This is to certify that the

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Epidemiology and Control of Cherry Leaf Spot Disease Caused by Coccomyces hiemalis Higgins

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Major professor

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EPIDEMIOLOGY AND CONTROL OF CHERRY LEAF SPOT DISEASE CAUSED BY COCCOMYCES HIEMALIS HIGGINS

By

Scott Preston Eisensmith

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ABSTRACT

EPIDEMIOLOGY AND CONTROL OF CHERRY LEAF SPOT DISEASE CAUSED BY COCCOMYCES HIEMALIS HIGGINS

BY

Scott Preston Eisensmith

Models which predict terminal and spur leaf emergence and expansion of sour cherry (Prunus cerasus L. 'Montmorency') were developed. Leaf number and area were more highly correlated with degree-day accumulation at a base of 4°C starting April 19, than with time. At full leaf expansion terminal leaves were 50% larger than spur leaves; however, final spur and terminal leaf size was not constant between years.

A regression model relating wetness and temperature to infection of sour cherry by Coccomyces hiemalis was developed and validated in the field. The model is $EFI = [-11.0 + 0.2858W + 1.4639T - 0.0019W^2 - 0.389T^2 - 0.003WT]^2$, where T = temperature C, W = hours of leaf wetness, and EFI = environmental favorability index from 0 to 100. An EFI of 14 delineated the minimum conditions for infection under field conditions. Daily EFI values were linearly related to disease increase in 1978 and 1979. When the model was used to schedule fungicide applications, CGA-64251 provided leaf spot control regardless of spray timing, and dodine provided control when applied after EFI $\geq$ 14 and $\geq$ 28, but not $\geq$ 42.

Effects of leaf age, inoculum concentration, and interrupted wetting on infection were investigated. With

increasing leaf age from 5 to 36 days, there was a linear decrease in ln lesions/cm^2 of leaf area with 10^5 and 10^6, but not 10^4 spores/ml; with leaves 35 to 70 days old, the decrease in ln lesions/cm^2 occurred only at 10^6 spores/ml. No changes in ln lesions/cm^2 were observed in leaves 103 to 126 days old. With 1- to 32-day-old leaves, lesions/cm^2 did not increase between 10^2 and 10^4, increased tenfold between 10^4 and 10^5, and increased less than tenfold between 10^5 and 10^6 spores/ml. Fewer lesions/cm^2 of leaf resulted from interrupted (IWP) than continuous (CWP) wet periods. Infection decreased with increasing dry interruption length. Infection from IWP with an initial 4 hr wet period, 1 to 48 hr dry interruptions, and a final 8 hr wet period was greater than from a 4 hr CWP but not statistically different from an 8 hr CWP.

To my parents

"Just a few more months!"

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GENERAL INTRODUCTION AND LITERATURE REVIEW

Cherry leaf spot is widespread in the cherry growing regions of the world. It has been recorded in Japan, South Africa, Europe, and across Canada and the United States (2). It is prevalent in Michigan, Pennsylvania, Wisconsin, and New York (12) and is economically important in nursery and commercial production systems. In one case in Nebraska, a loss of $40,000 was recorded in 1903 in nursery stock due to leaf spot (13). Even today with many fungicides available to control this disease, serious losses can still occur.

This disease is characterized by purple necrotic lesions on the upper side of the foliage, leaf yellowing, and premature defoliation (12); which if severe, may predispose the tree to winter injury (8, 16), and reduce fruit set, fruit size, and shoot growth the following year (9). The disease may appear on the fruit as small brownish spots. Fruit quality may be reduced in the same year if infection becomes severe early in the season (18).

Cherry leaf spot is caused by the fungus Coccomyces hiemalis Higgins. This fungus is classified as an ascomycete in the order Phasidiales and family Phasidiaceae (1). The asexual stage of this organism was first described by Karsten

(17) in 1884 in Europe on Prunus padus and named Cylindrosporium padi. Arthur (3, 4) in New York, described a similar fungus on plums and cherries, but did not name it. In Iowa in 1891, Pammel (22) inferred that the many separate fungal species thought to cause this disease were probably one species. Higgins (14, 15) described the sexual stage of the fungus and designated three species in the genus Coccomyces: C. hiemalis on Prunus cerasus, P. avium, and P. pennsylvanicum; C. prunophorae on P. domestica, P. spinosae, P. insititia, and P. americana; and C. lutescens on P. serotina, P. virginiana, and P. mahaleb. Higgins also elucidated the complete life cycle and described in detail the various stages involved. Backus (6, 7) investigated the initiation of the ascocarp and development of the ascus of this fungus. In 1952, Nannfeldt (20) grouped this fungus in the genus Higginsia which contained five species. Later von Arx (5) revised Nannfeldt's work and combined all the European and American species as one, under the name Blumeriella jaapii (Rehm) v. Arx. However, I will use the name Coccomyces hiemalis in this thesis because it is well established in plant pathological literature and because there is doubt whether the European and American species are the same.

The disease cycle of this fungus consists of saprophytic and pathogenic phases (21). The pathogenic phase begins when mature ascospores are released from apothecia in overwintered leaves on the orchard floor. Ascospore discharge begins near

petal-fall and continues during rainy periods in May and June (19). Air currents and rain splashing disseminate the spores to the trees (8). Once on the leaf surface the ascospores germinate and penetrate through the stomata. Infection frequency is governed primarily by duration of leaf wetness and air temperature (19). An incubation period ensues and at 18°C, the lesions become visible in seven days (1).

On the lower leaf surface opposite the purple lesions on the upper surface, white sporulating masses can be seen during humid conditions (23). These structures, called acervuli, are approximately 2 mm in diameter and contain thousands of conidia. Once these sporulating lesions are present in the orchard a secondary repeating cycle commences during favorable environmental periods. These secondary infection periods cause extensive disease spread and disease severity is dependent on the frequency and favorability of wetting periods and amount of inoculum in the orchard. Severe infection causes the leaves to turn yellow and abscise. This color change and premature abscission has been correlated with production of large amounts of ethylene by the diseased leaves (25). Under certain conditions a cork layer will form around each lesion and the cork layer and lesion drop out, leaving a hole in the leaf (23). Cherry trees may be completely defoliated as early as 15 July (11).

The fungus begins the saprophytic phase in the leaves that fall to the ground (21). Fungal hyphae ramify through the leaf tissue and produce microconidia and archicarps

which are the initials of the sexual stage (7). Further development is retarded while the pathogen overwinters in diseased leaf tissue on the orchard floor. In late March ascospores form and begin to mature (6, 7). Mature ascospores are forcibly discharged during wet periods in the spring and initiate the pathogenic phase for that growing season.

Current control practices consist of five to six protective fungicide sprays from petal-fall through post-harvest on a 10- to 14-day schedule (10). With the development of fungicides possessing after-infection eradicant activity (24), new management strategies can be employed when the time of infection is known. These management strategies require accurate knowledge of the favorability of the weather for infection, the susceptibility of the host, how much tissue is present in the orchard, and the inoculum level of the pathogen in the orchard. This information can be obtained by coupling models with biological and environmental monitoring systems.

The objectives of this research were: 1) develop models for predicting leaf emergence and expansion of cherry leaf tissue so that estimates of the amount of susceptible tissue present can be made, 2) develop a model to identify and quantify favorable environmental conditions for infection and disease development, 3) test the infection model as a tool for timing eradicant fungicides, 4) investigate the effects of leaf age and inoculum concentration on the susceptibility of sour cherry, and 5) study the effects of interrupted

wetting on infection. The results of my research on each of these objectives are given in the major sections of this thesis.

LITERATURE CITED

1. ANDERSON, H. W. 1956. Diseases of fruit crops. McGraw-Hill, New York. 501 pp.

2. ANONYMOUS. 1976. Distribution maps of plant diseases. Map No. 58. Commonwealth Mycological Institute, Kew, Surrey. England.

3. ARTHUR, J. C. 1887. Report of the botanist. N. Y. Agric. Expt. Stn. Rept. 5:259-298.

4. _____. 1888. Report of the botanist. N. Y. Agric. Expt. Stn. Rept. 6:343-371.

5. ARX, J. A. VON. 1961. Über Cylindrosporium padi. Phytopath. Z. 42:161-165.

6. BACKUS, M. P. 1933. The development of the ascus and the occurrence of giant ascospores in Coccomyces hiemalis. Bull. of the Torrey Club 60:611-632.

7. _____. 1934. Initiation of the ascocarp and associated phenomena in Coccomyces hiemalis. Contributions from Boyce Thompson Institute of Plant Research 6:339-379.

8. COONS, G. H. 1921. Cherry leaf spot. Mich. Agric. Expt. Stn. Quart. Bull. 3:93-96.

9. DUTTON, W. C., and H. M. WELLS. 1925. Cherry leaf spot: residual effects and control. Mich. Agric. Expt. Stn. Spec. Bull. 147:1-15.

10. FLORE, J. A., A. L. JONES, and L. G. OLSON (Eds.). 1979. Fruit Pesticide Handbook. Michigan State University Ext. Bull. E-154, East Lansing, MI. 86 pp.

11. GLOYER, W. D., and H. GLASGLOW. 1928. Defoliation of cherry trees in relation to winter injury. N. Y. Agric. Expt. Stn. Bull. 555:1-27.

12. HEALD, F. D. 1926. Manual of plant disease. McGraw-Hill, New York. 891 pp.

13. _____. 1943. Introduction to plant pathology. McGraw-Hill, New York. 579 pp.

14. HIGGINS. B. B. 1913. The perfect stage of Cylindrosporium on Prunus avium. Science 37:637-638.

15. _____. 1914. Contribution to the life history and physiology of Cylindrosporium on stone fruits. Amer. J. of Bot. 1:145-173.

16. HOWELL, G. S., and S. S. STACKHOUSE. 1973. The effect of defoliation time on acclimation and dehardening in tart cherry (Prunus cerasus L.). J. Amer. Soc. Hort. Sci. 98:132-136.

17. KARSTEN, P. A. 1884. Cylindrosporium padi Karst (n. sp.). Symb. Mycol. Fenn. 16:159.

18. KEITT, G. W. 1918. Control of cherry leaf spot in Wisconsin. Wis. Agric. Expt. Stn. Bull. 286:1-11.

19. _____, E. C. BLODGETT, E. E. WILSON, and R. O. MAGIE. 1937. The epidemiology and control of cherry leaf spot. Wisc. Agric. Expt. Stn. Res. Bull. 132. 118 pp.

20. NANNFELDT, J. A. 1952. Studien über die Morphologie und Systematik der Nicht-lichenisierten Inoperuculaten Discomyceten. Nova Acta Regiae Soc. Sci. Upsaliensis. 8:1-368.

21. OATMAN, E. R., and C. G. EHLER. 1962. Cherry insects and disease in Wisconsin. Wisc. Agric. Expt. Stn. Bull. 555:1-43.

22. PAMMEL, L. H. 1891. Spot disease. Iowa Agric. Expt. Stn. Bull. 13:47-48.

23. SCHNEIDERHAN, I. J. 1938. Control of cherry leaf spot in West Virginia. West Virginia Agric. Expt. Stn. Bull. 288:1-13.

24. SZKOLNIK, M. 1979. Broad-spectrum after-infection activity by CGA-64251 against tree fruit diseases (Abstr.) Phytopathology 69:1047.

25. WILLIAMSON, C. E. 1950. Ethylene, a metabolic product of diseased or injured plants. Phytopathology 40:205-208.

PART I

DEVELOPMENT OF MODELS TO PREDICT LEAF EMERGENCE AND EXPANSION OF SOUR CHERRY FROM DEGREE-DAY ACCUMULATIONS

LEAF EMERGENCE

ABSTRACT

A model which predicts terminal and spur leaf emergence of sour cherry (*Prunus cerasus* L. 'Montmorency') grown near East Lansing, Michigan was developed from biological and temperature observations made in orchards near Egg Harbor, Wisconsin. Leaf number of spur and terminal shoots was more highly correlated with degree-day accumulation at a base of 4°C starting April 19, than with time. Leaf number on individual shoots was linear with respect to degree-day accumulation; however, not all growth on an individual tree was synchronous, and the plot of average leaf number versus time was slightly curvilinear. Terminal buds set about 350 and 850 degree-days after first leaf emergence for spur and terminal shoots, respectively, regardless of location. Leaf size increased linearly with degree-day accumulation until full leaf expansion. At maturity terminal leaves were about 50% larger in area than spur leaves. Foliage growth was greatest during stage I and early stage II of fruit growth, and may compete with the fruit for assimilates needed for growth.

INTRODUCTION

The ability to predict leaf emergence and expansion of Montmorency sour cherry based on degree-day accumulation would be a useful tool for both the horticulturist and plant pathologist. Such a model could be used in conjunction with research on the effect that defoliation may have on yield, the leaf area available for deposition and/or absorption of a growth regulator or pesticide, canopy development in relation to light quality and distribution, vegetative development in relation to fruit growth, or as part of a whole tree growth model used to study host-pathogen interactions.

The degree-day system (1) used for predicting growth or maturity has found widespread use in several biological systems, particularly for predicting vegetable maturity in the processing industry (5), for predicting the completion of rest (2, 10), predicting bloom (11), and for predicting harvest dates for tree fruits (6). Although considerable information relating growth to degree-day accumulation is available for several fruit crops, little exists for Montmorency cherry.

Foliage development of sour cherry can be classified as either terminal and lateral shoots or as spur shoots. Kenworthy (8) has categorized the longer terminal and lateral

shoots according to tree vigor, 25 cm in length or less for low and 45 cm in length or more for high, and the spur shoots as lateral shoots less than 5 cm in length. The proportion of each depends on the age and vigor of the tree and its crop load. Generally younger trees that are vigorous have a high percentage of terminal and lateral shoots and few spur shoots. This trend reverses as the tree ages and begins to bear fruit. A foliage growth model based on degree-day accumulation can be constructed by observing tree growth and associating it with temperature data. In cherry, leaf emergence does not occur until a sufficient chilling requirement has been met to break rest (2) and after a minimum number of growing degree-days have accumulated if other environmental parameters are not limiting. Based on data recorded in orchards in Egg Harbor, Wisconsin, I report herein a leaf emergence model which has been verified in East Lansing, Michigan, that will predict terminal and spur leaf emergence and number based on degree-day accumulations.

MATERIALS AND METHODS

Tree growth and model development. Data on leaf emergence from mature Montmorency sour cherry trees (15 years old in 1951, planted 6.1 x 6.1 m, on Prunus mahaleb rootstock, in silt loam, trained to a modified central leader, from Horseshoe Bay Farms, Egg Harbor, Wisconsin) and temperature records during the 1951-1953 growing seasons were obtained from Dr. J. D. Moore, University of Wisconsin. An interactive FORTRAN IV program (Appendix A) was used to calculate and accumulate degree-days according to the Baskerville and Emin (3) method, which assumes the sine curve as an approximation of the diurnal temperature curve. Regression analyses (4) were performed using degree-day accumulations at bases 1 to 5°C by 1° increments, calendar days, and days from initiation of growth as the independent variables and the leaf number per terminal or spur as the dependent variable. A Control Data Corporation 6500 computer and the Statistical Package for the Social Sciences Regression subprogram (9) were used to analyze the data, and develop a leaf emergence model based on degree-day accumulation.

Model verification. Biological data were obtained for three different research orchards (KL1, BU2, and DE3) in the East Lansing, Michigan area during the 1978 growing season

and for one orchard in Wisconsin during the 1972 and 1973 growing seasons. Since data were similar between years and locations, only the 1978 East Lansing data are presented. The orchards were trained to a modified central leader, were 20-, 12-, and 6-years-old and were planted 6.1 x 7.3 m, 6.1 x 6.1 m and 4.5 x 1.8 m, respectively. The model was validated by predicting and then counting the mean number of leaves which had unfolded on each of five terminal and spur shoots on each of four trees in each orchard at 3 to 4-day-intervals. Average area per leaf was determined by measuring 50 terminal and 50 spur leaves selected by chance from the BU2 and DE3 orchards with a portable area meter (Lambda Instrument Corporation Model LI-3000, Lincoln, NE 68504). Average fruit weight was determined several times throughout the season in orchard DE3 by weighing 100 fruit selected by chance from each of four trees. These data were used to indicate the relationship between fruit growth and leaf emergence. Sampling was initiated when the first growth appeared and continued until bud set. Maximum and minimum temperature data were derived from hygrothermographs at the Horticulture Research Center, Michigan State University, East Lansing. Degree-day accumulation and statistical analysis were conducted as described above.

RESULTS

Foliage growth and model development. Regression and coefficient of variation analysis of degree-day accumulations at base temperatures of 1 to 5°C indicated that a 4° base temperature and an initial accumulation date of April 19 (the earliest available) resulted in the "best" fit for observations (Table 1, Figures 1, 2) made in Wisconsin from 1951-1953. The mean number of leaves per spur and per terminal shoot was highly correlated (r for spur=0.93; r for terminal=0.98) with degree-day accumulations (Table 2). Number of leaves per individual terminal and per individual spur were linear with respect to degree-day accumulation. All spur or terminal growth on an individual tree is not synchronous, and therefore average leaf number is slightly curvilinear (Figure 2). The following foliage development prediction equations were derived from the data:

$$\text{Spur leaf no.} = 5.02 + .05D - 6.02 \times 10^{-5} D^2$$

$$\text{Terminal leaf no.} = 2.14 + .026D - 1.12 \times 10^{-5} D^2$$

where D = degree-day accumulation above 4°C beginning April 19.

Model verification. Use of a Chi-square test showed good agreement between expected leaf numbers and observations made in the three orchards in 1978 (Table 3). Observed leaf

Figure 1. Number of leaves per spur and per terminal produced by mature Montmorency sour cherry trees at Egg Harbor, WI, during the 1951-1953 growing seasons.

