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A Revision of Mills's Criteria for Predicting Apple Scab Infection Periods

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ABSTRACT

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A review of published investigations of the relationship between leaf wetness, temperature, and infection of apple leaves by *Venturia inaequalis* indicated that infection by ascospores requires approximately 3 hr less than the interval reported by Mills and Laplante (Cornell Ext. Bull. 711, rev. 1951). Conidia require approximately 2.5 hr more than ascospores to infect apple foliage, rather than two-thirds the time required by ascospores, as stated by Mills. The discrepancy with ascospore infection could be explained by the daily periodicity of ascospore discharge, in which nearly all ascospores are released during the daytime. A revision of Mills's warning system is proposed, which computes primary infection periods from 0700 hr when the rain begins at night and utilizes a new polynomial equation for predicting infection. The impact of the revised criteria on scab warning systems is discussed.

Additional keywords: epidemiology, spore trapping.

In the early 1920s, W. D. Mills, a plant pathologist at Cornell University, began to study sulfur dusts as a replacement for lime sulfur to control apple scab and to develop a strategy to apply sulfur fungicides during rain before infection occurred. The study spanned 20 yr before it was published in 1944 (21). In the mid-1920s, Keitt and Jones (11,12), in Wisconsin, published a laboratory study that related temperature to the minimal hours of continuous wetting needed for infection by ascospores of *Venturia inaequalis*. Mills prepared a table from their data that provided the best fit for temperatures between 5 and 26 C (14). From the mid-1920s to the late 1930s, Mills adjusted the table for orchard conditions on the basis of information from commercial orchards provided by extension agents in New York. Mills quickly found that wet intervals required for infection in orchards were about 1.5 times the number of hours reported by Keitt and Jones (11,12) and altered his table to reflect this difference (F. H. Lewis, *personal communication*). Mills continued to make slight revisions in the table, based on the information received from the extension agents, and by 1937 he had constructed a table that specified the time by which spraying or dusting with sulfur must be completed during a rainy period to control scab (14,15). The table was validated by Lewis (13) in a 3-yr study that included replicated plots in a high-inoculum orchard of susceptible McIntosh apple trees.

The figure in Mills's 1944 publication (21) depicted the approximate hours of leaf wetting required for light, moderate, and severe infection in an orchard containing an abundance of inoculum. This publication was a milestone in plant pathology in that it was the first warning system that included an assessment of risk, i.e., the conditions necessary for three levels of infection. This report and other reports by Mills and co-workers (22–24) provided what is referred to here as the Mills system: 1) a table or figure for predicting three levels of infection by ascospores on the basis of temperature and the duration of leaf wetness and 2) the criterion that the time required for infection by conidia is about one-third shorter than that indicated in the table for infection by ascospores.

Scientists throughout the world have examined the accuracy of Mills's table in their localities. Orchard studies in Italy (25), Belgium (8), and France (7) concluded that Mills's table worked, but no data were reported. Orchard studies with data generally supportive of Mills's criteria were reported from Australia (31), Belgium (41), Yugoslavia (45), and England (34). However, several orchard studies (2,27,29,30,38,40,42) and laboratory studies (11,12,16,25,36,37,39,44) provided data that do not agree with Mills's table, and scab warning systems in Belgium (44), France (30), South Africa (39), and Switzerland (2,38) have modified Mills's scab prediction curves. In England, Preece and Smith (35) validated the Mills system but found that periods of high relative humidity (Smith periods) could be substituted for periods of leaf wetness (Mills periods) to predict infection. In the United States, Jones et al (10) reported that Mills's table more accurately accounted for the appearance of lesions if hours of high relative humidity (90% or greater) after the leaves were recorded as dry were added to the hours of leaf wetness. Numerous laboratory studies (11,12,16,25,36,37,39,44) contradict Mills's statement that conidia can infect in two-thirds the time required for ascospores.

Discrepancies between the Mills system and the studies cited above may be related to differences in identifying the time of inoculation. Ascospores of *V. inaequalis* are discharged primarily in daylight (3–5,18,30,32), and this suggests that ascospores released at night may account for allow percentage of the lesions that develop from any primary infection period. If this is true, then the hours of wetting required for infection reported by Mills would be overestimated, because significant ascospore release would be delayed 1–12 hr for rainy periods that begin at night. Mills did not include this delay when computing his infection periods.

