with a maximum daily range of 7–14°C, depending on the season. The monthly mean temperature in winter (November to April) ranged from 16 to 23°C, and in summer (June to October) it ranged from 24 to 30°C. Rainfall was in the range 150–250 mm and 800–1000 mm during the winter and summer seasons, respectively. Irrigation was practised at 10-day intervals during the winter; summer crops were rainfed and irrigation was used only for sowing. The relative humidity (RH) during the winter season is normally above 70%, and 10–15 cloudy or foggy days are recorded monthly. The soil at the station is described as a fluvisol. The maize materials used were the open-pollinated CIMMYT Pools 15, 19, 20 and 21, and the French hybrid LGII. Agricultural practices included shredding of maize straw, which was then superficially incorporated into the soil, followed by irrigation. Seeds were placed on top of ridges 15–20 cm high at a spacing of 70 × 25 cm. Weeds and insects were chemically controlled. Nitrogen and P_2O_5 were applied at 100 and 80 kg/ha at sowing and 80–100 kg/ha of ammonium sulphate was applied at the 6- to 8-leaf stage. Crops were sown on 28 November 1985, 2 December 1986 and 30 November 1987.

Weather data

Temperature, RH and leaf wetness duration were recorded hourly in the maize canopy in the centre of the 21 × 22 m experimental plot by means of a thermohygrograph combined with a leaf wetness recorder (Lufft, Stuttgart, Germany) in 1986. Leaf wetness was always measured with the Lufft equipment at a height of 1 m. Temperature and RH were recorded at a height of 1·5 m. In 1987 and 1988, measurement of temperature and RH was continued by recording data with a Datapod Digital Recorder (model DP 220 mm). The data were subsequently downloaded to a PC and transferred to a mainframe computer for processing. Daily data for sunshine, precipitation and wind speed were supplied by the station's meteorological service.

Disease progress

The holistic field experiments (Kranz & Rotem, 1988) were conducted during the winter seasons of 1986, 1987 and 1988, with sowing in late November/early December. Seeds of the resistant and susceptible fractions of Pool 15 were sown in the winter of 1986, but in 1987 and 1988 only the susceptible fraction was sown. In the plot of 21 × 22 m, 40 plants were tagged in a grid of dimensions 2·6 × 3·0 m. Plant growth

