Use of a Rainfall Frequency Threshold to Adjust a Degree-Day Model of Ascospore Maturity of *Venturia inaequalis*

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ABSTRACT

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Estimates of ascospore maturity generated by a model developed previously in New Hampshire, United States, were compared with the cumulative release of ascospores in southern Norway as monitored by volumetric spore traps at one site for 12 years, and at two additional sites for 2 years. In locations and years with frequent rain events, model-estimated ascospore maturity closely approximated observed ascospore release. However, in years with protracted dry periods of 1 to 3 weeks with no or little rain, not only was spore release delayed, but release continued to lag behind predicted maturity even after several rain events subsequent to the dry interval. By halting degree-day (base = 0°C) accumulation if 7 consecutive days without rain occurred, accuracy of the model during “dry” years was greatly improved, without substantially affecting accuracy in “wet” seasons. With minimal additional effort on the part of the user, this simple modification increases the accuracy of model-derived estimates of ascospore maturity when lack of rain slows ascospore maturation.

Additional keywords: integrated pest management

Apple scab is caused by the ascomycete *Venturia inaequalis* (Cooke) G. Wint. Ascospores formed within pseudothecia in infected, overwintered apple leaves serve as primary inoculum during periods of rain in spring and early summer. Many authors have studied the seasonal distribution of ascospore release in *V. inaequalis* (1–5,10–12,15,22,23,25,26,33–38,40). Although the primary season for ascospore release typically lasts 6 to 10 weeks, the period of major spore release can be much shorter. Usually, the first mature ascospores are ready to be released at bud break of the apple tree. Depending on the frequency of rainfall, the peak in release usually occurs from the tight cluster stage to the petal fall stage of fruit bud development. A critical time for spraying against apple scab is during the major period of ascospore release, which is concurrent with the prebloom expansion of cluster leaves. When the ascospore supply is depleted in early summer, the interval between fungicide sprays for scab usually is extended and, in some cases, spraying for scab may cease. Thus, it is of great utility to accurately

describe the distribution of ascospore maturity and release in *V. inaequalis*, in particular the exhaustion of the ascospore supply.

Models have been developed to estimate the maturation of ascospores in *V. inaequalis* (5,14,16,21). These models are based on temperature sums or temperature sums combined with moisture data. Gadoury and MacHardy (5) in New Hampshire, United States, developed a model (NH model) to estimate the cumulative percentage of matured ascospores, based on degree-day (DD) accumulation starting at the first appearance of mature ascospores. The model predicts 50, 95, and 99% spore maturation at 250, 420, and 490 DD (base temperature 0°C), respectively. The model is widely used and appears to provide estimates of ascospore maturity that are as accurate as many direct methods of assessment in areas with relatively frequent rain, such as New Hampshire and New York, United States (7).

St-Arnaud and Neuman (29) evaluated the New Hampshire model in Québec, Canada. In most cases, the model predicted 100% maturation much earlier than the observed cessation of spore trapping. Cumulative ascospore release sometimes lags behind cumulative maturity due to the temporal distribution of rain events, incomplete release during brief rains, or suppressed release during nighttime rains (8,9,17); thus, the lag observed by St-Arnaud and Neuman (29) was not unusual.

However, periods of extremely dry weather can slow or stop ascospore maturation (13–15,24,27,39). James and Sutton (13) in North Carolina found that dry periods in spring delayed ascospore maturation in the field. In the laboratory, the pseudothecial development rate was retarded at a water saturation deficit greater than 85%, and there was no pseudothecial development in air-dried leaves. James and Sutton (14) obtained the best correlation between DD accumulation and pseudothecial development by excluding DD accumulation on days where rainfall was 0.25 mm or less and duration of 100% relative humidity (RH) was 12 h or less per day.

Weather in spring and early summer in the fruit-growing regions of Norway varies greatly with location and year. Southwestern Norway receives more frequent rain than southeastern Norway. In the latter region, periods of 1 to 3 weeks with little or no rain are common during the season for ascospore release in *V. inaequalis*. Under these circumstances, we have observed that estimates of ascospore maturity generated by DD models deviate greatly from observed trapping of ascospores (30,31). The model first described by Gadoury and MacHardy (5) has certain practical advantages for integrated pest management programs, in that it is very simple to use and has been widely studied under high-rainfall conditions (7). The present investigation was conducted to adapt the above model to areas where drier conditions prevail in some years.