In this paper we analyze and compare published orchard and laboratory data that relate temperature and hours of leaf wetness to scab lesion development, investigate the contribution of ascospores released at night to scab incidence, propose a revision of Mills's criteria for predicting infection by ascospores and conidia, discuss the effect of the revised criteria on the prediction of scab infection under New Hampshire conditions, and discuss the impact of the revised criteria on scab warning systems.

MATERIALS AND METHODS

Assessment of previously published studies. Several graphs were derived from previously published studies that related temperature and hours of leaf wetness to lesion development. In our analysis, the hours of leaf wetness used was the minimum time reported for infection or, if an interval of time was reported, the middle of the interval. For example, if initial infection occurred after 5–8 hr, the time we used was 6.5 hr.

New Hampshire studies. In 1984, seedlings grown from open-pollinated McIntosh apples harvested from the Mast Road Research Orchard, in Durham, NH, were placed 2–3 m from a Burkard spore trap during each rainy period. When rain began during the day (between 0700 and 1800 hr), the seedlings remained in the orchard until 1800 hr, were removed, and then replaced by seedlings that remained until 0600 or 0700 hr the following morning. If the leaves on orchard trees were still wet the following morning, the seedlings were replaced with a third set of seedlings, which remained until 1700–1800 hr. This procedure was repeated as long as the leaves on orchard trees remained wet. Seedlings were hand-misted when replaced in the orchard if it was not raining. When rain began at night (between 1800 and 0700 hr), seedlings remained in the orchard until 0700 hr, when they were replaced as described above. Seedlings removed from the orchard were placed in a mist chamber for at least 12 hr at 15.0 ± 0.2 C to allow deposited ascospores to infect the leaves and were examined 24 days later for lesion development.

The density of airborne ascospores in the orchard was sampled with a Burkard 7-day recording volumetric spore sampler (Burkard Scientific Sales, Ltd., Rickmansworth, England). Recording weather instruments, housed in a standard U.S. Weather Service instrument shelter approximately 3 m from the spore sampler, provided hourly records of rainfall (amount and intensity), temperature, relative humidity, and leaf wetness (20). All times reported are eastern standard time.

A rainy period was referred to as "nighttime" if it began between 1800 and 0700 hr and as "daytime" if it began between 0700 and 1800 hr. The nighttime and daytime intervals were selected to be coincident with the discharge of ascospores, which occurred almost entirely during the daytime interval (18). Six distinct categories of leaf wetness associated with rainy periods of less than 36 hr were examined: day (D) began and ended during a single daytime interval; night (N) began and ended during a single nighttime interval; day/night (D/N) began during the day and ended during the following nighttime interval; night/day (N/D) began during the night and ended during the following daytime interval; day/night/day (D/N/D) began during the day and ended during the following daytime interval; night/day/night (N/D/N) began during the night and ended during the following nighttime interval. Rainy periods of more than 36 hr were composites of the above categories. For each category, the relationship between the prediction of infection according to the Mills system and the prediction according to the criteria we propose was examined.

RESULTS

Assessment of published laboratory and orchard studies. Figure 1A depicts curves for light infection by ascospores (Mills/a) derived from Mills's table (23) and for light infection by conidia (Mills/c) based on Mills's statement that conidia infect in two-thirds the time required for infection by ascospores. These curves are included in Figure 1B–H for comparison with other published data. Table 1 presents the polynomial equations used to generate the curves drawn in Figure 1.

When the minimum hours for infection by ascospores reported in laboratory studies by Keitt (11), Keitt and Jones (12), Moore (26), Sys and Soenen (46), and Schwabe (39) are combined, a curve (Lab/a) fit to the data by multiple regression is nearly identical to the Mills/c curve (Fig. 1B). When the minimum hours for infection by conidia reported in laboratory studies by Schwabe (39), Sys and Soenen (44), Moore (26), and Louw (16) are combined, a curve (Lab/c) fit to the data by multiple regression nearly overlays the Mills/c curve between 4 and 9 C, but at higher temperatures it more closely approximates the Mills/a curve (Fig. 1C). At 15 of 18 temperatures from 4 to 26.5 C, the time required for infection by conidia is longer than that indicated by Mills.

From 14 to 24 C, the average minimum times for infection by ascospores and conidia derived from the Mills system and from the laboratory studies are nearly reversed. The Mills system indicates that ascospores require 3 hr more than conidia to infect leaf tissue at these temperatures, whereas the laboratory data indicate that ascospores require 2.9 hr less than conidia.