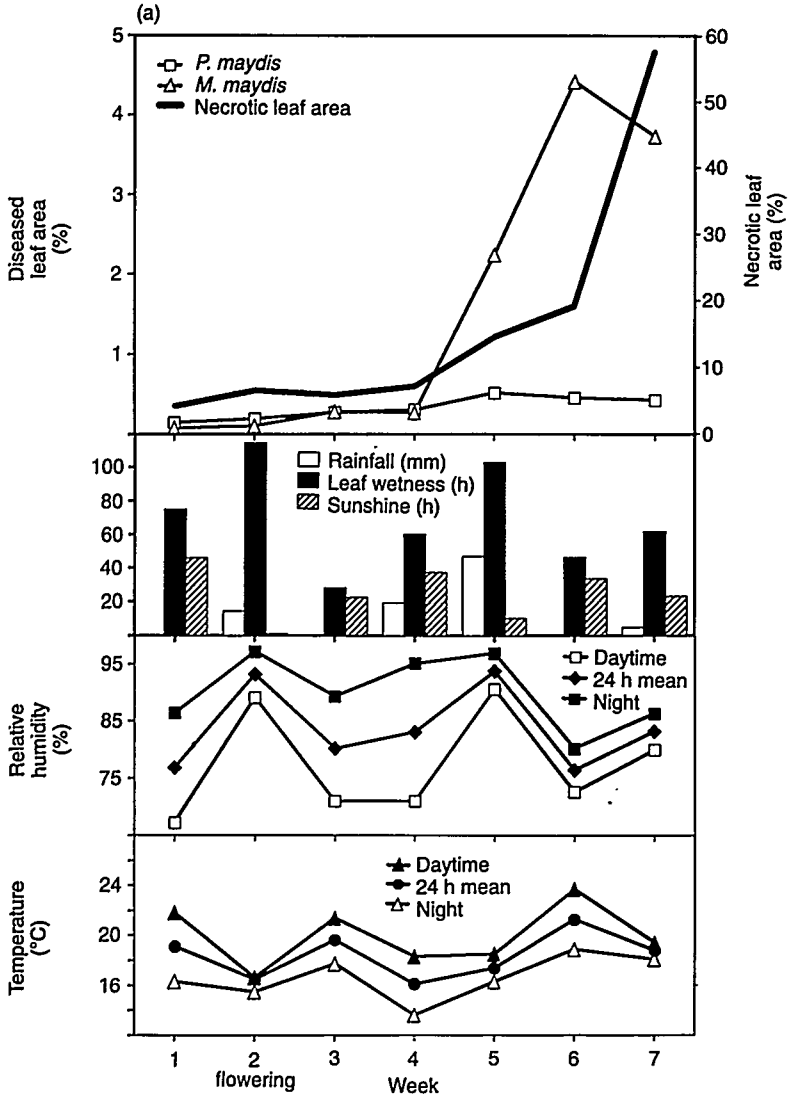

Fig. 1. (a) Disease progress curves for *Phyllachora maydis*, *Monographella maydis* and the total necrotic leaf area with pertinent weather variables, recorded weekly during winter 1987, starting on 17 February 1987. The crop was sown on 2 December 1986.

and disease intensity were recorded weekly, and disease was assessed on all leaves of the tagged plants. Disease recording started with the first appearance of symptoms of *P. maydis*, and severity was assessed by means of standard diagrams (Kranz, 1970; Hau *et al.*, 1989; Table 1). For assessment, a distinction was made between the leaf area covered by the true symptoms and the total necrotic leaf area, which was regarded as a secondary effect due to premature senescence and extensive leaf necrosis.

Spore catches

Spores were trapped in two ways. First, in each of the four corners of the plot, iron bars 2 cm in diameter were installed and petroleum-jelly-coated slides were fixed with clips in a horizontal position at 0·5 m and 1·5 m above the ground.

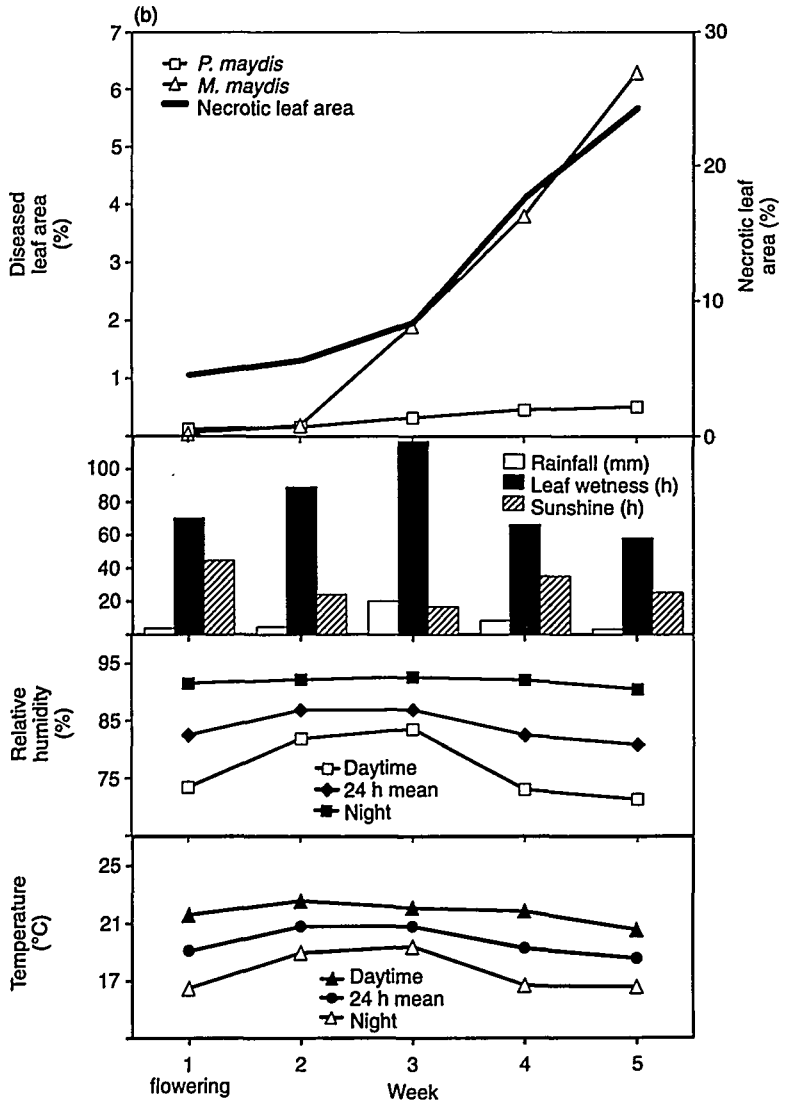

Fig 1. (b) Disease progress curves for *Phyllachora maydis*, *Monographella maydis* and the total necrotic leaf area with pertinent weather variables, recorded weekly during winter 1988, starting on 24 February 1988. The crop was sown on 30 November 1987. Although the last data point was not taken due to rapid drying of plants, disease expression was even more severe than in 1987.

