Factors Affecting Dispersal of Conidia of the Apple Scab Fungus

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ABSTRACT

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Dispersal of conidia of *Spilocea pomi*, the imperfect stage of *Venturia inaequalis*, was monitored in air during the summers of 1973 and 1974 with a Burkard recording volumetric spore trap and in rainwater during 1974 using funnel traps. Rain was an important mechanism for disseminating conidia; however, significant numbers of conidia also were detected in air. Aerial dissemination was diurnal with peak conidium frequency occurring between 1400 and 1600 hours Eastern Standard Time (EST) and with a subsidiary peak around 2100 to 2200 hours EST. Correlation and multiple regression analyses were used to relate counts of trapped conidia to several meterological factors and to determine their relative importance in the release of conidia. Trap counts of conidia were not related to any dominant environmental parameter, but to the interaction of several. Release of conidia was positively correlated with temperature, wind velocity, and solar radiation, but negatively correlated with leaf wetness and relative humidity. Analysis of disease progress data in relation to availability of conidia and to infection periods suggests that airborne conidia contribute to disease increase, particularly during dry periods.

Additional key word: epidemiology.

Apple scab, a major disease of apple in eastern North America, is caused by *Venturia inaequalis* (Cke.) Wint. Ascospores from perithecia in overwintering apple leaves initiate the primary disease cycle by infecting emerging leaves, flower buds, and fruits in the spring. Secondary disease cycles, which are repeated through the summer and fall, are initiated by the conidial stage of *V. inaequalis* (*Spilocea pomi* Fries).

Before 1960, it was considered that scab conidia were disseminated primarily by rain. Although Howitt (6) believed conidia were freely scattered by wind, airborne conidia were detected infrequently in other studies (3, 7) and under laboratory conditions excessive air velocities (300-500 m/second) were necessary to detach substantial numbers of conidia (11). Because of these findings, the significance of airborne conidia was generally discounted until recently, when conidia were found in the orchard air during dry weather (1, 4, 10). In this study we reassessed aerial dispersal of conidia of *S. pomi* and investigated the significance of meterological factors on aerial dissemination, an area which has been largely neglected.

MATERIALS AND METHODS

Airborne conidia of *S. pomi* were collected from 2 May to 28 September 1973, and 2 June to 28 September 1974, in a block of Red Delicious trees on Malling 2 rootstock planted in 1954 at the Graham Experiment Station, Grand Rapids, Michigan. A Burkard 7-day recording volumetric spore trap [Burkard Scientific (Sales) Limited, Rickmansworth, Hertfordshire, England] was located with its orifice about 2.3 m above ground level within the crown of an unsprayed tree. Traps were adjusted to sample 10 liters of air per minute. Hourly counts of conidia were made by treating the Melinex tape from the trap with cotton blue in lactophenol and traversing the width of the tape at 2-mm intervals. Counts were corrected to compensate for the area sampled, but not for trap efficiency, and were recorded as numbers of conidia per cubic millimeter of air sampled each hour.

Water dispersal of conidia was measured in 1974 by collecting rainwater at random under the tree canopy with four funnels, 10.5 cm in diameter. Funnels and 400-ml plastic collection bottles were supported 1.5 m above ground level on wooden posts. Ten ml of 11.5% phenylmercury monoethanol ammonium acetate (Puratized Apple Spray, Niagara Chemical Corp., Middleport, N.Y.) were added to each bottle before use to prevent spore germination.

We determined the number of conidia in the collection bottles by filtering a 2-ml sample through a 25-mm diameter (1.0-μm pore size) gridded filter and counting the conidia in five randomly-selected grid squares. Samples were suspended in 25 ml of distilled water before filtering to assure uniform distribution of the conidia on the filter. Before being counted the conidia were stained with cotton blue in lactophenol. Grid counts were adjusted to give the total number of conidia in each bottle.