In Figure 1D, minimum hours for infection by ascospores from studies by Tosic and Vasic (45), Preece (34), and Schwabe (39) are plotted and compared to values reported in Mills's table (23). The infections occurred on mature trees or on seedlings left in the orchard. A polynomial curve (Orchard/a) fit to the data is closely aligned with the Mills/c curve between 7 and 21 C.

Forecasts for infection by ascospores from three European scab warning systems are compared to the Mills system in Figure 1E. The Belgium curve, reported by Sys and Soenen (44), is closely aligned with the Mills/c curve. It was tested in southern France by Gendrier (7) and rejected in favor of Mills's curve because it led to an excessive number of fungicide applications. The Angers curve, which requires fewer hours than the Mills/a curve to predict infection, is recommended in the Loire Valley in France for orchards with a large amount of overwintered inoculum (30). The Switzerland curve is actually Mills's curve (23) for moderate infection by ascospores, and in eastern Switzerland it is used in scab warning systems that recommend curative fungicide treatments (2,38).

Some researchers (33,39,43) have reported minimum degree-hour accumulations needed during periods of leaf wetness for infection by ascospores. These degree-hour accumulations are plotted in Figure 1F. According to Post et al (33), Scharinga and Meyneke were the first to propose that the hours for light infection reported by Mills could be determined by an equation based on degree-hours. Schwabe (39) developed an infection index based on degree-hour accumulations. Infection was rarely associated with an infection index value of less than 100, and a curve representing this index value nearly overlies the Mills curve for infection by conidia between 5 and 20 C (Fig. 1F). An index value of 125 represented the minimum hours required for light infection (less than 10%) in a high-inoculum orchard (39), and the curve representing this index value is intermediate between the Mills curves for infection by ascospores and conidia. According to Schwabe, control measures were seldom necessary after light infection periods (index 100–149). Average indices required for moderate leaf infection (10–40%) and heavy leaf infection (greater than 40%) in South Africa were 170 and 287, respectively. The wetting intervals required to predict moderate infection in South Africa approximate the Switzerland curve for predicting light infection in Switzerland (Fig. 1E). Studt and Weltzien (43) calculated 140 and 300 degree-hours for light and heavy infection, respectively, in Lebanon. The 140-index curve is similar to the Mills/a curve between 6 and 18 C, and the 300-index curve is similar to the 287-index curve for heavy infection reported by Schwabe (39). All curves based on degree-hours differ from the Mills curves as temperatures increase above 16 C, where the

