Patterns of Ascospore Discharge by *Venturia inaequalis*

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ABSTRACT

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Discharge of ascospores of *Venturia inaequalis* was monitored with a Burkard volumetric spore trap for 4 yr in an apple orchard with a large overwintering population of the apple scab pathogen. The major discharges occurred during clearly defined intervals. When rain began before 0700 hours, the leaves remained wet through 2400 hours, and temperatures were above 10 C, 97.9% of the ascospores trapped by 2400 hours were trapped between 0700 and 1800 hours. When rain began between 0700 and 1300 hours, 98–100% of the spores were trapped before 2100 hours. Even when the rain began later in the day, between 1400 and 1800 hours, 90% or more of the ascospores were trapped before 2100 hours. No spores were trapped until the following morning when the rain began after 1800 hours. The extremely low density of ascospores in the air between 1800 and 0700 hours has significant implications for determining Mills' infection periods and for selecting and scheduling postinfection fungicides, because spore discharge and the subsequent initiation of infection often occur several hours after rain begins rather than at the start of rainfall.

Additional key words: apple scab, spore trapping.

The primary inoculum for apple scab, caused by *Venturia inaequalis* (Cke.) Wint., is comprised of ascospores produced within pseudothecia in infected leaves that overwinter on the orchard floor. The length of the primary infection season is determined by temperature, which governs the rate of maturation of ascospores (5,8,9), and rainfall, which causes the spores to be discharged.

Work done in the 1920's established that wetting of pseudothecia by rain was required for significant discharge of ascospores and that the discharge began within minutes after the leaves were wetted by rain (1,7,18,26). As little as 0.25 mm of rain has resulted in measurable spore discharge (2,15), but wetting of leaves by dew resulted in comparatively low densities of spores in the air (3,22,15,18).

Numerous studies have reported a relationship between rainfall and spore discharge, but four reports of ascospores being trapped during fair weather have not been adequately explained (2,6,18,23). The interval and pattern of spore release accompanying or following rain is also not clear. Keitt and Jones (18) reported that spores were trapped for 3–5 hr after wetting. Von Arx (28) trapped few ascospores during the first hour of rain. Most spores were trapped during the day in the third hour of rain, and few were trapped after 8 hr. Hirst and Stedman (15) reported that 75% of all spores trapped were collected within 3 hr after a brief rain and within 6 hr when rains of all duration were considered. Miller and Waggoner (23) reported a bimodal distribution of ascospore trapping during continuous rain, with a second peak occurring several hours after the first. Hirst et al (16) observed only one peak within 24 hr in a 2-yr study, but Hirst and Stedman (15) later noted three patterns of ascospore trapping: a rapid increase to a single peak after the start of rain, two distinct peaks with variable intervals between peaks, and release delayed several hours after the start of rain. Seem et al (27) reported a correlation between temperature, humidity, duration of leaf wetness, and the time required to reach a peak of ascospores trapped. Between 3 and 6 C, the rate of release was slowed by decreasing temperature, but temperatures between 6 and 18 C had little effect on ascospore trapping. However, in a wind tunnel experiment Hirst and Stedman (15) reported that the temperature of the 4 hr after wetting affected the time of peak ascospore liberation at temperatures between 6 and 13 C. They also noted that the concentration of spores during the daytime was not explained by the distribution of rain, and suggested that a circadian rhythm might be involved in ascospore discharge.

Brook (3) reported that light has a profound influence on spore release, and was second only to leaf wetness in triggering spore release. Spores trapped during darkness accounted for only 0.5% of all spores trapped (2), and during the first hour of light 20 times more spores were trapped than during the first hour of darkness (3). Appreciable discharge occurred only when wetted pseudothecia were exposed to far red wavelengths of light between 716 and 730 nm, and declined drastically after 15 min of darkness (4). Brook concluded that after wetting, spores may be released continuously, but at a very low rate during darkness and at a high rate during daylight. However, Gilpatrick and Szkolnik (14) suggested that the greater discharge of spores during the daylight was due to the daily periodicity of temperature and its effect on ascospore maturation, rather than to a direct effect of light on release of spores. Thus, there remain uncertainties that must be resolved before information on ascospore release can be incorporated into management programs for apple scab.