Each installation was protected by a rain shelter consisting of four wooden legs, 2 m high, with a 1·2 × 1·2 m transparent plastic roof. Slides were recovered at 7-day intervals for spore counts. Secondly, a volumetric Burkard spore trap was placed about 3 m away from the weather recording devices, 1·5 m above the ground, and set to record spore catches at hourly intervals.

Spatial spread

To study the distance of spore flight, plots of dimensions 1·5 × 1·5 m containing six plants of Pool 15 (susceptible) were sown in a lawn that had been free from any crop for 10 years. These were sown on 15 December 1987 at 10, 20, 30 and 40 m downwind of infected maize fields, and on 30 November 1988 at 15, 30, 45, 60 and 75 m.

From the appearance of the first symptoms of *P. maydis* the disease severity was assessed weekly on the flag leaf and the second leaf beneath this.

Incubation period

The incubation period for *P. maydis* was recorded on plants of the susceptible hybrid LG II. Single plants were grown in pots under disease-free conditions at El Batan until flowering, and were then transported to Poza Rica for infection and incubation. The plants were exposed in a plot of infected plants and monitored daily for 15 days. The experiment was repeated eight times at 3- to 4-day intervals, exposing plants on 16 March, 20 March, 23 March, 26 March, 29 March, 1 April, 4 April and 7 April 1988.

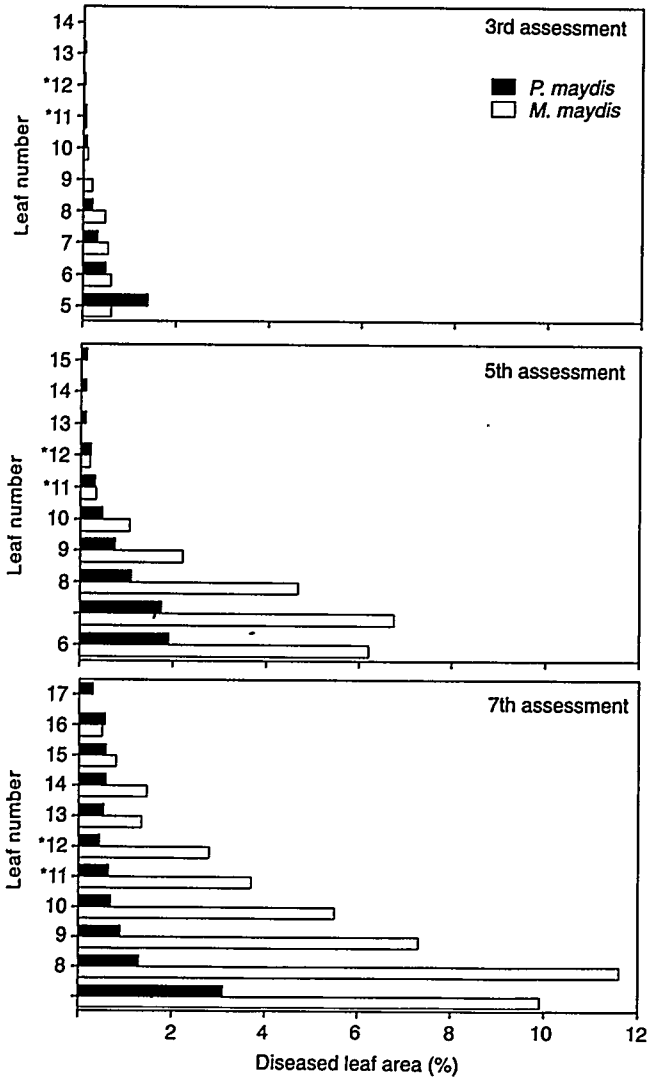

Fig. 2. Mean disease severity of *Phyllachora maydis* and *Monographella maydis* recorded in winter 1987 on different leaf insertions of tagged plants in the field. * Leaf insertion at which the ear was formed. The results for winter 1988 show a very similar distribution.