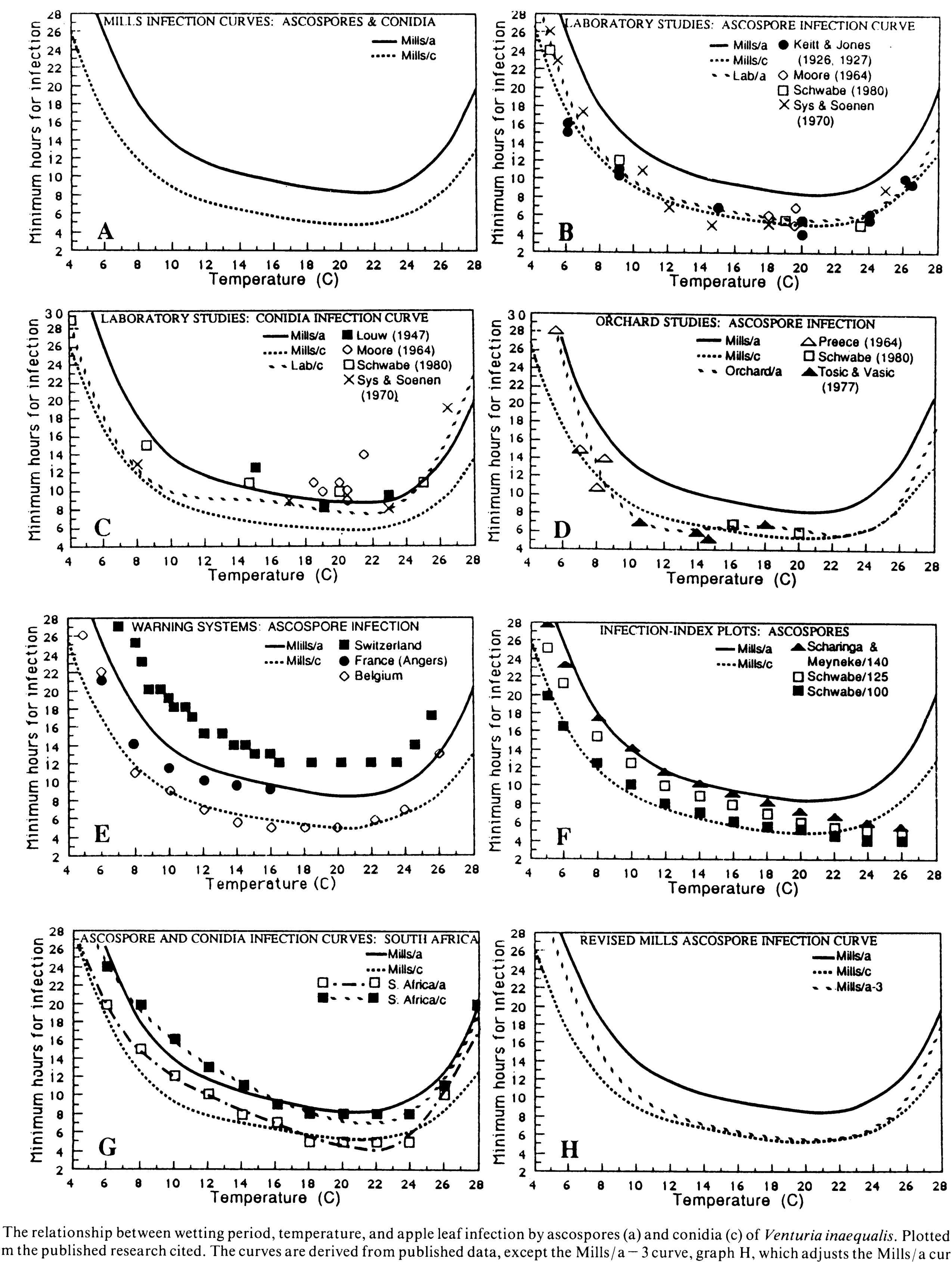

Fig. 1. The relationship between wetting period, temperature, and apple leaf infection by ascospores (a) and conidia (c) of *Venturia inaequalis*. Plotted data are from the published research cited. The curves are derived from published data, except the Mills/a − 3 curve, graph H, which adjusts the Mills/a curve to compensate for the daily periodicity of ascospore discharge.

degree-hour formulae do not reflect decreasing favorability of temperatures for infection above the optimum level.

Figure 1G compares the Mills curves with curves for light infection by ascospores and conidia reported by Schwabe (39). Between 14 and 24 C, Schwabe's data indicate that ascospores require 2.8 hr less than conidia to infect leaf tissue, which is nearly identical to 2.9 hr less for infection by ascospores at these temperatures estimated from the laboratory studies included in Figure 1B and C.

New Hampshire studies. Four rainy periods were analyzed. In each instance, relatively few ascospores were released at night, and they accounted for a very low percentage of the lesions that developed (Table 2). Of 1,009 lesions and a seasonal total of 47,099 ascospores recorded for the four rainy periods, 4% of the ascospores were trapped at night, and 3% of the total lesions developed on seedlings in the orchard during the same nighttime intervals.

Seventy-six rainy periods occurred during the primary scab season in 1981 through 1986 in Durham, NH. Of these, 54 were short rainy periods, with 25 beginning during the day and 29 beginning at night. For each category of short rainy period, the number of rainy periods that occurred, the mean wetting interval, the mean number of infection severity hours (ISH), and the number of light infection periods predicted from Mills's table (24) or the Mills/a − 3 curve in Figure 1H, proposed for our revised Mills (RM) criteria, are summarized in Table 3. ISH is defined as the number of hours of additional time remaining in a wetting period after the minimum requirement for infection (by either the Mills or the RM criteria) has been met.

The basis for developing the Mills/a − 3 curve, shown in Figure 1H, lies in the diurnal periodicity of ascospore discharge and the fact that this phenomenon was unknown to Mills when he developed the curve referred to here as Mills/a (Fig. 1A). If it is assumed that rains beginning at night result in a 1- to 12-hr delay of ascospore release and that the onset of rain is randomly timed, then the mean delay of ascospore release in night rains would be 6 hr. If this mean delay is averaged with numerous daytime infection periods over several years, the end result is that infection by ascospores would appear to take approximately 3 hr longer than the actual minimum time required for infection. Hence, the subtraction of 3 hr from the Mills/a curve to yield the Mills/a − 3 curve. To be used properly, however, one counts wetness duration beginning at 0700 hr. Consider, for example, a wet interval of 15 hr and a mean temperature of 20 C, with the rain beginning at 2400 hr and the leaves drying at 1500 hr. By the Mills criteria, infection would occur 9 hr after the rain commenced, and there would be 6 ISH. By the RM criteria, infection would occur 6 hr after 0700 hr (the first significant discharge of ascospores), and there would be 2 ISH. Use of the RM criteria resulted in a decrease of 4 ISH. The analysis of ISH allows a comparison of the six categories with respect to their potential for scab development; i.e., the greater the value of ISH, the more favorable the infection period for scab development.