MATERIALS AND METHODS

Burkard 7-day recording volumetric spore traps (Burkard Manufacturing Co Ltd., Rickmansworth, Hertfordshire, UK) were installed in different apple-growing regions of Norway during the primary inoculum seasons of 1990–95, 1997–2001, and 2003 at Ås, 1991 and 1992 at Svelvik, and 1993 and 1994 at Hjelmeland. The first two locations are in southeastern Norway and the latter in southwestern Norway. Approximately 4 m² of the orchard floor at each site was covered with heavily infected apple leaves in the fall, and the spore trap was installed at the center of this area prior to bud break the following spring. Leaves were held in place over winter with a plastic screen and exposed to rain and snow. To prevent earthworms from consuming the leaf litter during winter and spring, the soil

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of the study area was drenched with endosulfan (Thiodan 50WP, Bayer CropScience, RTP, NC, USA) at 12 g a.i./liter, thiophanate-methyl (Topsin-M WG, KVK Agro A/S, Lyngby, Denmark) at 0.5 g a.i./liter, or copper oxychloride (Kopperkalk Bayer, Bayer CropScience, RTP, NC, USA) at 2.1 g a.i./liter prior to placing the leaves. Operation of the traps and microscopic preparation of recording tapes was carried out as described previously (30), and the number of ascospores of *V. inaequalis* recorded each hour was noted.

Electronic data loggers (model KMS-P, Anton Paar KG, Graz, Austria; or model Instrumenttjenesten A/S, Ås, Norway) provided hourly records of precipitation, temperature, RH, and leaf wetness at each site. Each device had two leaf wetness sensors, one placed above the canopy and the other within the canopy of an apple tree. Temperature and RH were measured 1.5 to 2 m aboveground in weather shelters or radiation shields. Additional precipitation data at Ås in 1990 and 1991 were obtained from a rain gauge with 0.1-mm accuracy at a meteorological station situated approximately 1 km from the orchard. The rain gauge at Svelvik in 1991 measured rain in 0.1-mm increments, whereas the gauges at other locations and years measured rain in 0.2-mm increments.

For the purpose of generating estimates of ascospore maturity from the previously-described model (5), DDs (base = 0°C) were accumulated beginning when 50% of the flower buds on either cv. Gravenstein or Summerred showed the first green tissue, a phenological stage closely associated with the first appearance of mature ascospores (5,7,35). The estimated cumulative ascospore maturity in *V. inaequalis*, according to the New Hampshire DD model (5), was compared with actual cumulative ascospore release as recorded by the spore traps.

To adjust the estimates provided by the NH model for periods of dryness, we used a variable number of rain-free days, from 4 to 10 in number at 1-day increments, to “turn off” DD accumulation, thereby halting any increase in estimated maturity. Unadjusted DD accumulation was calculated from the average of daily maximum and minimum temperatures. Adjusted DD accumulations began at green tip, but accumulation ceased after 4 to 10 days without measurable precipitation. No precipitation was defined as less than 0.2 mm (the minimum measurable by the data loggers) and days on which only dew or fog occurred for less than 12 h were considered dry days.

Effects of the various rainfall frequency thresholds (RFTs) upon model performance were evaluated as follows. Because the NH model had provided acceptably accurate estimates under conditions where moisture was nonlimiting in Norway (31) and elsewhere (7), performance during “dry” versus “wet” years was evaluated

separately, to insure that any improvements of forecasts for “dry” years did not come at the expense of accuracy in the more common “wet” years. “Dry” years were defined as years in which the difference between unadjusted versus adjusted DD accumulation at 95% estimated maturity, using an RFT of 4 days, exceeded 200 DDs; and included the years in which the largest deviations between observed discharge and estimated maturity occurred. Using this criterion, dry years were identified for six site-year combinations at Ås in 1990, 1991, 1992, 1994, and 1997, and at Svelvik in 1992. Performance of the model using adjusted or unadjusted DD accumulations calculated using each RFT value in wet and dry years was evaluated by (i) linear regression of observed ascospore discharge against estimated ascospore maturity for the pooled data of all wet or dry years and (ii) comparison of the date of 95% ascospore release to the date of estimated 95% ascospore maturity for each site-year combination.

