Forecasting the Seasonal Maturation of Ascospores of *Venturia inaequalis*

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Scientific Contribution 1299 from the New Hampshire Agricultural Experiment Station.
Accepted for publication 8 October 1984.

ABSTRACT

MacHardy, W. E., and Gadoury, D. M. 1985. Forecasting the seasonal maturation of ascospores of *Venturia inaequalis*. Phytopathology 75:381-385.

A system is presented that, at the time of apple bud break, can forecast maturity of ascospores of *Venturia inaequalis* for an entire growing season. The system was developed in two steps. In the first step, a regression equation based on historical weather data was used to forecast degree-day accumulation from a phenological date to some future date. Based on the forecasted degree-day accumulation, ascospore maturity was then estimated by using a second model that described the relationship between ascospore maturity and degree-day accumulation. From 1979 to 1984, the forecasting system predicted the date of 10% ascospore maturity to within 4 days and the date of 90% ascospore maturity to within 2 days in 5 of 6 yr. The forecasting system can be adapted to areas other than New Hampshire and may be used to supplement or replace microscopic assessments of ascospore development in apple scab management programs. The system can identify periods of relatively rapid or slow inoculum accumulation during ascospore maturation. Applications of the forecasting system in timing fungicide sprays to control apple scab are discussed.

Scab is a serious disease of apples in temperate regions because the causal fungus, *Venturia inaequalis* (Cke.) Wint., can infect the leaves and fruit from bud break to harvest whenever wet periods of sufficient duration occur. The primary inoculum is produced within pseudothecia in infected leaves that overwinter on the orchard floor. In New Hampshire, mature ascospores are usually available for discharge during rainy periods from the silver tip or green tip stage to the petal-fall stage of McIntosh fruit bud development.

There have been several approaches to assessing the progress of ascospore maturation. Methods of direct assessment, such as microscopic examination of crushed pseudothecia (5,16) or the quantification of ascospores collected in wind tunnels (3,8,9), can provide accurate measurements of ascospore maturity, but they are time-consuming, especially when used extensively in disease management programs. Szkolnik (17) monitored ascospore maturation for 16 yr in New York to determine if ascospore maturation was correlated with apple tree phenology. The first mature ascospores usually appeared between the silver tip and green tip stages of fruit bud development of cultivar McIntosh, but the yearly variation in ascospore maturity at various later growth stages was too great to allow use of tree phenology as an indicator of ascospore development. Indirect methods of assessing ascospore maturity have focused on the use of mathematical models to relate the cumulative percentage of matured ascospores to degree-day accumulation. The starting point for degree-day accumulation may be a calendar date, e.g., 1 February (10), or a phenological date (such as leaf fall [13] or the first appearance of mature ascospores [6]). Three such models have been reported (6,10,13). One model, which was developed in North Carolina (10), was used to estimate pseudothecial development from the initiation of asci to the final stages of ascospore maturation, but it was not suitable for estimating ascospore maturity from 1979 to 1984 in New Hampshire (D. M. Gadoury, *unpublished*). A second model, which was developed in New York, was not accurate in Michigan (13), North Carolina (15), or New Hampshire (4). A third model, which was developed in New Hampshire (6), was validated by field studies in New Hampshire, New York (6), and Pennsylvania (D. M. Gadoury, *unpublished*). The New Hampshire model (4), based upon degree-day accumulation after the first appearance of mature ascospores, was used to estimate the cumulative percentage of mature ascospores. A limitation shared by all of these models is that they can only estimate the cumulative percentage of mature ascospores up to the current date. They cannot be used to forecast the cumulative percentage of mature ascospores for any future date, and to call them predictive models would be a misnomer.

Forecasts of ascospore maturity would provide valuable information for scheduling fungicide sprays during the primary infection season for apple scab. Long-range forecasting of ascospore maturity could also be useful in integrating fungicide, insecticide, and miticide applications. Our objective was to develop a means of forecasting the cumulative percentage of mature ascospores of *V. inaequalis* with a level of accuracy suitable for incorporation into integrated disease and pest management programs.