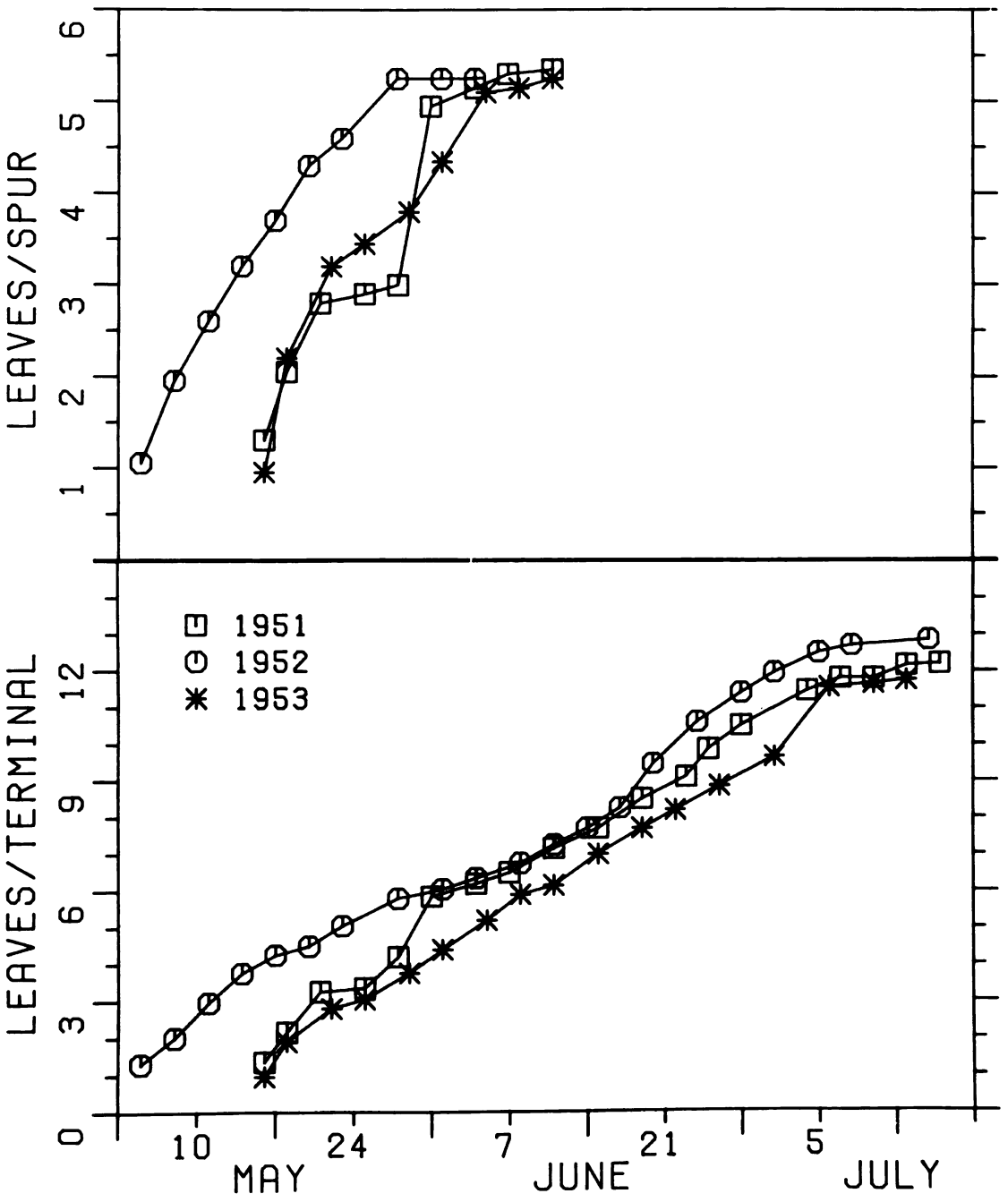

LEAVES/SPUR
1
2
3
4
5
6
LEAVES/TERMINAL
0
3
6
9
12
1951
1952
1953
10
24
7
21
5
MAY
JUNE
JULY

Figure 2. Number of leaves per spur and per terminal as a function of degree-day accumulation, base 4°C beginning April 19, for mature Montmorency sour cherry trees at Egg Harbor, WI, during the 1951-1953 growing seasons (...line for equation).

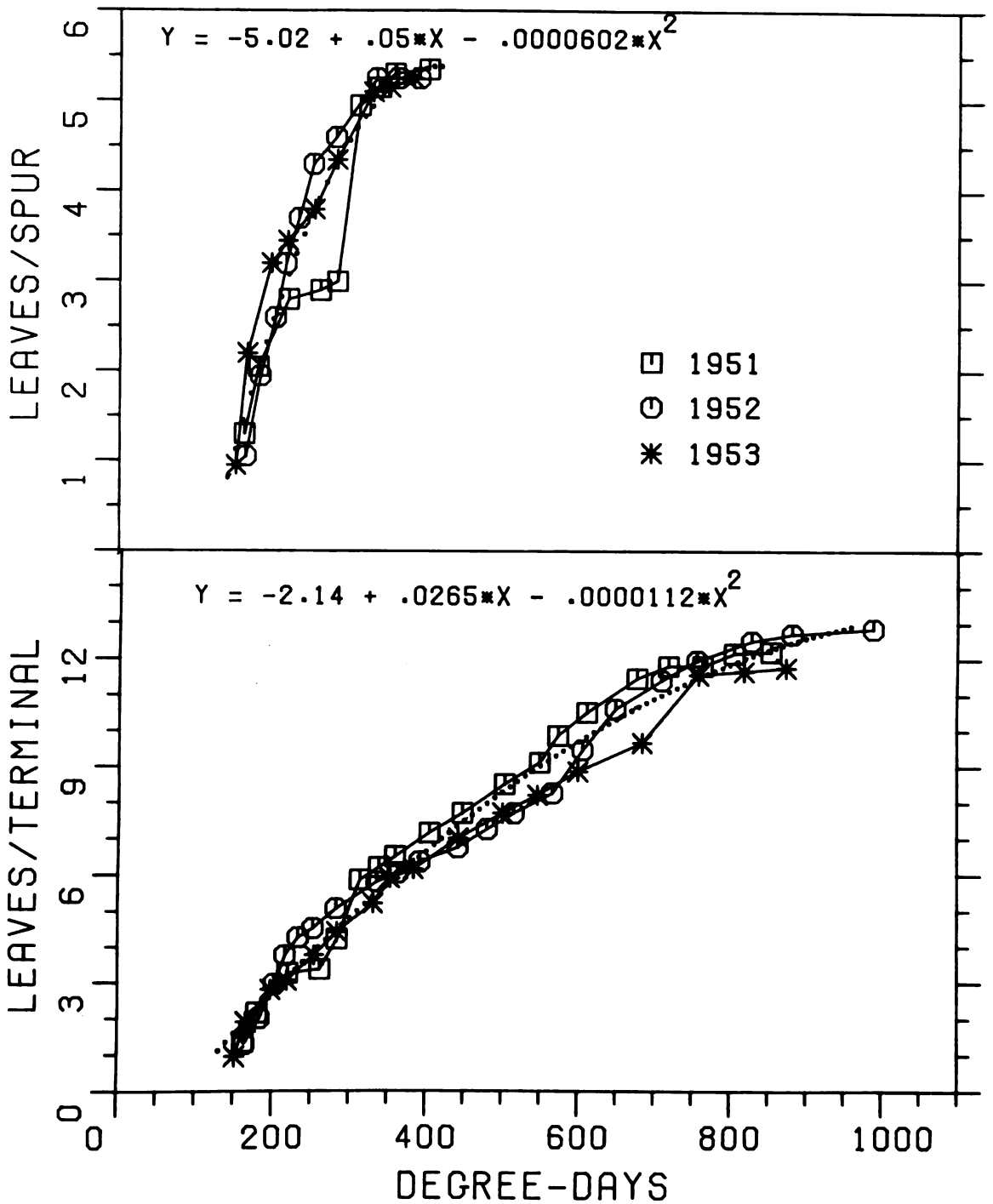

Y = -5.02 + .05*X - .0000602*X^2
LEAVES/SPUR
1
2
3
4
5
6
1951
1952
1953
Y = -2.14 + .0265*X - .0000112*X^2
LEAVES/TERMINAL
0
3
6
9
12
0
200
400
600
800
1000
DEGREE-DAYS

Table 1. Regression statistics for degree-day accumulation at base temperature 1-5°C beginning April 19 in relation to spur and terminal leaf development in Montmorency sour cherry.

Statistic	Shoots	Base Temperature (°C)				
		1	2	3	4	5
Coefficient of variance	Spur[y]	12.1	11.8	11.7	12.1	12.8
	Terminal[z]	7.5	7.4	7.3	7.2	7.3
Coefficient of determination	Spur[y]	0.912	0.916	0.917	0.911	0.901
	Terminal[z]	0.978	0.979	0.979	0.979	0.979
Overall F Value	Spur[y]	129.3	136.7	137.7	128.4	114.2
	Terminal[z]	1191.6	1231.4	1256.9	1269.3	1254.7

[y]Based on 28 observations.

[z]Based on 57 observations.

Table 2. Regression statistics for degree-day accumulation, base 4°C beginning April 19, in relation to spur and terminal leaves in Montmorency sour cherry.

		Spur leaf number				
		Source	DF	SS	MS	Overall F[y]
R^{2}[z]	0.911	Regression	2	51.32	25.66	128.4
Std. Deviation	0.477	Residual	25	5.00	0.20	

Variable	Coefficient	Std. Error	Beta	Partial F Value
Constant	-5.02	1.196		17.60
Degree-days	0.05003	0.9252×10^{-2}	2.73	29.24
(Degree-days)^2	-0.6019×10^{-4}	0.1678×10^{-4}	-1.18	12.87

		Terminal leaf number				
		Source	DF	SS	MS	Overall F[y]
R^{2}[z]	0.979	Regression	2	685.97	342.99	1269.3
Std. Deviation	0.520	Residual	54	14.59	0.27	

Variable	Coefficient	Std. Error	Beta	Partial F Value
Constant	-2.139	0.337		40.21
Degree-days	0.02645	0.1498×10^{-2}	1.73	311.62
(Degree-days)^2	-0.1121×10^{-4}	0.1425×10^{-5}	-0.77	61.87

[y]All F values are significant at P=0.001.

[z]Coefficient of determination.

Table 3. A comparison of expected and observed leaf emergence based on degree-day accumulations and leaf development in three orchards near East Lansing, Michigan, 1978.

Date:	5/15	5/19	5/23	5/26	5/30	6/2	6/6	6/9	6/13	6/16	6/20	6/23	6/27	6/30	7/7	Chi-Square[y]
DD[z]	162.5	216.5	257.6	304.6	382.6	432.6	479.1	515.1	572.6	606.1	677.6	718.6	791.1	847.1	955.1	
Leaf Development																
Expected																
L/S[x]	1.52	2.99	3.88	4.64	5.31	5.36										
L/T[w]	1.86	3.06	3.93	4.88	6.34	7.20	7.96	8.51	9.33	9.77	10.63	11.07	11.76	12.22	12.89	
Observed																
KL1[v]																
L/S	1.05	2.65	4.20	4.95	5.20	5.30										0.24
L/T	0.30	1.65	3.35	4.65	6.05	6.85	7.35	7.95	8.55	9.15	9.65	9.80	10.20	10.30	10.40	3.50
BU2[v]																
L/S	1.10	3.00	3.80	4.60	5.10	5.65										0.14
L/T	0.75	2.60	3.60	4.60	5.70	6.90	7.15	7.80	8.50	8.75	9.10	9.30	9.30	9.30	9.30	3.96
DE3[v]																
L/S	1.21	3.16	4.00	4.53	4.74	4.79										0.20
L/T	0.39	2.28	3.50	4.67	5.89	6.44	7.00	7.67	8.39	9.00	10.22	10.61	11.67	12.17	12.78	1.92

[z]Degree-days calculated from April 19 using base of 4°C.

[y]All chi-square values are non-significant at the P=0.01.

[x]Mean leaves per spur.

[w]Mean leaves per terminal.

[v]Orchard designation.

number for both older, less vigorous, trees (KL1, BU2), and young, vigorous trees (DE3) were closely related to the predicted values, differing only in time of cessation of growth.

Canopy and fruit development. Fruit weight followed the typical double sigmoid pattern (Figure 3) reported for cherry (12). Spur leaf emergence terminated approximately 21 days (about 350 degree-days) after the first leaf emerged, and coincided with early stage II of fruit development. Terminal leaf number increased until approximately 60 days (about 850 degree-days) after first leaf emergence, and growth terminated near the end of stage III of fruit development, prior to harvest. Rate of leaf production, as measured by adding spur and terminal leaf number (Figure 3), was greatest during stage I of fruit growth, remained relatively constant during stage II and early stage III, then declined to zero at the end of stage III. Average area per leaf increased with degree-day accumulation until all leaves were fully expanded. At that time terminal leaves were 50% larger than spur leaves (Table 4).

Figure 3. Mean fruit growth (weight), number of leaves per spur and per terminal, and spur plus terminal leaf number for Montmorency sour cherry in orchard DE3 at East Lansing, MI, during the 1978 growing season.

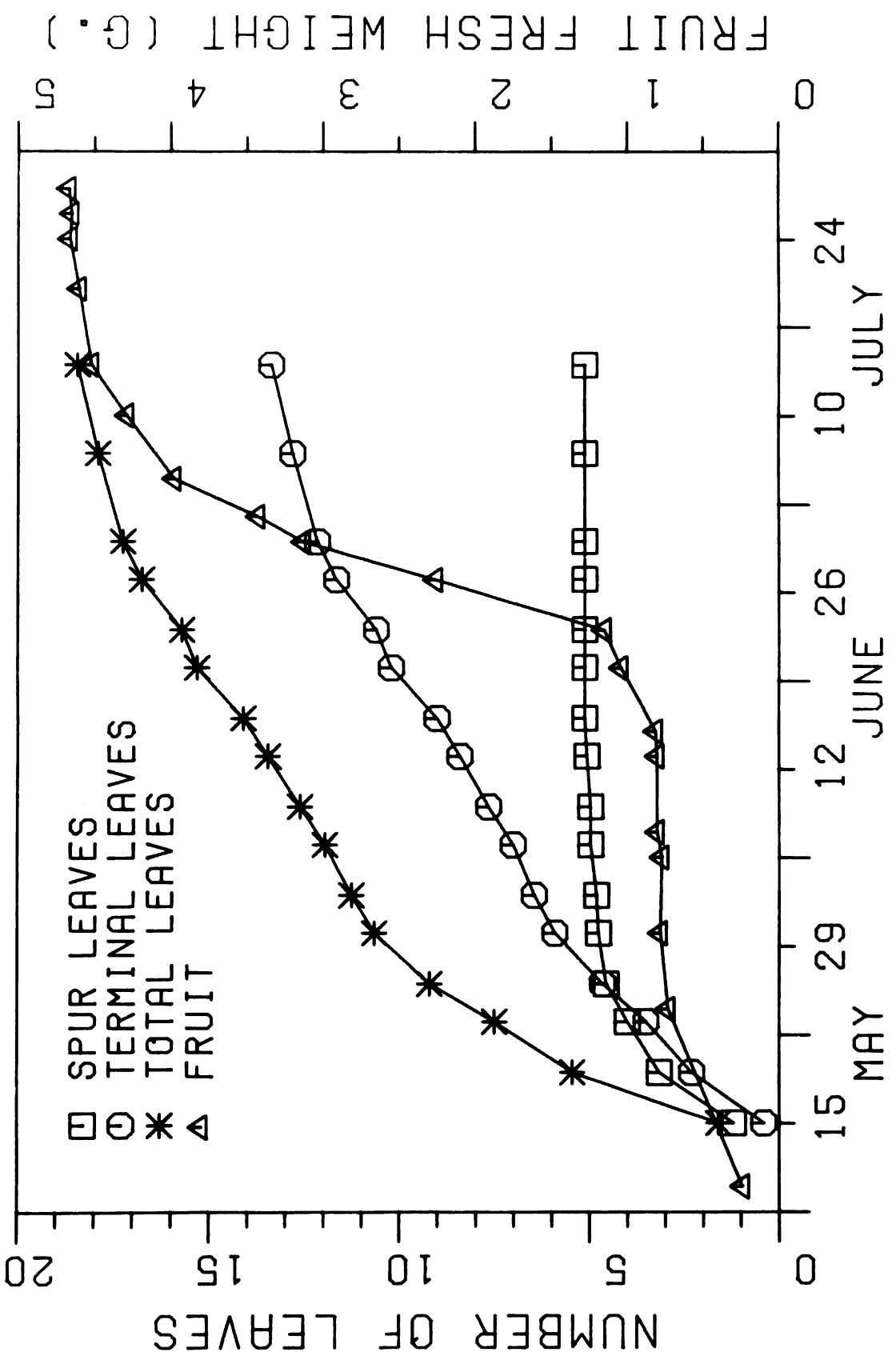

NUMBER OF LEAVES
0
5
10
15
20
SPUR LEAVES
TERMINAL LEAVES
TOTAL LEAVES
FRUIT
15 MAY
29
12 JUNE
26
10 JULY
24
FRUIT FRESH WEIGHT (G.)
0
1
2
3
4
5

Table 4. Average terminal and spur leaf areas in relation to degree-days and leaf number of Montmorency sour cherry.[z]

Degree-days	Terminal		Spur	
	Leaf number[y]	Area/Leaf[x] (cm^2)	Leaf number[y]	Area/Leaf[x] (cm^2)
216	2.28	6.56	3.16	5.88
258	3.50	9.72	4.00	9.44
304	4.67	15.10	4.53	13.15
383	5.89	21.18	4.74	16.34
433	6.44	24.87	4.79	17.42
479	7.00	32.03		20.58
515	7.67	29.49		20.90
572	8.39	31.29		20.59
606	9.00	33.15		21.19
678	10.22	35.11		23.35
719	10.61	32.51		23.02
791	11.67	31.90		20.53
847	12.17	30.24		21.46
955	12.78	32.73		20.56

[z]Based on observations from the DE3 block, 1978.

[y]Mean of 20 shoots.

[x]Mean of 50 shoots.

DISCUSSION

The model based on data obtained from cherry orchards in Egg Harbor, Wisconsin, can be used to predict leaf emergence and number of leaves on terminal and spur shoots of Montmorency cherry in East Lansing, Michigan (Tables 2, 3; Figures 1, 2). The model will not predict cessation of growth, since other factors such as age, vigor, and crop load greatly influence total growth (8). However, a good approximation of bud set could be built into the model from previous terminal node numbers or shoot lengths.

Sufficient phenological data were not available from the Wisconsin observations to enable the prediction of bud break or the completion of the rest period. A basic limitation of this model is that the accumulation of energy is begun on a fixed calendar date and not on some physiological parameter, such as the completion of rest. Accuracy, especially early in the season, could be improved with additional data which could be used to predict the completion of rest and the beginning of growth. Models which predict completion of rest and spring bud development based on accumulation of chill units or growing degree hours, have been developed for peach (10, 11) and could be developed for sour cherry. For the East Lansing location, degree-day

accumulation, based on a fixed calendar date (April 19), provided an acceptable model (Table 3) which could be used to predict growth and emergence.

It is interesting to note that canopy development is completed prior to fruit harvest (Figure 3), and that it may compete with fruit development during stage I and the early part of stage III of fruit development when fruit are growing at their maximum rate. Since most fruit do not produce a significant amount of photosynthate, they must rely on efficient translocation of assimilates from leaves or storage tissues for growth. Therefore, any environmental, cultural, or physiological limitation during these critical periods of maximum assimilate demand could have a profound effect on fruit growth, tree vigor, and flower bud initiation and/or differentiation for the following year. This model provided a method for monitoring foliage development, which can be used to study the interrelationships between vegetative and reproductive growth.

Other potential uses for the model are: 1) to study foliage/disease or foliage/insect relationships, 2) to determine the amount of leaf area available for pesticide deposit or growth regulator absorption, and 3) for the development of a whole tree growth model for cherry. For example, a similar model could be used in conjunction with a disease model for cherry leaf spot (7) to study pathogen-host interactions. In these studies, growth initiation, initial growth rates, bud set, and total canopy developed have

special meaning. They signify the presence of susceptible tissue, the concomitant establishment of the disease under favorable conditions, and the termination of vegetative growth, all of which could be used to develop the most appropriate control program for the disease.