The short D and N rainy periods accounted for very few or no

TABLE 1. Polynomial equations for curves depicted in Figure 1

Curve	Polynomial equation[a]	R value[b]
Mills/a	$y = 89.3749 - 18.0034x + 1.5703x^2 - 0.062x^3 + (9.198\text{E}{-}04)x^4$	0.99
Mills/c	$y = 58.8899 - 11.7951x + 1.0244x^2 - 0.0403x^3 + (5.969\text{E}{-}04)x^4$	0.99
Lab/a	$y = 71.2009 - 14.881x + 1.3252x^2 - 0.0534x^3 + (8.062\text{E}{-}04)x^4$	0.97
Lab/c	$y = 76.5384 - 17.6803x + 1.7201x^2 - 0.0731x^3 + 0.0011x^4$	0.96
Orchard/a	$y = 122.3869 - 28.7786x + 2.6028x^2 - 0.1019x^3 + 0.0015x^4$	0.98
S. Africa/a	$y = 64.7714 - 13.0094x + 1.2163x^2 - 0.0532x^3 + (8.673\text{E}{-}04)x^4$	1.00
S. Africa/c	$y = 60.3741 - 9.8398x + 0.8325x^2 - 0.0352x^3 + (5.782\text{E}{-}04)x^4$	0.99
Mills/a − 3	$y = 86.3749 - 18.0034x + 1.5703x^2 - 0.062x^3 + (9.198\text{E}{-}04)x^4$	0.99

[a] y = minimum hours of leaf wetness required for infection; x = mean temperature during wetting interval.

[b] Coefficient of simple correlation that describes the relationship between the model's predicted values and the observed data.

TABLE 2. The development of primary scab lesions on McIntosh seedlings placed in an orchard during the night or day and the number of ascospores of *Venturia inaequalis* trapped, 1984

Rain period				Interval during which seedlings were in the orchard	Lesion development				Ascospores trapped				Ascospores trapped per lesion	
					Number[a]		Percentage of total[b]		Number[c]		Percentage of total[d]			
Number	Date	Begin	End		Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
(1)	5/3–4	2200		2100–0700		14		4		485		2		35
	5/4			0700–1700	388		95		19,160		88		52	
	5/4–5		0700	1700–0700		5		1		2,111		10		422
(2)	5/8	1100		1130–1700	161		95		17,058		99.9		106	
	5/8–9		0700	1700–0700		8		5		50		<0.5		6
(3)	5/13–14	2200		2200–0700		4		1		120		2		30
	5/14		1300	0700–1700	324		99		6,374		98		20	
(4)	5/28	0900		0930–1800	117		94		1,350		78		12	
	5/28–29			1800–0745		0		0		0		0		
	5/29			0745–1700	5		4		361		21		72	
	5/29–30			1700–0700		1		1		20		1		20
	5/30–6/1		0800	0700–0800	2		1		10		1		5	
Season total					977	32	97	3	44,313	2,786	96	4	—	—

[a] Total lesions on 12 McIntosh seedlings.

[b] Percentage of total lesions recorded for the rainy interval.

[c] Total trapped ascospores recorded.

[d] Percentage of total trapped ascospores recorded for the rainy interval.

infection periods with either the Mills or the RM criteria, and only one N/D rainy period was an infection period when computed with the RM criteria. Twenty-two short rainy periods were infection periods according to both the Mills and the RM criteria, and the infection periods differed only in the value of ISH. These 22 infection periods were computed with the RM criteria and compared with the periods computed with the Mills criteria: seven were N/D/N periods, which had a mean increase of 3 ISH with the RM method; seven were D/N periods, which had a mean increase of 2 ISH; and eight were D/N/D periods, which had a mean decrease of 4 ISH. Discrepancy in the prediction of infection periods was found in 10 other short rainy periods: seven (two N and five N/D) of the 30 Mills infection periods were not RM infection periods, and three (one D and two D/N) of the 26 RM infection periods were not Mills infection periods. Nineteen of 22 extended rainy periods were infection periods with the Mills criteria and our criteria.

