Northern Leaf Blight of Maize in New Zealand: Release and Dispersal of Conidia of Drechslera turcica

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ABSTRACT

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To determine the relations of spore release to changes in meteorological conditions, the incidence of conidia of the fungus *Drechslera turcica* was monitored continuously for 6.5 mo over a diseased maize crop at Pukekohe, New Zealand. Continuous measurements of wind, rain, relative humidity, duration of leaf wetness, and air temperature were made during the same period. Three types of spore release were discerned: (i) forcible discharge of conidia induced by rapidly falling relative humidity and exposure to solar radiation (diurnal discharge); (ii) wind release which occurred when wind velocities were greater than about 3 m/sec; and (iii) rain release. On many days, all three forms of release occurred and overlapped. Conidiophores also were trapped, particularly on dry, windy days not favorable for conidium development. The possibility that airborne conidiophores of *D. turcica* may act as infective propagules is discussed. Immature conidia (three or fewer septa) often were trapped and were capable of germination even when aseptate. Conidia containing chlamydospores were trapped during the late part of the growing season following periods of low night temperatures (10 C). Most airborne conidia were trapped during the day; few were trapped at night. Highest incidence of spores occurred during February-April (1974).

Additional key words: *Helminthosporium, Zea mays.*

Northern leaf blight of maize (*Zea mays* L.) caused by the fungus *Drechslera turcica* (Pass.) Subram. & Jain (perfect stage *Trichometasphaeria turcica* Luttrell), occurs in many of the maize-growing regions of the world (5) including New Zealand (6). The fungus may overwinter in the soil as chlamydospores (4, 7) or within infected leaves and husks (15). Under favorable weather conditions, conidia are produced on leaf lesions from whence they become airborne and are dispersed (14).

The precise quantitative measurement of airborne spores of a specific pathogen above a diseased crop, coupled with good meteorological records, can provide clues on the relationship of environmental factors to sporulation, spore release, and dispersal, all of which are important components in the epidemiology of the disease. Even though certain aspects of the epidemiology of northern leaf blight have been investiaged extensively in North America (3, 4, 14, 18), the relationships of environmental factors to the development of a disease epidemic still are not well understood.

In a study of airborne spores of *D. turcica* over a maize crop in Nebraska, Meredith (14) observed a regular diurnal periodicity in spore release trapped at night and a maximum at noon. He postulated that forcible discharge of conidia occurred as water vapor pressure decreased (13). Subsequently, Leach (11) has shown that forcible discharge of conidia is induced both by decreasing relative humidity (RH) and also by increasing RH and exposure to infrared radiation. Spore discharge due to these factors has been termed "diurnal release". Meredith (14) also suggested that under certain conditions wind and rain may be involved in spore release. Before considering mechanisms of spore release, it must be emphasized that spore release cannot be divorced from the preceding meteorological and conditions that favor or limit sporulation. Other studies (C. M. Leach, *unpublished*) have shown that sporulation only occurs after fairly long (approximately 8 hr), continuous nocturnal periods with RH above 90%.

MATERIALS AND METHODS

Spore trapping.—A 24-hr Hirst spore trap (9) was placed within a 35- × 48-m block of maize, cultivar XL45, located on the D.S.I.R. vegetable research station near

Pukekohe (37° 12′S, 174° 52′E), New Zealand. The maize, planted on 17 October 1973, began tasseling on 15 January 1974. To ensure uniform infection, all plants were inoculated on three occasions (16, 21, and 28 November 1973) using spore suspensions obtained from heavily sporulating agar cultures. Colonies from five different isolates were comminuted together and applied to plants with a knapsack sprayer. When the spore trap was placed in the maize block on 30 November, well-formed lesions were evident, but sporulation had not begun as evidenced by microscopic examination of lesions. Twenty lesions were examined microscopically twice weekly to detect the first occurrence of sporulation. At the end of spore trapping, 6.5 mo later, the maize plants were severely and uniformly blighted and leaves without large lesions were a rarity. The research area was approximately 90 km from the major maize-growing region and there were no commercial plants within 5 km of the experimental plot. Because of this isolation, and because the incidence of northern leaf blight was extremely low in North Island maize (a very dry summer), we have assumed that all trapped spores of *D. turcica* were from the artificially inoculated experimental planting.

