Changes in the Susceptibility of Developing Apple Fruit to *Venturia inaequalis*

W. F. S. Schwabe, A. L. Jones, and J. P. Jonker

Visiting professor and professor, Department of Botany and Plant Pathology and the Pesticide Research Center, Michigan State University, East Lansing 48824, and research technician, Fruit and Fruit Technology Research Institute, Stellenbosch 7600, South Africa, respectively.

Michigan Agricultural Experiment Station Journal Article 10872.

This research was conducted at the Fruit and Fruit Technology Research Institute, Stellenbosch 7600, South Africa. Data analysis and manuscript preparation were done during the study leave of W. F. S. Schwabe at Michigan State University. This material is based in part upon work supported by the U.S. Department of Agriculture under Agreement 82-CRSR-2-1000. We thank Estelle van Blerk for technical assistance, and Errol van Kerwel and Martin Arnolds for maintenance of experimental trees.

Accepted for publication 26 July 1983.

ABSTRACT

Schwabe, W. F. S., Jones, A. L., and Jonker, J. P. 1984. Changes in the susceptibility of developing apple fruit to *Venturia inaequalis*. Phytopathology 74:118-121.

In greenhouse studies, potted apple trees with fruit in various stages of development were inoculated with conidia of *Venturia inaequalis*, exposed to different durations of wetting, and rated after a suitable incubation period for the severity of scab infection on the fruit. Wetting duration required for infection increased with increased age of the fruit. At high inoculum levels, fruit showed light (about 2%) infection at infection indices (hours of wetting × mean temperature C) of >120, 260, 370, 455, 525, and 590 when they were inoculated 1, 5, 10, 15, 20, and 25 wk after full bloom, respectively. A curve describing this relationship increased exponentially with time and was linearized with a square root transformation of fruit age. When the duration of wet periods was adjusted to account for changes in fruit susceptibility with age, it was possible to develop a linear regression model relating hours of wetness at 9.3 to 20.0 C to the severity of scab infection on the fruit.

The wetting and temperature requirements for infection of young leaves and fruit of apple by *Venturia inaequalis* (Cke.) Wint. were assumed to be identical by Mills and LaPlante (6). However, Tomerlin and Jones (12) reported that as apple fruits matured, conditions of temperature and wetting that resulted in scab infection of foliage often failed to result in infection of the fruit. Bratley (1,2), Folson and Ayers (3), and Schwabe and Matthee (11), noted that long continuous wet periods were necessary in late summer for infection of mature fruit. Recently, Schwabe (10) reported infection indices (fruit wetting period [hr] × mean temperature [C]) of 44–600, >600–1,000, and 1,000 were required for light, moderate, and heavy infection, respectively, of mature cultivar Granny Smith apples. These infection indices were much higher than those required for leaf infection early in the growing season. The probable reason fruit infection occurs more readily early in the season than late in the season is that, as the fruits develop, their susceptibility to scab decreases.

Information on the decline in susceptibility of apple fruit to infection by *V. inaequalis* may make it possible to control apple scab more efficiently and economically. Current mid- to late-season scab-control strategies assume fruit have similar infection requirements throughout the season. However, a control strategy that assumes a decline in fruit susceptibility should result in fewer fungicide applications than are currently practiced. This approach is particularly relevant to production areas such as South Africa and Michigan where scab is the major disease of importance on apple fruit.

This study was conducted to determine the relative susceptibility of apple fruit to infection by *V. inaequalis* at various stages of development.

MATERIALS AND METHODS

Experiments on harvested fruit. These experiments were previously described by the first author (10) and those results are included in this investigation. Briefly, mature fruit of the cultivar Granny Smith were harvested 23 wk after full bloom from orchard

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

trees and arranged one layer deep on the floor of inoculation chambers, inoculated with freshly prepared conidial suspensions, covered with moist cotton wool or fresh scab-free apple leaves, and exposed to continuous wet periods of 24–144 hr at 9.3, 15.0, and 20.0 C. After removal from the inoculation chamber and drying, the fruit were held at 1–2 C for 6 mo when disease assessments were made. Each treatment was replicated 40 times with 10 fruit per replicate.