LITERATURE CITED

1. ARNOLD, C. Y. 1959. The determination and significance of base temperature in a linear heat unit system. Proc. Amer. Soc. Hort. Sci. 74:430-445.

2. ASHCROFT, G. L., E. A. RICHARDSON, and S. D. SEELEY. 1976. A statistical method for determining chill requirements of fruit buds. Appendix D in: Reducing fruit losses caused by low spring temperatures, Final Rept. Utah Agr. Expt. Station to Four Corners Regional Commission, Project No. 562-366-084, Document No. 10550101.

3. BASKERVILLE, G. L., and P. EMIN. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50:514-517.

4. DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. Wiley, New York. 407 pp.

5. EDEY, S. N. 1977. Growing degree-days and crop production in Canada. Agriculture Canada Publication 1635.

6. FISHER, D V. 1962. Heat units and number of days required to mature some pome and stone fruits in various areas of North America. Proc. Amer. Soc. Hort. Sci. 80:114-124.

7. KEITT, G. W., E. C. BLODGETT, E. E. WILSON, and R. O. MAGIE. 1937. The epidemiology and control of cherry leaf spot. Wisc. Agr. Expt. Stn. Res. Bul. 132. 118 pp.

8. KENWORTHY, A. L. 1974. Sour cherry tree vigor as related to higher yields and better fruit quality. Mich. Agr. Expt. Stn. Rept. 223.

9. NIE, H. C., H. HULL, J. G. JENKINS, K. STEINBRENNER, and D. H. BENT. 1975. Statistical package for the social sciences. McGraw-Hill, New York. 675 pp.

10. RICHARDSON, E. A., S. D. SEELEY, and D. R. WALKER. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. HortScience 9:331-332.

11. _____, _____, _____, J. L. ANDERSEN, and G. L. ASHCROFT. 1975. Pheno-climatology of spring peach bud development. HortScience 10:236-237.

12. TUKEY, H. B. 1931. Growth of the embryo, seed, and pericarp of the sour cherry (Prunus cerasus) in relation to season of fruit ripening. Proc. Amer. Soc. Hort. Sci. 31:125-144.

LEAF EXPANSION

ABSTRACT

Linear and non-linear models which predict spur and terminal leaf expansion of sour cherry (*Prunus cerasus* L. 'Montmorency') were developed from biological and temperature observations made in orchards near East Lansing, Michigan. Average leaf area per leaf was more highly correlated with degree-day accumulation at a base of 4°C starting April 19, than with time. Leaf area per leaf increased linearly with degree-day accumulation until full leaf expansion; however, final spur or terminal leaf size was not constant between years.

INTRODUCTION

A canopy development model for Montmorency sour cherry would be useful in i) the study of foliage/pest relationships, ii) determining the amount of leaf area available for pesticide deposit or growth regulator absorption, iii) the study of the effect defoliation may have on yield, and iv) correlating vegetative development with fruit growth.

Development of a canopy model could be subdivided into models for leaf emergence and leaf expansion. We developed a method for predicting leaf emergence of Montmorency sour cherry based on degree-day (DD) accumulation (5). Degree-day accumulation has been used for predicting completion of rest (1,12), bloom (13), and harvest dates for tree fruits (7), and vegetable maturity in the processing industry (4). I report herein research on predicting leaf expansion of Montmorency sour cherry.

For canopy development I followed Kenworthy's (9) classification of shoots as either terminal and lateral shoots or spur shoots. The length and proportion of each shoot type varies with tree vigor, age, and crop load; however, younger trees generally have a higher percentage of terminal and lateral shoots and few spur shoots. These

percentages change as the tree ages and are affected by pruning and light quality and distribution.

MATERIALS AND METHODS

Data on leaf expansion from Montmorency sour cherry were obtained from two research orchards (BU2 and DE3) near East Lansing, Michigan, in 1978, 1979, and 1980. The orchards were trained to a modified central leader, were 12- and 6-years-old in 1978, and were planted 6.1 x 6.1 m and 4.5 x 1.8 m, respectively. Average area per leaf for 50 terminal and 50 spur leaves selected by chance from each orchard was determined from measurements with a portable area meter (Lambda Instr. Corp., Model LI-3000, Lincoln, NE 68504). Sampling began when the first unfolded leaves appeared and continued until two weeks after terminal bud set.

Daily maximum and minimum temperatures were obtained from hygrothermograph recordings made at the Horticulture Research Center, Michigan State University, East Lansing. An interactive FORTRAN IV program (Appendix A) was used to calculate and accumulate DD according to the Baskerville and Emin (2) method, which assumes the sine curve as an approximation of the diurnal temperature curve. Regression analyses (3) were performed using DD accumulation at base 4°C beginning April 19 and calendar days of the year as the independent variables and the average area per leaf for terminal and spur shoots as the dependent variable. Individual spur and terminal shoot data

sets for orchards BU2 and DE3 were combined for use in the regression analyses.

Ten models (Table 5) were selected from three categories of equations commonly used in plant growth modeling; the polynomial, reciprocal, and rectangular hyperbolic type functions. A Control Data Corporation 170/750 computer and the Statistical Package for the Social Sciences (SPSS) linear regression subprogram (11) were used to fit the regression models to the spur and terminal leaf expansion data of 1978. The linear regression models with the highest coefficients of determination and no discernable patterns in the residuals were then used to predict the leaf expansion observations for 1979 and 1980. Chi-square goodness of fit tests (15) were performed on the predicted areas for both spur and terminal leaves for both orchards in each of the three years. The ten linear regression models in Table 5 were fitted to the spur and terminal leaf expansion data for 1979, 1980, and all three years combined to verify that the "best" linear model had been selected.

The SPSS non-linear regression subprogram (11) was used to fit non-linear models to the 1978 data. Chi-square goodness of fit tests were performed on the spur and terminal leaf areas predicted from the non-linear models and the areas observed in 1978, 1979, and 1980. All three years of data were then used to develop linear and non-linear models to predict spur and terminal leaf expansion from DD accumulations. These models were compared graphically and statistically.

RESULTS AND DISCUSSION

Average spur and terminal shoot areas per leaf increased in a curvilinear fashion during the 1978-1980 growing seasons (Figure 4). Similar patterns of expansion were observed in older, less vigorous trees (BU2), and in young, vigorous trees (DE3); however, growth began on different days of the year in each of the three years the trees were observed. The variance in growth initiation among years was reduced when average areas per leaf were plotted against DD accumulations (Figure 5); with unfolded leaves being observed after approximately 200 DD had accumulated since April 19. Average area per leaf increased linearly with time and DD accumulation during the first three weeks of growth, but the final average leaf size for both spur and terminal shoots was not constant among years.

Of ten linear regression models fitted to the spur and terminal leaf expansion data of 1978 (Table 5), the second order rectangular hyperbola model using DD accumulation was selected as the "best" model based on the coefficient of determination and Durbin-Watson statistics (3). When spur and terminal areas per leaf predicted from this model were compared to the observed areas for 1979 in orchards BU2 and DE3, an acceptable fit was obtained for both orchards

Figure 4. Average areas per leaf on Montmorency sour cherry spur and terminal shoots observed in orchards BU2 and DE3 near East Lansing, Michigan, during the 1978-1980 growing seasons.

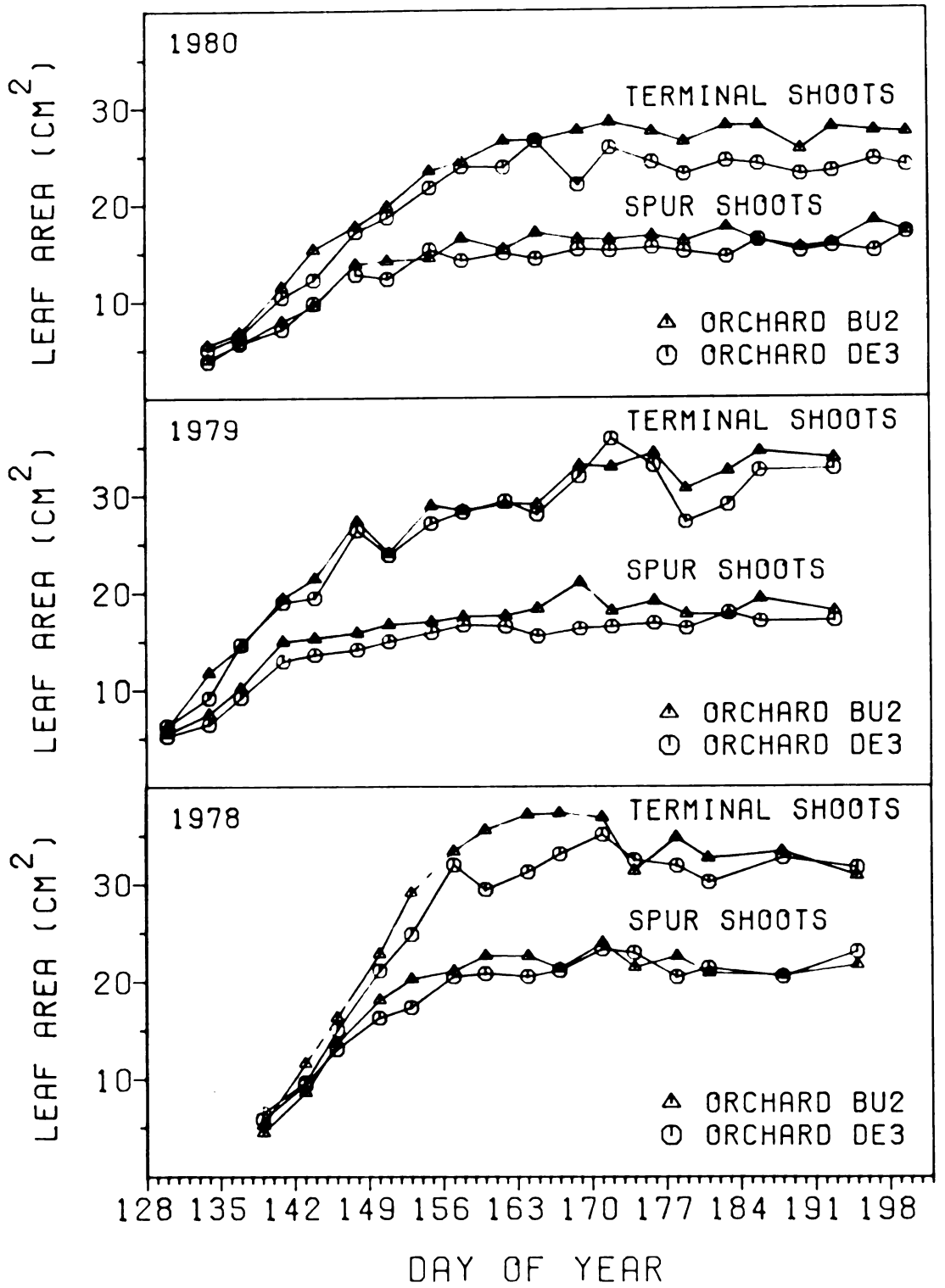

1980
TERMINAL SHOOTS
SPUR SHOOTS
ORCHARD BU2
ORCHARD DE3
1979
TERMINAL SHOOTS
SPUR SHOOTS
ORCHARD BU2
ORCHARD DE3
1978
TERMINAL SHOOTS
SPUR SHOOTS
ORCHARD BU2
ORCHARD DE3
LEAF AREA (CM2)
10
20
30
128 135 142 149 156 163 170 177 184 191 198
DAY OF YEAR

Figure 5. Predicted average spur and terminal areas per leaf as linear (A) and non-linear (B) functions of degree-day accumulation, base 4°C beginning April 19, and observed areas for Montmorency sour cherry in orchards BU2 and DE3 near East Lansing, Michigan, during the 1978-1980 growing seasons.

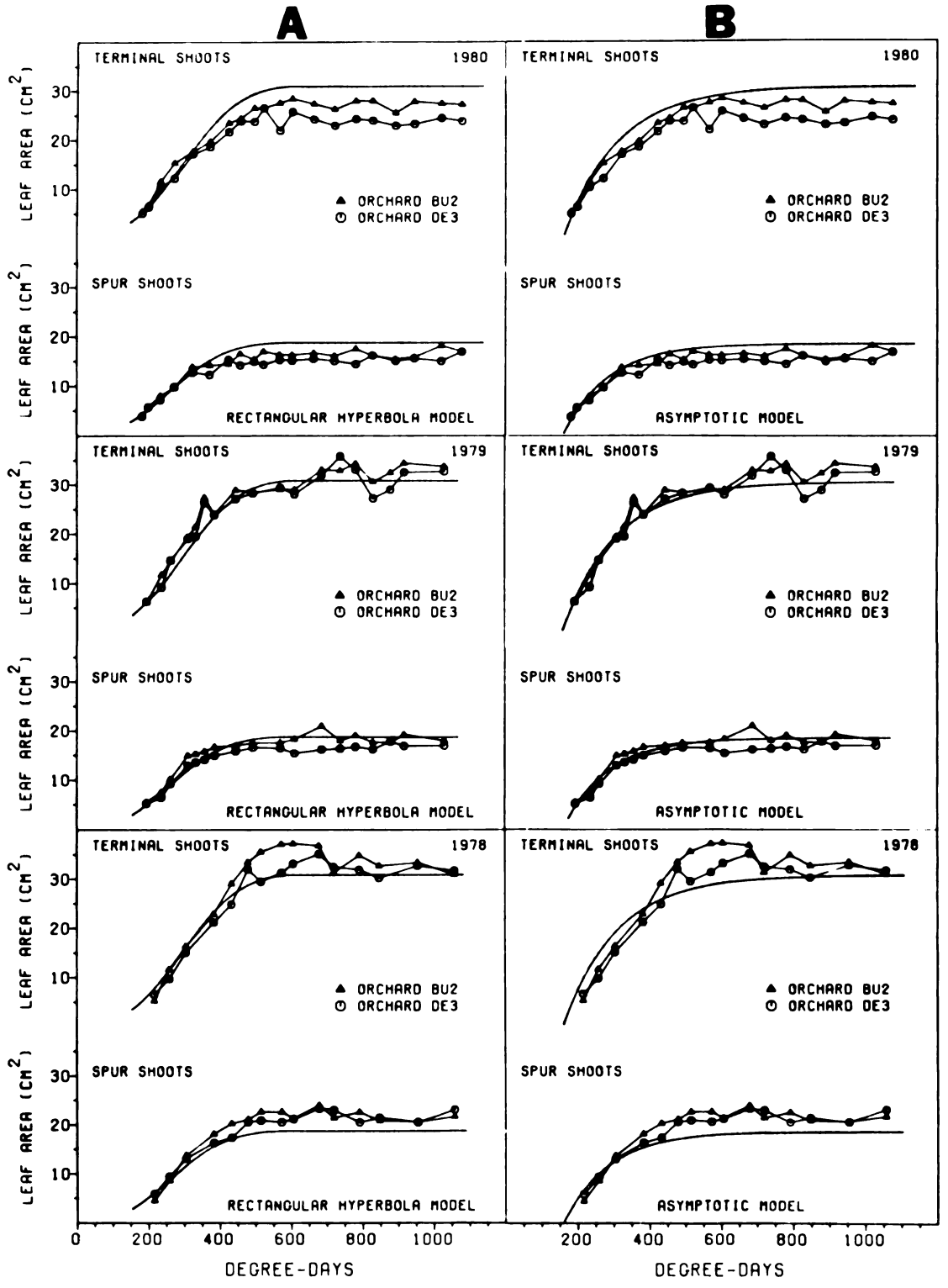

A
B
TERMINAL SHOOTS
1980
SPUR SHOOTS
RECTANGULAR HYPERBOLA MODEL
ASYMPTOTIC MODEL
1979
1978
ORCHARD BU2
ORCHARD DE3
LEAF AREA (CM2)
DEGREE-DAYS
0
200
400
600
800
1000
10
20
30

Table 5. Coefficient of determination values for ten linear regression models which relate Montmorency sour cherry spur and terminal leaf expansion to degree-day accumulation at base 4°C beginning April 19 (DD) or to day of the year (DOY). Data sets for individual years contain observations from research orchards BU2 and DE3 at East Lansing, Michigan.

	Coefficient of determination							
	Spur shoots				Terminal shoots			
Model/Equation	1978	1979	1980	Combined	1978	1979	1980	Combined
1st Order Reciprocal with 2 variables								
$Y = a + b(\frac{1}{DOY}) + c(\frac{1}{DD})$	.956	.896	.947	.779	.915	.940	.929	.857
1st Order Rectangular Hyperbola with 2 variables								
$\frac{1}{Y} = a + b(\frac{1}{DOY}) + c(\frac{1}{DD})$	.946	.913	.921	.903	.962	.916	.941	.922
2nd Order Polynomial with 1 variable								
$Y = a + b(DOY) + c(DOY)^2$	.885	.870	.880	.690	.908	.937	.916	.777
$Y = a + b(DD) + c(DD)^2$	.887	.806	.843	.704	.908	.893	.886	.810
2nd Order Logarithmic Reciprocal with 1 variable								
$\ln Y = a + b(\frac{1}{DOY}) + c(\frac{1}{DOY})^2$	.901	.909	.925	.773	.939	.945	.952	.815
$\ln Y = a + b(\frac{1}{DD}) + c\ (\frac{1}{DD})^2$	.979	.941	.976	.889	.969	.973	.973	.916
2nd Order Reciprocal with 1 variable								
$Y = a + b(\frac{1}{DOY}) + c(\frac{1}{DOY})^2$	.933	.902	.921	.702	.936	.950	.935	.767
$Y = a + b(\frac{1}{DD}) + c(\frac{1}{DD})^2$	.944	.899	.941	.756	.890	.940	.917	.809
2nd Order Rectangular Hyperbola with 1 variable								
$\frac{1}{Y} = a + b(\frac{1}{DOY}) + c(\frac{1}{DOY})^2$	.796	.876	.873	.735	.836	.861	.899	.745
$\frac{1}{Y} = a + b(\frac{1}{DD}) + c(\frac{1}{DD})^2$	.952	.961	.970	.937	.969	.976	.981	.943

(Table 6). However, when predicted areas were compared to the observed average areas per leaf for 1980, a lack of fit was observed. The lack of fit occurred because the final leaf sizes for spur and terminal leaves were not the same among years.

A non-linear asymptotic regression model of the form

$$\text{Average area per leaf} = A\,[1 - e^{-r(DD-Biofix)}]$$

was fitted to the 1978 data sets in order to obtain a predictive model with more biological meaning. The parameters in this model are: A = the asymptote or maximum average area per leaf for the season, r = an exponential leaf expansion rate constant, DD = the degree-day accumulation from April 19, and Biofix = the degree-days from April 19 to full bloom. Full bloom is used as a reference or biological fixpoint (Biofix) for predicting leaf expansion after the bloom period. The value of Biofix was determined empirically by plotting accumulated degree-day values for each day from April 19 against the residual (i.e., the difference between the original data points and those predicted by the model) sum of squares. The minimum sum of squares occurred with a DD accumulation of 150 to 180 DD. Because Biofix values for each year varied by only 30 DD, a value of 160 DD was selected as the Biofix value in the asymptotic model.