MATERIALS AND METHODS

Degree-day accumulation model. Twenty-six years of daily temperature minima and maxima for Durham, NH (1949–1975 inclusive) were used to develop a quadratic equation for forecasting degree-day accumulation (base, 0 C) from 15 March to 15 June, which is the period during which ascospores of *V. inaequalis* can mature in New Hampshire. The temperature data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) Environmental Data Service in Asheville, NC. Regression of degree-day accumulation against time yielded the following equation:

$$Y = 1.30 + 1.17\ X + 0.0949\ X^2,\ R^2 = 0.93,$$

in which Y = degree-day accumulation since 15 March and X = days elapsed since 15 March. Actual degree-day accumulation was monitored from 1979 to 1984 by a recording thermograph housed in a standard U.S. Weather Service instrument shelter at the Mast Road Research Orchard in Durham, NH. Degree-day accumulation in 1982 was also monitored as above at Gould Hill Orchard in Contoocook, NH, and at Moose Hill Orchard in Londonderry, NH. Durham is approximately 16 km west of the Atlantic coast of New Hampshire; Contoocook lies 60 km west of Durham, in the foothills of the White Mountain range; and Londonderry is 50 km southwest of Durham, in the Merrimack River Valley.

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System to forecast ascospore maturity. A model developed in an earlier study (6), shown in Fig. 1, describes the relationship between ascospore maturity and degree-day accumulation from the first appearance of mature ascospores. Originally (6), the starting point for degree-day accumulation (phenological date) was the first appearance of mature ascospores. In the present study, we used the date when at least 50% of McIntosh fruit buds had reached the silver tip phenophase as the phenological date of the ascospore maturity model, since others had found that the first mature ascospores generally appear either at the time of, or shortly after, bud break (9). The use of tree phenology to determine the phenological date of the model rather than actual microscopic assessments (5) of pseudothecial maturity greatly simplified the task of forecasting ascospore maturity. Once the silver tip phenophase had been reached, the ascospore maturity forecast was based on degree-day accumulation as predicted by the above equation. For example, silver tip occurred on 10 April 1979. The prediction based on the degree-day model was that 274 degree-days would accumulate between 10 April and 10 May. Use of this prediction for the ascospore maturity model resulted in an estimate that 60% of the season's ascospores would mature 274 degree-days after the phenological date. Therefore, the forecasted ascospore maturity for 10 May 1979 was 60%.

Ascospore maturity of *V. inaequalis* was assessed at approximately weekly intervals at the Mast Road Research Orchard from 1979 to 1984 as described previously (5), and the phenophase of McIntosh fruit buds at the time of each assessment was recorded. Ascospore discharge was also monitored at the research orchard with a Burkard volumetric spore trap.

RESULTS AND DISCUSSION

Evaluation of the forecasting system. There was no consistent deviation of actual degree-day accumulation from that forecasted by the degree-day model from 1979 to 1984 in Durham (Fig. 2). Regression of actual degree-day accumulation against forecasted degree-day accumulation yielded a quadratic equation with an R^2 of 0.95. The model also was used to forecast degree-day accumulation between 1 and 30 May 1982 at Contoocook and Londonderry, with less than 10% error (Table 1). Thus, the method used to forecast degree-day accumulation was valid for Durham, and quite possibly for the southern third of New Hampshire, where the majority of that state's apple orchards are located.

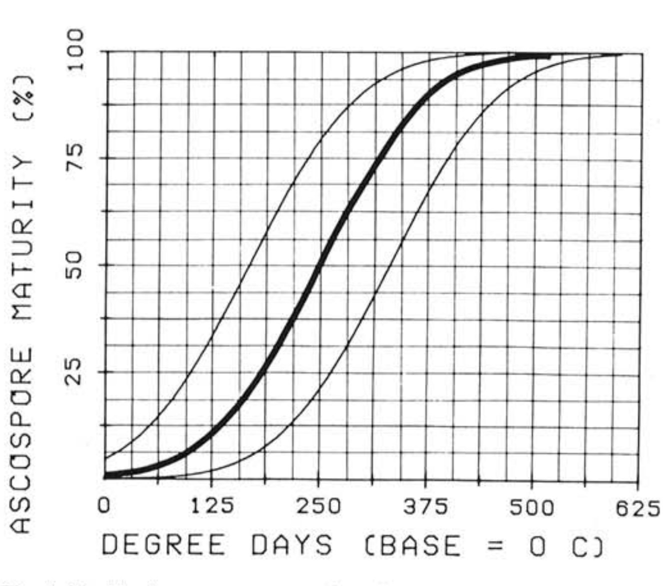

Fig. 1. Model of ascospore maturation of *Venturia inaequalis* developed from field and laboratory studies of Gadoury and MacHardy (6). Degree-day accumulation begins with the first appearance of mature ascospores. The central curve indicates ascospore maturity as estimated by the model; the outer curves are the limits of the 90% confidence bands.