DISCUSSION

When Mills's figures are adjusted to account for the overwhelming predominance of ascospore discharge during the daytime, the resultant curve, Mills/a − 3 (Fig. 1H), nearly overlies the curves for infection by ascospores developed from laboratory and orchard studies (Lab/a and Orchard/a). Such studies provided a more accurate assessment of the minimum hours of wetting required for infection by ascospores than the orchard studies of Mills (21), Mills and Laplante (23), and Lewis (13), because the time of inoculation was known. The similarity between the Lab/a and Orchard/a curves for infection by ascospores, derived from the laboratory studies using controlled inoculations, and orchard studies by Tosic and Vasic (45), Preece (34), and Schwabe (39), suggests that the minimum periods for infection by ascospores recorded under controlled laboratory conditions are reliable indicators of the minimum periods for infection under orchard conditions if the time of inoculation in the orchard is known.

When conidia are studied, the time of inoculation is known with a fair degree of precision. In the laboratory, suspensions of conidia are placed directly onto the leaves of potted trees; in the orchard, conidia are splash-dispersed from a sporulating lesion to adjacent tissue or to leaves in close proximity at the beginning of rainy periods. Thus, the curves for infection by conidia developed from Mills's study and the laboratory studies should be similar, but longer intervals of leaf wetting were required in the laboratory at all temperatures.

The Lab/c curve, plotted from laboratory data, may identify more accurately the minimum hours for infection by conidia in the orchard than the Mills/c curve, developed from Mills's data. Warning systems that have used the Mills/a curve through the primary and secondary scab seasons for many years have been successful, indicating that it is not necessary to employ the Mills/c curve during the secondary scab season. Warning systems that have used the Mills/a curve only during the primary season have very likely been operating at times when sporulating lesions were present. If conidia require fewer hours than ascospores to infect, then there should have been more failures during the primary scab season. The Lab/c curve is also more closely aligned than the Mills/c curve with the S. Africa/c curve (Fig. 1G), based on Schwabe's data (39) for infection by conidia.

When failures in Mills's warning system have occurred, the cause has been attributed to an error in the method of determining the length of the wetting period or to a high inoculum potential. Jones et al (10) reported that the failures with Mills's table in Michigan could be corrected if the hours of high relative humidity (90% or greater) after the leaves dried were added to the hours the leaves were recorded as wet. Thus, with this procedure, more rainy periods would become infection periods, by the addition of time to certain rainy periods. This approach is questionable, however, since a film of water is required for *V. inaequalis* to infect apple leaves (1,12,17,46,47). An explanation better supported by published studies is that infection actually occurred in fewer hours than Mills's table indicates. Jones's method was incorporated into an electronic scab predictor (9), which was tested successfully in Poland (27) but not in Australia (31). In Australia, Penrose et al (31) reported that Jones's method predicted an unnecessary number of infection periods, compared with a modified Mills system that they had used successfully for 20 yr. This would be expected, particularly with rainy periods that begin at night. The Australian system reduced the length of wetting periods that begin at night by computing infection periods beginning from 0600 hr.

The Angers curve, developed for the Loire Valley in France (29,30), the infection curve developed for Belgium (44), and the 125-degree-hour index curve associated with light infection in South Africa (39) all require fewer hours for predicting infection by ascospores than does Mills's table. In most instances, these curves were developed because Mills's table sometimes failed to predict an infection period, and they support our conclusion that Mills's table overestimates the number of hours required for infection when ascospore release and the start of rain are coincident. In South Africa, Schwabe (39) reported that the 125-degree-hour curve (index 100–149) gives rise to light infection in a high-inoculum orchard. This curve nearly overlies the Angers curve and appears to lend credence to Olivier's conclusion (30) that attributed failures with Mills's table in the Loire Valley to high inoculum levels. However, this seems unlikely, since Mills's table was developed when foliar scab incidence of at least 10% was common in commercial orchards in New York, and the table was validated by Lewis (13) in a high-inoculum orchard. We suggest that these new curves are more accurate because they identify D and D/N infection periods that are not predicted with Mills's curve. The shorter wetting intervals needed to predict infection more accurately identify the number of hours required by ascospores to infect leaf tissue, as reported in the laboratory studies. Failures