The flow rate of the Hirst spore trap was adjusted to 11 liters/min through a 2-mm × 14-mm orifice located 0.5 m above ground. Spores were trapped on greased slides moving past the orifice at 2 mm/hr. The slides were changed daily between 0630 and 0830 hr. Each slide (25 × 75 mm) was examined microscopically in a systematic manner and the total number of conidia deposited in successive 1.2 mm bands across the slide were recorded. The widths of these bands equalled the diameter of the microscope field and also equalled approximately 30 min of slide movement past the orifice.

Meteorological measurements.—A sheltered hygrothermograph (Model 3A, Ota Keiki Seisakusho Co., Tokyo) and an anemometer (Woelfle-type

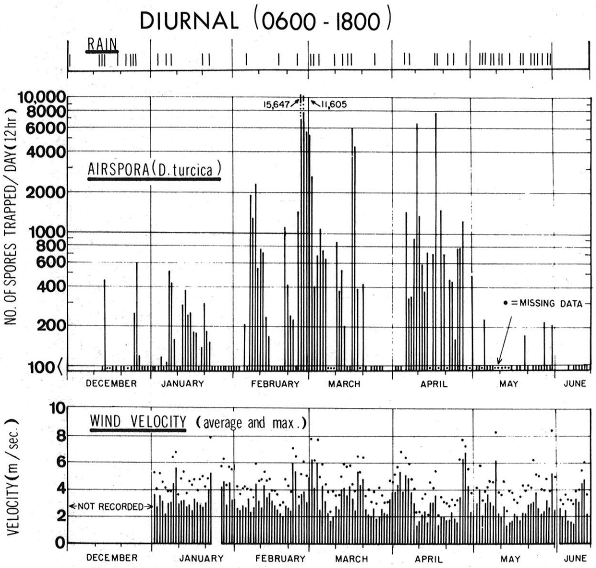


Fig. 1. Daily incidence (log scale) of airborne conidia of *Drechslera turcica* within a severely diseased maize planting located near Pukekohe, New Zealand, and summarized records of wind and rain for the same period.

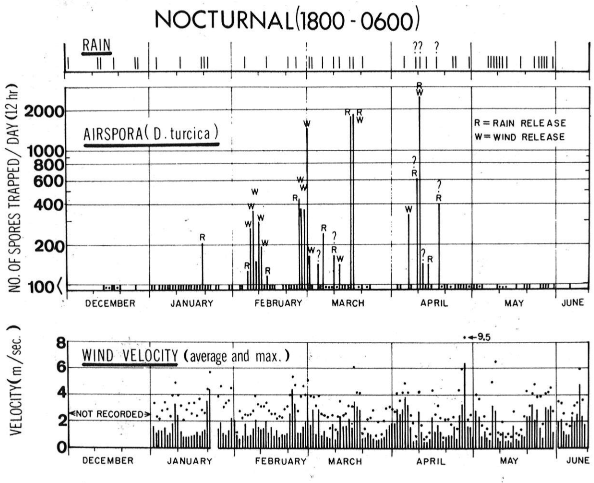


Fig. 2. Nocturnal incidence (log scale) of airborne conidia of *Drechslera turcica* within a severely diseased maize planting located near Pukekohe, New Zealand, with summarized records of wind and rain for the same period.

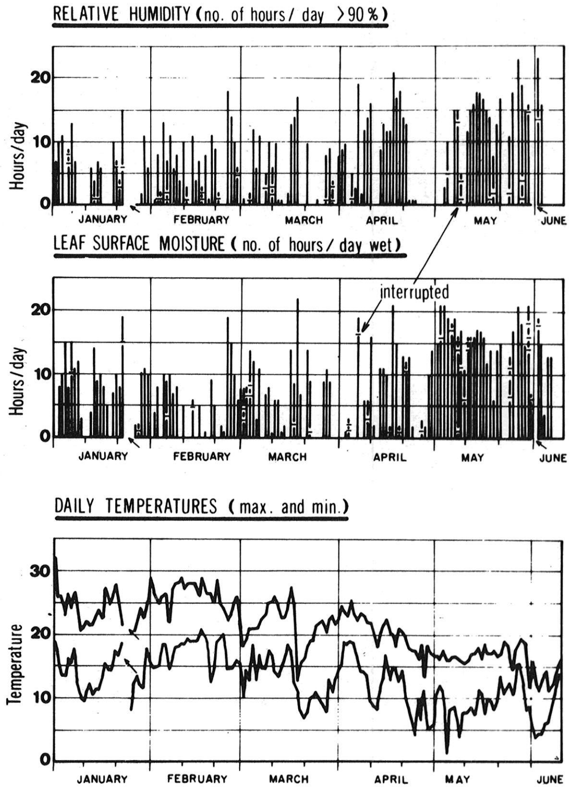


Fig. 3. Summarized daily records of air temperature (shade), leaf wetness, and relative humidity for a *Drechslera turcica*-infected maize planting located near Pukekohe, New Zealand (small arrows along absissa indicate missing records).