The use of the silver tip phenophase of McIntosh fruit buds as the phenological date of the ascospore maturity model provided essentially the same results as using actual assessments of ascospore development for that purpose. From 1980 to 1984, ascospores first matured within 2 days of the occurrence of silver tip, and an average of 13 degree-days accumulated between the two events (Table 2). In 1979, even though mature ascospores were found 17 days before silver tip, only 47 degree-days accumulated between the first appearance of mature ascospores and the date of silver tip (Table 2). The degree-day model predicted that only 4–6 degree-days would accumulate per day during early April in Durham. Thus, even though initial ascospore maturity does not always coincide precisely with the silver tip phenophase of McIntosh, the results of the error are likely to be inconsequential in forecasting ascospore maturity in New Hampshire. Our results are in agreement with those of Gilpatrick and Szkolnik (9) who found (over a 16-yr period) that approximately 1% of the ascospores of *V. inaequalis* was mature at the silver tip phenophase of McIntosh fruit buds.

When the degree-day model was used in conjunction with the ascospore maturity model (Fig. 1), critical periods in the development of *V. inaequalis* could be identified as long as 4 wk in advance. The curve in Fig. 1 depicts a sigmoid relationship between degree-day accumulation and the percentage of the season's total inoculum that has matured. Three distinct phases in the development of a population of ascospores can be identified: a lag phase from 0 to 125 degree-days (0–10% maturity), an accelerated phase from 126 to 375 degree-days (11–90% maturity), and a final phase above 375 degree-days (91–100% maturity). The system used to forecast ascospore maturity was evaluated for accuracy in predicting the date of the shift from the lag phase to the accelerated phase and the date of the shift from the accelerated phase to the final phase. The temporal error in forecasting the date of 10% ascospore maturity was 4 days or less in each of the six infection seasons (Table 3). The forecasting system was more accurate in predicting the date of 90% ascospore maturity; the temporal error was 2 days or less, except in 1981, when the temporal error was 9 days (Table 3). The larger temporal error in 1981 may have been related to unusually dry weather during the first part of the accelerated phase of ascospore maturation. A slower rate of maturation from 125 to 250 degree-days after silver tip (Fig. 3) may have resulted in a shift of the entire curve for ascospore maturity. There were 83 hr of leaf wetness, 12 mm of rain, and nine rainless days during this period in 1981, compared to an average of 118 hr of leaf wetness, 33 mm of rain, and seven rainless days in the other 5 yr

TABLE 1. Actual and forecasted degree-day accumulation between 1 May and 30 May 1982 at Contoocook and Londonderry, NH

Date	Degree-days accumulated from 1 May		
	Contoocook	Londonderry	Forecasted[a]
10 May	110	108	100
20 May	254	247	230
30 May	390	380	378

[a] Forecasted degree-day accumulation based on a model equation developed from 26 yr of weather data for Durham, NH.

TABLE 2. Dates of initial ascospore maturity of *Venturia inaequalis* and the silver tip phenophase of McIntosh fruit buds, and the degree-day accumulation[a] between these events for Durham, NH

Year	Date of first mature ascospores	Date of silver tip phenophase	Degree-day accumulation
1979	24 March	10 April	47
1980	13 April	14 April	7
1981	8 April	6 April	16
1982	16 April	18 April	24
1983	7 April	8 April	12
1984	18 April	17 April	7

[a] Degree-day accumulation base = 0 C.

of the study. James and Sutton (10) reported that ascospore maturation was halted on days with <0.25 mm of rain or <12 hr of leaf wetness. However, except for the atypical period in 1981, we have not detected a delay of ascospore maturation in New Hampshire due to dryness, even though James and Sutton's (10) criteria are frequently not satisfied. The phase of development (i.e., lag or accelerated) during which dryness occurs may be as important as the dry conditions themselves.