When spur and terminal leaf areas predicted from the asymptotic models were compared to the observed average areas per leaf for 1979 in orchards BU2 and DE3, acceptable fits were obtained (Table 6). The asymptotic model predicted

Table 6. Chi-square statistics for goodness of fit of linear and non-linear models constructed from 1978 data to Montmorency sour cherry spur and terminal leaf area observations in research orchards BU2 and DE3 near East Lansing, Michigan for the 1978-1980 growing seasons.

	Orchard		
	BU2	DE3	Combined
1978[z]			
Spur shoots			
Rectangular Hyperbola Model	1.74	2.81	4.55
Asymptotic Model	3.31	2.41	5.72
Terminal shoots			
Rectangular Hyperbola Model	2.90	5.38	8.29
Asymptotic Model	9.90	9.99	19.89
1979[y]			
Spur shoots			
Rectangular Hyperbola Model	13.38	22.17	35.55
Asymptotic Model	7.70	17.80	25.50
Terminal shoots			
Rectangular Hyperbola Model	13.97	14.82	28.78
Asymptotic Model	3.66	7.83	11.50
1980[x]			
Spur shoots			
Rectangular Hyperbola Model	28.76*	39.35*	68.11*
Asymptotic Model	20.22	30.16*	50.38*
Terminal shoots			
Rectangular Hyperbola Model	32.87*	53.39*	86.26*
Asymptotic Model	19.56	41.63*	61.19*

[z]Based on 15 observations.

[y]Based on 18 observations.

[x]Based on 20 observations.

*Chi-square values significant at P=0.001.

average area per leaf better than the rectangular hyperbolic model. However, when predicted areas from the asymptotic models were compared to the observed areas for 1980, an acceptable fit was observed for orchard BU2 for both spur and terminal shoots but not in orchard DE3. This lack of fit in orchard DE3 resulted from a smaller final spur and terminal average area per leaf for that season.

To verify that the second order rectangular hyperbola model was the "best" linear regression model, ten models were fitted to the data of 1979, 1980, and all three years (Table 5). These analyses supported the selection of the rectangular hyperbola model. The spur and terminal leaf expansion models based on the combined data from both orchards for all three years reproduced the observed data well for each year even though different final leaf areas were observed (Figure 5A). The following leaf expansion prediction equations were derived from the combined data and used to generate the predicted lines in Figure 5A:

Spur leaf area = $0.0897 - 43.206/DD + 12806.26/DD^2$

Terminal leaf area = $0.0606 - 34.831/DD + 10756.75/DD^2$

where DD = degree-day accumulation above 4°C beginning April 19.

Non-linear asymptotic regression models developed from the combined yearly data for both spur and terminal leaf expansion also reproduced the data well for each year (Figure 5B) when a Biofix value of 160 DD was used. Marginally better fits were obtained by using the DD accumulation

at which bloom occurred each year instead of 160 DD. The following leaf expansion prediction equations were derived from the combined data and used to make the predictions in Figure 5B:

$$\text{Spur leaf area} = 18.57\ [1 - e^{-0.008\ (DD - 160)}]$$

$$\text{Terminal leaf area} = 30.68\ [1 - e^{-0.0067\ (DD - 160)}]$$

where DD = degree-day accumulation above 4°C beginning April 19. Goodness of fit testing for both the linear and non-linear models indicated acceptable reproduction of the observed data for both spur and terminal shoots in both orchards for all three years (Table 7).

To explore why the final average areas per leaf were not the same each year, climatological data were obtained for East Lansing, Michigan, for monthly average temperature, rainfall, and percent of maximum possible sunshine (Table 8). Sunshine during April of 1979 and 1980 was less than the 25 yr normal and corresponded to the two years which had smaller final spur leaf areas. Percent sunshine for June of 1980 was lower than normal and that year had the smallest final spur and terminal leaf areas. These observations contradict shading studies (10,14) which have shown large leaf areas to be correlated with low light levels. The effect of temperature should be captured by using degree-days and no trend of final leaf size with temperature was observed. Total rainfall for April, May, and June was lowest for 1978, the year with the largest final leaf area.

Table 7. Chi-square statistics for goodness of fit of linear and non-linear models constructed from combined data of three years to Montmorency sour cherry spur and terminal leaf area observations in research orchards BU2 and DE3 near East Lansing, Michigan for the 1978-1980 growing seasons[w].

	Orchard		
	BU2	DE3	Combined
1978[z]			
Spur shoots			
Rectangular Hyperbola Model	7.80	5.21	13.00
Asymptotic Model	10.97	7.21	18.18
Terminal shoots			
Rectangular Hyperbola Model	7.48	2.22	9.69
Asymptotic Model	14.73	7.10	21.84
1979[y]			
Spur shoots			
Rectangular Hyperbola Model	2.06	2.94	5.00
Asymptotic Model	1.51	2.42	3.93
Terminal shoots			
Rectangular Hyperbola Model	5.43	4.42	9.85
Asymptotic Model	3.62	3.96	7.58
1980[x]			
Spur shoots			
Rectangular Hyperbola Model	4.29	9.25	13.54
Asymptotic Model	3.15	7.38	10.53
Terminal shoots			
Rectangular Hyperbola Model	6.89	20.09	26.98
Asymptotic Model	4.45	17.50	21.95

[z]Based on 15 observations.

[y]Based on 18 observations.

[x]Based on 20 observations.

[w]Chi-square values are non-significant at P=0.001.

Table 8. Climatological data for three years during collection of leaf expansion data and normals for East Lansing, Michigan, obtained from National Weather Service.

	March	April	May	June
Average Temperature (°C)				
1978	-3.28	6.67	14.5	18.7
1979	2.28	6.72	18.2	19.7
1980	-2.11	6.83	14.0	16.7
1940-1969 Normals	0.67	7.94	13.7	19.3
Average Rainfall (cm)				
1978	5.51	3.73	5.89	5.74
1979	3.58	7.21	5.38	10.80
1980	5.00	7.01	7.32	9.65
1949-1980 Normals	5.31	7.21	6.83	9.25
Average Sunshine (% of maximum possible)				
1978	51	55	61	72
1979	33	44	61	70
1980	53	46	64	59
1955-1979 Normals	47	53	63	66

CONCLUSIONS

I have demonstrated that both linear and non-linear models, based on field observations from one year, can acceptably predict average area per leaf of spur and terminal leaves in other years. My models do not account for many factors which affect growth (i.e., tree age, vigor, pruning practices, crop load, etc.); however do reproduce the overall patterns observed for spur and terminal shoots of Montmorency sour cherry trees. Like my model for leaf emergence (5), these leaf expansion models unfortunately accumulate energy from a fixed calendar date and not from some physiological event such as completion of rest. Research on rest completion of sour cherry is needed and may improve the accuracy of these models.

Because it is unreasonable to expect canopy development to be governed by a few parameters throughout its course, development of a mechanistic model which explains how the parts of the system work has not met with much success. I have, however, been successful in developing empirical models which redescribe the growth patterns in the observed data. These empirical models summarize many observations in a convenient way, free from the random fluctuation of sampling error. Such models have utility in monitoring foliage

development, which may be part of a larger pest management model. For example, our leaf emergence and expansion models could be used to study pathogen-host interactions for cherry leaf spot disease (6,8). Estimates of how much new foliage has developed since a fungicide application would be of value in deciding whether another application is needed. In addition, knowledge of the percentage new growth comprises of the total canopy will facilitate estimates of overall susceptibility of trees to the leaf spot fungus (6).

Of the two models, the asymptotic model is preferred because it contains parameters with biological meaning. Moreover, it is derived from the negative exponential growth function, which we have observed to fit leaf expansion rate data from the greenhouse (6) very well. The asymptotic model reproduces the data better than the rectangular hyperbola model in two of the three years studied, regardless if the parameters were determined from all three years or just from the 1978 data (Tables 6 and 7). The accuracy of the asymptotic model would improve if the value of "A" could fluctuate for each data set. Research is needed on determining what causes the final average leaf area to be smaller or larger than normal for a season.

LITERATURE CITED

1. ASHCROFT, G. L., E. A. RICHARDSON, and S. D. SEELEY. 1976. A statistical method for determining chill requirements of fruit buds. Appendix D in: Reducing fruit losses caused by low spring temperatures, Final Rpt. Utah Agr. Expt. Station to Four Corners Regional Commission, Project No. 562-366-084, Document No. 10550101.

2. BASKERVILLE, G. L., and P. EMIN. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50:514-517.

3. DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. Wiley, New York. 407 pp.

4. EDEY, S. N. 1977. Growing degree-days and crop production in Canada. Agriculture Canada Publication 1635.

5. EISENSMITH, S. P., A. L. JONES, and J. A. FLORE. 1980. Predicting leaf emergence of 'Montmorency' sour cherry from degree-day accumulations. J. Amer. Soc. Hort. Sci. 105:75-78.

6. EISENSMITH, S. P., T. M. SJULIN, A. L. JONES, and C. E. CRESS. 1981. Effects of leaf age and inoculum concentration on infection of sour cherry by Coccomyces hiemalis. Phytopathology 71:(In Press).

7. FISHER, D. V. 1962. Heat units and number of days required to mature some pome and stone fruits in various areas of North America. Proc. Amer. Soc. Hort. Sci. 80:114-124.

8. KEITT, G. W., E. C. BLODGETT, E. E. WILSON, and R. O. MAGIE. 1937. The epidemiology and control of cherry leaf spot. Wisc. Agr. Expt. Sta. Res. Bul. 132:1-118.

9. KENWORTHY, A. L. 1974. Sour cherry tree vigor as related to higher yields and better fruit quality. Mich. Agr. Expt. Stn. Rept. 223.

10. MAGGS, D. H. 1960. The stability of the growth pattern of young apple trees under four levels of illumination. Ann. Bot. 24:434-450.

11. NIE, H. C., H. HULL, J. G. JENKINS, K. STEINBRENNER, and D. H. BENT. 1975. Statistical package for the social sciences. McGraw-Hill, New York. 675 pp.

12. RICHARDSON, E. A., S. D. SEELEY, and D. R. WALKER. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. HortScience 9:331-332.

13. _____, _____, _____, J. L. ANDERSEN, and G. L. ASHCROFT. 1975. Pheno-climatology of spring peach bud development. HortScience 10:236-237.

14. SAMS, C. E. 1980. Factors affecting the leaf and shoot morphology and photosynthetic rate of sour cherry (Prunus cerasus L. 'Montmorency'). Ph.D. Dissertation. Michigan State University. 128 pp.

15. STEEL, R. G. D., and J. H. TORRIE. 1980. Principles and procedures of statistics. 2nd Ed. McGraw-Hill, New York.

PART II

DEVELOPMENT AND VALIDATION OF A MODEL TO DETECT INFECTION PERIODS OF COCCOMYCES HIEMALIS ON SOUR CHERRY

ABSTRACT

A regression model relating hours of continuous moist chamber exposure and temperature to infection of sour cherry by conidia of the cherry leaf spot fungus was developed from published data. The model is $EFI = [-11.0 + 0.2858W + 1.4639T - 0.0019W^2 - 0.0389T^2 - 0.003WT]^2$, where T = temperature C, W = hours of leaf wetness, and EFI = environmental favorability index from 0 to 100. An EFI of 14 was selected to delineate the minimum conditions for infection under field conditions. EFI was $\geq$ 14 in 62 of 65 validations where infection was detected by observing marked shoots of orchard trees every 4 to 7 days, and < 14 in 15 of 18 validations where no infection occurred. In 34 of 35 cases where infection was detected by exposing potted trees during putative infection weather, EFI was $\geq$ 14; and in 20 of 39 cases where no infection occurred, the EFI was < 14. The infection model is useful between 8 and 28 C, and for leaf wetness periods up to 70 hr. Daily EFI values were linearly related to rates of disease increase in Michigan in 1978 and 1979.

INTRODUCTION

Cherry leaf spot, caused by Coccomyces hiemalis Higgins, is a major disease of sour cherry (Prunus cerasus L. 'Montmorency') throughout Michigan cherry growing regions. Ascospores from apothecia in leaves overwintering on the orchard floor initiate primary infection in spring. Conidia from acervuli on infected leaves initiate secondary infection, a process repeated several times throughout the growing season.

Infection by ascospores and conidia is governed by the duration of wetting from rain and by temperature. A predictive system, similar to that of Mills for predicting infection by the apple scab fungus (7), might be useful in developing disease management strategies for leaf spot control. The objectives of this study were to develop and validate a model for identifying environmental periods favorable for infection by the leaf spot fungus and to relate the frequency and severity of these periods to disease progress.

MATERIALS AND METHODS

A multiple regression equation relating infection of leaves to hours of wetting in the chamber and temperature was generated from numerical values published in Figure 22 of Keitt et al (5). These workers inoculated sour cherry trees with conidial suspensions of C. hiemalis and incubated them continuously in a moist chamber for 4 to 70 hr and at temperatures of 8 to 28 C. These data, furnished to me by J. D. Moore, University of Wisconsin, Madison, WI, and the corresponding values predicted by the regression equation were plotted with a three-dimensional plotting program (12). Although Keitt et al (5) expressed infection as the average number of lesions per maximally infected square inch per leaf, I converted the published values to a relative percentage of the maximum disease intensity observed for their combined data. This relative scale of 0 to 100 was called an environmental favorability index (EFI). Various regression models were applied to the moist chamber data to find one which would explain the greatest percentage of variability.

Disease data for validation of the model were obtained by monitoring leaf spot infection and disease progress in three Montmorency cherry orchards and one nursery planting.

Orchards J04 and KL1 were located near East Lansing, MI, and consisted of 9- and 21-yr-old trees, respectively, in 1978. Orchard SH5A consisted of 7-yr-old trees in a mixed cultivar planting and SH5B consisted of a 5-yr-old planting of open-pollinated Montmorency seedlings. Both plantings were located at the South Haven Experiment Station, South Haven, MI. Orchard KL1 was used in 1978, SH5B in 1979, and J04 and SH5A in 1978 and 1979. Five spur and five terminal shoots on each of four unsprayed trees in each planting were selected for assessing disease development during the growing season. The number of lesions on all leaves, the number of leaves, and the number of leaf nodes on these spurs and shoots were counted every 4-7 days. Occurrence of infection was determined by the appearance of new lesions on leaves of the same terminal shoot. The mean number of lesions per leaf on 40 shoots for SH5A, SH5B, and KL1 and 20 shoots for J04 was calculated for each observation date, then expressed as a percentage of the maximum average number of lesions per leaf observed at each orchard.

To establish which wetting periods were suitable for infection, potted Montmorency cherry trees on Prunus mahaleb rootstock were exposed during each rainy period. In 1978, two groups of four trees were placed in orchard KL1 and four groups of three trees were placed in orchard J04. In 1979, single groups of twelve and nine trees were exposed in planting J04 and SH5B, respectively. After each rain, the exposed trees were removed from the orchards and placed in a

cold frame. After a two week incubation period, the trees were examined for lesions and classified as infected or non-infected. Trees grown in the cold frame throughout the season served as controls.

Relative humidity, air temperature, leaf wetness and rainfall data were collected at each location for use in testing the model and for assessing the favorability of the environment for infection. Relative humidity and air temperature were measured with a 7-day recording hygrothermograph (Bendix Co., Inc., Baltimore, MD 21204) placed in a standard weather shelter 2 m above the ground. Calibration of the hygrothermograph was checked bi-weekly with a sling psychrometer. A 7-day recording leaf wetness meter (M. deWit, Hengelo, Holland) was placed 1 m above the ground in the drip line of a tree to measure the duration of leaf wetness. Rainfall was measured daily with a dip-stick rain gauge and the data were used to verify that periods of leaf wetness recorded by the wetness meter were initiated by rain.

I assumed rather arbitrarily that intermittent wetting with individual dry periods < 8 hr would allow infection to proceed. Therefore, rain-initiated leaf wetness periods were not terminated until the lapse of an 8 hr dry period. Initiation and termination times of wetting were rounded to the nearest hour. Average air temperatures were the arithmetic means of hourly observations during the wet period.

To establish if ascospores and conidia of the leaf spot fungus were disseminated in each wetting period, three battery powered Rotorod spore samplers (Ted Brown Associates, Los Altos Hills, CA 94022), activated by a moisture sensor (9), were located 0.5 m above the ground and within 2 m of a group of exposed plants. Each sampler was protected by a rain shield placed 4 cm above the collection head. Type U collection heads with 64 mm long plastic 'I' rods coated with silicone compound G-697 (General Electric, Waterford, NY 12188) were used in orchard KL1 and retractable collection heads with 32 mm long rods coated with G-697 were used in orchards J04 and SH5B. After each rainy period the plastic rods were collected and mounted in cotton blue-lactophenol for examination with a light microscope at 400X.