TABLE 3. A comparison of the Mills and revised Mills (RM) criteria for predicting apple scab infection periods during the primary scab season in Durham, NH

Rainy period category[a]	Number of rainy periods[a]	Mean duration of leaf wetness (hr)	Number of infection periods		Infection severity hours (ISH)[b]		RM criteria
			Mills	RM	Mills	RM	
Day	5	5.0	0	1	—	2.0	Increased the number of predicted infection periods
Night	6	9.5	2	0	1.5	—	Decreased the number of predicted infection periods
Day/night	12	15.5	7	9	7.8	9.5	Increased the number of predicted infection periods and the mean ISH interval
Night/day	9	10.0	6	1	3.3	2.0	Decreased the number of predicted infection periods and the mean ISH interval
Day/night/day	12	21.9	8	8	10.4	14.4	Increased the mean ISH interval
Night/day/night	10	29.0	7	7	17.4	14.4	Decreased the mean ISH interval
Total	54	—	30	26	—	—	

[a] Includes only rainy periods with three or fewer intervals.

[b] ISH is the mean number of hours leaf wetness available for spores to infect the leaves after the minimum number of hours required for infection has been satisfied according to the prediction criteria.

with Mills's table may have been simply more conspicuous in orchards with higher inoculum levels.

The relationship between temperature and hours of foliar wetting required for ascospores and conidia to infect apple leaves is described mathematically by a fourth-order polynomial equation. It has been reported that the degree-hour formula represents this relationship. However, degree-hour formulae predict infection periods with progressively fewer hours of leaf wetting as the temperature during wetting increases (Fig. 1), and in some instances this causes unnecessary predictions of infection and, consequently, unnecessary fungicide applications. For this reason, we recommend that warning systems employ a curve based on a polynomial equation.

It is not unreasonable to assume that during Mills's extended study approximately 50% of the rainy periods began at night and that the mean delay in significant ascospore release for all rainy periods was approximately 3 hr. In New Hampshire during the primary scab season in 1981–1986, 39 of 76 rainy periods began at night, with a mean delay in significant ascospore discharge of 7.5 hr, and 37 rainy periods began during the day. Thus, nearly 50% of the rainy periods began at night, and the mean delay in ascospore release was 3.75 hr.

The Mills/a − 3 curve is similar to the curve used in Belgium (2,38), to the curve for light infection by ascospores reported by Schwabe (39), to the Angers curve (27,28) and the 125-degree-hour curve (39) at lower temperatures, and to the Lab/a and Orchard/a curves. The Mills/a − 3 curve is best suited for orchards with highly susceptible cultivars and high inoculum potential, since most of the curves that are similar were developed under these conditions. Curves that require more hours of leaf wetting to predict an infection period may be more efficient in scheduling fungicides in orchards with low inoculum potential or with cultivars less susceptible to scab. Warning systems in South Africa (39) and Switzerland (2,38) utilize such curves, presumably because commercial orchards there have a low inoculum potential, but the extent of weather favorable for scab infection may also be important.

The RM warning system we propose for predicting primary and secondary apple scab infection periods is presented below. In the primary season before lesions appear, when a rainy period begins during the day, between 0700 and 1800 hr, an infection period is computed from the first hour rain is recorded; when a rainy period begins at night, between 1800 and 0700 hr, an infection period is computed from 0700 hr; the Mills/a − 3 curve (Fig. 1H) is consulted to predict an infection period. In the primary season after lesions appear, an infection period is computed from the beginning of all rainy periods; the Mills/a − 3 curve is consulted to predict an infection period. (The Mills/a − 3 curve should be consulted even though lesions are present, because the minimum time for infection by ascospores is less than that for conidia at each temperature.) In the secondary season (after 95% of the ascospores have been discharged), infection periods should be computed from the beginning of all rainy periods; the S. Africa/c curve (Fig. 1G) is consulted to predict an infection period.

We are not the first to recommend that ascospores released at night should be ignored when primary infection periods are determined. A warning system that includes this concept has been used successfully for more than 20 yr in Australia (31), and Schwabe (39), in South Africa, recommended that wetting periods beginning at night should be measured from dawn if an orchard has a low inoculum potential and conidial inoculum is absent. The warning system we propose differs from Schwabe's in several respects: the delay in identifying the beginning of an infection period should be used only with rainy periods that begin between 1800 and 0700 hr; 0700 hr should replace dawn as the beginning time for computing infection periods when the rain begins between 1800 and 0700 hr; and this criterion should be used in orchards with low or high inoculum potential.