In 1973, temperature (C) and relative humidity (RH) were measured within the orchard area with a 7-day recording hygrothermograph at 1.5 m above ground level in a weather instrument shelter, rainfall (mm) with a dip-stick rain gauge at ground level, and leaf wetness with a DeWit 7-day recording leaf wetness meter (M. DeWit, Hengelo, The Netherlands) at 1.5 m above ground level and in the drip line of the tree. Wind velocity data (kilometers per hour) were obtained from the Grand Rapids airport about 16 km away. In 1974, temperature and RH at 1.5 m above ground level, rainfall at ground level, and wind velocities in the mid-canopy region of the trees were measured at an automatic weather station within the orchard. A mechanical pyranograph measured solar radiation in m-cal/cm^2/minute. Leaf wetness was recorded as in 1973. In taking data from the leaf-wetness charts, wetness from rain was recorded in a separate category from wetness due to fog, dew, and light rain.

In 1974, 25 fruit spurs and 25 terminals were tagged and the number of scab lesions on the upper and lower surfaces of the leaves was counted every 3-5 days from full bloom through mid-July, then at 2-week intervals until mid-August.

Multiple linear regression model-building techniques (2) were used to relate hourly trap counts to meterological factors. These analyses were computed for individual monthly data for the 1973 and 1974 seasons using dummy variables to account for certain hour-to-hour and day-to-day variability in the data. There was a set of dummy (categorical) variables for the hour-to-hour variation and another set for the day-to-day variation. The dummy representing a particular hour (or day) took on the following values:

$X = +1$, if the Y-variable reading was taken for that particular hour (or day),

$X = -1$, if the Y-variable reading was taken for the last hour (or day), or

$X = 0$, if otherwise.

This system resulted in individual earlier hours (or days) being contrasted with the final hour (or day) and permitted accounting for the final variation due to hour (or day) effects. The number of dummy variables for hours (or days) was one less than the number of hours (or days). The regression coefficients representing these dummy variables have little interpretational value. Partial regression coefficients were tested for statistical significance with Student's t-test.

RESULTS

Spore trapping and disease development.—The low counts of conidia trapped in May probably were caused, at least in part, by placement of the trap at ground level under the tree canopy rather than in the tree (Fig. 1). Moreover, differences in numbers of conidia trapped before and after 29 May cannot be compared directly because of changes in location of the trap. The first conidia were caught on 8 May when the trees were approaching the full bloom stage of bud development. Disease increased rapidly through May. By 6 June, 94.7% of the cluster leaves were infected and defoliation was

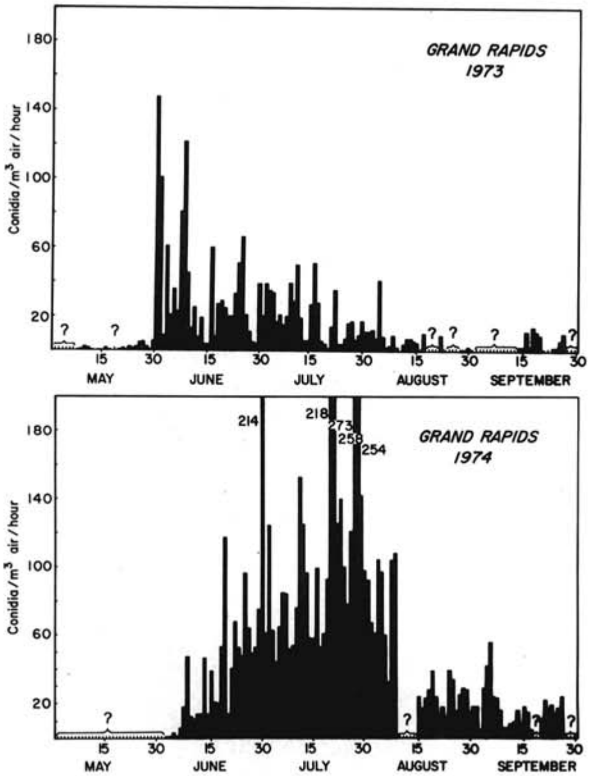

Fig. 1. Mean hourly counts (no. per m^3 per hour) of conidia of *Spilocea pomi* (top) 2 May to 28 September 1973 and (bottom) 2 June to 28 September 1974 at Grand Rapids, Michigan. Question marks indicate periods during which data were not gathered.