Mechanical Wind Recorder, W. Lambrecht KG, Göttingen, Germany) were placed within 10 m of the spore trap. Precise and continuous measurements also were made at an automatic meteorological station located 150 m from the maize. Recorded at this station were: wind direction and velocity at 2 m height, relative humidity (thermocouple-psychrometer), duration of leaf wetness (double resistance coil), time and amount of rain (photocell drop counter), and temperature at 1.4 m (normal screen height). Details of these instruments can be obtained by direct correspondence with K. Young.

RESULTS

Seasonal incidence of airborne conidia of Drechslera turcica.—A summary of continuous spore trapping for 6.5 mo are shown in Fig. 1 and 2. The diurnal incidence (0600-1800 hours) of airborne condida is summarized in Fig. 1 and the nocturnal incidence (1800-0600 hours) in Fig. 2. Records of wind and rain also are included in Fig. 1 and 2. Leaf wetness, RH, and air temperature for the same period are summarized in Fig. 3. Relative humidity is plotted as the number of hours above 90%, because little sporulation occurs when RH is below 90% (C. M. Leach, *unpublished*).

First visual observation of sporulation on leaf lesions occurred on 14 December, which also coincided with the first trapping of conidia in the spore trap. Incidence of airborne spores of *D. turcica* was low during December and January, increased to a maximum during late February, and continued at a high level through mid-April. The highest daytime (12-hr) total counts occurred during late February (Fig. 1). On 2 days, totals of 15,647 and 11,605 conidia were trapped. At the time of highest spore counts (26 February), kernels were filled and the plants were beginning to mature and die.

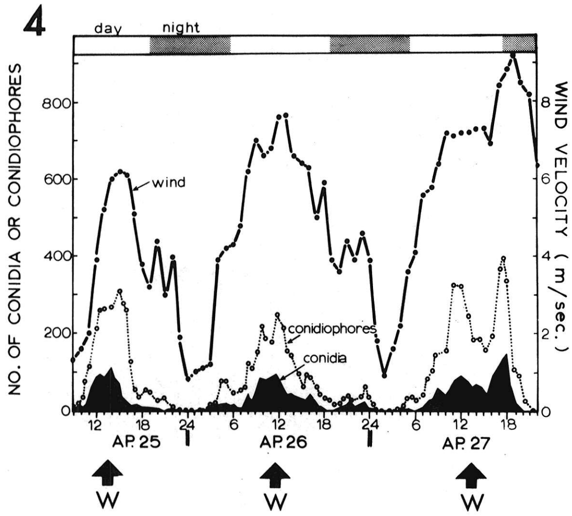
Daily incidence of spores.—A comparison of Fig. 1 and 2 shows that the incidence of airborne conidia differed markedly between day and night; relatively few spores were trapped at night.

When daily incidences of spores were plotted (0.5-hourly slide counts) and related to variations of wind, rain, and RH, three patterns of spore release were evident: those caused by wind, rain, and diurnal release. Although there were clear relationships between these environmental factors and spore release on numerous occasions, only a few examples are presented in the results (Fig. 4-9).

Wind release of conidia and conidiophores.—Representative patterns of spore release due to wind are presented in Fig. 4 and 5. During and preceding the 3-day periods shown, nocturnal RH was low and not conducive to sporulation. All trapped conidia were "old conidia"; i. e., the products of earlier sporulation. During the periods 25-27 April (Fig. 4) and 1-3 March (Fig. 5), wind was the principal cause of spore release. Certain subsidiary peaks evident on 1-2 March (0400-0600 hours) are attributable to rain. Other examples of wind release are shown in Fig. 6 (26 February, 0800-1800 hours) and Fig. 7 (28 February, 0800-0200 hours).

Conidiophores often were observed on trap slides, usually mixed with many conidia. On occasions, conidia were few when conidiophores were numerous. For example on 1 March at 1300 hours (Fig. 5), nearly 600 conidiophores were trapped in a 30-min period. Incidence of both spores and conidiophores were closely correlated with wind velocity; even relatively small changes in wind were reflected as changes in spore and conidiophore catches. The presence of conidiophores always was associated with relatively strong wind. Whenever average wind exceeded about 3 m/sec, conidiophores were trapped.