Our criteria for recording nighttime rains may have avoided the failures of Mills's system in an orchard study in Belgium (41), in which scab was not recorded for 27% of the infection periods predicted with Mills's criteria. In New Hampshire during the primary season in 1981–1986, 23% of the wetting periods (two N and five N/D) were predicted infection periods with Mills's criteria but not with our criteria. Also, in Belgium there were two instances of scab that were not predicted, and in New Hampshire one D and two D/N rainy periods were predicted as infection periods with our criteria but not with Mills's criteria. We did not record whether infection actually occurred, nor do we know which categories of rainy periods were associated with the failures of Mills's criteria in Belgium. However, the similarity between the percentage of failures of Mills's criteria in Belgium and the percentage of corrections with our criteria suggests that our criteria could account for the failures.

Our system does not distinguish between light, moderate, and heavy infection periods. Mills (21) was the first to use these terms to identify the severity of scab development, but he never defined them, and consequently they have often been misused. The curves were determined by Mills after examining a few wet periods when growers sprayed at different times after infection (F. H. Lewis, *personal communication*). The amount of infection that occurred was compared with the time of fungicide application. Mills established a simple ratio (hours of leaf wetness to noticeable increase in scab incidence) that explained the data and then developed the curves for moderate and heavy infection. Unfortunately, Mills never published information that identified the percentage of increase in scab associated with each curve. It is our understanding that with a given amount of inoculum, the curves for moderate and heavy infection identify the additional time the leaves must remain wet for a noticeable increase in scab incidence. The curves have been misinterpreted to mean that the prediction of a moderate or heavy infection period will actually result in moderate or heavy infection. However, variables such as the amount of inoculum available, cultivar susceptibility, and tree growth stage must also be considered to forecast severity of infection. The development of a system that integrates an infection curve with the variables inoculum dose and cultivar resistance, as proposed by MacHardy and Jeger (19), Oberhofer (28), and Olivier (29), would provide a more meaningful and comprehensive value for assessing risk and making scab management decisions.

Our warning system implies that ascospores released during the nighttime interval should be ignored, but is there sufficient evidence to justify ignoring these ascospores and the lesions they cause? The triggering of ascospore discharge by light and the major release of ascospores during the daytime are well documented (2–4,18,32), and the results of our seedling study suggest that ascospores released at night account for a very low percentage of the lesions that develop from an infection period. We are not aware of any published studies that investigated the contribution of spores discharged at night during individual primary infection periods to the incidence of foliar and fruit scab at harvest. However, we have not detected fruit infection in New Hampshire orchards when trees were left unsprayed during infection periods when the airborne inoculum density exceeded what could reasonably be expected to occur at night in a commercial orchard. If we assume that an orchard in which 10% of the leaves are scabbed at the time of leaf fall produces approximately 100,000 ascospores per square meter in a year (6), we can estimate the maximum nighttime airborne ascospore dose and can compare this to levels of scab that have resulted from leaving trees unsprayed during infection periods with known airborne ascospore doses. If 50% of the ascospores in such an orchard were mature and capable of being discharged (50,000 ascospores per square meter), no more than 5% (2,500 ascospores per square meter) of those available would be discharged during darkness (18). If these ascospores were discharged at a uniform rate over a period of 2 hr and were uniformly dispersed in the air 2 m above the orchard floor, and if individual spores settled to a substrate or drifted from the orchard within 12 min of being discharged, then the airborne ascospore density would not exceed approximately 63 ascospores per cubic meter. This is a very conservative estimate of the maximum airborne ascospore dose for a commercial orchard during night hours. It assumes a high inoculum dose, 100% efficiency in discharge and dispersal, and a long residence time for inoculum after release. During 1981–1985, we left McIntosh and Cortland trees unprotected during five infection periods in which the airborne ascospore dose, as measured by a Burkard volumetric spore trap, was less than or equal to 63 ascospores per cubic meter. No significant increase in fruit infection resulted from the exposure of trees to this level of airborne inoculum. Although these ascospores were not all released at night, there is no reason to believe that the results would not apply to similar airborne ascospore densities at night. Thus, it seems unlikely that the low incidence of scab lesions caused by ascospores released at night during the early portion of the primary scab season would result in significant fruit scab at harvest if fungicides effective in controlling apple scab are timed according to the RM criteria and are applied properly.

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