In this study we describe the effect of various environmental factors on ascospore discharge of *V. inaequalis* and explain the diurnal periodicity of ascospore discharge, the occurrence of double peaks of ascospore discharge, and the occasional occurrence of fair-weather discharges. We further clarify the relationship between dew and ascospore discharge, and finally suggest how our current understanding of spore discharge may be useful in a disease management program.

MATERIALS AND METHODS

The intervals we refer to as daytime and nighttime do not coincide precisely with intervals determined by sunrise and sunset. In Durham, NH, from 15 April to 15 June, sunrise occurs between 0502 and 0404 hours EST, and sunset occurs between 1827 and 1918 hours EST. The intervals of day and night in this paper (0700–1800 hours and 1800–0700 hours, respectively) are established by ascospore trapping records and provide a convenient means of delimiting intervals when the airborne ascospore density was relatively high or low.

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The 4-yr study was conducted on a 1-acre block of 30-yr-old McIntosh and Cortland trees on M-7 rootstocks at the Mast Road Research Orchard in Durham, NH. Several trees were not sprayed with fungicide each year, resulting in a high level of inoculum compared with commercial orchards. The percentage of leaves with scab on unprotected McIntosh trees for the 1981–1984 seasons was 21, 59, 62, and 83%, respectively, and the percentage of fruit with scab on the unprotected trees was 29, 99, 93, and 100%, respectively. The land on which the orchard was planted had a northern slope of approximately 5°.

A Burkard 7-day recording volumetric spore sampler (Burkard Scientific Sales, Ltd., Rickmansworth, England) was installed in the orchard and operated continuously from 5 April to 12 June 1981, from 28 April to 3 June 1982, from 7 April to 28 May 1983, and from 17 April to 3 June 1984. Recording weather instruments, housed in a standard U.S. Weather Service instrument shelter approximately 3 m from the trap, provided hourly records of rainfall (amount and intensity), temperature, relative humidity, and leaf wetness (22). The leaf wetness sensor used a hemp sensing element similar to that described by MacHardy and Sondej (22). The sensor was placed within the canopy of a tree approximately 2 m from the station at a height of approximately 1.5 m. A second tipping bucket rain gauge and event recorder (Weathertronics, Sacramento, CA) was also installed in the station to provide records of onset, intensity, and duration of rain. Records of the time of sunrise and sunset were obtained from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration's Environmental Data Service, Asheville, NC.

The Burkard volumetric spore sampler was operated using a 12-v DC power source, and was adjusted to sample air at 10 L/min. The Melinex tape that served as the trapping surface was prepared for trapping, removed, and dissected for microscopic examination as previously described (14). The tape was examined microscopically (675×) by scanning transects across the long axis of the tape at 2-mm (1-hr) intervals. The number of ascospores of *V. inaequalis* observed in each transect was corrected for the proportion of the tape examined and the volume of air sampled. The spore counts were not adjusted for trap efficiency.

RESULTS

Although the size of the overwintering population of *V. inaequalis* varied greatly from year to year, the ratio of ascospores trapped during daylight to spores trapped during darkness varied only slightly from year to year. During 1981–1984, the cumulative hourly observations totaled 1,702, 27,269, 177,808, and 70,524 ascospores per cubic meter of air sampled, with 95.2, 96.2, 97.1, and 95.1% trapped during the day and 4.8, 3.8, 2.9, and 4.9% trapped during the night, respectively. The mean airborne ascospore density per observation also varied greatly from year to year. There were 140, 164, 194, and 142 hr of leaf wetness during daylight hours and 152, 179, 239, and 211 hr of leaf wetness during the night during 1981–1984, respectively. Thus, the mean airborne ascospore density per hour of leaf wetness was 12, 160, 891, and 472 ascospores per cubic meter during the day and 0.5, 6, 22, and 16 ascospores per cubic meter during the night in 1981–1984, respectively. The 4-yr means of the percentage of ascospores trapped at 1-hr intervals are shown in Figure 1. When all spore trappings were considered, nearly 80% of the ascospores were trapped between 0700 and 1400 hours and 97.4% were trapped between 0700 and 1800 hours.