Survival of inoculum

Diseased leaf material was collected in October 1986, then dried and stored in metal containers at 35–55% RH and 19–23°C for about 100 days. A total of 200 *P. maydis* and *M. maydis* lesions were examined for spore viability. For the test of field survival of *M. maydis*, leaves with fisheye symptoms were placed in bags of plastic mesh on the lawn of the CIMMYT's Poza Rica station without protection from the environment from 23 August 1987 to 26 December 1987. Leaves in the same number of bags were stored under ambient laboratory conditions out of direct sunlight. All data were entered on field record forms and analysed using SAS Version 5.

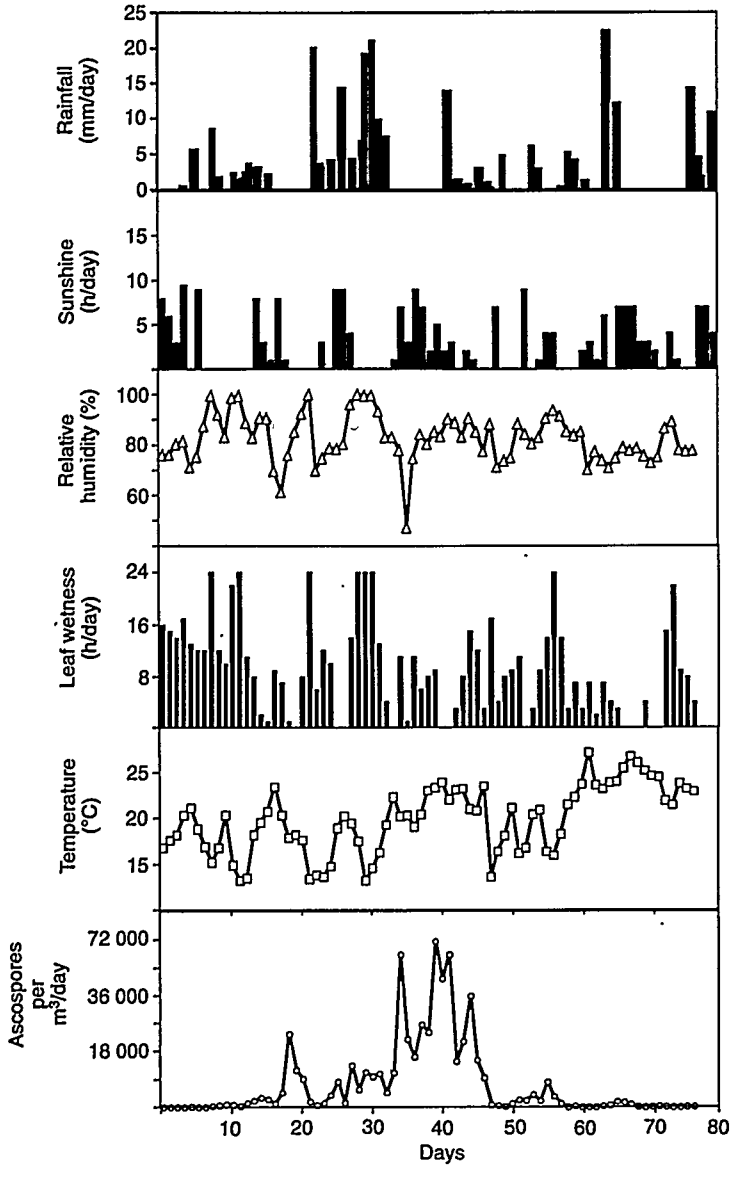

Fig. 3. Catches of ascospores of *Phyllachora maydis* during winter 1987 in relation to precipitation, sunshine, mean daily RH, mean daily temperature and leaf wetness duration.