RESULTS

Infection model development. A regression model was developed for relating temperature and length of moist chamber exposure to infection. A suitable second-order model was of the form:

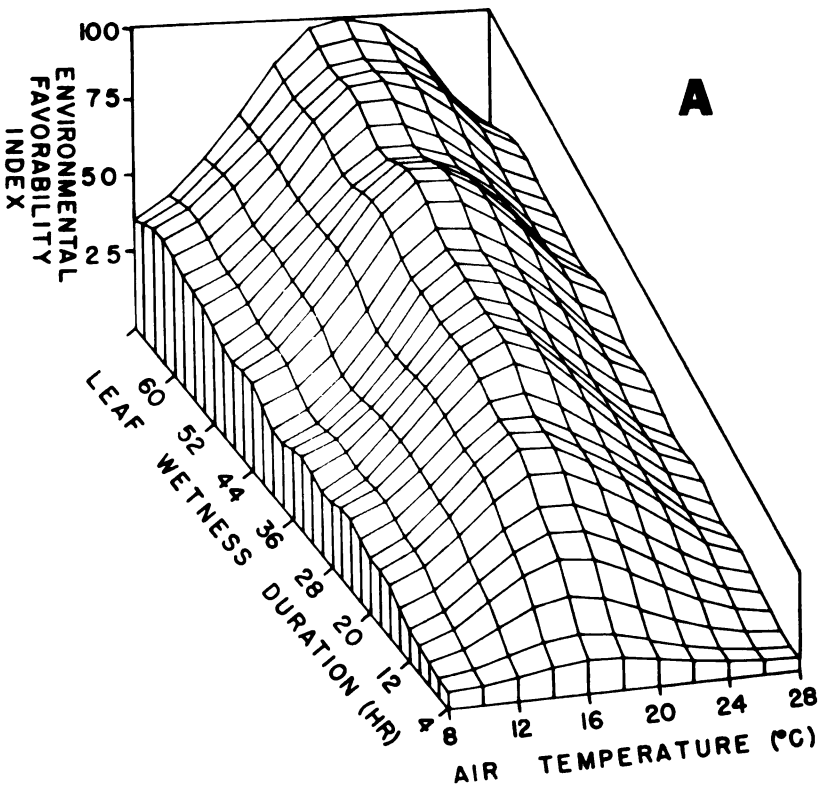
$$EFI = b_0 + b_1W + b_2T + b_{11}W^2 + b_{22}T^2 + b_{12}WT + \epsilon$$

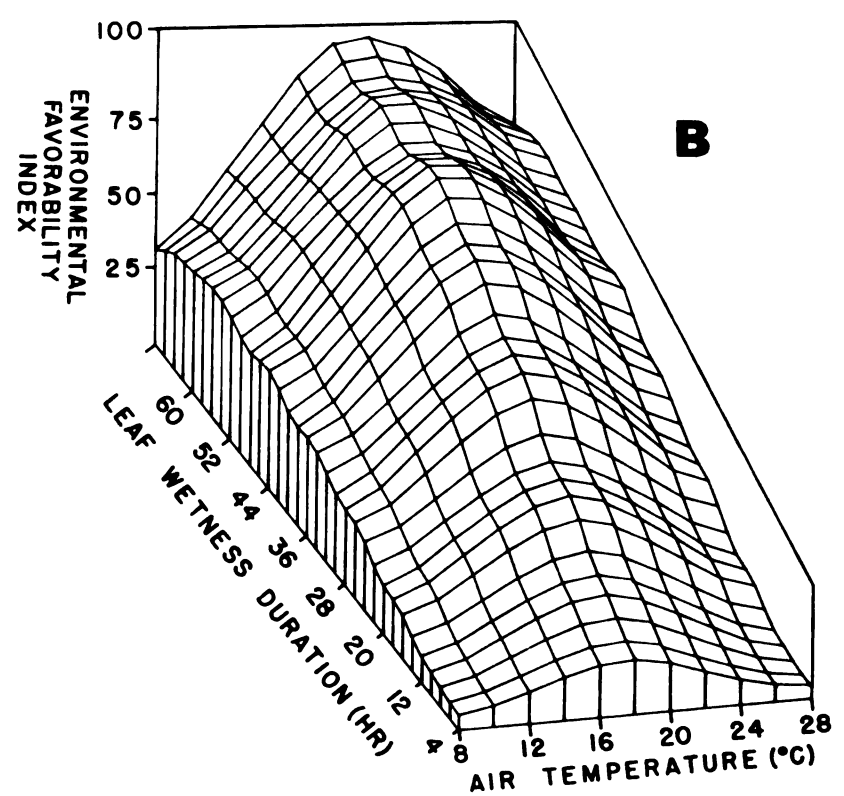
where W = hours of continuous moisture and T = temperature C. The b values are least squares estimates of the partial regression coefficients and ϵ is a normally distributed random variable with mean zero and variance σ^2. This model accounted for 93% of the observed variation in infection and all estimated coefficients were statistically significant ($P = 0.01$). The actual equation is:

$$EFI = [-11.0 + 0.2858W + 1.4639T - 0.0019W^2 - 0.0389T^2 - 0.0030WT]^2$$

The relationship of temperature and wetting to infection is shown in a surface generated from the original 54 data points (Figure 1A). A comparative surface generated from predicted points (Figure 1B) indicates a good fit of the model for temperatures of 8 to 28 C and wetting durations up to 68 hr. Examination of residuals (2), i.e., the difference between the original data points and those predicted by the regression model, supports the assumption that errors are independent and normally distributed with a mean of zero and

Figure 1. Relationship of temperature and wetting to infection by Coccomyces hiemalis of Montmorency sour cherry leaves from empirical data by G. W. Keitt et al, 1937. Wisconsin Agric. Exp. Stn. Res. Bull. 132 (A) and predicted from regression equation (B). Levels of leaf infection are plotted on a relative scale.


A
ENVIRONMENTAL FAVORABILITY INDEX
100
75
50
25
LEAF WETNESS DURATION (HR)
60
52
44
36
28
20
12
4
8
12
16
20
24
28
AIR TEMPERATURE (°C)


B
ENVIRONMENTAL FAVORABILITY INDEX
100
75
50
25
LEAF WETNESS DURATION (HR)
60
52
44
36
28
20
12
4
8
12
16
20
24
28
AIR TEMPERATURE (°C)

a constant variance (Figure 2). The model tends to overpredict with EFI values less than 20 and underpredict with EFI values greater than 70.

Infection model validation. The following assumptions were made for predicting infection by C. hiemalis with the model in the field: (i) temperature was the average air temperature during a wetness period, (ii) wetness was the hours of wetting recorded by the deWit recorder, and (iii) conditions were not favorable for infection unless EFI $\geq$ 14. An EFI of 14 fits Keitt's (4) conclusion that 5 hr of wetting at 20 C were the minimum conditions for infection.

Putative infection periods were verified by monitoring the weather, trapping spores, and observing subsequent disease development in three orchards in 1978 and two orchards in 1979. After each rain, temperature and wetness duration values from the recording charts were used in the infection model to calculate EFI values. In 95% of 65 cases where infection was detected by the appearance of new lesions on leaves of terminal shoots observed every 4-7 days, the EFI was > 14; and in 83% of 18 cases where no infection occurred, the EFI was < 14 (Figure 3B). In 97% of 35 cases where infection was detected by exposing potted cherry trees during each wetting period, the EFI was > 14; and in 51% of 39 cases where no infection occurred, the EFI was < 14 (Figure 3A). Examination of the other 49% (19 cases), where infection was predicted but the exposed plants were not infected, revealed that in 14 cases no spores were trapped and in five cases no

Figure 2. Plot of residuals against predicted environmental favorability index (EFI) indicating that the errors are independent, have zero mean, and a constant variance. Dotted line indicates EFI value considered to delineate minimum environmental conditions for infection of Montmorency sour cherry by Coccomyces hiemalis.

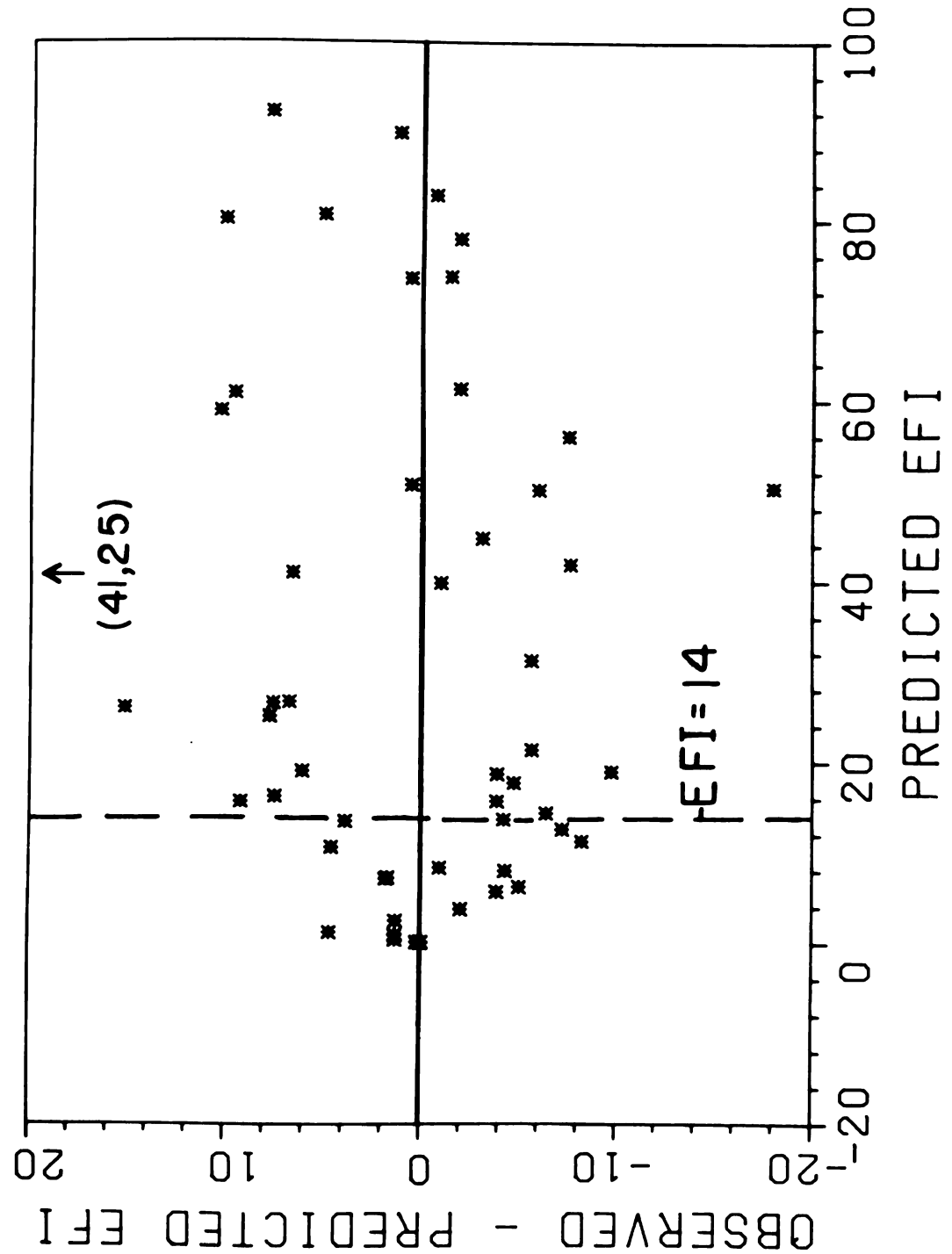
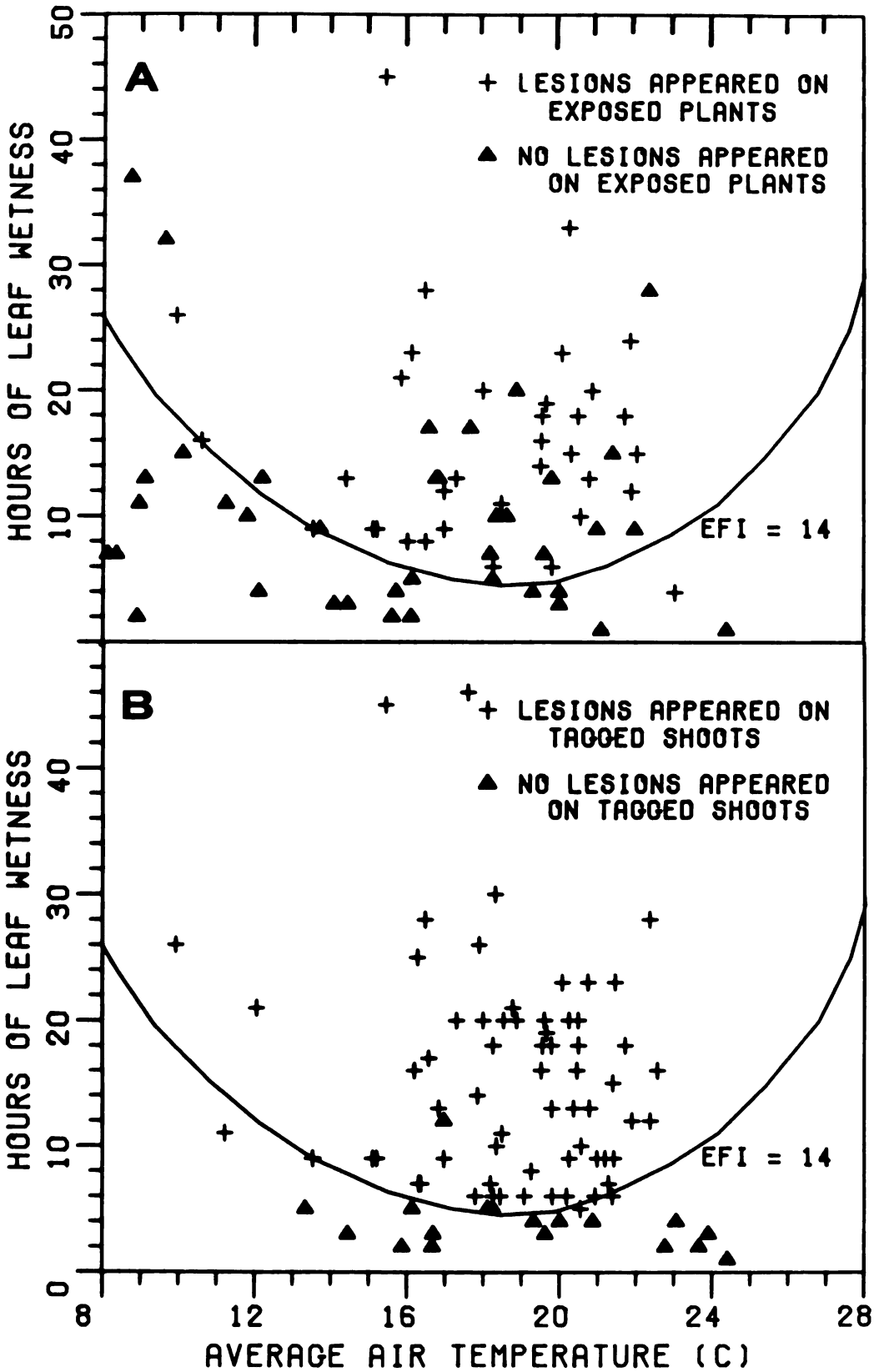

OBSERVED - PREDICTED EFI
20
10
0
-10
-20
PREDICTED EFI
100
80
60
40
20
0
-20
EFI=14
(41,25)

Figure 3. Wetting periods followed and not followed by infection of Montmorency sour cherry leaves by Coccomyces hiemalis on potted trees exposed per wetting period (A) and on shoots of orchard trees observed every few days for leaf spot development (B) in relation to an infection curve generated from an infection model. Data are for orchards KL1, J04, and SH5B in 1978 and J04 and SH5B in 1979.


A
+ LESIONS APPEARED ON EXPOSED PLANTS
▲ NO LESIONS APPEARED ON EXPOSED PLANTS
EFI = 14
B
+ LESIONS APPEARED ON TAGGED SHOOTS
▲ NO LESIONS APPEARED ON TAGGED SHOOTS
EFI = 14
HOURS OF LEAF WETNESS
0
10
20
30
40
50
8
12
16
20
24
28
AVERAGE AIR TEMPERATURE (C)

spore trapping data were taken. However, in five of the 14 and in three of the five cases, new lesions were observed on leaves of terminal shoots in the orchard. Overall, the model predicted correctly in 93% of the cases using marked terminal shoots and 75% of the cases using exposed potted trees.

Relation of environmental favorability index to infection rate. The percentage data for orchard J04 in 1978 and orchard SH5A in 1979 were plotted against EFI values calculated with the infection model (Figure 4). It was observed that intervals with several high EFI values (20-27 July 1978 for J04) were followed by increases in disease (28 July to 10 August for J04) and intervals with low EFI values (5-27 July 1979 for SH5A) were followed by periods of little or no disease increase (13 July to 4 August for SH5A). Similar patterns were observed to occur in orchards SH5A and KL1 in 1978 and J04 and SH5B in 1979.

The hypothesis that the EFI, which reflects the combined effects of temperature and wetness on infection, is related to the rate of disease increase was tested using regression analysis. Proportional rates of change in lesions per leaf and average daily EFI values were calculated for time intervals where defoliation did not hamper disease assessment (Table 1). EFI values were summed for the interval 8 days prior to the disease change interval, since incubation periods have been reported to range from 5 to 11 days (5). A linear regression model of the form:

$$Y = b_0 + b_1X$$

Figure 4. The relation of the progress of cherry leaf spot epidemics in two orchards to the frequency and favorability of wetting periods as expressed by daily environmental favorability index (EFI) values.

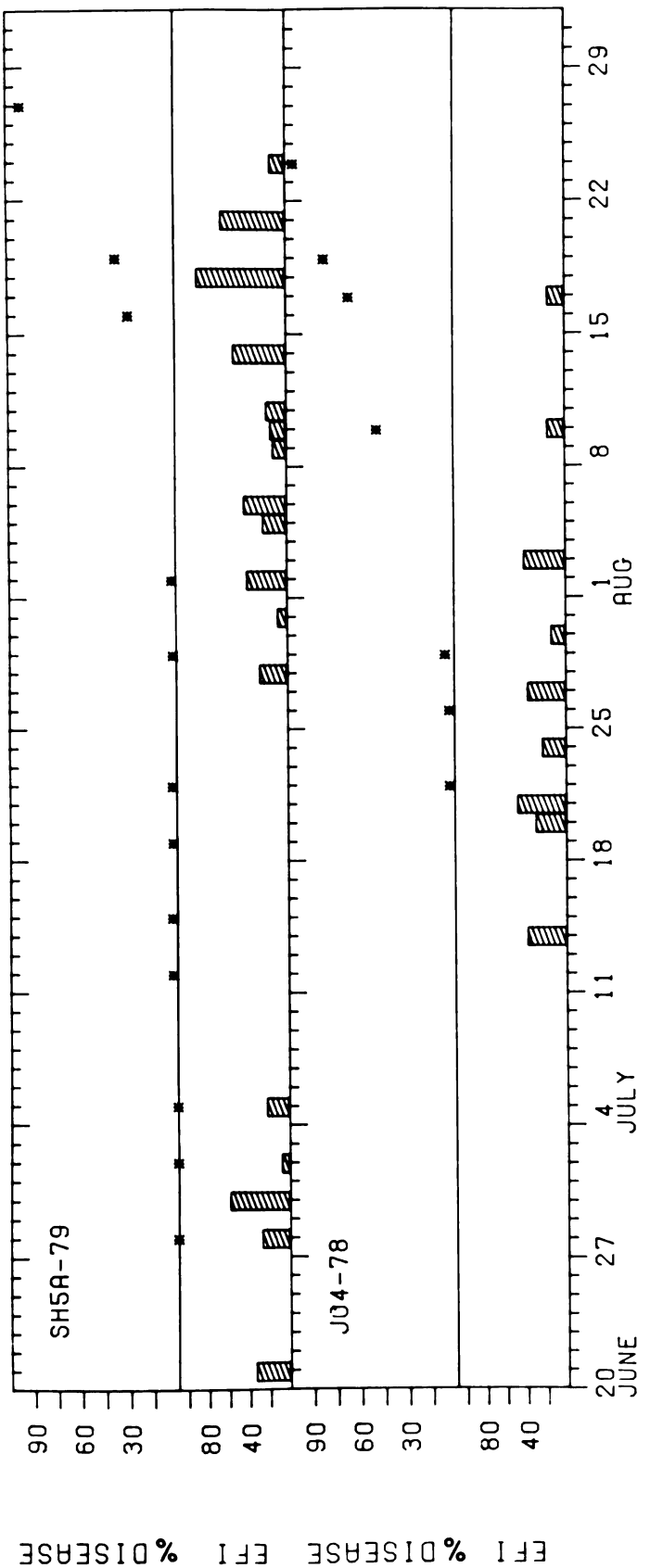

SH5A-79
J04-78
90
60
30
80
40
90
60
30
80
40
20
JUNE
27
4
JULY
11
18
25
1
AUG
8
15
22
29
EFI %DISEASE EFI %DISEASE

Table 1. Proportional rates of change in cherry leaf spot severity and average daily environmental favorability index calculated with an infection model from temperature and leaf wetness data taken in six sour cherry orchards in Michigan.