Large deviations from forecasted maturity were not uncommon during the accelerated phase of ascospore maturation (Fig. 3), and they should not have been unexpected. In the ascospore maturity model, the confidence bands for estimated maturity (Fig. 1) are wider during the accelerated phase; i.e., the greater the percentage of the population that is maturing, the more difficult it is to estimate the percentage that have matured at any one time. Conversely, the ascospore maturity model is more precise during

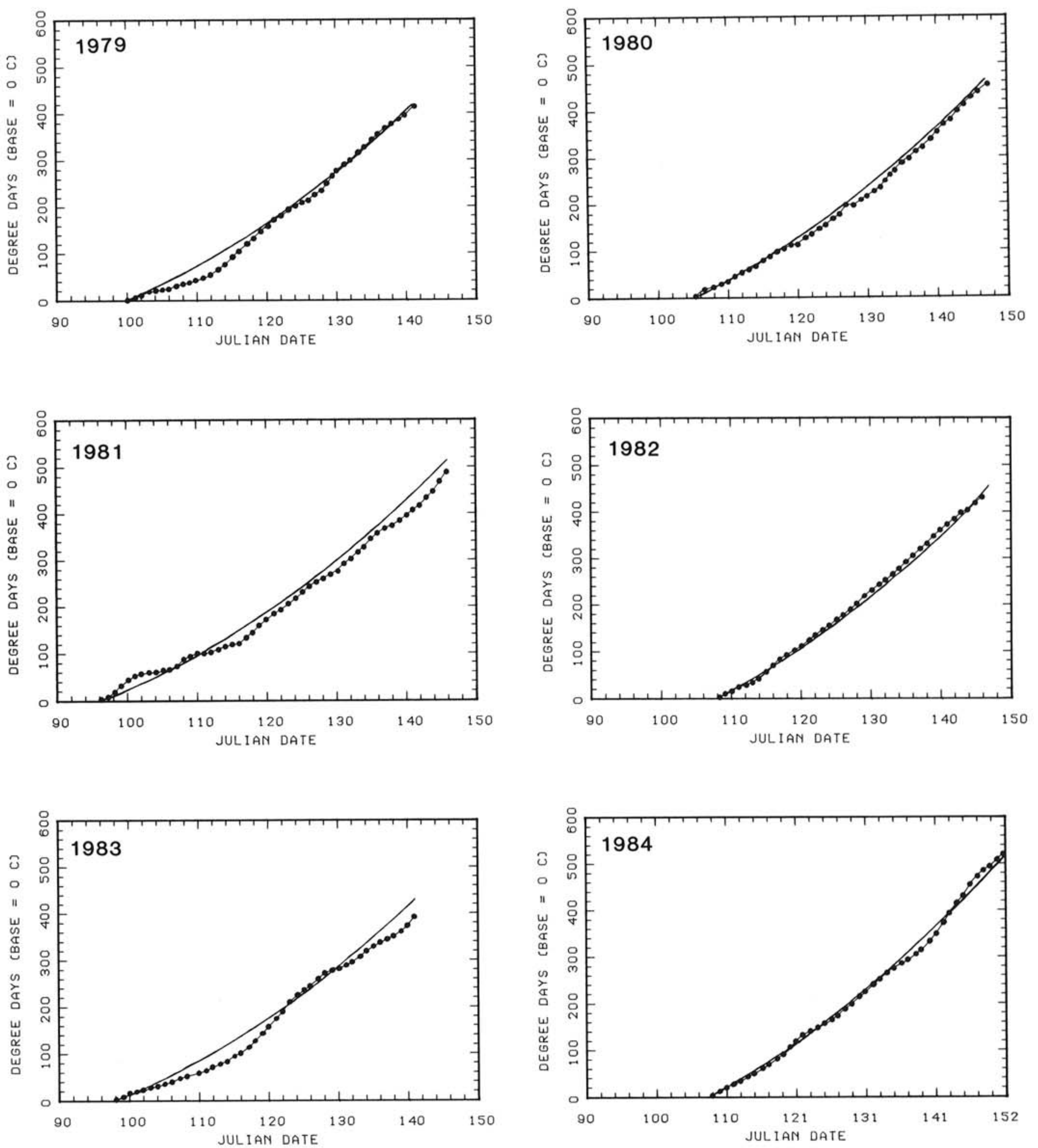

Fig. 2. Actual (dotted line) and forecasted (solid line) degree-day accumulation in Durham, NH, from 1979 to 1984. Forecasted degree-days were predicted from an equation developed from historical weather data for Durham, NH.

the lag phase and after the accelerated phase of ascospore maturation. For example, on 23 April 1980, forecasted maturity was 4% and observed maturity was 5%. On 5 May 1980, forecasted maturity was 28%, but the observed maturity was 68%. Finally, on 18 and 19 May 1980, forecasted maturity was 84 and 87%, respectively, whereas observed maturity was 87 and 88%, respectively (Fig. 3).