Many of the trapped conidiophores were thick-walled and contained one or two cells. When several spore trap



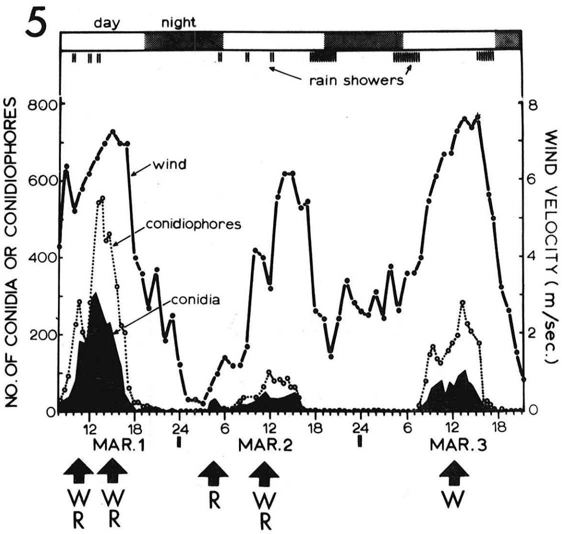


Fig. 4-5. Influence of wind, and to a lesser degree rain, on the incidence of airborne conidia and conidiophores within a maize planting infected with *Drechslera turcica* (W = wind release; R = rain release; relative humidity was unfavorable for sporulation the nights of **4**) 24-27 April and the nights of **5**) 28 February - 3 March; conidia and conidiophore counts are not cumulative).

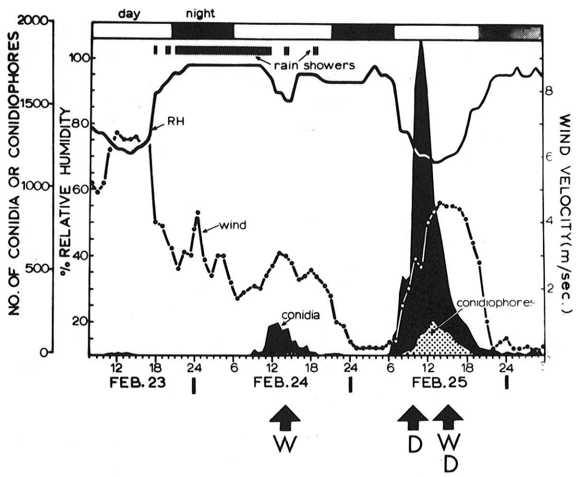
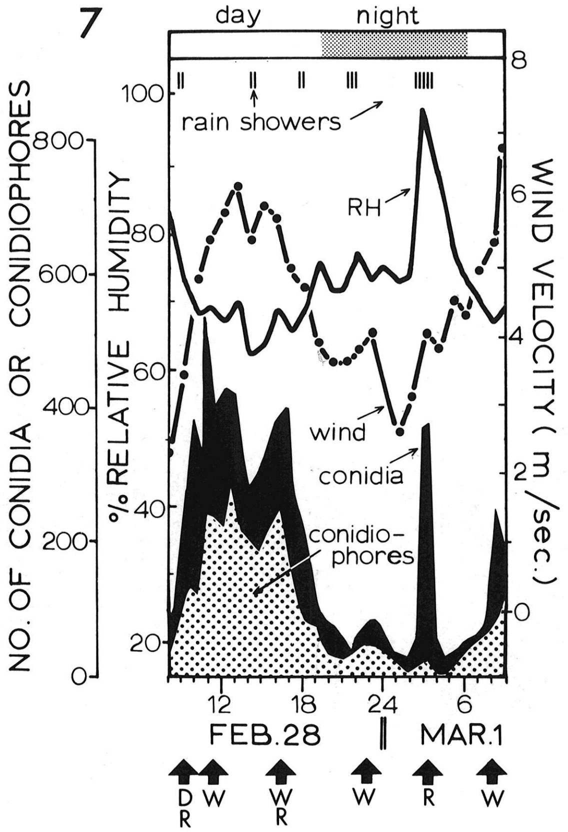


Fig. 6. The influence of wind and diurnal release on the incidence of airborne conidia and conidiophores of *Drechslera turcica* within a maize planting (W = wind release, D = "diurnal" or violent release; relative humidity was unfavorable for sporulation on the night of 22-23 February but was ideally suited on the nights of 23-24 February and 24-25 February; conidia and conidiophore counts are not cumulative).

slides with high counts of conidiophores were placed in a moist chamber, their surfaces moistened with distilled water and incubated at 22 C for 3 days, 23% of conidiophores (300 counted) and 42% of conidia (300 counted) germinated.