Experiments with fruit on potted trees. Grafted apple trees of the cultivars most important in South Africa (Golden Delicious, Granny Smith, Starking Delicious, Starkrimson Delicious, and White Winter Pearmain) were grown in 35-cm-diameter pots each containing 20 L of soil. Fruit produced on these trees were inoculated 0.5, 1.5, 3, 3.5, 5, 6, 7, 10, 12, 15, and 18 wk after full bloom with freshly prepared suspensions of conidia of *V. inaequalis* from infected apple leaves. Spore concentrations were adjusted to 10^5 spores per milliliter. Spore suspensions were applied until runoff with a low-pressure paint sprayer. After inoculation, trees were given wet periods of various durations with a low-volume irrigation system operated 20 sec every 30 min in inoculation chambers. These chambers were as described in 1977 (8) except the surface of the floor was increased to 4 × 5 m and the polyethylene ceiling was omitted. After the trees were removed from the inoculation chamber, water drops were blown from the leaves with compressed air. The trees were then set in a wind tunnel or outside the greenhouse in the sun to be sure the surface of the fruit dried.

To determine if interrupting a wet period influenced the incidence of fruit infection, fruit on 70 trees were inoculated 6 wk after full bloom and exposed to a total of 48 hr of wetting. After a continuous wet period of 24 hr, 60 trees were removed from the inoculation chamber and their fruits were dried. The trees were subdivided into six groups of 10 trees each and subjected to dry periods of 1, 2, 4, 8, 16, and 32 hr before returning them to the inoculation chamber for 24 hr. The mean temperature during the dry intervals was 23.5 C and the mean relative humidity was 44%. This experiment was repeated 18 wk after full bloom. In this experiment, the fruit were given a 48-hr wet period before and again after the various dry interruptions. The temperature during the dry periods fluctuated from 15 to 27 C and the relative humidity from 30 to 70%.

Following either a continuous or interrupted wet period, the trees were incubated in a greenhouse at approximately 20 C for at least 1 wk and then placed outside. The fruit were examined weekly for symptoms. When inoculations were carried out on fruit that matured before symptoms could develop, the fruit were harvested and placed in a cold storage room at 1–2 C for 6 mo. Each continuous, and each interrupted wet period was replicated 10 times on individual trees with 5–40 apples each.

Disease assessment. The number of lesions per fruit was counted and the fruit grouped according to the following scale: 0 = no lesions, 1 = 1 lesion, 2 = 2–5 lesions, 3 = 6–10 lesions, 4 = 11–20 lesions, and 5 = >20 lesions per fruit. Percentage infection was calculated from these groupings by using the formula proposed by Kremer and Unterstenhöfer (4).

Statistical analysis. For each fruit age, the value for the wet period with the highest mean percent infection of the fruit was set at 100% and the remaining infection values were adjusted proportionately. In the experiment with harvested fruit, maximum infection was obtained with the longest wet period at 20 C. The percentage infection for this treatment was set at 100% and infection values for lower temperatures and other wet periods were adjusted proportionately. A Control Data Corporation Cyber 170/750 computer and the Statistical Package for the Social Sciences (SPSS) linear regression subprogram (7) were used to fit regression models to the fruit infection data.

RESULTS

Continuous wet periods. The susceptibility of the fruit to scab did not differ perceptibly among cultivars. Therefore, the results from the different cultivars were combined.

Percent infection data for selected ages of fruit were plotted against hours of wetness to illustrate that as the fruit increased in age the duration of wetting required for infection also increased (Fig. 1). For example, a wet period of 24 hr resulted in about 43, 24, 7, 0, and 0% infection to 1.5-, 3-, 6-, 10-, and 23-wk-old fruit, respectively. By interpolation, it was estimated that wet periods of 8, 13.5, 17.5, 28.5, and 36 hr were required to give 2% fruit infection when fruit were inoculated 1.5, 3, 6, 10, and 23 wk, respectively, after full bloom.