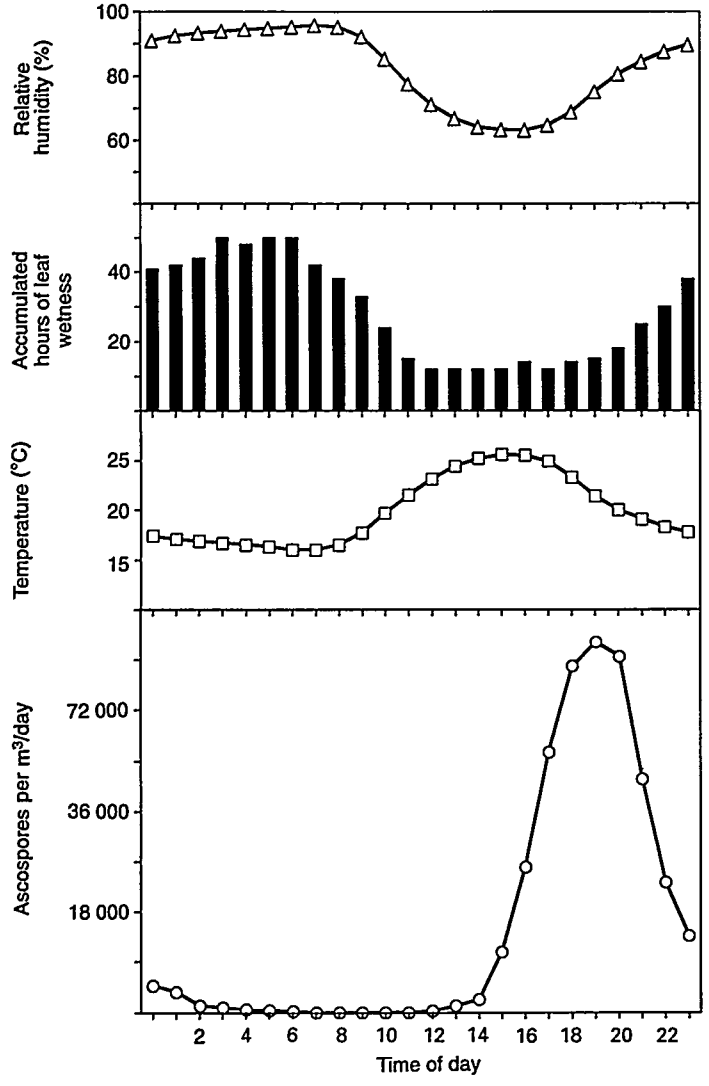

Fig. 4. Mean catches of ascospores of *Phyllachora maydis* per hour in relation to mean hourly temperature, RH and leaf wetness duration over 80 days during winter 1987.

RESULTS

Disease progress

Disease severity was highest during the winter seasons as measured in three staggered planting trials (data not shown), and reached a maximum in the winter of 1988. In the summer trials of 1986, 1987 and 1988, the disease severity of *P. maydis* and *M. maydis* always remained low. Thus only data for the winter seasons of 1987 and 1988 are included in which TCD progress was recorded in relation to host development influenced by weather conditions (Fig. 1).

The epidemics caused by the two main pathogens started 2–3 weeks before flowering each year, and maximum disease severity occurred about 4 weeks after flowering. *P. maydis* always appeared first, with little effect on the host. *M. maydis* followed and had colonized 52% and 85% of the tar spots by 8 days and 21 days, respectively, after their appearance in 1987. The mean size of necrotic fisheye lesions of *M. maydis* was 10 to 20 times

Table 2. Percentage of *Phyllachora maydis* ascospore catches classified in five temperature ranges and three relative humidity ranges; the χ^2 tests refer to a test of the number of observations against the proportion of time spent in temperature ranges

Temperature range (°C)	Percentage of spore catches at specific RH			Number of observations	χ^2/*P*-test
	<70%	70–85%	>85%		
1987[a]					
10·0–14·5	0·7	7·2	92·1	290	0·2 NS
14·6–16·5	4·5	8·3	87·2	202	0·8 NS
16·6–21·5	9·1	15·2	75·7	680	23·9**
21·6–23·5	22·8	27·6	49·6	210	9·8**
>23·6	70·8	24·2	5·0	434	5·8*
1988[b]					
10·0–16·0	0·0	12·4	87·6	113	NS
16·1–18·0	6·1	8·7	85·6	11	8·2**
18·1–23·0	5·3	7·5	87·1	583	64·3**
23·1–25·0	14·4	39·4	46·2	132	8·6**
>25·1	155·8	42·2	2·0	301	17·1**

* Significant at probability level of 0·05; ** significant at probability level of 0·01; NS, not significant.
[a] Catches started on 11 February 1987, lasting 80 days.
[b] Catches started on 17 February 1988, lasting 55 days.

larger than that of *P. maydis*. Microscopic examination showed that *C. phyllachorae* formed pycnidia inside the ascostromata of *P. maydis*. Two weeks before harvesting in both seasons almost 50% of the ascostromata were hyperparasitized, which often resulted in a smaller necrotic lesion of *M. maydis*. The respective disease severities in 1987 and 1988 were 4·4% and 6·5% for *M. maydis* at 4 weeks after flowering, whereas the disease severity for *P. maydis* was about 0·5% and represented only as much as 11% and 8%, respectively, of the leaf area diseased by *M. maydis*. In the unusually hot winter of 1986 (mean temperature 21·7°C), the respective disease severities of *P. maydis* and *M. maydis* were very low, at 0·1 and 0·2%, and were not considered to be representative. The correlation coefficients for disease severity between *P. maydis* and *M. maydis* in 1987 and 1988 were $r^2 = 0{\cdot}62$ and 0·55 ($P = 0{\cdot}01$) (Fig. 2), respectively.