On 15 days when the leaves were first wetted by rain at night (before 0700 hours EST), remained wet through 2400 hours, and the temperature remained above 10 C, 1.3% of the ascospores were trapped before 0700 hours, 97.9% were trapped between 0700 and 1800 hours and 0.8% were trapped after 1800 hours (Fig. 2B). Regression of the probit of ascospores trapped against time yielded a linear model (Fig. 2A) with an R^2 of 0.98.

The rate of ascospore discharge was slowed when the mean temperature after 0700 hours was below 10 C. (Fig. 3). On 7 days when the mean daytime temperature was below 10 C, the times at which 25 and 90% of the ascospores were trapped were delayed 1 hr and 2.5 hr, respectively, compared with 15 days when the temperatures were above 10 C.

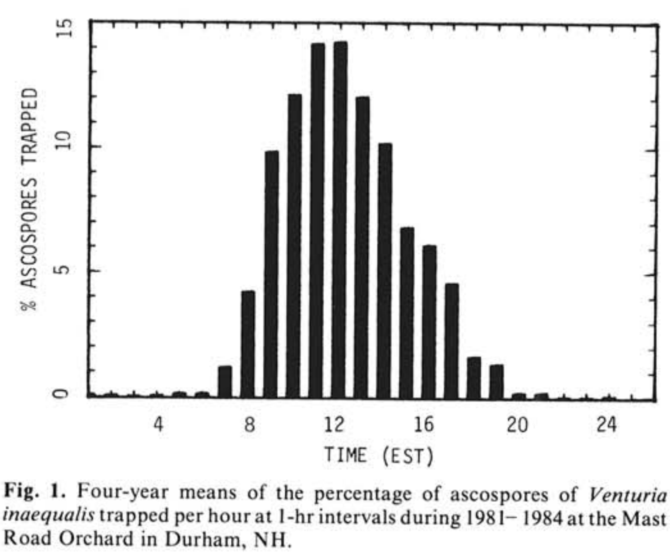

Fig. 1. Four-year means of the percentage of ascospores of *Venturia inaequalis* trapped per hour at 1-hr intervals during 1981–1984 at the Mast Road Orchard in Durham, NH.