To better compare experiments conducted at different temperatures or durations of wetting, temperature and wetness duration values were multiplied to give an infection index value for each treatment. Index values corresponding to 2% infection were plotted against weeks after full bloom. The resulting curve increased exponentially as the age of the fruit increased (Fig. 2).

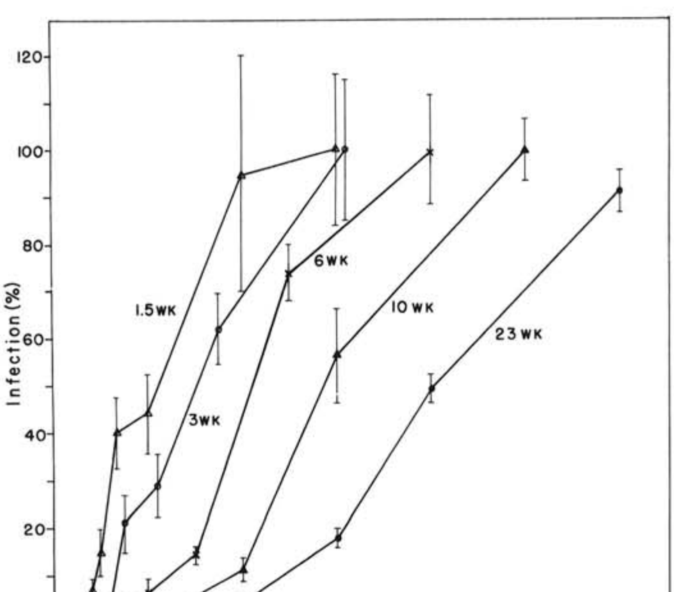

Fig. 1. Effect of wet periods at 15 C on infection of apple fruit by *Venturia inaequalis* at various times after full bloom.

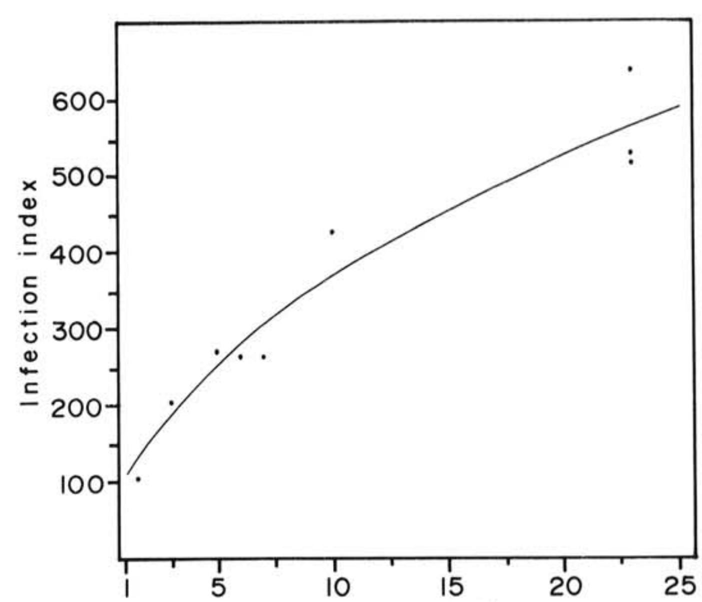

Fig. 2. Infection indices (hours of wetting × mean temperature C) required for a level of 2% infection of apple fruit by *Venturia inaequalis* at various times after full bloom.

Infection indices of about 120, 260, 370, 455, 525, and 590 were required for 2% infection of the fruit 1, 5, 10, 15, 20, and 25 wk, respectively, after full bloom.

The relationship between index values and fruit age was linearized by regression analysis. With 1- to 23-wk-old fruit, the regression of infection index on the square root of fruit age accounted for 93% of the variation in the infection index. The equation was:

$$\hat{Y} = -6.482 + 119.4\, X^{0.5} \quad (1)$$

in which $\hat{Y}$ is the estimated infection index value for 2% infection and X is the number of weeks past full bloom.