Temperatures in winter 1988 ranged from 17 to 22°C, and RH exceeded 75% during more hours than in 1986 or 1987. Hence, leaf wetness duration was longer and more consistent than in those seasons. Apparently this had a greater effect on disease progress and final disease severity (Fig. 1) than rainfall, which was sporadic and only about 20 mm/week each year. The weather conditions that favour severe disease can be summarized as a temperature in the range 17–22°C, a minimum of 7 h/night of leaf wetness, and a RH > 75%.

Spore catches

During the epidemics, ascospores of *P. maydis* were generally found to be aggregated on the sticky tape of the Burkard trap, with 40% as 4-spore clusers, 27% with 3 spores, 3% as a single spore, 6% as complete asci with 8 spores and 24% with an indistinct number of spores. The number of ascospores caught with the slide traps represented 5–10% of the amount of spores sucked in by the Burkard spore trap. Of the total amount of ascospores, 55–70% were found on the slide trap at a height of 0·5 m, and the remainder at 1·5 m. There was a high correlation in capture rates between the four slide traps ($r^2 > 0{\cdot}9$, $P = 0{\cdot}01$) and between the slides and the Burkard trap ($r^2 > 0{\cdot}8$, $P = 0{\cdot}01$). Therefore the results are based on the more precise hourly catches of the Burkard spore trap. However, the slide traps represent an effective, low-cost method for monitoring ascospore dispersal.

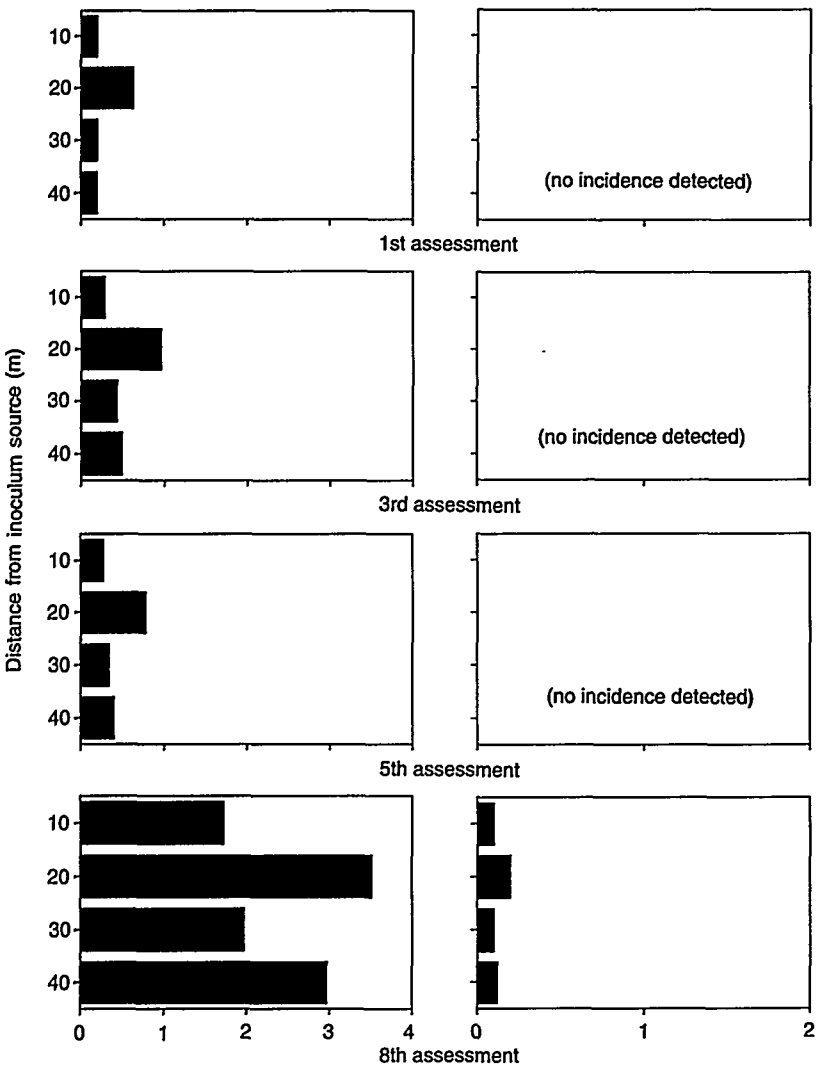

Fig. 5. Spread of *Phyllachora maydis* (left) and *Monographella maydis* (right) from the nearest known source of inoculum over time into small plots of susceptible Pool 15 at various distances. *P. maydis* was assessed on a scale of 1–9, and *M. maydis* was estimated as a percentage of diseased leaf area (see Table 1).