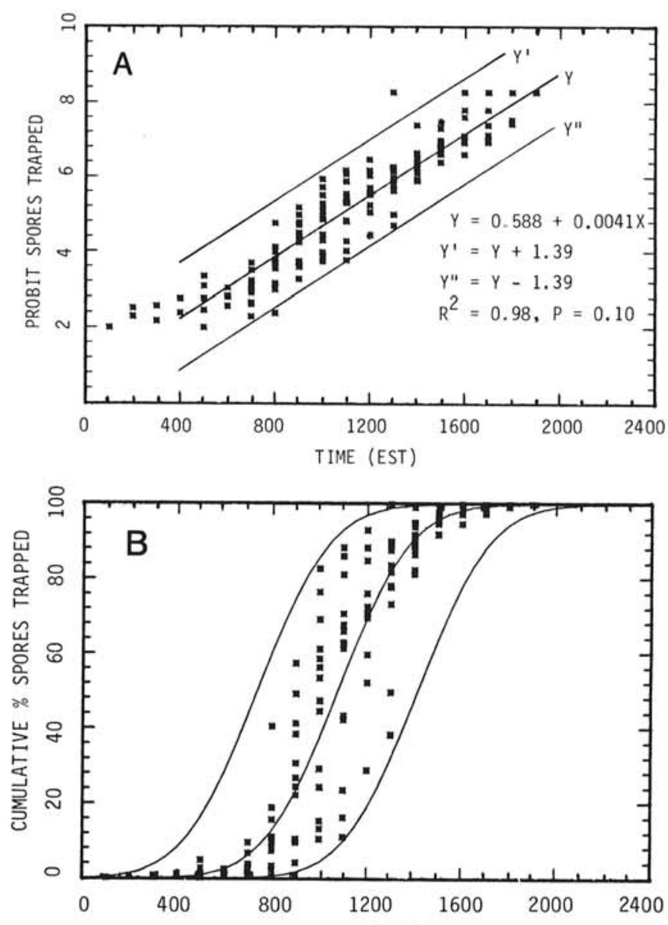

Fig. 2. Ascospores of *Venturia inaequalis* trapped at the Mast Road Research Orchard in Durham, NH, on 15 days during 1981–1984 when rain began before 0700 hours EST, the leaves remained wet through 2400 hours EST, and the mean daytime (0700–1800 hours EST) temperature was above 10 C. **A,** Relationship of the probit of ascospores trapped to the time of day. Y′ and Y″ are the upper and lower bounds, respectively, of the 90% confidence bands for the prediction. **B,** Cumulative percentage of ascospores trapped. The central curve indicates the percentage of spores trapped as predicted by the model shown in **A,** whereas the outer curves are the upper and lower bounds of the 90% confidence bands for the prediction.

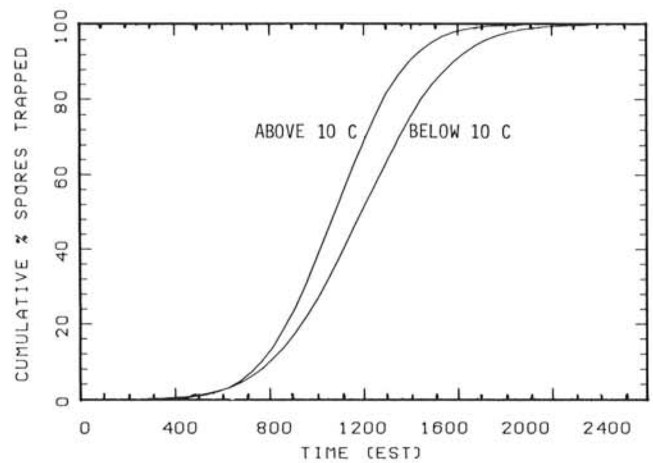

Fig. 3. Effect of temperature on the cumulative percentage of ascospores of *Venturia inaequalis* trapped at the Mast Road Research Orchard in Durham, NH, during 1981–1984. After probit transformation of the percentage of spores trapped, linear regression analysis, and detransformation, curves were generated to describe (1) ascospore discharge on 15 days during 1981–1984 when rain began before 0700 hours EST, the leaves remained wet through 2400 hours EST, and the mean daytime (0700–1800 hours EST) temperature was above 10 C, and (2) ascospore discharge on 7 days during 1981–1984 when rain began before 0700 hours EST, the leaves remained wet through 2400 hours EST, and the mean daytime temperature was below 10 C.

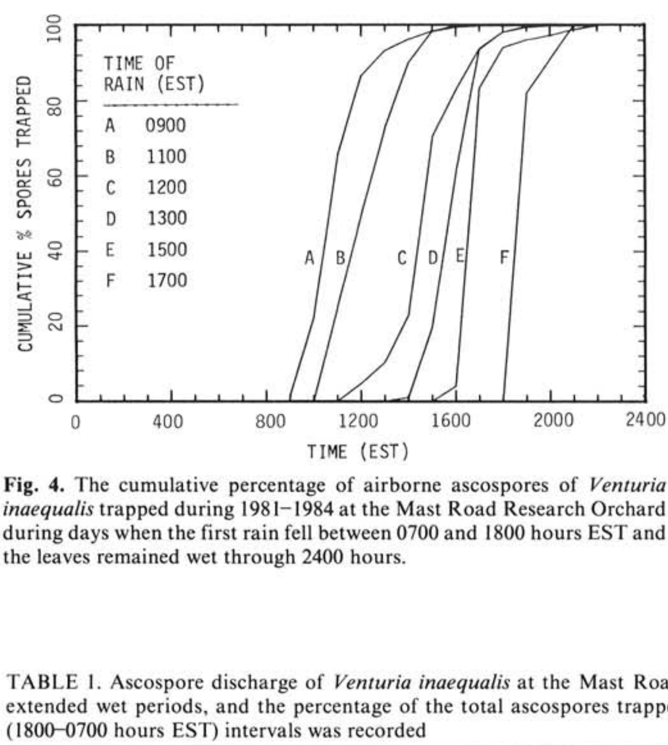

Fig. 4. The cumulative percentage of airborne ascospores of *Venturia inaequalis* trapped during 1981–1984 at the Mast Road Research Orchard during days when the first rain fell between 0700 and 1800 hours EST and the leaves remained wet through 2400 hours.