Applications of the forecasting system. It matters little to a commercial apple grower whether 28 or 68% of the ascospores of *V. inaequalis* are mature, because this is only a relative measure of inoculum levels. The actual size and density of the pathogen population, i.e., the absolute inoculum level, is usually not known, although progress has recently been made in forecasting this variable (7). At present, the only effects that assessments, estimations, or forecasts of ascospore maturity have upon decisions made by commercial growers in scheduling fungicide sprays are that spraying begins when mature ascospores and susceptible tissue are present and the intervals between sprays and the rates of

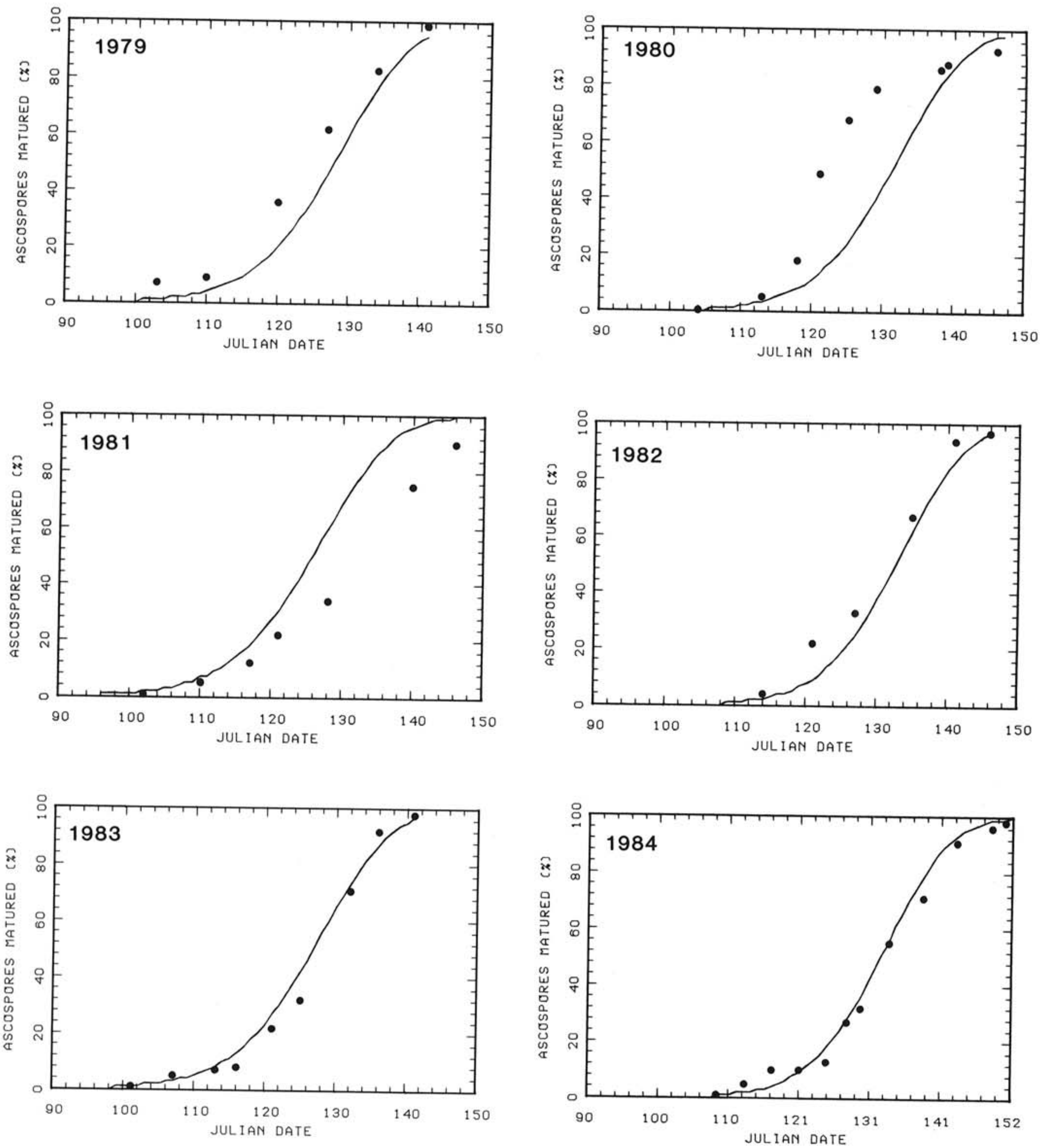

Fig. 3. Actual (circles) and forecasted (line) ascospore maturity of *Venturia inaequalis* in Durham, NH, from 1979 to 1984. Forecasted maturity was based on two models, one that forecasted degree-day accumulation and a second model that used the forecasted degree-day accumulation to estimate forecasted ascospore maturity. Actual maturity was determined by microscopic examination of crushed pseudothecia.