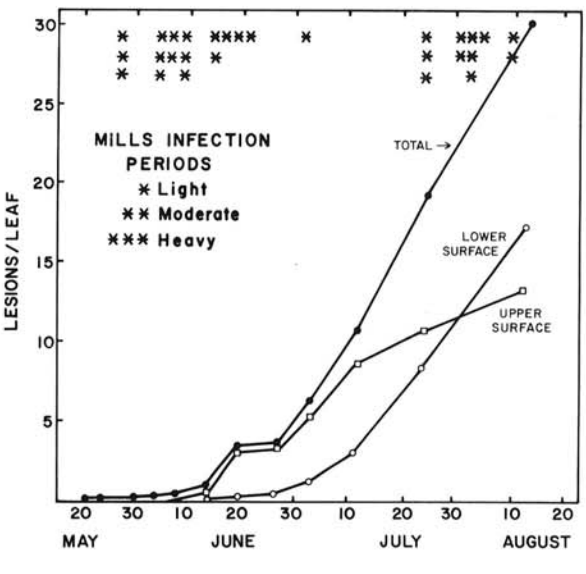

Fig. 2. The number of apple scab lesions on the upper and lower surface of 25 tagged groups of cluster leaves and 25 terminals for 1 May to 15 August 1974 in relation to total lesions and Mills' infection periods at Grand Rapids, Michigan.

occurring. The greatest number of conidia trapped per hour were recovered on 30 May, soon after the trap was located in the tree. Thereafter, conidia counts decreased through the season and reflected the heavy defoliation (~85%) that occurred through mid-July.

In 1974, conidia were caught on 2 June (Fig. 1), which was the day the spore trap was set up and about 17 days after the first primary scab lesions were noted on cluster leaves. Numbers of conidia increased through late July, then declined thereafter. Disease development on leaves also increased as the season progressed, even though terminal growth was complete in early July (Fig. 2). In early summer, the greatest increase in lesion numbers occurred on the upper leaf surface, but later lesion numbers increased faster on the lower surface. The greatest increase in lesion numbers on the upper leaf surface occurred 12 June to 19 June and 26 June to 12 July and on the lower surface from 12 July to 16 August. It is interesting that total disease increase was nearly linear after 26 June although only one infection period (based on Mills' criteria) occurred between 22 June and 25 July. However, during this time, periods of fog and/or dew of sufficient duration for a "light" infection period occurred on the mornings of 26 and 29 June and 5, 6, 8, 15, 16, 17, and 24 July.

During both seasons spore shower peaks occurred between 1400 and 1600 EST with a subsidiary peak around 2100 to 2200 hours (Fig. 3).

Numbers of conidia in rainwater increased from late May through mid-July, then decreased somewhat thereafter (Fig. 4). The maximum number of conidia per funnel trap was 1.6×10^6 following 15 mm of rain on 1 July. The greatest concentration (6,996 conidia per ml) was recorded on 23 July following 3.8 mm of rain. The number of conidia in rainwater tended to increase when numbers of new lesions on the upper leaf surface were high or when several days elapsed between rains.