Day of year		Lesions per leaf (Mean number)		Rate of disease increase[a]	Average daily environmental favorability index[b]
t_1	t_2	$D(t_1)$	$D(t_2)$		
Orchard J04-1978					
206	209	0.24	0.43	0.187	9.53
209	221	0.43	3.67	0.179	9.80
221	228	3.67	4.99	0.044	5.69
228	230	4.99	6.17	0.106	7.90
230	235	6.17	7.61	0.042	3.10
Orchard SH5A-1978					
179	192	0.04	0.97	0.239	10.08
206	213	0.79	5.82	0.285	9.96
213	220	5.82	6.54	0.017	4.66
220	227	6.54	15.45	0.123	10.14
227	234	15.45	19.18	0.030	2.99
234	242	19.18	45.59	0.109	4.99
Orchard KL1-1978					
181	188	0.19	0.77	0.197	8.99
188	195	0.77	1.32	0.077	5.10
213	216	0.98	2.31	0.287	14.23
216	220	2.31	3.13	0.076	4.05
223	228	2.43	6.28	0.190	8.62
228	234	6.28	7.27	0.025	2.72

Table 1 (cont'd)

Orchard J04-1979					
188	203	0.07	3.51	0.269	9.98
203	215	3.51	4.13	0.014	1.70
215	228	4.13	38.86	0.172	9.83
Orchard SH5A-1979					
178	185	0.04	0.05	0.028	4.69
185	195	0.05	1.57	0.355	11.20
213	227	1.39	15.22	0.171	9.68
230	238	19.35	50.29	0.136	6.39
Orchard SH5B-1979					
185	195	0.03	1.48	0.393	11.20
213	227	1.48	7.26	0.113	9.68
230	238	8.38	22.04	0.121	6.39

---

[a]Defined as the $\log_e D(t_2) - \log_e D(t_1)$ divided by t_2-t_1.

[b]Defined as the sum of the EFI values from t_1-8 to t_2-8 divided by t_2-t_1.

Table 2. Regression statistics for testing the linear relationship between average daily environmental favorability index and proportional rate of change in cherry leaf spot disease severity for six orchards in Michigan.

Orchard-year	Intercept[a]	Slope[a]	Standard error of slope	F-statistic[a]	Coefficient of determination
J04-1978	-0.055 NS	0.0231	0.0053	19	0.86
SH5A-1978	-0.063	0.0276	0.0093	9	0.69
KL1-1978	-0.026 NS	0.0231	0.0018	158	0.98
J04-1979	-0.031 NS	0.0254 NS	0.0098	7 NS	0.87
SH5-1979[b]	-0.186 NS	0.0439	0.0125	12	0.71
Combined[c]	-0.065	0.0281	0.0034	68	0.73

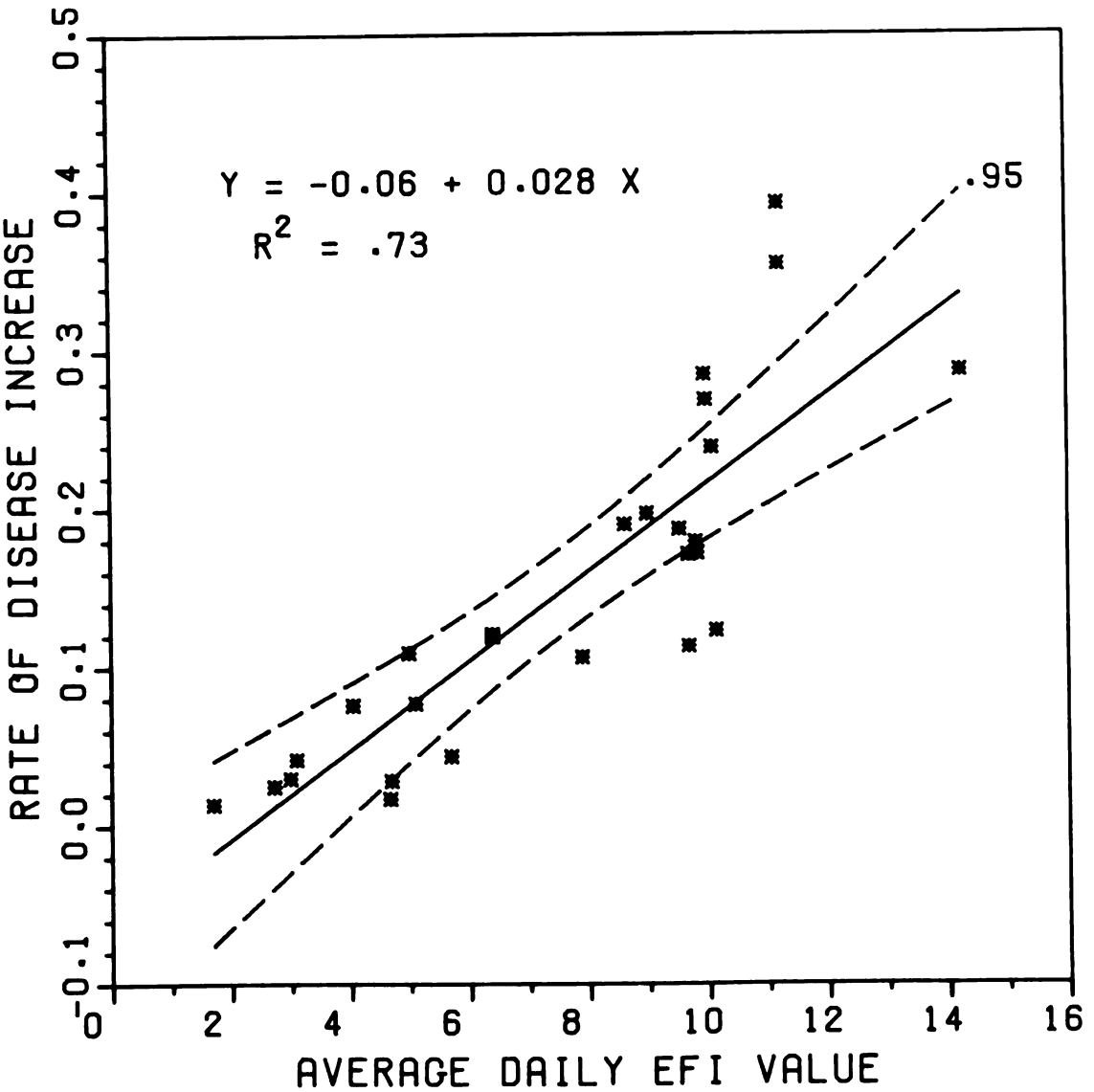
[a]All values are significant at P=0.05 except when followed by NS.

[b]Data from orchards SH5A-1979 and SH5B-1979 were combined.

[c]Data from all orchards were combined.

where Y is rate of change in disease per day, X is the average daily EFI, and the b values are the estimated regression coefficients, was fitted to the data from each orchard, except that data for SH5A-1979 and SH5B-1979 were combined (Table 2). Before pooling the five data sets for regression analysis, tests for homogeneity of regression coefficients (1, 10) were performed. The resultant F-statistics were not significant (P=0.05), indicating that the hypothesis that all five regression coefficients are homogeneous cannot be rejected. The combined model (Figure 5) shows that frequency and favorability of wetting periods, as measured by average daily EFI values, are directly related to infection rates.

Figure 5. Fitted regression line and 95% confidence limits for data from Table 1 relating proportional rate of change in mean number of cherry leaf spot lesions per leaf to average daily environmental favorability index 8 days prior to the interval of disease increase.


Y = -0.06 + 0.028 X
R^2 = .73
.95
RATE OF DISEASE INCREASE
AVERAGE DAILY EFI VALUE
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0
2
4
6
8
10
12
14
16

DISCUSSION

A multiple regression model was developed for identifying rainy periods favorable for infection by the cherry leaf spot fungus. The term "environmental favorability", rather than "relative disease severity", was used in this model because the EFI does not account for variations in inoculum levels or host susceptibility. Therefore, EFI may indicate that considerable infection is expected at times when little or no infection is seen because of limited inoculum.

The model was developed from conidial infection data and validated primarily on secondary infection periods having air temperatures between 15 and 23 C. Additional data are needed to determine the effectiveness of the model in detecting primary infection periods. Most wet periods that appeared favorable for infection but failed to give detectable infection occurred in May and early June when infection was caused by primary inoculum. Keitt et al (5) observed little or no disease development following ascospore discharges from some continuous wet periods under conditions that appeared favorable for infection. Ascospore discharge was heaviest at the end of these wet periods, when leaves containing apothecia were drying (5). Thus, split wet periods may be

more favorable than continuous wet periods for severe primary infection.

The method used in this study to connect split wetting periods was taken from an apple scab infection prediction system (4). Extending wetting periods when relative humidity is above 90% has been used to determine the length of leaf wetness duration for apple scab (3, 8) and may increase the model's ability to predict cherry leaf spot disease severity. Additional work is needed to determine the best criteria for connecting wetting periods that are not contiguous.

The model allows for consideration of new disease management strategies based on the use of fungicides having post-infection eradicant activity against the leaf spot fungus (6, 11). Work is currently underway to test the effectiveness of fungicide applications applied after leaf spot infection is detected with the model. The relationship between average daily EFI and proportional rate of change in disease severity may be used to determine if a fungicide application is necessary when more is known about the economic threshold of cherry leaf spot.

LITERATURE CITED

1. CHOW, G. C. 1960. Tests of equality between sets of coefficients in two linear regressions. Econometrica 28:591-605.

2. DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. J. Wiley and Sons, Inc., New York, NY. 407 pp.

3. JONES, A. L., S. L. LILLEVIK, P. D. FISHER, and T. C. STEBBINS. 1980. A microcomputer-based instrument to predict primary apple scab infection periods. Plant Dis. 64:69-72.

4. KEITT, G. W. 1927. Studies of apple scab and cherry leaf spot infection under controlled conditions. Phytopathology 17:45.

5. KEITT, G. W., E. C. BLODGETT, E. E. WILSON, and R. O. MAGIE. 1937. The epidemiology and control of cherry leaf spot. Wis. Agric. Exp. Stn. Res. Bull. 132:1-118.

6. KLOS, E. J., and F. R. FRONEK. 1964. Chemical eradication of cherry leaf spot fungus. Mich. Agric. Exp. Stn. Quart. Bull. 47:65-68.

7. MILLS, W. D. 1944. Efficient use of sulfur dusts and sprays during rain to control apple scab. N. Y. Agric. Exp. Stn. (Ithaca) Ext. Bull. 630. 4 pp.

8. PREECE, T. F., and L. P. SMITH. 1961. Apple scab infection weather in England and Wales, 1956-1960. Plant Path. 10:43-51.

9. SMALL, C. G. 1978. A moisture-activated electronic instrument for use in field studies of plant diseases. Plant Dis. Rep. 62:1039-1043.

10. STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc. New York, NY. 481 pp.

11. SZKOLNIK, M. 1974. Unusual post-infection activity of a piperazine derivative fungicide for the control of

cherry leaf spot. Plant Dis. Rep. 58:326-369.

12. WITTICK, R. I. 1974. GEOSYS: A computer system for the description and analysis of spatial data. Computer Institute for the Social Sciences Research Technical Report 74-53. Dept. of Geography, Michigan State University, East Lansing, MI 48824. 35 pp.

PART III

USE OF THE INFECTION MODEL FOR TIMING FUNGICIDE APPLICATIONS TO CONTROL CHERRY LEAF SPOT

ABSTRACT

A model relating leaf wetness duration and mean air temperature to infection of sour cherry by Coccomyces hiemalis was evaluated for timing fungicide applications of dodine and CGA-64251 (1-[[2-(2,4-dichlorophenyl)-4-ethyl-1,3-dioxolan-2-yl]methyl]-1H-1,2,4-triazole) for leaf spot control. Infection periods were identified and classified as LOW, MODERATE and HIGH based on predicted environmental favorability indices (EFI) of $\geq$ 14, $\geq$ 28, and $\geq$ 42, respectively. In 1979 and 1980, CGA-64251 provided good leaf spot control regardless of application timing, and dodine provided good control when applied after LOW and MODERATE but not HIGH infection periods. In a second trial in 1980, dodine and CGA-64251 applied on an 11-day schedule or as post-infection applications after infection periods with an EFI $\geq$ 28 gave comparable control. Secondary infection was prevented with eradicant sprays applied against conidial inoculum available during infection periods. Use of the infection model for timing sprays for leaf spot is a promising alternative to fixed time interval spray schedules.

INTRODUCTION

Cherry leaf spot, a serious disease of sweet and sour cherry in New York and Michigan, is initiated each spring by ascospores of *Coccomyces hiemalis* Higgins from apothecia in overwintering cherry leaves. Extensive spread of the disease in late spring and summer is caused by the conidial stage of *C. hiemalis* (*Cylindrosporium hiemalis* Higgins).

Protective fungicide programs are used to prevent infection by the leaf spot fungus (2). However, the recent development of a model for identifying environmental periods suitable for infection of cherry trees (1) and the reported control of leaf spot with experimental fungicide CGA-64251 applied 24 hr after inoculation under greenhouse conditions (11) should make eradicant fungicide programs possible as well. This section assesses the effectiveness of combining predictions and the use of eradicant fungicides for controlling leaf spot.

MATERIALS AND METHODS

Dodine (Cyprex 65% a.i. WP, American Cyanamid Co., Princeton, NJ 08540) and CGA-64251 (1-[[2-(2,4-dichlorophenyl)-4-ethyl-1,3-dioxolan-2-yl]methyl]-1*H*-1,2,4-triazole 10% a.i. WP, Ciba-Geigy Co., Greensboro, NC 27409) were applied with a handgun sprayer at 24.6 kg/cm^2 (350 psi) at a rate of 0.45 g/L (6 oz/100 gal) of formulation in a 10-yr-old Montmorency sour cherry orchard in 1979 and in 22- and 30-yr-old Montmorency sour cherry orchards near East Lansing, MI, in 1980. Each treatment was replicated three times using single tree plots, and each tree was sprayed to the point of drip (approximately 15 L of spray per tree). All eradicant sprays were applied within 48 hr after the inception of wet periods predicted to give infection, except that no additional sprays were made for 7 days after a fungicide was applied.

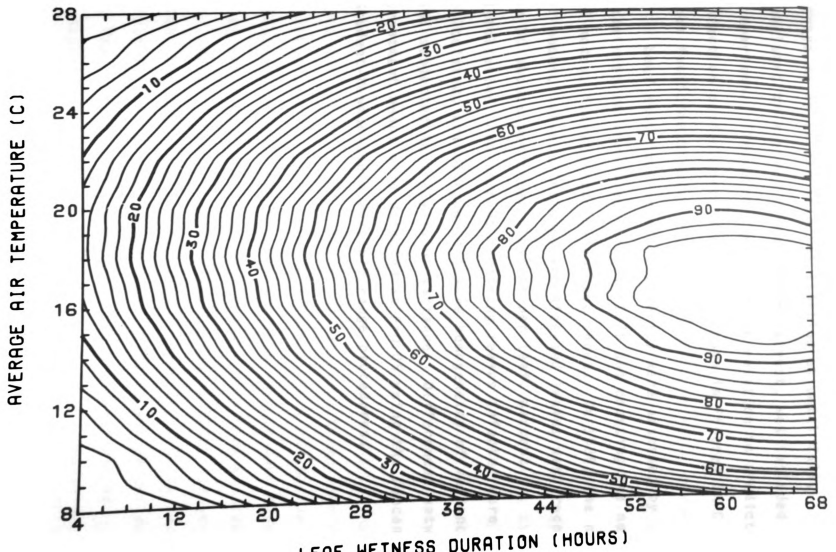
The model used to identify infection periods of *C. hiemalis* on sour cherry is described elsewhere (1). Hours of wetness from rain and mean air temperature (C) during the wet period are used to compute an environmental favorability index (EFI) from 0 to 100. Under orchard conditions and high inoculum levels, an EFI value of 14 is considered to represent the minimum conditions for infection. In this

study, EFI values were computed directly with the model, or were taken from a nomogram (Figure 1). The nomogram was constructed using a computer plotting package (8) and a set of 363 points generated by varying the temperature (T) and leaf wetness (W) values in the model, i.e., EFI = f(T,W) where T = 8, 10, 12, ... 28 and W = 4, 6, 8 ... 68.

Weather data were collected in each orchard each year for determining the EFI values. Air temperature was measured with a 7-day recording hygrothermograph (Bendix Co., Inc., Baltimore, MD 21204) placed in a standard weather shelter 2 m above the ground. A 7-day recording leaf wetness meter (M. deWit, Hengelo, The Netherlands) was placed 1 m above the ground in the drip line of a tree to record the duration of leaf wetness. Rainfall was measured with a 7-day recording tipping bucket rain gauge (Weathermeasure Corp., Sacramento, CA 95841) in 1979 and 1980 and with a dip-stick rain gauge at a second location in 1980.

To test EFI values for timing fungicides, sprays were applied in 1979 following wet periods when EFI values were $\geq$ 14, $\geq$ 28, and $\geq$ 56, and in 1980 when EFI values were $\geq$ 14, $\geq$ 28, and $\geq$ 42. Infection periods corresponding to these categories of EFI values were designated as LOW, MODERATE, and HIGH, respectively. In 1979, a protective schedule (2) with sprays on a 10-day interval starting at petal fall, concluded by a spray 1 week after harvest, was included for comparison. In 1980, a second trial consisted of applying the fungicides after primary, secondary, and all infection

Figure 1. Nomogram relating the duration of leaf wetness and mean air temperature to infection by Coccomyces hiemalis of Montmorency sour cherry leaves. Intervals are values of an environmental favorability index from 0 to 100 generated from an infection model.


AVERAGE AIR TEMPERATURE (C)
28
24
20
16
12
8
4
12
20
28
36
44
52
60
68
LEAF WETNESS DURATION (HOURS)
10
20
30
40
50
60
70
80
90

periods with EFI values $\geq$ 28. A protective schedule with sprays on an 11-day interval starting at petal fall, concluded by a spray 1 week after harvest, was included for comparison. Timing of the sprays in relation to predicted infection periods and rainfall is shown in Figures 2A-C for each fungicide trial.

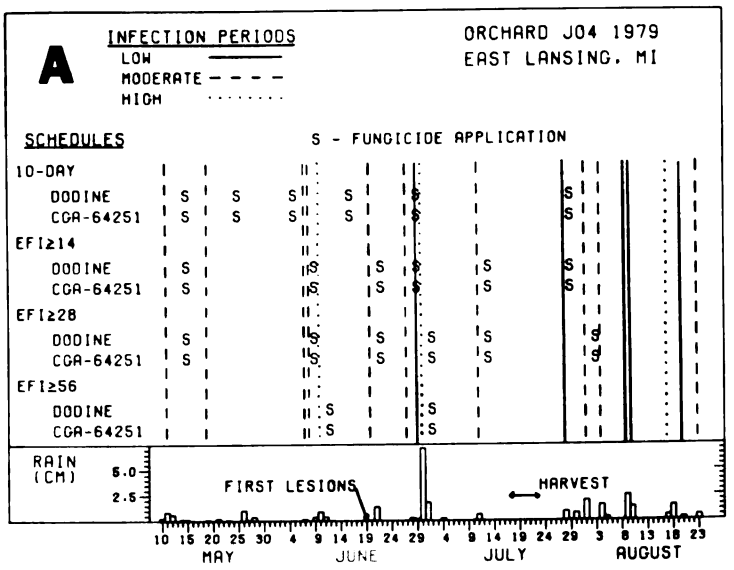
Leaf spot incidence and severity were assessed by examining 20 shoots per tree in 1979 and counting the number of nodes, leaves, and lesions per shoot. In 1980, the number of nodes, leaves, lesions, and diseased leaves were recorded on 30 shoots per tree. Lesions per leaf, percent defoliation, and percent remaining leaves infected were calculated, transformed to insure homogeneity of variance, and subjected to analysis of variance. Differences between treatment means were detected at P=0.05 using the Duncan or Student-Newman-Keuls multiple range procedures.