When rain began between 0700 and 1300 hours EST, 98–100% of the total ascospores trapped by 2400 hours were trapped before 2100 hours (Fig. 4). Even when the rain began later in the day, between 1400 and 1800 hours, 90% or more of the spores were trapped before 2100 hours. Relatively few spores were trapped immediately following rains beginning after 1700 hours compared with rainy periods initiated earlier in the day. When the rain began after 1800 hours, no spores were trapped until early the following morning.

Ascospores were not trapped when dew occurred unless the dew was closely associated with rain. On 16 days, dew occurred two to several hours before the first 0.25 mm of rain was recorded, but ascospores were never trapped until after rain began. On 11 days, dew followed a rainy period after a 2- to 14-hr interval when the leaves were dry. No ascospores were trapped during nine of the 11 dew periods. On two days when only a 2-hr dry interval separated the rain and dew, a small percentage of ascospores was trapped during the dew periods, i.e., 1.0 and 0.3% of the total ascospores recorded during the combined rain and dew periods.

A fair-weather day was designated as a day without fog or mist and less than 0.25 mm of rain recorded between 0400 and 2000 hours. Rain beginning after 2000 hours had no influence on spore trapping earlier in the day and a negligible effect on spores trapped at night after 2000 hours. Ascospores were trapped on only 10 fair-weather days, and each of these days was closely associated with rain on the previous day. Weather conditions varied on the fair-weather days: three were overcast, two were overcast in the morning but were sunny by noon, three were sunny all day, and two were hazy. Rain the preceding day was light (0.1 cm) on one occasion, moderate (0.53 cm) on two occasions, and heavy (1.12–7.62 cm) on eight occasions. Leaves in the orchard were wet until at least 0500 hours on all 10 fair-weather days on which spores were trapped, but dried by 0900 hours on 7 days, by 1100 hours on 1 day, and by 1300 hours on 1 day. One clear but humid (75–95% relative humidity) fair-weather day was preceded by a day with 6.38 cm of rain, and leaves in the orchard remained wet throughout the day. Six of the fair-weather days were preceded by days with rain beginning by noon, and ascospores recorded during the fair-weather day accounted for 1.9, 3.0, 3.3, 5.5, 8.0, and 38.7% of the total ascospores trapped for the 2-day periods.

Each year there was at least one wet period during which leaves remained wet for 48 hr or more. An examination of these extended wet periods allowed a comparison of airborne ascospore densities on successive days (Table 1). In four of the six extended rainy periods, ascospore density peaked on the first day, and the first two days accounted for 69–100% of the total ascospore catch, regardless of the duration of the wet period. As before, 93–100% of the ascospores were trapped during the daytime interval.

Thirty-one rainy intervals were of sufficient timing and duration to provide a comparison of spore emission during the night and

TABLE 1. Ascospore discharge of *Venturia inaequalis* at the Mast Road Research Orchard in Durham, NH. Spore discharge was monitored during extended wet periods, and the percentage of the total ascospores trapped during the wet period in successive day (0700–1800 hours EST) and night (1800–0700 hours EST) intervals was recorded

Wet interval[w]					Total ascospores trapped during successive day and night intervals (%)										Spores trapped (%)	
Began		Ended		Ascospores[x]												
Hour	Date	Hour	Date	trapped	1800–0700	0700–1800	1800–0700	0700–1800	1800–0700	0700–1800	1800–0700	0700–1800	1800–0700	0700–1800	Night	Day
1700	23 Apr 81	0600	26 Apr 81	51	0	40.4	0	59.6	0	...[y]	...	...	...	...	0	100.0
0700	29 May 82	1400	2 Jun 82	6,030	...	27.5	0	41.9	0.7	6.4	0.2	7.0	0.2	16.2	1.1	98.9
1300	23 May 82	1000	25 May 82	15,834	...	56.4	3.8	27.0	1.0	11.8	...	...	...	...	4.8	95.2
0600	24 Apr 83	0600	27 Apr 83	44,471	0	71.2	0.1	3.8	0.2	18.0	6.7	...	...	...	7.0	93.0
0900	28 May 84	0700	3 Jun 84	1,741	...	77.5	0	20.2	0.6	0.6	1.1	0	0	0[z]	1.7	98.3
0100	23 May 83	0700	25 May 83	453	2.2	93.2	0	4.5	0	...	...	...	...	...	2.2	97.7