The curve for spore catches in 1986 is omitted because of the very low disease severity during that year. *C. phyllachorae* spore catches were not systematically counted. However, spores were observed regularly and reached up to 40% of the *P. maydis* catches in 1987 and 1988. A great number of spores was caught in 1988, almost twice as many as in 1987, but the conditions of spore release in both years were very similar (Fig. 3).

The maximum catches occurred about 40 days after the first catches, but smaller peaks were also recorded between 10 and 20 days. Temperatures between 18 and 25°C with 6 to 12 h/day of leaf wetness were associated with these peaks. The effects of rain and sunshine are less clear. The quantity of *P. maydis* ascospores caught was not strongly correlated with weather conditions, but there was a close relationship between the quantity of spores trapped and the subsequent maximum disease severity during each season.

Table 3. Mean time between exposure of maize seedlings and the appearance of symptoms of *Phyllachora maydis*, with pertinent weather factors in winter 1988

Exposure date	Incubation period[a] (days)	Temperature[b] (°C)	Leaf wetness (h/day)	Rainfall (mm/day)	Sunshine (h/day)
16 March	13	21·5	6·8	0·3	4·9
20 March	12	22·8	6·6	1·8	6·3
23 March	13	24·9	5·8	1·7	5·7
26 March	13	24·4	6·5	2·4	4·8
29 March	12	24·0	6·5	3·1	4·1
01 April	15	23·2	6·3	3·2	5·0
04 April	14	23·0	6·2	3·4	5·5
07 April	15	23·6	5·1	2·6	6·8

[a] Number of days to appearance of first symptoms.
[b] The weather variables are calculated as daily means for each exposure date according to the incubation period.

Diurnal spore dispersal

The diurnal spore catches of *C. phyllachorae* were rather irregular, but often occurred between 02.00 and 09.00 hours. In contrast, the mean hourly spore catches of *P. maydis* during the epidemics (Fig. 4) began at about noon and reached a maximum between 17.00 and 21.00 hours. These times of maximum spores catches coincided with a decrease in temperature and a rise in RH. Parbery (1963) observed that spore release from ascostroma occurred after 1 h of leaf wetness. However, continuous leaf wetness for 24 or even 72 h resulted in no significant increase in the number of spores released. Since the maximum wind speed of 2–3 m/s occurred at 15.00–18.00 hours, we assumed that wind plays a minor role in the detachment of the spores from the leaf surface, serving mainly to increase spore propagation.

The effect of weather on *P. maydis* dispersal

Multiple correlations between weather variables and the number of spores were highest for temperature and RH. Hence, for the subsequent frequency analyses, temperature and RH ranges were defined so as to describe the frequency with which ascospores were caught by the Burkard trap in 1987 and 1988. The largest number of

Table 4. Time-course of survival and germination of the *Monographella maydis* anamorph on maize leaves placed outdoors on a lawn or in the laboratory

Days of exposure (1987)	Lawn			Laboratory		
	Number of conidia[a]	Percentage germination		Number of conidia	Percentage germination	
		PDA	MBA[b]		PDA	MBA
28[c]	+++	91	92	+++	93	90
58	++	72	67	+++	22	26
93	+	23	25	+++	3	1
126	+	1	5	++	0	0

[a] +, few; ++, some; +++, many.
[b] PDA, potato-dextrose-agar; MBA, mungbean agar.
[c] First sampling data after 28 days of exposure with subsequent incubation on PDA and MBA.

leaves were found to be infected, and there was no evidence of deeper penetration. Whether *M. maydis* is endophytic still has to be studied.

Collateral hosts

In surveys to investigate possible collateral hosts of the two pathogens at 20 sites (Hock *et al.*, 1989) *Phyllachora* spp. were found to be common on various grass species in Mexico. The symptoms expressed on *Paspalum virgatum* were similar to those of TCD on maize (Fig. 6), but the causal organism was identified as either *P. urvillana* or *P. minutissima*, as described by Parbery (1967, 1978).