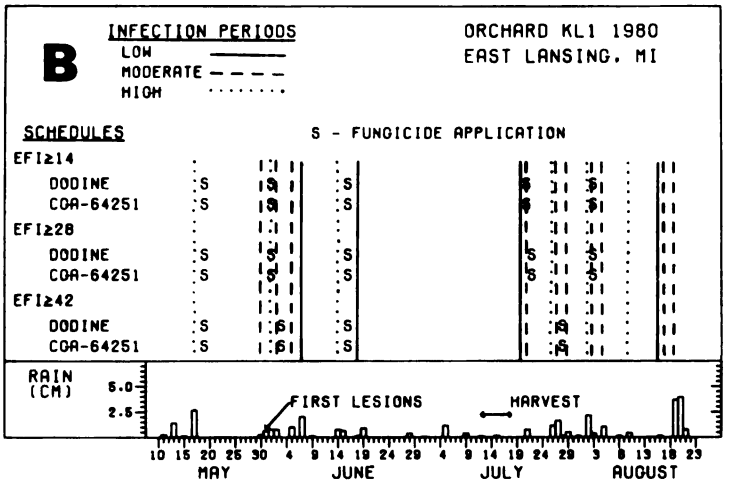
RESULTS

In 1979, of 18 infection periods identified, three were HIGH, ten MODERATE, and five LOW (Figure 2A). Lesions were first observed on 19 June resulting from rainy periods during 9-11 June. Analysis of data taken 15 July indicates infection in all spray treatments was significantly less than infection on untreated trees (Table 1). Infection in the dodine treatment applied after infection periods with EFI $\geq$ 56 was significantly higher than infection in the CGA-64251 treatment applied after the same infection periods, and significantly higher than infection in the other dodine and CGA-64251 schedules. On 31 August, defoliation from leaf spot was significantly greater on untreated trees than on treated trees. Defoliation and infection in the dodine treatment applied after HIGH infection periods were identified was more severe than in the other fungicide treatments.

Of 20 infection periods identified in 1980, six were HIGH, ten MODERATE, and four LOW (Figure 2B). On 31 May the first lesions were observed from a HIGH infection period on 17 May. Analysis of disease assessment data taken on 1 August indicated infection in all spray treatments was significantly less than infection on untreated trees (Table 2). Infection in the dodine treatment applied after

Figure 2. Timing of spray schedules for control of cherry leaf spot in relation to predicted infection periods and rainfall in three orchards (A, B, C) near East Lansing, MI. Predicted sprays were not applied when a fungicide had already been applied within 7 days.


A
INFECTION PERIODS
LOW
MODERATE
HIGH
ORCHARD J04 1979
EAST LANSING, MI
SCHEDULES
S - FUNGICIDE APPLICATION
10-DAY
DODINE
CGA-64251
EFI≥14
DODINE
CGA-64251
EFI≥28
DODINE
CGA-64251
EFI≥56
DODINE
CGA-64251
RAIN (CM)
5.0
2.5
FIRST LESIONS
HARVEST
10 15 20 25 30 4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18 23
MAY
JUNE
JULY
AUGUST


B
INFECTION PERIODS
LOW
MODERATE
HIGH
ORCHARD KL1 1980
EAST LANSING, MI
SCHEDULES
S - FUNGICIDE APPLICATION
EFI≥14
DODINE
CGA-64251
EFI≥28
DODINE
CGA-64251
EFI≥42
DODINE
CGA-64251
RAIN (CM)
5.0
2.5
FIRST LESIONS
HARVEST
10 15 20 25 30 4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18 23
MAY
JUNE
JULY
AUGUST

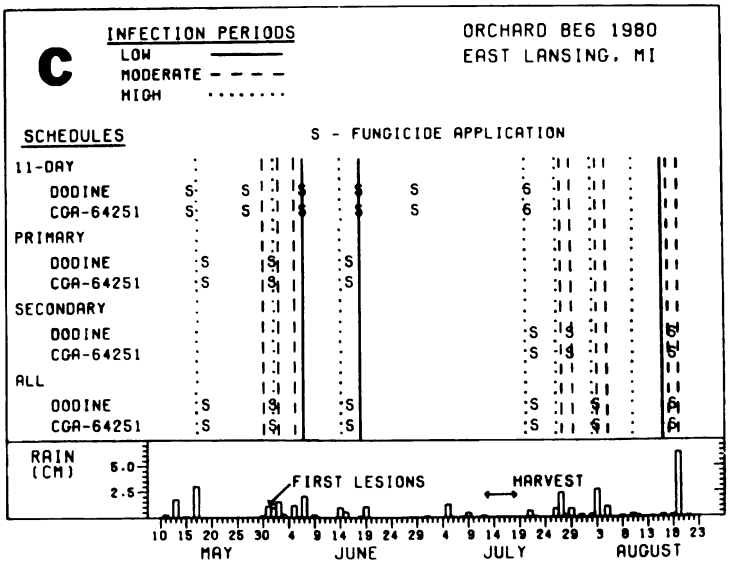

C
INFECTION PERIODS
LOW
MODERATE
HIGH
ORCHARD BE6 1980
EAST LANSING, MI
SCHEDULES
S - FUNGICIDE APPLICATION
11-DAY
DODINE
CGA-64251
PRIMARY
DODINE
CGA-64251
SECONDARY
DODINE
CGA-64251
ALL
DODINE
CGA-64251
RAIN (CM)
5.0
2.5
FIRST LESIONS
HARVEST
10 15 20 25 30 4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18 23
MAY
JUNE
JULY
AUGUST

Table 1. Use of an infection model in scheduling fungicide applications for cherry leaf spot on Montmorency sour cherry at East Lansing, MI in 1979.

Timing of fungicides[v]	Number of sprays	Incidence of leaf spot on terminal leaves: 15 July, Lesions/leaf, Mean		Std. error	31 August, Percent defoliation, Mean		Std. error	31 August, Lesions/leaf, Mean		Std. error
10-day schedule[w]										
Dodine	6	0.007[y]	a	0.004	2.5	a	2.06	3.82	a	1.97
CGA-64251	6	0.003	a	0.001	0.0[z]		0.0	0.009	a	0.009
EFI[x] ≥ 14										
Dodine	6	0.121	a	0.103	0.3	a	0.28	0.239	a	0.237
CGA-64251	6	0.002	a	0.001	0.0[z]		0.0	0.019	a	0.017
EFI ≥ 28										
Dodine	6	0.012	a	0.012	0.1	a	0.14	0.038	a	0.038
CGA-64251	6	0.001	a	0.001	0.0[z]		0.0	0.003	a	0.003
EFI ≥ 56										
Dodine	2	0.435	b	0.111	8.6	b	1.9	6.44	b	2.62
CGA-64251	2	0.012	a	0.006	0.9	a	0.46	1.09	a	0.78
Untreated	0	1.56	c	0.257	80.5	c	16.9	----		----

[v]Fungicides, both at 0.45 g/L (6 oz/100 gal), were applied within 48 hr of the inception of leaf wetness.

[w]Five sprays were applied on a 10-day interval and one spray was applied 1 wk after harvest.

[x]Environmental favorability index (EFI) was calculated with an infection model from duration of leaf wetness and mean air temperature.

[y]Values followed by the same letter are not significantly different from each other at P=0.05 using the Student-Newman-Keuls multiple range test.

[z]Information was not used in range test.

Table 2. Use of an infection model in scheduling fungicide applications for cherry leaf spot on Montmorency sour cherry at East Lansing, MI in 1980.

Timing of fungicides[x]	Number of sprays	Incidence of leaf spot on terminal leaves			
		1 August		5 September	
		Defoliation (%)	Infected leaves (%)	Defoliation (%)	Infected leaves (%)
EFI[y] ≥ 14					
Dodine	5	0.0	0.47[z] a	0.0 a	5.85 a
CGA-64251	5	0.0	0.17 a	0.0 a	2.69 a
EFI ≥ 28					
Dodine	5	0.0	0.0 a	3.06 a	7.44 a
CGA-64251	5	0.0	0.0 a	0.65 a	2.82 a
EFI ≥ 42					
Dodine	4	0.0	0.22 a	20.0 b	54.7 b
CGA-64251	4	0.0	0.62 a	1.34 a	20.8 a
Untreated	0	0.95	24.5 b	88.2 c	-----

[x]Fungicides, both at 0.45 g/L (6 oz/100 gal), were applied within 48 hr of the inception of leaf wetness.

[y]Environmental favorability index (EFI) was calculated with an infection model from duration of leaf wetness and mean air temperature.

[z]Values followed by the same letter are not significantly different from each other at P=0.05 using Duncan's multiple range test.

infection periods with EFI $\geq$ 42 was not significantly different from the other schedules. On 5 September, defoliation from leaf spot was significantly higher on untreated trees than on treated trees. Defoliation and infection in the dodine treatment applied after HIGH infection periods were significantly higher than in the other schedules.

In a second orchard in 1980, of 19 infection periods identified, seven were HIGH, nine MODERATE, and three LOW (Figure 2C). Lesions were first observed on 31 May from a wet period on 17 May. Analysis of data taken 6 August indicated that defoliation was significantly greater on untreated than on treated trees (Table 3). Infection and defoliation in treatments sprayed only during secondary infection periods were significantly greater than in other schedules. Differences in defoliation and infection between dodine- and CGA-64251-sprayed trees on the same schedule were not significant. On 5 September, differences in defoliation from leaf spot between dodine- and CGA-64251-sprayed trees on similar schedules were not significant, but dodine-sprayed trees on a protective schedule had significantly more infection than CGA-64251-sprayed trees on a protective schedule. Dodine and CGA-64251, when applied to control secondary infection on trees with primary infections, substantially reduced further increase in disease. A marked increase in disease was observed in trees sprayed after primary, but not secondary infection periods.

Table 3. Use of an infection model in scheduling fungicide applications for cherry leaf spot on Montmorency sour cherry at East Lansing, MI in 1980.

Timing of fungicides[u]	Number of sprays	Incidence of leaf spot on terminal leaves: 6 August Defoliation (%)	6 August Infected leaves (%)	5 September Defoliation (%)	5 September Infected leaves (%)
11-day schedule[v]					
Dodine	6	0.45[z] ab	0.75 a	1.52 abc	34.0 cd
CGA-64251	6	0.0 a	0.10 a	0.31 a	7.70 ab
Primary infection[w]					
Dodine	3	0.0 a	1.68 a	6.64 bcd	64.5 d
CGA-64251	3	1.14 ab	1.93 a	26.3 d	72.4 d
Secondary infection[x]					
Dodine	3	2.15 bc	30.0 b	6.50 cd	29.0 cd
CGA-64251	3	4.06 c	29.6 b	4.34 bcd	20.3 bc
All infection periods[y]					
Dodine	6	0.89 ab	0.19 a	0.68 ab	2.56 a
CGA-64251	6	0.16 a	0.19 a	0.97 abc	2.11 a
Untreated	0	13.5 d	58.1 b	70.6 e	-----

[u]Fungicides, both at 0.45 g/L (6 oz/100 gal), were applied within 48 hr of the inception of leaf wetness.

[v]Five sprays were applied on an 11-day interval and one spray was applied 1 wk after harvest.

[w]Sprays applied when the infection model predicted an EFI $\geq$ 28 between 5/15 and 7/1.

[x]Two sprays were applied 1 wk apart when 5% defoliation was observed and remaining spray was applied when infection model predicted an EFI $\geq$ 28 between 7/1 and 8/31.

[y]Sprays were applied when infection model predicted an EFI $\geq$ 28 between 5/15 and 8/31.

[z]Values followed by the same letter are not significantly different from each other at P=0.05 using the Duncan's multiple range test.

DISCUSSION

Forecasting systems to time fungicides have been developed for late blight of potato (5), early blight of tomato (6), Cercospora leafspot on peanut (9), and apple scab (7). In all of these systems, except for apple scab, disease control is achieved by limiting inoculum increases by timely applications of fungicides. The success of these systems indicates that fungicide applications timed by monitoring the environment often control disease as effectively as fixed time interval schedules with fewer sprays. These data also show that disease control can be obtained with fewer sprays. Two applications of CGA-64251 resulted in statistically equivalent disease levels as six sprays on a fixed time interval schedule in 1979 (Table 1). The 6 August 1980 assessment (Table 2) resulted in statistically equivalent disease control with six 11-day sprays or three after primary infection period sprays. Furthermore, if the goal of the disease management program is to keep disease below a threshold which the tree can tolerate without affecting its potential yield, adequate control should be achieved with a reduction in spray number by applying dodine or CGA-64251 only after secondary infection periods (Table 2).

The use of infection models in timing fungicide sprays

increases the effectiveness of disease control during moderately wet or dry seasons, but not in very wet years. Rainfall during June through August in 1979 and 1980 was above the 1940-1969 normal for East Lansing, MI. Therefore, the potential increase in effectiveness of using the infection model for disease control was not demonstrated. Some drawbacks to the use of infection models to time fungicide sprays are: 1) the inability to plan applications; 2) the necessity of monitoring the environment; 3) the inability of the grower to apply chemicals within the post-infection activity period of the compound; and 4) the necessity of complete spray coverage of susceptible host tissue.

Our data indicate that the experimental fungicide CGA-64251 possesses the postinfection control activity needed for use in an eradicant schedule for cherry leaf spot. However, the apparent lack of persistence may mandate the use of a more persistent fungicide if a single postharvest spray is expected to control leaf spot for the remainder of the season. Fungicide CGA-64251 could replace benomyl, now ineffective due to resistance by the fungus (4), as a highly effective broad-spectrum compound for the combined control of leaf spot, brown rot (Monilinia fructicola (Wint.) Honey), and powdery mildew (Podosphaera oxyacanthae (D.C.) DeBary). CGA-64251 could also replace cycloheximide which was formerly used to suppress sporulation in established lesions (3). Our field results are consistent with Szkolnik's greenhouse work with CGA-64251 (11) and should allow for the use of other

eradicant fungicides for leaf spot when they become available (10).

The nomogram relating leaf wetness duration and mean air temperature to the favorability of the environment (Figure 1), offers several potential advantages to growers. It is faster to use than an equation, there is less chance of error because no mathematical calculations are required, and the high operating and maintenance costs of computerized pest management delivery systems are avoided. The use of the infection model is a promising alternative to fixed time interval schedules and may be used by growers who prefer not to apply sprays until they have a prediction of whether and to what extent infection from leaf spot has occurred during a natural wet period.

LITERATURE CITED

1. EISENSMITH, S. P., and A. L. JONES. 1981. A model for detecting infection periods of Coccomyces hiemalis on sour cherry. Phytopathology 71:728-732.

2. FLORE, J. A., A. L. JONES, and L. G. OLSON (eds.). 1979. Fruit Pesticide Handbook. Mich. State Univ. Ext. Bull. E-154. 86 pp.

3. HAMILTON, J.M., and M. SZKOLNIK. 1953. Factors involved in the performance of Cycloheximide (Actidione) against Coccomyces hiemalis. (Abstr.) Phytopathology 43:109.

4. JONES, A. L., and G. R. EHRET. 1980. Resistance of Coccomyces hiemalis to benzimidazole fungicides. Plant Dis. 64:767-769.

5. KRAUSE, R. A., L. B. MASSIE, and R. A. HYRE. 1975. Blitecast: A computerized forecast of potato late blight. Plant Dis. Rep. 59:95-98.

6. MADDEN, L., S. P. PENNYPACKER, and A. A. MACNAB. 1978. FAST, a forecast system for Alternaria solani on tomato. Phytopathology 68:1354-1358.

7. MILLS, W. D. 1944. Efficient use of sulfur dusts and sprays during rain to control apple scab. N.Y. Agric. Expt. Stn. (Ithaca) Ext. Bull. 630. 4 pp.

8. SAMPSON, R. G. 1975. Surface II Graphics System. Series on Spatial Analysis #1. Kansas Geological Survey. Lawrence, KS 66044. 240 pp.

9. SMITH, D. H., F. L. CROSBY, and W. J. ETHREDGE. 1974. Disease forecasting facilitates chemical control of Cercospora leaf spot of peanuts. Plant Dis. Rep. 58:666-668.

10. SZKOLNIK, M. 1974. Unusual post-infection activity of a piperazine derivative fungicide for the control of cherry leaf spot. Plant Dis. Rep. 58:326-329.

11. SZKOLNIK, M. 1979. Broad-spectrum after-infection activity by CGA-64251 against tree fruit diseases. (Abstr.) Phytopathology 69:1047.

PART IV

FACTORS AFFECTING CHERRY LEAF SPOT DISEASE SEVERITY ON SOUR CHERRY

LEAF AGE AND INOCULUM CONCENTRATION

ABSTRACT

Effects of leaf age and inoculum concentration on infection of Montmorency cherry by conidia of Coccomyces hiemalis were investigated in the greenhouse. With increasing leaf age from 5 to 36 days at inoculation, there was a linear decrease in the ln of leaf spot lesions per square centimeter of leaf area 11 days after inoculation with 10^5 and 10^6, but not 10^4 spores per milliliter. With leaves 35 to 70 days old, there was a decrease in ln lesions per square centimeter only at a inoculum concentration of 10^6 spores per milliliter. No changes in the ln of lesion numbers were observed in leaves inoculated at 103 to 126 days of age. Leaves expanded fully within 16 days of unfolding. Resistance did not increase in the same manner as leaf growth, but continued after growth was completed. With 1- to 32-day-old leaves, mean lesions per square centimeter of leaf at inoculation did not increase between inoculum concentrations of 10^2 and 10^4, increased tenfold between 10^4 and 10^5, and increased less than tenfold between 10^5 and 10^6 spores per milliliter. Germination on water agar was reduced at 10^6 spores per milliliter.

INTRODUCTION

A system for predicting infection of sour cherry (Prunus cerasus L. 'Montmorency') leaves by Coccomyces hiemalis Higgins was described (1) and used to time fungicide applications for the control of cherry leaf spot disease in the field (2). This system is based on an environmental favorability index computed from hours of leaf wetness and average air temperature during the wet period. Most forecasting schemes (5) assume that inoculum and a susceptible host are present, and evaluate the suitability of the weather for infection or disease development. However, variations in host susceptibility or inoculum density can affect disease severity even under favorable environmental conditions (6). The environmental favorability index in the cherry leaf spot model could be modified to account for variation in host susceptibility and inoculum levels if the relationship of these variables to infection frequency were known. The purpose of this study was to investigate the effects of leaf age and inoculum concentration on infection frequency under greenhouse conditions.