[w] Wet interval began when the first 0.25 mm of rain was recorded and ended when leaves on trees in the orchard were dry.
[x] Total number of ascospores of *V. inaequalis* observed while scanning the tape from a Burkard volumetric spore trap at 2-mm (1-hr) intervals, corrected for the proportion of the tape examined and the volume of air sampled.
[y] Leaves dry during the interval, and no ascospores trapped.
[z] No ascospores trapped during the remainder of the wet period.

day (Table 2). On three occasions when rain began at night before 0000 hours and the leaves remained wet until 1200–1400 hours, more than than 98% of the ascospores were trapped between 0700 and 1800 hours. On 21 occasions when rain began at night and the leaves remained wet through 2400 hours the following day, 1.9% of the ascospores were trapped before 0700 hours, 96.7% were trapped between 0700 and 1800 hours, and 1.4% were trapped after 1800 hours. On 6 days when the rain began between 0500 and 1100 hours and the leaves remained wet through 2400 hours, all of the ascospores trapped through 2400 hours were trapped by 1800 hours on 5 days and 99.8% were trapped by 1800 hours on one day. When all 31 trapping intervals were considered, 97.7% of the ascospores were trapped between 0700 and 1800 hours EST, and 2.3% were trapped between 1800 and 0700 hours. Seventy-nine percent of the ascospores trapped at night were trapped from 1800–2000 hours. The highest percentage of ascospores trapped at night compared with the day was 6.7% on 27 April 1983, a cold day with a mean temperature of 6.9 C between 0700 and 2000 hours. Approximately 80% of the spores trapped at night on 27 April 1983 were trapped between 1800 and 2000 hours.

DISCUSSION

The major emissions of ascospores by *V. inaequalis* occurred during clearly defined intervals of the day. Each year nearly all (>97%) of the ascospores were trapped between 0700 and 1800 hours during wet intervals initiated by rain. Most of the remaining 2–3% were trapped during the 2 hr preceding and after the daytime interval. Nearly all of the remaining ascospores were trapped during dew intervals and fair-weather days preceded by moderate to heavy rain and poor drying conditions. These findings are consistent with several earlier studies (2,7,15,18,23) in which few ascospores of *V. inaequalis* were trapped at night. Brook (3) also demonstrated in wind tunnel and laboratory experiments that the release of ascospores from wetted pseudothecia was accelerated 6–8 hr after sunrise, which would correspond to 1000–1300 hours in New Hampshire, the hours when the highest percentage of ascospores were trapped in the present study.

Other orchard spore trapping studies (7,15,18,23) did not compare daytime and nighttime spore trappings, but the data included in these reports are similar to ours and those of Brook (2). Keitt and his co-workers in Wisconsin conducted the first extensive spore trapping studies beginning in 1917. During a rainy period on 21–22 May 1917, when 53.4% of that season's ascospores were trapped, 97.6% were trapped during the daytime (7). In 1924 during rainy periods on 12–15 and 23–24 May that accounted for 98% of the trapped spores for the season, 99.1% were trapped during the daytime (14). We estimate that approximately 90% of the ascospores trapped by Hirst and Stedman in England in 1961 (15) were trapped between 0600 and 1800 hours. The daily periodicity of ascospore liberation is clearly evident in the wet interval from 2 through 5 April 1961 (15). Patterns of ascospore discharge by *V. pirina* Aderh. (19), the pear scab pathogen, are similar to those we observed in *V. inaequalis*.