Defoliation increased through the season as a function of the number of lesions per leaf such that:

$$Y = 0.0805\,X - 0.0588\,X^2 + 0.0021\,X^3$$

where Y = predicted percent defoliation and X = number of lesions per leaf. The decline in conidia counts in 1973

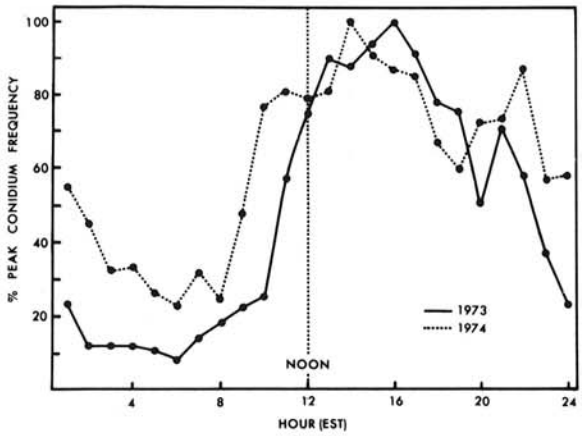

Fig. 3. Hourly levels of airborne conidia of *Spilocea pomi*. Conidium frequency is expressed as a percentage of the peak arithmetic mean frequency for the period 2 May to 28 September 1973 and 2 June to 28 September 1974 at Grand Rapids, Michigan.

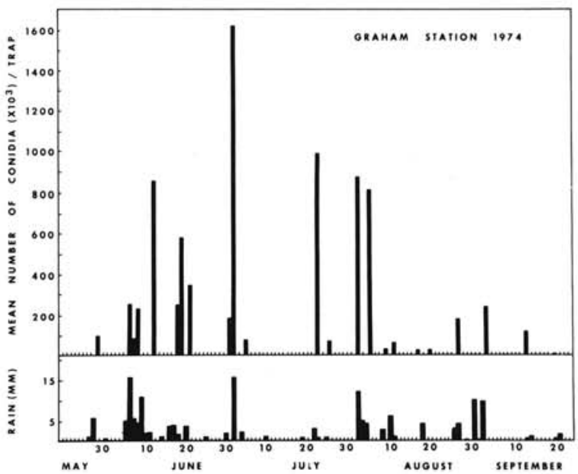

Fig. 4. Numbers of conidia of *Spilocea pomi* in water traps and rainfall at Grand Rapids, Michigan, for 1 May to 20 September 1974.

TABLE 1. Correlation of $\log_e$ (*Spilocea pomi* conidia trap counts +1) with meterological factors for four summer months in 1973 and 1974 at Grand Rapids, Michigan

Meterological factors	Simple correlation coefficients							
	1973				1974			
	June	July	August	September	June	July	August	September
Temperature (C)	0.299**[a]	0.324**	0.182**	0.086	0.102*[a]	0.249**	0.233**	0.039
Relative humidity	−0.230**	−0.397**	−0.226**	−0.200**	−0.233**	−0.383**	−0.221**	−0.267**
Wind velocity (km/hr)	0.310**	0.130**	0.140**	−0.048	−0.093*	0.205**	0.116*	−0.019
Rainfall amount (mm)	. . .	. . .	. . .	. . .	−0.029	−0.184**	0.003	−0.057
Solar radiation[b]	. . .	. . .	. . .	. . .	0.165**	0.271**	0.172**	0.141**
Wetness from rain	−0.301**	−0.073	−0.093*	−0.201**	−0.175**	−0.331**	−0.136**	−0.243**
Wetness from light rain, dew, or fog	−0.387**	−0.157**	−0.218**	−0.288**	−0.105**	−0.281**	−0.257**	−0.230**

[a]Asterisks (**) indicate significant correlation coefficients at $P = 0.01$; the single asterisk (*) indicates significant correlation coefficients at $P = 0.05$.

[b]= m-cal/cm²/minute.

and in August and September 1974, were associated with heavy defoliation.

Spore trap counts and meterological factors.—Correlation analysis of numbers of conidia trapped daily each month in 1973 and 1974 (Table 1) indicated the $\log_e$ of daily spore concentration was positively correlated with temperature and wind velocity except in September, and negatively correlated with RH and leaf wetness. In 1974, spore concentration also was positively correlated with solar radiation throughout the season. Amount of rainfall was positively correlated with spore concentration in July 1974, but no significant trends occurred in the other months.