RESULTS AND DISCUSSION

The total seasonal number of airborne ascospores counted in microscopic transects of the recording tape from the Burkard traps averaged 31,189, and ranged from 3,511 to 92,108. The mean hourly density of airborne spores at each study site exceeded 10 ascospores/m³, the minimum level of detection of the volumetric trap (6), during all rain events, and was adequate to construct seasonal distributions of ascospore discharge. The duration

of ascospore trapping ranged from 46 to 97 days. The number of days from the initial spore release to 95% spore release ranged from 39 to 88 days. DD accumulation (base = 0°C) at the time of 95% ascospore release ranged from 393 to 1,305.

In previous reports on the ascospore maturity model (5,7), the green tip stage of apple fruit bud development has been suggested as a starting time (biofix) for DD accumulation, because this growth stage generally is coincident with the first appearance of matured ascospores (20). If several days separate the two events, the cooler prevailing temperatures at bud break typically result in little DD accumulation during the interval (18). We found this to be the case in the present study (Table 1). In 11 of 16 site-year combinations (Ås 1990, 1991, 1994, 1995, 1997, 1998, 2001, and 2003; Svelvik 1991 and 1992; and Hjelmeland 1993), ascospores were trapped during the first rain event following green tip (Table 1), and not before. In two of the remaining cases (Ås 1992 and 1993), ascospores were first trapped during the rain event which immediately preceded green tip (Table 1), but with less than 50 DDs separating the rain event from the date of green tip. In the remaining three cases (Ås 1999 and 2000, and Hjelmeland 1994), no airborne ascospores were detected during the three to four rain events that occurred after green tip. However, during the above rain events, temperatures averaged 3.4°C, and ranged from 1.0 to 6.6°C, which were within the temperatures shown to inhibit ascospore

Table 1. Temporal and heat unit (degree days, base = 0°C) proximity of the green tip phenophase of apple fruit buds to trapping of the season's first ascospores by a Burkard Volumetric Spore Sampler operated in three regions of Norway

Location, year	Date of green tip ^a	First spores trapped ^b	Degree days ^c
Ås			
1990	1 April	2 April	6
1991	15 April	27 April	79
1992	21 April	13 April	(35)
1993	16 April	5 April	(49)
1994	22 April	26 April	40
1995	17 April	17 April	0
1997	14 April	29 April	55
1998	15 April	16 April	4
1999	10 April	30 April	115
2000	14 April	21 April	46
2001	28 April	29 April	13
2003	20 April	27 April	53
Svelvik			
1991	10 April	11 April	7
1992	7 April	13 April	31
Hjelmeland			
1993	17 March	20 March	9
1994	1 April	13 April	25

^a Date upon which 50% or more of the fruit buds on cvs. Gravenstein or Summerred had reached the green tip stage of development.

^b Date of rain event in which first spores were trapped. This was the date of the first rain event after green tip at Ås in 1990, 1991, 1994, 1995, 1997, 1998, and 2001; at Svelvik in 1991 and 1992; and at Hjelmeland in 1993.

^c Degree days (base = 0°C) accumulated during the interval between the green tip stage of fruit buds and the first detection of airborne spores by a Burkard volumetric spore sampler. Values in parentheses indicate years in which ascospores were trapped during a rain event that occurred before green tip.

release in previous studies under laboratory (32) and field (19) conditions. Ascospores were trapped at Ås in 1999 and 2000 during the first rain event after green tip in which temperatures were above 8°C, and at Hjelmeland during a rain event with an average temperature of 5°C (Table 1). Relatively few DDs accumulated between green tip and the first detection of airborne ascospores, with the exception of Ås in 1999 (Table 1). We believe that the delayed detection of airborne ascospores in this case was most likely due to suppression of ascospore release by cold, rather than a

lack of mature ascospores. This is supported by an excellent fit of observed ascospore release to estimated ascospore maturity ($r^2 = 0.94$) for this site-year combination, and by the accurate estimation of the date of 95% ascospore discharge using both unadjusted and adjusted DD accumulations at Ås in 1999 (Table 2). The green tip stage of fruit bud development appears to be a useful, reliable, and easily assessed event (28) for the purpose of starting DD accumulations to drive the spore maturity model.