The necrotic halos contained a few conidia, and they were very similar in morphology to *Microdochium*, the anamorph of *M. maydis*. However, *P. virgatum* grows in swampy environments (Häfliger & Scholz, 1980) and is not common in areas where TDC of maize occurs. In the state of Michoacan, south-west Mexico, a *Phyllachora* sp. was found on teosinte, but it was not *P. maydis*.

DISCUSSION

A survey in Mexico revealed that the TDC can cause an estimated yield loss of up to 30% in maize, with an average loss of 8% in farmers' fields (Hock *et al.*, 1989). Grain yield loss in our trials at the Poza Rica was 11% in 1987 and 25% in 1988. Severe disease development was related to a monthly mean temperature of 17–22°C and 7 h/night of leaf wetness, 10 to 20 foggy days/month or a minimum monthly rainfall of 150 mm, and sunlight hours within the range 1800–1900 h/year. These findings are in agreement with the results of a survey in which TDC disease severity was related to weather data (Hock *et al.*, 1989). These conditions prevailed at Poza Rica station during winter 1988, when the disease was most severe. Disease assessment ceased about 10 days earlier in 1988 than in 1987. The canopy dried faster in 1988, and this was associated with a greater total necrotic leaf area.

In vitro, *P. maydis* ascospores show optimum germination at temperatures between 10 and 20°C, but outside this range germination declines sharply (Dittrich *et al.*, 1991). On the other hand, conidia of *M. maydis*, the most destructive pathogen and the next to cause symptoms in the complex, germinate optimally at 24–27°C. Favourable temperatures for *P. maydis* spore germination and disease development occur during the cooler months of December to February, whereas optimum temperatures for *M. maydis* occur in March and April. The peak of ascospore dispersal for *P. maydis* occurs between 17.00 and 21.00 hours, when RH increases to >85% and temperature decreases to 16·6–23°C, following a typical diurnal rhythm. Given that temperature and RH conditions between 17.00 and 21.00 hours are similar to those between 07.00 and 10.00 hours, it appears that the change in hours of light and darkness is also likely to play a role in spore release. In the field we always observed the lesions with ascostromata of *P. maydis* on maize leaves before *M. maydis* gave rise to the fisheye symptoms. In contrast, maize plants artificially inoculated with a conidial suspension of *M. maydis* showed typical necrotic symptoms without previous development of *P. maydis* lesions. It is not known how *P. maydis* survives in the absence of maize. Ascospores can survive in host debris for 3 months or longer, which would probably be enough to ensure a supply of primary inoculum.

Only four of 36 maize cultivars from diverse genetic backgrounds were found to have the ascostromata of *P. maydis* alone. The other 32 cultivars had both ascostromata and the typical fisheye symptoms of TDC (Hock *et al.*, 1992). Under favourable disease conditions, the leaves turned pale green in less than 5 days and dried up, which suggested the presence of a toxin. The ascostromata of *P. maydis* were frequently hyperparasitized by *C. phyllachorae*, a phenomenon that has previously been observed with other *Phyllachora* spp. (Parbery, 1978). Thus hyperparasitization at an early stage of infection restricted the lesion size of *M. maydis* and indicated the potential for biological control (Trutmann & Keane, 1982). Extensive leaf necrosis is caused by *M. maydis*, and a large number of conidia are found in the lesions. Conversely, only a small number of fusarium-like conidia of *Microdochium* were caught by either the Burkard or the slide traps. The way in which conidia disperse remains unclear, even though it was shown that the disease can spread as far as 75 m downwind. The progress of TDC on maize varies with weather conditions, but under favourable temperatures it increases with humidity and rises sharply at or shortly after flowering.

The disease severity of *P. maydis* never reached economically damaging levels in our trials but, when accompanied by infection with *M. maydis*,

extensive leaf damage and economic loss resulted. Fungicide trials at CIMMYT have shown that Corbel and Tilt are effective in controlling TDC (Renfro, 1987, personal communication).

Since infection by *P. maydis* is required for the development of TDC, tar spot severity can be used as a selection criterion in breeding for host plant resistance. Half-sib recurrent selection or a backcrossing programme are thus viable strategies for incorporating disease resistance in germplasm (Ceballos & Deutsch, 1992). As the temperature range of 17–22°C and a mean RH of >75% are most conducive to TDC development, disease-resistant germplasm should be primarily adapted to the mid-altitude zone (altitude 1300–2300 m), where these typical weather conditions are frequently found, and secondly to the tropical lowlands, which are considered to be less favourable for TDC development.

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