Numerous studies have reported that ascospore liberation required at least 0.25 mm of rain, but reports of ascospores trapped during dew intervals (2,6,15,18,23) or fair-weather days (15,25) suggested that the discharge mechanism may require less moisture or even no moisture at all and that the mechanism is perhaps more erratic and less predictable than other reports have indicated. An

TABLE 2. Ascospore discharge of *Venturia inaequalis* at the Mast Road Research Orchard in Durham, NH, during three time intervals that delimit early morning (0000–0700 hours EST), daytime (0700–1800 hours EST), and evening (1800–2400 hours EST)

Wet interval[x]				Spores trapped during interval (%)		
Began (hours)	Ended (hours)	Date	Ascospores[y] trapped	0000–0700 hours	0700–1800 hours	1800–2400 hours
Before 0000	1200	28 Apr 82	2,740	0.3	99.7	...[z]
Before 0000	1300	14 May 84	6,454	1.2	98.8	...
Before 0000	1400	2 May 83	23,006	0.1	99.9	...
Before 0000	After 2400	16 May 81	378	2.4	97.6	0
		24 May 82	4,473	0.9	95.7	3.4
		30 May 82	2,545	0	99.2	0.8
		31 May 82	414	4.8	92.8	2.4
		1 Jun 82	435	0	100.0	0
		11 Apr 83	282	3.5	93.0	3.5
		25 Apr 83	1,756	1.1	97.2	1.7
		26 Apr 83	10,997	0.5	99.1	0.4
		20 May 83	999	7.0	93.0	0
		19 Apr 84	1,585	0	97.5	2.5
		24 Apr 84	9,837	0	100.0	0
		4 May 84	21,745	2.2	91.0	6.8
		29 May 84	361	0	99.2	2.8
0000–02000	After 2400	12 May 81	558	1.4	96.2	2.4
		9 May 82	915	1.3	98.7	0
		5 June 82	374	2.7	94.6	2.7
		11 May 83	17,381	0.9	98.5	0.6
		23 May 83	423	2.4	97.6	0
		29 May 83	725	4.1	95.9	0
		12 May 83	8,423	0.7	99.2	0.1
		19 May 83	3,706	4.3	95.7	0
0500–11000	After 2400	29 May 82	1,656	...[z]	100.0	0
		24 Apr 83	31,718	...	99.8	0.2
		30 Apr 83	13,534	...	100.0	0
		13 May 83	2,443	...	100.0	0
		15 May 83	970	...	100.0	0
		28 May 83	1,350	...	100.0	0
		8 May 84	17,108	...	100.0	0

[x] Wet intervals began when the first 0.25 mm of rain was recorded and ended when leaves on trees in the orchard were dry.
[y] Total number of ascospores of *V. inaequalis* observed while scanning the tape from a Burkard volumetric spore trap at 2-mm (1-hr) intervals, corrected for the proportion of the tape examined and the volume of air sampled.
[z] Leaves dry during the interval and no ascospores trapped.

analysis of the weather preceding fair-weather and dew trappings in the present study indicates that in each instance ascospores were released from pseudothecia that had remained sufficiently wetted from a recent rainy period to continue the ascospore discharge in the presence of light. It should be noted that the leaf wetness indicator was adjusted to monitor the surface wetness of leaves on the trees and not the moisture conditions of fallen leaves. Following moderate to heavy rains and poor drying conditions, decaying leaves on the ground may have remained wet and released some ascospores after leaves on the trees had dried.

The fair-weather trappings reported by Hirst and Stedman (15) and Miller and Waggoner (23) may have occurred under similar conditions. Seven of the 10 fair-weather discharges reported by Hirst and Stedman occurred on mornings after rain at night. The remaining three fair-weather trappings were not associated with rain, but did follow dew at night. Comparatively few spores were trapped, and considering the relatively few ascospores involved and the dry conditions, it is not likely that these spores were important in the seasonal development of scab. Miller and Waggoner (23) reported fair-weather discharges on 5, 15, 19, and 24 May 1956. Each of these days was preceded by rain and a heavy discharge of ascospores. They presented no information to indicate when the leaves on the trees or ground dried, but we suggest that the fair-weather discharges were related to the previous day's rain.