Rain release of conidia.—There were numerous days and a few nights when rain caused release of conidia (Fig. 2, 7, 8, 9). Rain often was accompanied by high winds and it was not always possible to distinguish between the two types of release. At times that rain fell when the wind speed was very low, the rain unquestionably caused spore release. An example of rain release is shown in Fig. 7. During the preceding night (27-28 February) conditions favored sporulation (8 hr of RH > 90%). On 28 February, and the next day, 1 March, there were five separate rain showers and also periods of strong wind. Superimposed on the wind release (0800-1800 hours) are definite subsidiary peaks caused by the rain. The most distinct release of conidia by rain occurred the next night (1 March) between 0200 and 0400 hours. Another example of rain release is shown in Fig. 9 (9-11 April). Though the night of 8-9 April was unfavorable for sporulation (only 2 hr with RH > 90%), a heavy rain beginning 1400 hours on 9 April, caused a small release of conidia. The next night (9-10 April) was ideal for sporulation (approximately 16



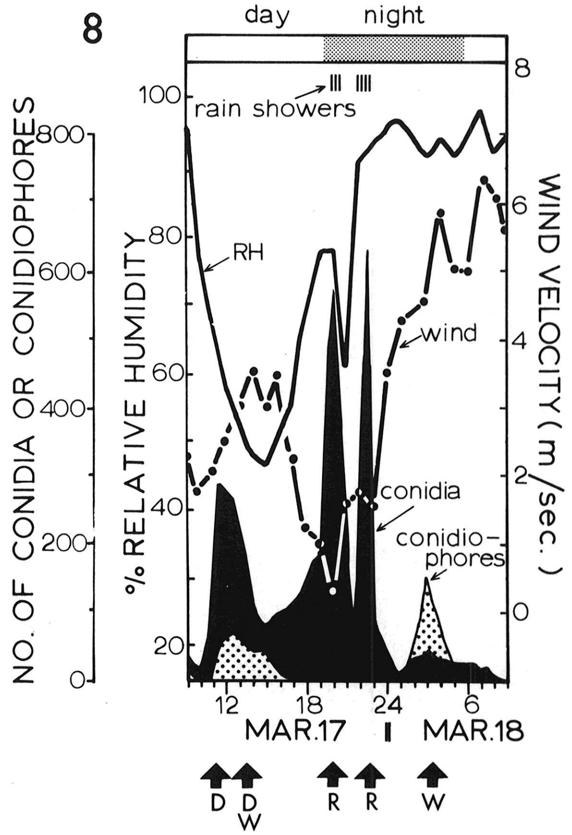


Fig. 7-8. The influence of a complex of factors (wind, rain, and diurnal release) on the incidence of airborne conidia and conidiophores of *Drechslera turcica* within a maize planting. (R = rain release, W = wind release, and D = "diurnal" or violent release; relative humidity during the night of **7**) 27-28 February was moderately favorable to sporulation, and ideal for sporulation the night of **8**) 16-17 March; conidia and conidiophore counts are not cumulative).

hr with RH > 90%) and rain at approximately 1600 hours (10 April), caused extensive release of spores. In this example, rain release is quite distinct from release due to other meteorological factors. Wind velocity at the time of the rain was less than 2 m/sec.

Under conditions that favored sporulation, even a slight shower sometimes caused massive spore release. At other times, however, rain did not cause spore release even though there was an abundance of conidia on lesions. For example, conditions on the night of 23-24 February (Fig. 6) were ideal for sporulation (24 hr with RH > 90%). It rained most of the night of 23-24 February. There were several showers the next day, but the release of spores was low, and that which occurred appeared to be caused by wind. Thus, factors other than rain must have been controlling spore release during this period.