Multiple regression analysis was used to relate percentage fruit infection to the infection index and fruit age. However, the infection index variable accounted for most of the observed variation in infection. Therefore, we related percentage fruit infection to hours of wetting and to temperature during the wet period. Before running the regression, hours of wetting (W) values from experiments with fruit >1 wk old were adjusted for the increased duration of wetting required for infection. This adjustment was made with the following equation:

$$\hat{W} = W/(\hat{Y}/120) \quad (2)$$

in which $\hat{Y}$ is the estimated infection index value from equation 1, 120 is the index value for 2% infection when the fruit are most susceptible, and $\hat{W}$ is the adjusted hours of wetting. Thus, the quantity $\hat{Y}$ divided by 120 is the scalar factor that adjusts the duration of wetness according to the age of the fruit.

Of the various regression models applied to the data, the most suitable regression model considered was:

$$D = b_0 + b_1\hat{W} + b_2T + b_{11}\hat{W}^2 + b_{22}T^2 + b_{12}\,\hat{W}T + \epsilon$$

in which D = square root of percent fruit infection, $\hat{W}$ = hours of wetting from equation 2, T = temperature (C), b values = partial regression coefficients, and ϵ = a random variable with mean zero and variance σ^2. This model accounted for 86% of the observed variation in infection. Therefore, the estimate for percent infection (P) was:

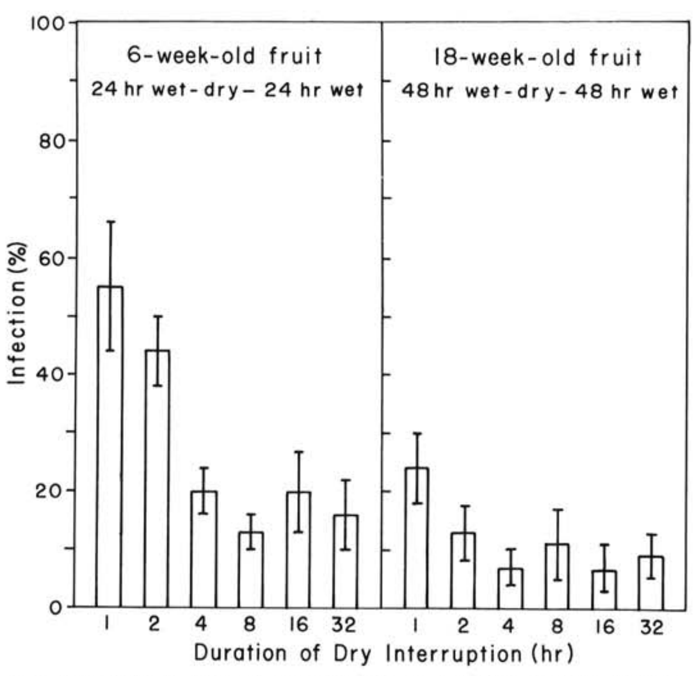

Fig. 3. Effect of interrupted wet periods on infection of apple fruit by *Venturia inaequalis* 6 and 18 wk after full bloom. Dry interruptions were imposed 24 and 48 hr after the beginning of the wet periods for the 6- and 18-wk-old fruit, respectively.

$$\hat{P} = (-6.7240 + 0.3407\,\hat{W} + 0.7265\,T - 0.0043\,\hat{W}^2 - 0.0228\,T^2 + 0.0070\,\hat{W}T^2 \quad (3)$$

The variation in infection accounted for by equation 3 was comparable to a similar equation in which percent infection rather than the square root of percent infection was predicted. However, this equation predicted low infection values with greater precision. precision.

Interrupted wet periods. Interrupted wet periods resulted in less fruit infection than did continuous wet periods (Fig. 3). Even an interruption of 1 hr resulted in significantly ($P = 0.05$) less infection. Interrupting the wet period was more detrimental to infection of 18-wk-old fruit than of 6-wk-old fruit. When 6-wk-old fruit were given dry intervals of only 1 or 2 hr, scab development was approximately 50% of that for fruit kept continuously wet, while for 18-wk-old fruit, scab development was less than 25% of that for fruit kept continuously wet.