TABLE 3. Temporal error in forecasting maturity of ascospores of *Venturia inaequalis* in Durham, NH

Forecasted[a] ascospore maturity (%)	Temporal error in forecasted maturity (days)[b]					
	1979	1980	1981	1982	1983	1984
10	+4	+4	−3	+4	−3	+4
90	+1	−1	−9	+2	+1	−2

[a] Forecasted maturity based on predicted degree-days from the silver tip phenophase of McIntosh fruit buds.

[b] Difference between date of forecasted maturity and date of actual maturity. Positive errors indicate that a given level of maturity was reached earlier than forecasted. Negative errors indicate that a given level of maturity was reached after the forecasted date.

TABLE 4. Estimated end of primary infection season of *Venturia inaequalis* in Durham, NH, 1979–1984

	1979	1980	1981	1982	1983	1984
Date of estimated end of primary infection season[a]	18 June	8 June	31 May	5 June	31 May	3 June
Cumulative percentage of spores trapped by estimated date[b]	100	96	91	100	100	100

[a] End of primary infection season estimated to occur when maturity equals 100% and daytime rain (from 0800 hours to 1700 hours EST) exceeds 2.5 mm on each of 2 days.

[b] Ascospores trapped by Burkard volumetric spore sampler.

application are altered when ascospore maturation is nearly complete. To aid growers in determining when the primary infection season has ended, extension personnel throughout New England regularly assess pseudothecial development (5,16) and ascospore discharge (8) and disseminate this information via newsletters, taped phone messages, and computer-based communications systems (1); these are expensive and time-consuming. A forecast of ascospore maturity for the entire season made on the date of silver tip would eliminate the need for much of this work. After the forecast was made, assessments would only be needed near the end of ascospore maturation to determine the time when ascospore discharge would be complete. We are currently developing rainfall-based guidelines for estimating ascospore discharge (11) that will eliminate the need for late-season assessments and allow growers with the appropriate weather monitoring instrumentation (12) to easily and simply make their own forecasts. For example, the end of the primary infection season (90% ascospore discharge) occurs when ascospore maturation is complete and rain has been sufficient to discharge the mature ascospores. The date of 100% ascospore maturity can be forecasted. As preliminary rules, we assumed that all mature ascospores were discharged after rain in excess of 2.5 mm fell during daylight hours on each of 2 days after the date of 100% ascospore maturity. We used this scheme to accurately estimate the end of the primary infection season from 1979 to 1984 (Table 4).

An interactive FORTRAN program that incorporates our forecasting system was developed in 1983 and was made available to extension agents and specialists through New Hampshire's version of SCAMP, a computer-based communications system developed at the New York Agricultural Experiment Station (1). The program was used to forecast ascospore maturity, forecast degree-day accumulation, and estimate ascospore maturity based on observed degree-day accumulations. Forecasts of ascospore maturity were made on the phenological date or later and were updated periodically throughout the growing season by using observed degree-day accumulation. This program can be easily adapted for areas other than New Hampshire by using the appropriate historical weather data to develop a new degree-day accumulation equation. Historical weather data for most areas of the United States are available from NOAA.

A second application of the forecasting system would be to consider the lag and final phases of ascospore maturation as periods of relatively low risk, i.e., suitable for using postinfection sprays to control apple scab or delaying sprays to coincide with insecticide sprays or sprays to control other diseases. The accelerated phase would be a high-risk period requiring protectant sprays and less manipulation in the timing of fungicides to coincide with other pesticide applications. Forecasted degree-day accumulation could also be used to predict the occurrence of the pink and petal-fall phenophases of apple fruit buds (14). These phenophases are important in New England pest management programs because insecticides are recommended at pink and petal fall (2) to control the tarnished plant bug (*Lygus lineolaris* L.) and plum curculio (*Conotrachelus nenuphar* Herbst).

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