Diurnal spore release.—Violent release of spores of *D. turcica* can occur when RH is lowered, raised, or when sporulating lesions are exposed to red-infrared radiation (11). An example of typical diurnal release is illustrated in Fig. 9. Spore release began at dawn (0630 hours) as the RH decreased and peaked near mid-morning. Wind velocities were less than 2 m/sec during this period. Diurnal release was common during the 6.5 mo of spore trapping, but it rarely occurred alone and usually was overlapped with wind release particularly when wind velocities increased during the morning. The combined effects of diurnal and wind release are shown (Fig. 6). Discharge of spores began at 0600 hours and peaked at about 1100 hours. Wind velocity began to increase later in the morning and from 1000 hours through 1900 hours, wind was an important component contributing to release.

Characteristics of airborne conidia.—Mature conidia of *D. turcica* are typically 6-7 septate (Fig. 12) and often slightly curved. On numerous occasions, many immature conidia were trapped. These conidia were much shorter, not curved, and had few or no septa (Fig. 10). Of 300 spores trapped and examined randomly on 6 February, 57% were aseptate, 11.4% had one septum, 8.1% had two septa, 22.8% had three septa, and none had more than three septa. The viability of immature conidia was tested by moistening a trap slide with distilled water and placing it in a moist chamber at 22 C for 12 hr. Twenty percent of immature conidia (including aseptate spores) germinated (Fig. 11), indicating that immature spores are viable propagules and should be included in spore counts of *D. turcica*.

The majority of airborne conidia usually were dehydrated and had collapsed walls. When placed in water, they immediately rehydrated and expanded. Spores in the hydrated form were trapped only during periods of high humidity that followed heavy rain.

During most of the spore-trapping period, conidia typically were thin-walled. On 14 April, 40% of trapped spores contained thick-walled, rounded chlamydospores (Fig. 13). Weather records for that period (Fig. 3) showed that this occurrence of chlamydospores was preceded by a period of fairly low night temperatures (minima of three preceding nights 9.5 C, 8.5 C, and 8.0 C). Although an earlier period of comparably low night temperatures had occurred, spore production was too low for evaluation of

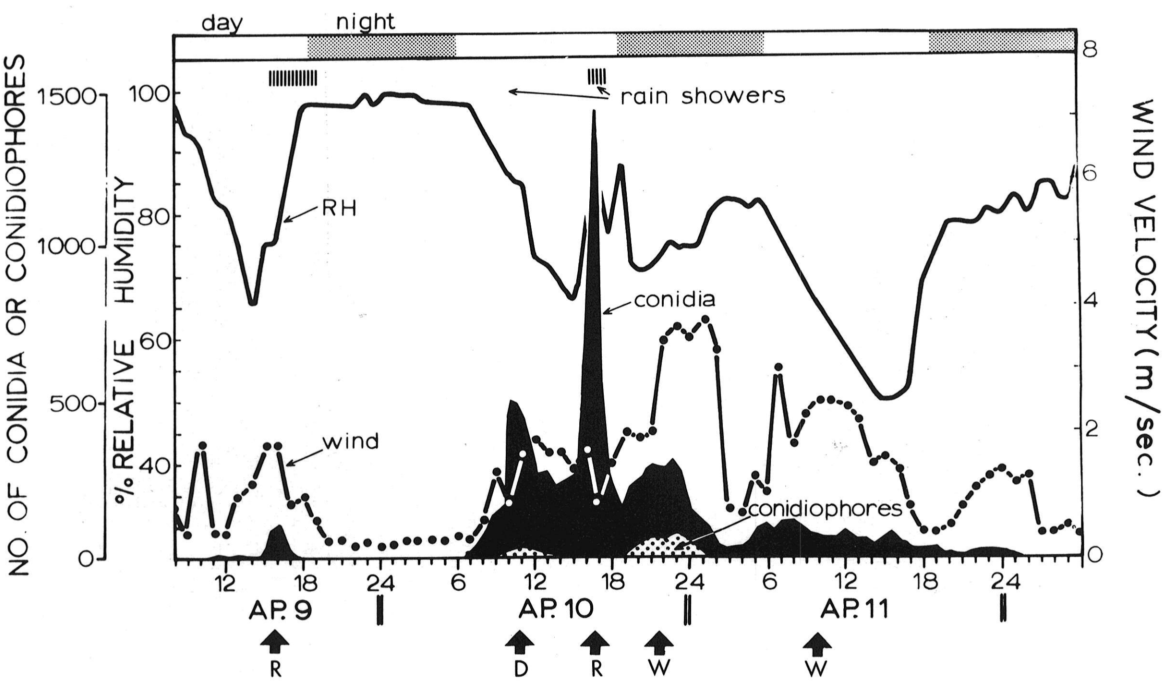


Fig. 9. The influence of environmental factors on the incidence of airborne conidia of *Drechslera turcica* within a maize planting (R = rain release, W = wind release and D = "diurnal" or violent release; nocturnal relative humidity was unfavorable for sporulation 8-9 April, favorable 9-10 April and unfavorable 10-11 April.