Results of multiple regression analyses for individual monthly data for the 1973 and 1974 seasons are reported in Table 2. Interaction and quadratic terms were used in the initial analysis, but generally were not significant and were omitted from the final analysis. Coefficients of determination (R^2) were 0.55 to 0.63 for all months except for the 0.42 in August and 0.48 in September 1973. Partial regression coefficients for temperature were significant in only two of the eight months. Leaf wetness, particularly wetness from rain, usually resulted in decreased trap counts and the partial regression coefficients were significant in four of the months. Partial regression coefficients for wetness (rain, dew, and fog combined), for RH, for rainfall amount, and for wind velocity were often nonsignificant or if significant, the relationship conflicted and thus was difficult to interpret. However, counts of conidia and solar radiation intensity appeared to increase together, particularly in September 1974.

Model construction was attempted also for relating conidial trap counts to meterological factors on an hour-by-hour basis during June 1974. The analysis was similar to the multiple regression described earlier except that categorical variables were not included in the model. Coefficients of determination values ranged from 0.20 at 1300 hours to 0.71 at 2000 hours. None of the partial regression coefficients was consistently significant and the analysis failed to indicate if one or more of the meterological parameters were correlated with conidia trap counts.

DISCUSSION

The results of these studies show that airborne conidia are more important in the epidemiology of apple scab than was suggested by those in Wisconsin (3, 7) and prove that conidia are not completely dependent upon rain for dissemination. Midsummer dissemination of airborne conidia was reported previously from England (4), Ireland (10), and Poland (1).

Aerial dissemination becomes important during summer and fall, particularly during periods without rain. Such a role for airborne conidia is suggested because much of the disease increase on foliage in summer of 1974 apparently was not associated with rainfall. One explanation for disease buildup without rainfall is that airborne conidia, deposited on leaves during the day, may germinate and infect at night when leaves are wet with dew. In summer, infection at the common night-time temperatures in Michigan would require only 6-8 hours of wetting (8, 9). Orchard observations and leaf-wetness recorder readings indicate that dew periods of this length were not uncommon through the summer. Although we have encountered periods when germination of field-collected conidia was poor, it seems unlikely, considering the large number of airborne conidia available, that there were too few viable conidia for development of epidemics.

From the standpoint of disease control, airborne conidia probably are important in the spread to scab-free but unprotected orchards, as suggested by Hirst and Stedman (4) and in increasing the rate of spread within orchards. Airborne conidia also could contribute to late-season infection after the normal orchard fungicide program is discontinued, helping to insure overwintering of the fungus.

The diurnal periodicity in counts of trapped conidia described by Hirst and Stedman (4) also was characteristic of our data, except that in ours the initial diurnal peak occurred slightly later in the afternoon. This time difference for peak spore counts may reflect regional environmental variables. The bimodal characteristic of the trap counts may relate to the two mechanisms of conidial release in *S. pomi*. The initial peak probably represents the period of maximum release in dry air and

TABLE 2. Partial regression coefficients and coefficients of determination for multiple regression equations of the $\log_e$ (*Spilocea pomi* conidia trap counts +1) with meterological factors at monthly intervals from June through September 1973 and 1974 at Grand Rapids, Michigan

Meterological factors	Partial regression coefficients							
	1973				1974			
	June	July	August	September	June	July	August	September
Temperature (C)	0.0251	−0.0341	−0.0156	0.0176	0.1218**[a]	0.0995*[a]	0.0224	0.0216
Relative humidity	0.0082	−0.0268**	−0.0003	−0.0165	0.0241*	−0.0149	0.0053	−0.0113
Wind velocity (km/hr)	0.0461**	−0.0105	0.0098	0.0039	−0.0183	−0.0331	0.0619	−0.0871
Rainfall amount (mm)	...	...	...	...	0.1193	−2.8779	0.0325	0.3580
Solar radiation[b]	...	...	...	...	−0.2958	0.8241	0.1402	1.7815**
Wetness from rain	−0.8389*	−0.5419**	−0.0827	−0.4519	0.0881	−2.4173**	0.0918	−1.0127**
Wetness from light rain, dew, or fog	−0.3267	0.3150	−0.2851	−0.3891	−0.1027	0.0354	−0.1882	0.0791
	R^2=0.59	R^2=0.56	R^2=0.42	R^2=0.48	R^2=0.61	R^2=0.55	R^2=0.63	R^2=0.58

[a]Asterisks (**) indicate significant correlation coefficients at $P = 0.01$; the single asterisk (*) indicates significant correlation coefficient at $P = 0.05$.