Our data support the conclusions of others that dew deposited on decaying leaves on the orchard floor can cause ascospore discharge, but, unless the dew is followed by rain, too few spores are released to be important in the epidemiology of apple scab (2,6,15,18,23). Brook (3) noted in a wind tunnel experiment that ascospores were released in dew at a low rate, and concluded that few ascospores were trapped from the orchard air during dew because few ascospores were released, not because they failed to disperse. Other factors, however, may also contribute to low levels of airborne ascospores during dew intervals. The thickness of the dew film may slow the rate of ascus emergence, and ascospores may be discharged into the water where they can remain trapped. Also, dew usually develops during low light or darkness and in the absence of wind, conditions that repress ascospore discharge and dispersal. Dew periods during the primary scab season in New Hampshire are usually too short to allow infection unless they follow rainy periods closely enough to allow continuous development of germ tubes and appressoria. Of 17 dew periods recorded during the primary scab season in 1984, none met the minimum criteria for infection as described by Mills (24).

Temperature had no measurable effect on the rate of release when the mean temperature during the daytime was above 10 C. Below 10 C the rate of release was slowed, and a slightly higher percentage of the day's ascospores were trapped in late afternoon compared with the warmer days. We noted a 2.5-hr delay in the time when 90% of the ascospores were trapped when temperatures were below 10 C. Hirst and Stedman (15) reported a similar 2-hr delay in trapping 90% of the spores when the temperature was below 11.6 C. The slowed release during cold weather will probably have little effect on scab incidence and management decisions in most instances, but it could be an important consideration when the rain begins in late afternoon, e.g., after 1600 hours. In that case, cold temperatures could delay the first major discharge of ascospores until 0700 hours the following morning, a delay of 15 hr.

The consistent pattern of major discharges of ascospores during the daytime in New Hampshire, Wisconsin, England, and New Zealand suggests that this pattern is widespread. The data also suggest that modification of the criteria for determining infection periods and post-infection activity of fungicides may be warranted. We propose that when rain begins at night, the starting time for determining either Mills' infection periods or after-infection activity of fungicides should be 0700 hours rather than the first recorded hour of rain. No modification of criteria is necessary when the rain begins during the daytime, because the beginning of the rain and the release of ascospores at a high rate are coincident or nearly so.

Our proposal has important implications for scab management strategies that use the identification of Mills' infection periods for scheduling fungicides and the beginning of rain for determining hours of postinfection activity of fungicides. The modification would affect only rainy periods beginning at night that were of sufficient duration to satisfy Mills' criteria (24) but of insufficient duration to satisfy our criteria. For example, a rainy period beginning at 2000 hours and ending (leaves dry) at 1400 hours the following day with a mean temperature of 12 C would satisfy the criteria for a Mills' infection period (24). However, if 0700 hours was the starting time for determining a Mills' infection period, only 7 hr would have elapsed before the wet interval ended; an interval that would be 5 hr less than required to meet the minimum criteria for a Mills' infection period at 12 C. Because an infection period would not have occurred between 0700 and 1400 hours, the interval when nearly all of the ascospores were being discharged, we suggest that for decision-making purposes no infection period should be recorded for the rainy period.

If the wet interval had continued through the day until 0900 hours the following morning (35 hr total wetting), infection would have been indicated by both Mills' criteria and ours. However, the hours of postinfection activity required if the spraying began at 0900 hr would be 26 hr by our criteria vs. 35 hr by Mills' criteria, because the hours of postinfection activity would also be calculated from 0700 hours rather than when the rain began. This difference could mean the selection of a different fungicide, perhaps of lower cost or with a broader spectrum of fungicide activity.

In a well-managed commercial orchard with 2% fruit scab at the time of harvest, our results indicate that ascospores released at night could account for no more than 3% of the toal amount of fruit scab, 0.06%, an insignificant amount of scab. The modification we have proposed assumes that the spores released at night would not cause enough lesions to warrant protection. We believe that this is a safe assumption, based on several years of trials in which trees were left unprotected during infection periods, where the airborne ascospore dose either equalled or far exceeded what could be reasonably expected to occur during night hours in a well-managed commercial orchard (11–13,17,20). These trials and our proposed modifications are the subject of a future paper.

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