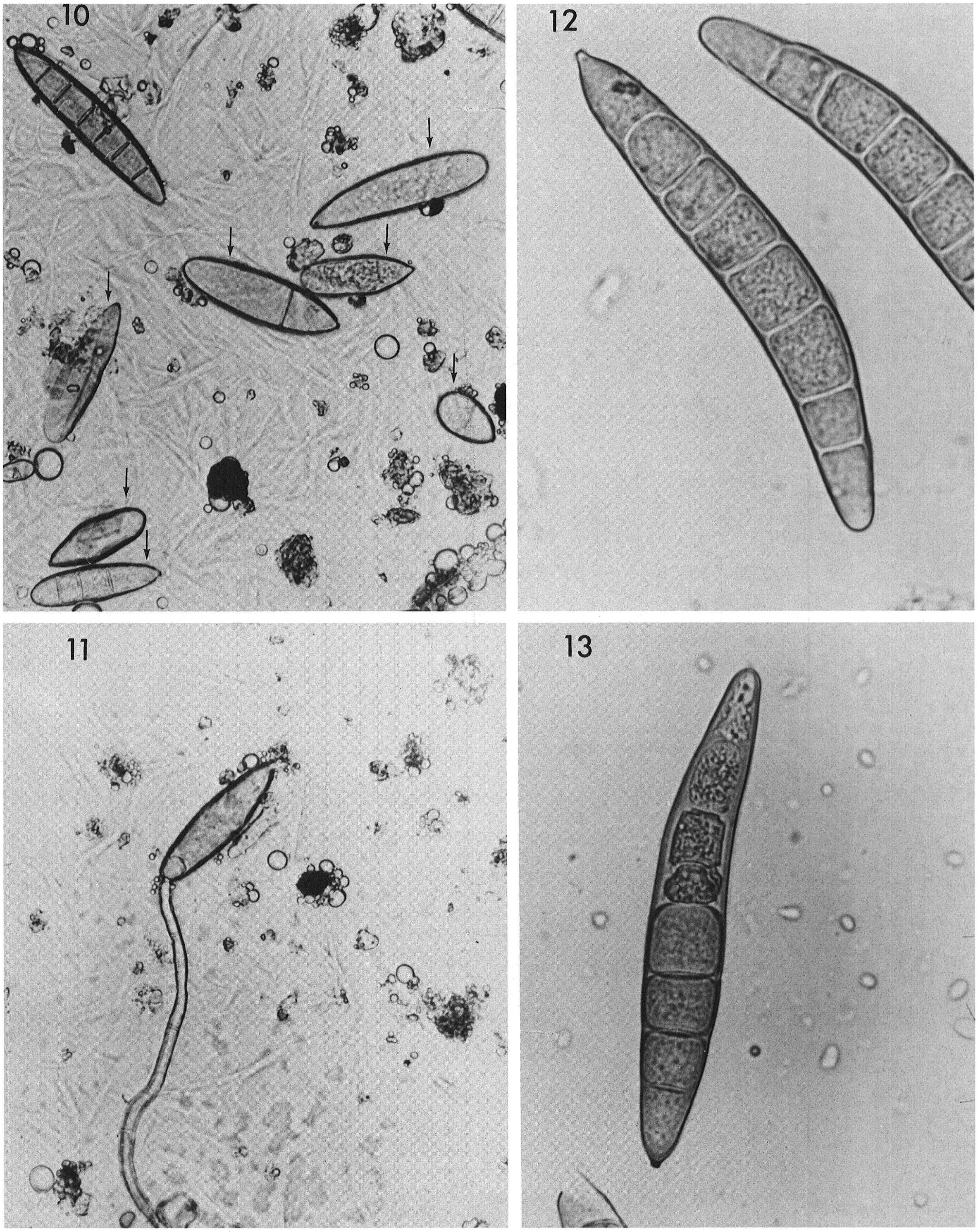


Fig. 10-13. Conidia of *Drechslera turcica.* **10)** Immature conidia on a spore trap slide (× 235). **11)** Germinating aseptate conidium (× 235). **12)** Mature conidium formed at 20 C (× 550). **13)** Formation of young chlamydospores (× 550).

chlamydospore formation. A second occurrence of chlamydospores (25 April) also was correlated with low temperatures during the preceding nights (7.5 C, 6.5 C, 5.5 C, 10 C, and 5.5 C). Many chlamydospores were trapped from 25-27 April. On 26 April, 33% of all spores trapped (1,432) contained chlamydospores. Later in the season when night temperatures were uniformly low, spore production was too low for accurate assessment of chlamydospore formation.