[b]= m-cal/cm^2/minute.

the second peak may be associated with the onset of dew, followed by release and dissemination.

The relation of meterological factors to dispersal of airborne conidia is far from clear. Visual inspection and correlation analysis of the data indicate that dissemination of conidia is associated with increasing temperature, sunshine, increasing wind speed, low RH, and dry foliage. The direct relation of temperature, or the inverse relation of RH to spore catch, could account equally well for the observed diurnal periodicity patterns. Rainfall probably has an initial effect of liberating spores through puff or splash dispersal (5); however, with continuing rain, conidia probably are removed from the air through its scrubbing effect. Because excessive wind velocities are required to remove scab conidia from leaves under controlled conditions (3, 11), wind speed may be less important than the data suggest. The positive correlation of spore release and increased wind velocity may in part reflect mechanical spore removal by leaf contact. The positive correlation with solar radiation may be spurious or confounded by the concomitant temperature increase and RH decrease. Solar radiation may be more important to viability than to release.

LITERATURE CITED

1. BORECKI, Z. 1967. Rozsiewanie sie zarodnikow workowych i konidialnych parcha jabloniowego w sadzie. (Dissemination of ascospores and conidia of apple scab in the orchard). Pr. Inst. Sadow. Skierniewic 11:131-152.
2. DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. John Wiley and Sons. New York. 407 p.
3. FREY, C. N., and G. W. KEITT. 1925. Studies of spore dissemination of Venturia inaequalis (Cke.) Wint. in relation to seasonal development of apple scab. J. Agric. Res. 30:529-540.
4. HIRST, J. M., and O. J. STEDMAN. 1961. The epidemiology of apple scab (Venturia inaequalis (Cke.) Wint). I. Frequency of airborne spores in orchards. Ann. Appl. Biol. 49:290-305.
5. HIRST, J. M., and O. J. STEDMAN. 1963. Dry liberation of fungus spores by raindrops. J. Gen. Microbiol. 33:335-344.
6. HOWITT, J. E., and W. G. EVANS. 1926. Preliminary report of some observations on ascospore discharge and dispersal of conidia of Venturia inaequalis (Cooke) Winter. Phytopathology 16:559-563.
7. KEITT, G. W., and L. K. JONES. 1926. Studies of the epidemiology and control of apple scab. Wisc. Agric. Exp. Stn. Res. Bull. 73:1-104.
8. MILLS, W. D. 1944. Efficient use of sulfur dusts and sprays during rain to control apple scab. N.Y. Agric. Exp. Stn. (Ithaca) Ext. Bull. 630. 4 p.
9. MILLS, W. D., and A. A. LAPLANTE. 1951. Control of diseases and insects in the orchard. Pages 18-21 *in* N.Y. Agric. Exp. Stn. (Ithaca) Ext. Bull. 711. 88 p.
10. O'KENNEDY, N. D. 1962. Observations on the trapping of spores of the apple scab fungus (Venturia inaequalis (Cke.) Wint.). Ireland J. Agric. Res. 1:200-203.
11. WISEMAN, R. 1932. Untersuchungen über die uberwinterung des apfelschorfpilzes Fusicladium dendriticum (Wallr.) Fckl. im toten blatt sowie die Ausbreitung der sommersporen (konidien) des apfelschorfes. Landwirtsch. Jahrb. Schweiz, Annu. Agric. Suisse 46:619-679.