DISCUSSION

The need for longer continuous wet periods for scab infection as the fruit develops from bloom to harvest supports our conclusion that the susceptibility of fruit to scab infection decreases through the growing season. This conclusion agrees, in general, with previous observations on natural and artificial infection periods needed for infecting fruit of various ages (1–3,10–12). Whether this change in susceptibility is due solely to changes in the cuticle, or to a combination of several anatomical and physiological changes has not been determined.

These studies were conducted with high concentrations of inoculum. Natural infections should be less severe because inoculum levels are low if primary scab has been well controlled. Schwabe (10) found that as the concentration of spores decreased from 3.7×10^5 to 1.24×10^2 viable conidia per milliliter of spore suspension, the severity of scab on mature fruit decreased from 97.8 to 1.1%. Therefore, in commercial orchards where fungicidal scab control has been effective, the risk of infection to the fruit should be less than expected from equation 3 because inoculum would be limiting.

The risk of fruit infection is reduced even more if the wet periods are interrupted rather than continuous. Schwabe (10) reached the same conclusion for mature (23-wk-old) fruit. How to cope with dry intervals in predicting fruit infection needs further study.

Infection index values necessary for a level of 2% fruit infection at various stages of development were defined. This information should make it possible to predict when infection of apple fruit has occurred from natural wet periods anytime during the season. This low infection limit was selected because no fruit scab can be tolerated if the fruit are produced for fresh market sale.

In apple-growing regions where scab is the main disease of importance in summer, fungicides are usually applied at 14- to 21-day intervals and may be discontinued altogether 1–2 mo before harvest. If unusually long wet periods occur late in the season, severe infection can occur if fungicide applications have been discontinued. By using the information reported here to time applications of curative fungicides, which control fruit infection when applied up to 72 hr after the beginning of wet periods suitable for infection (9), it should be possible to control fruit scab more efficiently prior to harvest. This model should be integrated with current methods of scab prediction (5) to determine if fungicide usage on apple can be reduced from current high levels.

LITERATURE CITED

1. Bratley, C. O. 1937. Incidence and development of apple scab on fruit during the late summer and while in storage. U.S. Dep. Agric., Tech. Bull. 563. 45 pp.
2. Bratley, C. O. 1940. Development of scab on stored apples, 1938–1939. Phytopathology 30:174-178.
3. Folson, D., and Ayers, T. T. 1928. Apple spraying experiments in 1926 and 1927. Maine Agric. Exp. Stn. Bull. 348.
4. Kremer, W., and Unterstenhöfer, G. 1967. Computation of results of

crop protection experiments by the method of Townsend and Heuberger. Pflanzenschutz-Nachr. 20:625-628.
5. Jones, A. L., Lillevik, S. L., Fisher, P. D., and Stebbins, T. C. 1980. A microcomputer-based instrument to predict primary apple scab infection periods. Plant Dis. 64:69-72.
6. Mills, W. D., and LaPlante, A. A. 1951. Diseases and insects in the orchard. N.Y. Agric. Exp. Stn. (Ithaca) Ext. Bull. 711.
7. Nie, H. C., Hull, H., Jenkins, J. G., Steinbrenner, K., and Gent, D. H. 1975. Statistical Package for the Social Sciences. McGraw-Hill, New York. 675 pp.
8. Schwabe, W. F. S. 1977. Tolerance of *Venturia inaequalis* to benzimidazole fungicides and dodine in South Africa. Phytophylactica 9:47-54.
9. Schwabe, W. F. S. 1980. Prevention of storage scab of apples. Phytophylactica 12:209-211.
10. Schwabe, W. F. S. 1982. Wetting and temperature requirements for infection of mature apples by *Venturia inaequalis* in South Africa. Ann. Appl. Biol. 100:415-423.
11. Schwabe, W. F. S., and Matthee, F. N. 1974. Storage scab. The Deciduous Fruit Grower 24:217-224.
12. Tomerlin, J. R., and Jones, A. L. 1983. Development of apple scab on fruit in the orchard and during cold storage. Plant Dis. 67:147-150.