RFT values from 4 to 7 days produced successively higher degrees of correlation

between observed ascospore release and estimated ascospore maturity, but RFT values of more than 7 days resulted in progressively lower correlations. For simplicity, utility, and illustration, only results for the unadjusted values and for RFT values of 4 and 7 days are shown graphically (Figs. 1 and 2). When data from the six site-year combinations identified as dry were pooled, regression of estimated ascospore maturity based upon unadjusted DD accumulation against observed ascospore release yielded the following (Fig. 1A):

$$Y = 0.87 + 1.44X, r^2 = 0.84, s = 12.5 \quad (1)$$

Similar regressions performed using RFT values of 4 (Fig. 1B) and 7 (Fig. 1C) yielded the following (Fig. 1B):

$$Y = -2.59 + 0.94X, r^2 = 0.91, s = 10.2 \quad (2)$$

and (Fig. 1C):

$$Y = 1.61 + 1.05X, r^2 = 0.96, s = 7.1 \quad (3)$$

Thus, in dry years, estimated maturity lagged considerably behind observed discharge (Fig. 1A). The use of an RFT of 4 days improved the correlation between observed release and estimated maturity (Fig. 1B), and increasing the RFT to 7 days further improved the correlation and decreased the standard error of the regression (Fig. 1C).

In wet years, regression of observed ascospore release against estimated ascospore maturity based upon unadjusted DD accumulation yielded the following (Fig. 2A):

$$Y = 2.12 + 1.00X, r^2 = 0.90, s = 13.5 \quad (4)$$

Similar regressions performed using RFT values of 4 (Fig. 2B) and 7 (Fig. 2C) yielded the following (Fig. 2B):

$$Y = -4.05 + 0.88X, r^2 = 0.81, s = 15.6 \quad (5)$$

and (Fig. 2C):

$$Y = 1.38 + 0.96X, r^2 = 0.86, s = 13.4 \quad (6)$$

Using an RFT of 4 days during wet years apparently overcorrected the DD

Table 2. Date of observed 95% ascospore release by *Venturia inaequalis* compared with the date of 95% ascospore maturity as estimated by an adjusted or unadjusted degree-day (DD) model

Location, year ^b	Observed 95% release ^c	Date of estimated 95% ascospore maturity ^a	
		Adjusted model	Unadjusted model
Ås			
1990*	31 May	20 May	5 May
1991*	19 June	18 June	30 May
1992*	10 July	13 June	24 May
1993	31 May	29 May	27 May
1994*	22 June	12 June	30 May
1995	3 June	5 June	5 June
1997*	22 June	15 June	4 June
1998	2 June	5 June	31 May
1999	3 June	4 June	3 June
2000	29 May	30 May	20 May
2001	8 June	14 June	3 June
2003	4 June	1 June	30 May
Svelvik			
1991	16 June	4 June	28 May
1992*	1 July	24 June	24 May
Hjelmeland			
1993	17 May	21 May	19 May
1994	31 May	1 June	31 May

^a Adjusted model initially uses DDs (base = 0°C) accumulated beginning at the green tip stage of apple fruit bud development to estimate the cumulative percentage of matured ascospores, but ceases to accumulate DDs after 7 consecutive days without measurable rain (rainfall frequency threshold [RFT] = 7). DD accumulation then resumes when a rain event terminates the dry interval. Unadjusted model uses all DDs accumulated beginning at the green tip stage of apple fruit development. In the original description of the spore maturity model (5), a DD accumulation of 420 DDs after green tip corresponded to an estimate of 95% cumulative ascospore maturity.

^b Years followed by an asterisk are defined as “dry”, in which the difference between unadjusted versus adjusted DD accumulation at 95% estimated maturity, using an RFT of 4 days, exceeded 200 DDs.

^c Date of observed 95% release. Ascospore release was recorded at each site by a Burkard volumetric spore sampler.

Fig. 1. Maturity of ascospores as estimated by a degree-day (DD) model versus the observed cumulative percentage of ascospores trapped for six site-year combinations in Norway categorized as “dry” years (i.e., >200 DDs difference between corrected and uncorrected DD accumulations at 95% ascospore maturity). **A**, Maturity estimated by DD accumulation from bud break of apple, no correction for lack of rainfall. **B**, Maturity estimated only from DDs accumulated within 4 days of a previous rain event. **C**, Maturity estimated only from DDs accumulated within 7 days of a previous rain event.

model, resulting in a substantially reduced correlation of observed versus estimated values, and inflation of the standard error of the regression. Although actual moisture levels in the leaf litter were not monitored in our study, our results indicate that, in general, leaf moisture content was sufficient for continued ascospore development for more than 4 days after a rain event.