DISCUSSION

The general pattern of spore release observed at Pukekohe was similar to that observed by Meredith (14) in Nebraska. This pattern is characterized by a regular diurnal periodicity with peak spore counts near noon; few were trapped at night. However, differences in weather conditions can modify this pattern.

Spore release of *D. turcica* can be caused by wind, rain, or diurnal release, a form of violent release affected by various factors including changes of RH and IR radiation (11). Meredith (13) first reported that decreasing vapor pressure causes the violent release of conidia of *D. turcica*, and attributed this to mechanical stresses induced into the conidium and conidiophore by loss of water. Leach (11) also has shown that spores are released violently as the RH decreases, but also has reported that release is initiated by an increasing RH and also by exposing sporulating lesions to infrared radiation. Leach (12) has theorized that this forcible discharge of spores is due to electrostatic repulsion.

The spore-trapping data from near Pukekohe suggest that diurnal release is one of the principal means of ejecting spores from their site of production through the static laminar boundary layer into the atmosphere. This mechanism failed to function only when RH remained high throughout the day (for example on a rainy day). The violent release of spores coincident with increasing RH, often evident in laboratory studies (11), was not observed in the field.

Wind was a common agent of spore release at Pukekohe. Even on days that followed nights unfavorable for sporulation, some conidia were trapped. These presumably were conidia formed during a previous period favorable for sporulation. Although the wind velocity needed to dislodge conidia was not determined precisely, our trapping data indicate that it is about 3 m/sec. In studies on the related fungus *Drechslera maydis*, Waggoner (19) reported that approximately 20% of its conidia were removed in 15 sec, by wind speeds of 3 m/sec and 80% by wind of 7 m/sec. Aylor and Lukens (2) have reported that, under field conditions, 75% of spores of *D. maydis* were removed by winds as low as 1 m/sec. Their estimate may be in error, however, because Aylor (1) subsequently has determined that the force necessary to break the conidiophore-conidium attachment of *D. maydis* is about 1×10^{-2} dynes (10^{-7} N) which he calculated is afforded by a wind speed of 10 m/sec. In estimating wind speed necessary for release of conidia, it is essential to consider several other factors such as age of conidium, state of hydration, intensity of electrical charge, and vibration of leaves, any of which may affect substantially the wind force needed to remove spores. It is likely that wind contributed significantly to the incidence of airborne spores at Pukekohe. Average wind speed commonly exceeded 3 m/sec; maximum speeds often were much higher. However, our data suggest that on most mornings, spores were removed by a combination of wind and diurnal release.

Splash dispersal of spores by rain is not a new concept (8, 10). Gregory (8) and others have demonstrated experimentally that spores can be dispersed by the fine droplets formed when large drops collide with a spore-bearing surface. Leach (11, 12) suggested that the mechanism of splash dispersal may involve both mechanical and electrostatic forces. Rain drops can be highly charged (17), which in part, could account for the large numbers of spores liberated during a light rain. Our data indicate that rain dispersal was much less important than wind and diurnal release. However, the study was done during an exceptionally dry season for the North Island of New Zealand and it is possible that, in years with higher rainfall, rain might be more important.

The occurrence of conidiophores in the airspora has been reported by Pady (16) and it probably is not uncommon. During our studies, conidiophores of *D. turcica* frequently were trapped, often in considerable numbers, but only when wind velocities were high. These conidiophores were capable of germinating when moistened, but when placed on leaves they failed to produce appressoria, nor did they infect the leaves (R. A. Fullerton, *unpublished*). Although airborne conidiophores may not function as infective propagules, they may be important in establishing saprophytic colonization of debris on which spores could be produced.

Chlamydospores formed within conidia of *D. turcica* are important in the overwintering of northern leaf blight of maize (4, 7). Our results suggest that chlamydospores are formed after periods of low night temperature and that air dispersal of chlamydospores may be epidemiologically significant.

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