Application of an RFT of 7 days during wet years also reduced the correlation reported for equation 4, but to a lesser degree than when an RFT of 4 days was used. Furthermore, there was no increase of the standard error of the regression, nor was there a significant difference ($P = 0.05$) between the slope coefficients of equations 4 and 6. In consideration of the above effects, we selected an RFT of 7 days as the most appropriate value to adjust DD accumulation during dry years, without adversely affecting the correlation between observed ascospore discharge and estimated ascospore maturity during wet years. Our results indicate that leaf moisture content, on average, declines to a level which markedly slows or completely stops ascospore maturation after approximately 7 days without measurable rain, at least in the climatic conditions of our study area.

The original spore maturity model described by Gadoury and MacHardy (5) has been shown to accurately describe the seasonal maturation of ascospores when moisture is not limiting, both in the present study (Fig. 2A) and in a recent article by Gadoury et al. (7), which compared unadjusted model estimates of ascospore maturity with observed ascospore discharge for 14 site-year combinations in New York and New Hampshire. The data reported by Gadoury et al. (7) were not analyzed separately as wet and dry years, because all but one of their site-year combinations would have been categorized as wet using the criteria applied in the present study (D. M. Gadoury, *unpublished*). However, protracted dry intervals can occur even in areas with relatively frequent rain. Several

previous studies have indicated that dry conditions retard the rate of ascospore maturation (13–15,24,27,39). The present study demonstrates the degree to which maturation can be slowed or stopped due to protracted dryness under field conditions, resulting in unadjusted estimates of cumulative ascospore maturity lagging behind observed cumulative discharge. For example, according to the maturity model, cumulative ascospore maturity should exceed 99% by 490 DDs after bud break (5). At Ås in the dry season of 1992, 490 DDs were accumulated before heavy daytime rains occurred on 8 June, and again on 13 June. Still, approximately 14% of the season's ascospores remained to be trapped after these rain events. A similar disparity between expected release (based upon estimated maturity) and observed release during rain events favorable for ascospore discharge was seen at Svelvik in 1992.

The use of RFTs in conjunction with the NH model (5), as suggested earlier by the present authors (31), was evaluated by Rossi et al. (25) in Italy. Rossi et al. (25) reported that model-estimated ascospore maturity was more closely aligned with observed ascospore trappings when an RFT of 4 days or less was applied to accumulated DDs. Unfortunately, Rossi et al. (25) used a separate and unrelated model from North Carolina (14) to identify the starting point of DD accumulation for the NH model, rather than the recommended stage of apple fruit bud development (5,18), and did not separately analyze wet versus dry years. Thus, it is difficult to make direct comparisons between their findings and the present study. Nonetheless, the improved fit of the NH model forecasts when used with RFT in a Mediterranean climate is encouraging.

The date upon which the supply of ascospore inoculum is exhausted is of particular interest to those involved in management of apple scab, because it can signal the switch to a less-intensive deployment

of fungicides. Thus, an important evaluation of our modifications to the spore maturity model would be to assess how it affected the prediction of the date of 95% ascospore release from the estimated date of 95% ascospore maturity during wet and dry years. This evaluation is reported in Table 2. As expected, there was little difference between the estimated dates of 95% ascospore maturity with or without use of an RFT of 7 days during wet years (Table 2). However, among the six dry site-year combinations, the date of 95% cumulative maturity differed from the observed date of 95% ascospore release by an average of 10.5 days, and the difference ranged from 1 to 27 days when the RFT of 7 days was applied (Table 2). In comparison, the date of 95% cumulative maturity differed from the observed date of 95% ascospore release by an average of 28.5 days, and the difference ranged from 18 to 47 days when no RFT was used (Table 2). The date of 95% ascospore release can be estimated to occur once a daytime rain event of sufficient quantity and temperature (e.g., >2.5 mm of rain at >10°C) follows the date of 95% ascospore maturity (8,19). Thus, the use of an RFT of 7 days would have provided a more accurate estimation of the date of 95% ascospore release in dry years.

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Fig. 2. Maturity of ascospores as estimated by a degree-day (DD) model versus the observed cumulative percentage of ascospores trapped for 10 site-year combinations in Norway categorized as "wet" years (i.e., <200 DD difference between corrected and uncorrected DD accumulation at 95% estimated maturity). A, Maturity estimated by DD accumulation from bud break of apple, no correction for lack of rainfall. B, Maturity estimated only from DDs accumulated within 4 days of a previous rain event. C, Maturity estimated only from DDs accumulated within 7 days of a previous rain event.

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