MATERIALS AND METHODS

The effects of inoculum concentration and leaf age on infection frequency were examined in seven factorial experiments conducted at different times over a 16-month period. Experiments I and II were performed with inoculum concentrations of 10^2, 10^3, 10^4, 10^5 and 10^6 spores per milliliter and experiments III to VII were performed with 10^4, 10^5, and 10^6 spores per milliliter. Experiment I contained 1- to 32-day-old leaves, experiments II and III contained 1- to 36-day-old leaves, experiment IV contained 5- to 40-day-old leaves, experiments V and VI contained 35- to 70-day-old leaves, and experiment VII contained 103- to 126-day-old leaves. Treatments were arranged in the mist chamber in a completely randomized design with five or six replications per treatment.

Three-yr-old Montmorency sour cherry trees on Prunus mahaleb rootstock were grown at 16 to 25 C in a greenhouse. Trees with three to five shoots were maintained in 3-L cans in a mixture of sand, peat moss, and soil (1:1:1, v/v). A 20% N - 20% P_2O_3 - 20% K_2O fertilizer (Robert B. Peters Co., Inc., 2833 Pennsylvania Street, Allentown, PA 18104) was mixed at 5.3 g/L of water and approximately 0.5 L was applied to each can biweekly. The age of a leaf was calculated from

the date of unfolding, i.e., when its laminar blades were separated by an angle greater than 90°. All leaves unfolding within a 4-day period were assigned to an age class. Thus, 1- to 4-day-old leaves were assigned to class 1, 5- to 8-day-old leaves to class 2, etc. All trees used in an experiment had a range of leaf ages present at the time of inoculation. Leaves of appropriate ages were selected at random for use in each experiment.

Leaves were inoculated with conidial suspensions of C. hiemalis prepared by washing infected cherry leaves with distilled-deionized water. Concentrations of conidia in the suspensions were determined with a haemocytometer. The spore suspension was sprayed uniformly onto the undersurface of each leaf with an atomizer (The DeVilbis Co., Somerset, PA 15501) and compressed air at a pressure of 1.4 kg/cm^2 (20 psi).

Percent germination of conidia on 2% water agar was determined in experiment I. At the time of inoculation spores were sprayed onto agar blocks in a petri dish and incubated at 20 C for 24 or 48 hr. Germinated and ungerminated spores were counted at 200X with a light microscope. Percent germination was determined from a total of 100 to 400 spores per inoculum concentration.

Within 1 hr after inoculation, the trees were placed in a mist chamber at 20 to 24 C for 48 hr. After removal from the mist chamber, the trees were placed under a cheesecloth tent on a greenhouse bench. The cheesecloth was wetted to

maintain a humidity as measured with a hygrothermograph of 90 to 100% around the plants. Under these conditions chlorotic flecks were visible 6 days after inoculation, but lesions were not counted until 11 days after inoculation.

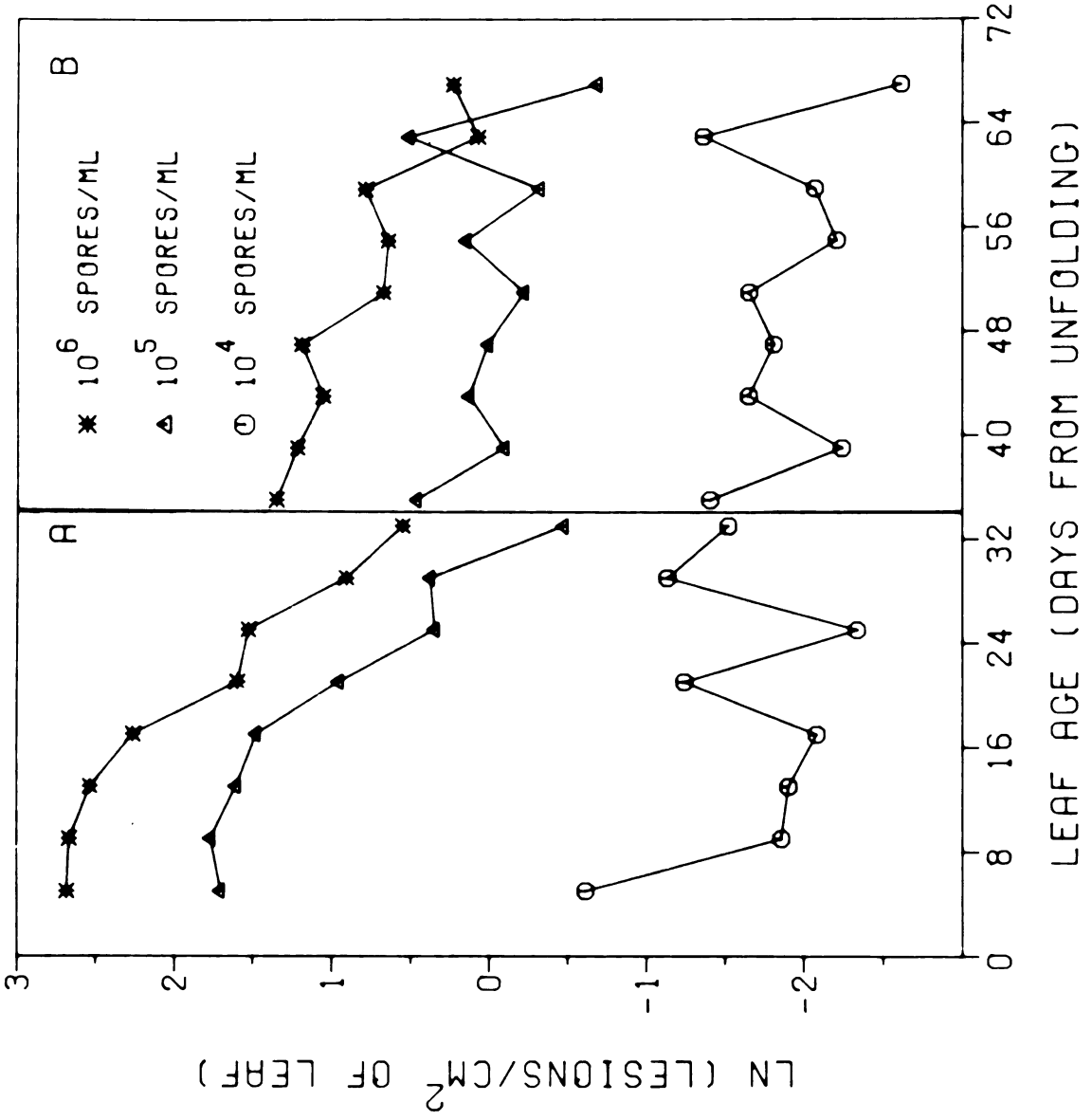
The area of each leaf was measured with an area meter (Model LI-3000, Lambda Instrument Corp., Lincoln, NE 68504) on the day of inoculation and again 11 days later. These measurements were used to determine if leaf size and rate of expansion were constant among different leaf age classes. Leaf spot severity was assessed by counting the number of lesions per leaf and adjusting the data based on the leaf area on the day of inoculation or on the day of assessment. The data for each experiment were subjected to analysis of variance to determine if differences in disease severity between leaves could be attributed to leaf age or inoculum concentration and if an interaction existed between leaf age and inoculum concentration. Differences among treatment means were detected (P=0.05) with the Student-Newman-Keuls procedure.

RESULTS

Combined data from experiments I, II, III, and IV showed that leaves become more resistant with age. For leaves 5-36 days old at inoculation there was a highly significant ($P=0.01$) decrease in the number of lesions per square centimeter of leaf area measured at assessment with increases in leaf age at inoculation. The decrease in lesion number with increasing leaf age occurred at inoculum concentrations of 10^5 and 10^6 spores per milliliter; no significant trend was observed at 10^4 spores per milliliter (Figure 1A). Combined data from experiments V and VI, showed a highly significant decrease ($P=0.01$) in lesion number with increasing leaf age from 35 to 70 days when 10^6 spores per milliliter were used, but when 10^4 or 10^5 spores per milliliter were used there was no significant difference in lesion number (Figure 1B). For leaves 103 to 126 days old at inoculation (experiment VII), lesion numbers did not decline significantly with increasing leaf age at any spore concentration. Mean numbers of 0.31, 1.19, and 1.42 lesions per square centimeter of leaf were obtained from inoculations with 10^4, 10^5, and 10^6 spores per milliliter, respectively.

The relationship between lesion number and successive leaf age classes was determined by regression analyses of

Figure 1. Number of leaf spot lesions on Montmorency sour cherry leaves of increasing ages inoculated with Coccomyces hiemalis at three inoculum concentrations. Lesion numbers were adjusted for leaf area at time of assessment and each value is the average of four (A) and two (B) experiments, respectively.


A
B
* 10^6 SPORES/ML
Δ 10^5 SPORES/ML
Θ 10^4 SPORES/ML
LN (LESIONS/CM^2 OF LEAF)
3
2
1
0
-1
-2
0
8
16
24
32
40
48
56
64
72
LEAF AGE (DAYS FROM UNFOLDING)

combined data from experments I, II, III and IV, and of combined data from experiments V and VI. With 5- to 36-day-old leaves, a linear relationship between ln ($\log_e$) lesions per square centimeter and leaf age accounted for 90 and 94% of the variation in lesion numbers from inoculation with 10^5 and 10^6 spores per milliliter, respectively (Figure 2). Slopes for the two regression lines were not significantly different (P=0.01) from each other. With 35- to 70-day-old leaves, a linear relationship between ln lesions per square centimeter and leaf age accounted for 85% of the variation in lesion numbers from inoculations with 10^6 spores per milliliter (Figure 3). At 10^6 spores per milliliter, the slope of the regression line for 35- to 70-day-old leaves was about half the slope for 5- to 36-day-old leaves. This indicates the rate resistance increases in older leaves is only half that of younger leaves.

Highly significant differences (P=0.01) in lesion numbers between leaves were observed in each of four experiments (I, II, III, and IV) involving leaves less than 40-days-old (Table 1). Five to 20-day-old leaves had significantly more (P=0.05) leaf spot lesions than did 21- to 40-day-old leaves. Lesions per leaf did not appear to differ among 5- to 20-day-old leaves. However, when adjustments were made for variations in leaf area at time of inoculation or at 11 days later, 5- to 8-day-old leaves had significantly higher (P=0.05) lesion numbers than older leaves.

Figure 2. Linear regression of ln lesions per square centimeter of leaf area 11 days after inoculation on Montmorency sour cherry leaves of increasing age inoculated with Coccomyces hiemalis at concentrations of 10^6 spores per milliliter (A) and 10^5 spores per milliliter (B) versus leaf age at time of inoculation.

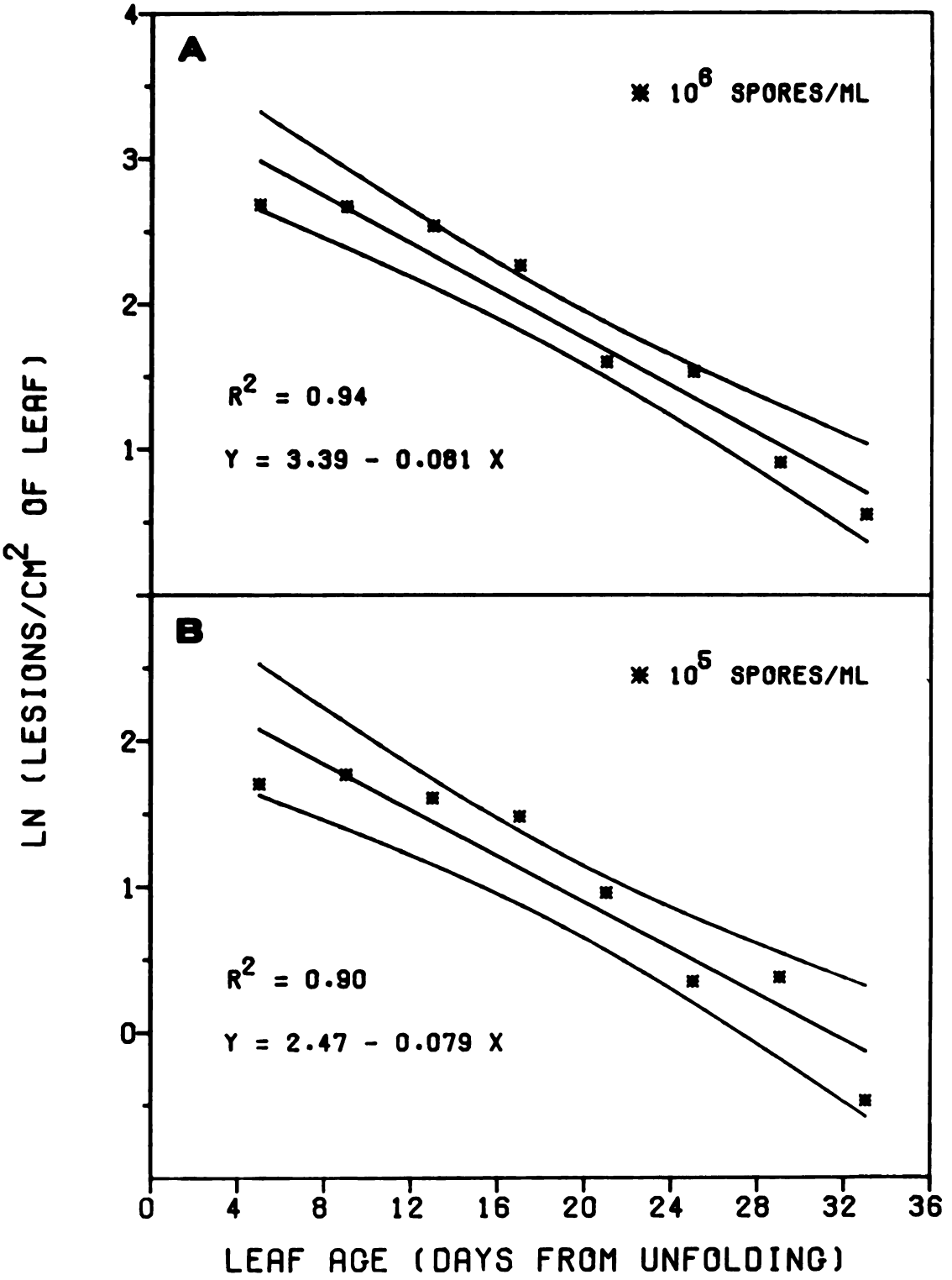

A
* 10^6 SPORES/ML
R^2 = 0.94
Y = 3.39 - 0.081 X
B
* 10^5 SPORES/ML
R^2 = 0.90
Y = 2.47 - 0.079 X
LN (LESIONS/CM^2 OF LEAF)
LEAF AGE (DAYS FROM UNFOLDING)
0
4
8
12
16
20
24
28
32
36
1
2
3
4

Figure 3. Linear regression of ln lesions per square centimeter of leaf area 11 days after inoculation on Montmorency sour cherry leaves of increasing age inoculated with Coccomyces hiemalis at a concentration of 10^6 spores per milliliter versus leaf age at time of inoculation.

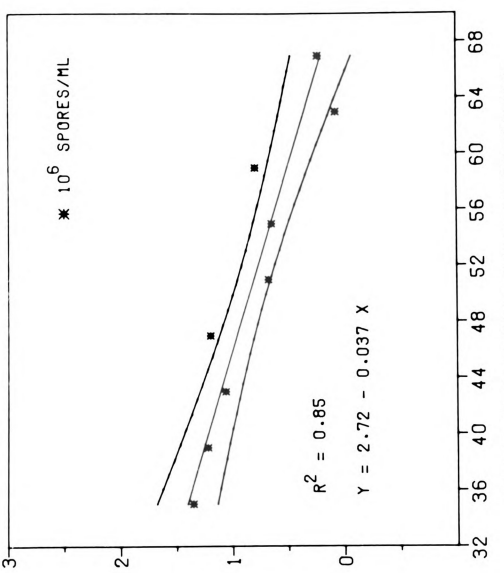

* 10^6 SPORES/ML
R^2 = 0.85
Y = 2.72 - 0.037 X
LN (LESIONS/CM^2 OF LEAF)
LEAF AGE (DAYS FROM UNFOLDING)
3
2
1
0
32
36
40
44
48
52
56
60
64
68

Table 1. Number of leaf spot lesions, before and after adjustment for changes in leaf area, on Montmorency sour cherry leaves of different ages following inoculation with approximately 0.5 ml of 1 x 10^5 conidia per milliliter of Coccomyces hiemalis.

Age of leaves (days)	Leaf area[y]		Leaf spot lesions[y]		
	Day of inoculation (cm^2)	Day 11 after inoculation (cm^2)	Number per leaf	Number per cm^2 of leaf on Day of inoculation	Number per cm^2 of leaf on Day 11 after inoculation
5-8	15 a[z]	21 a	444 b	31.0 c	22.0 c
9-12	26 b	31 ab	395 b	15.0 b	12.7 b
13-16	32 bc	35 b	454 b	14.7 b	13.4 b
17-20	37 bc	37 b	376 b	10.7 b	10.6 b
21-24	36 bc	37 b	160 a	4.4 a	4.4 a
25-28	46 c	46 b	88 a	1.8 a	1.8 a
29-32	46 c	47 b	85 a	1.8 a	1.7 a
33-36	43 c	43 b	77 a	1.9 a	1.9 a
37-40	43 c	44 b	93 a	2.4 a	2.4 a

[y]Means of five replications from experiment IV.

[z]Values in a column followed by the same letter do not differ significantly (P=0.05) using the Student-Newman-Keuls procedure.

Five to 8-day-old leaves had significantly smaller (P=0.05) areas at time of inoculation than leaves 9 days or older. Leaves 13 days or older did not significantly differ (P=0.05) in area at time of inoculation (Table 1). Newly unfolded leaves expanded fully within 16 days, with expansion rate decreasing exponentially with time. Lesion numbers at 10^5 spores per milliliter declined gradually over the 36-day-period and at 10^6, lesion numbers remained high for 16 days then declined rapidly (Figure 4).

The relationship of inoculum concentration to lesion number was examined in each experiment to determine if lesion number was proportional to inoculum concentration as reported by Keitt et al (4). Significant differences (P=0.05) in lesion numbers could be attributed to inoculum concentration in all experiments. With 1- to 32-day-old leaves (experiment I), lesion numbers did not differ significantly (P=0.05) between 10^2 and 10^4 spores per milliliter, but did increase significantly between 10^4 and 10^5 and between 10^5 and 10^6 spores per milliliter (Figure 5). The increase from 10^5 to 10^6 was significantly less (P=0.05), as determined with a t-test, than the tenfold increase expected when a tenfold higher inoculum concentration was applied. Spore germination on water agar was 90.8, 92.4, and 40.3% after an incubation period of 24 hr and 93.0, 93.0, and 55.7% after 48 hr for 10^4, 10^5 and 10^6 spores per milliliter, respectively.

Figure 4. Relationship of percent of maximum lesion frequency on 1- to 4-day-old Montmorency sour cherry leaves inoculated with Coccomyces hiemalis at 10^5 and 10^6 spores per milliliter to leaf expansion rate for 1- to 36-day-old leaves.

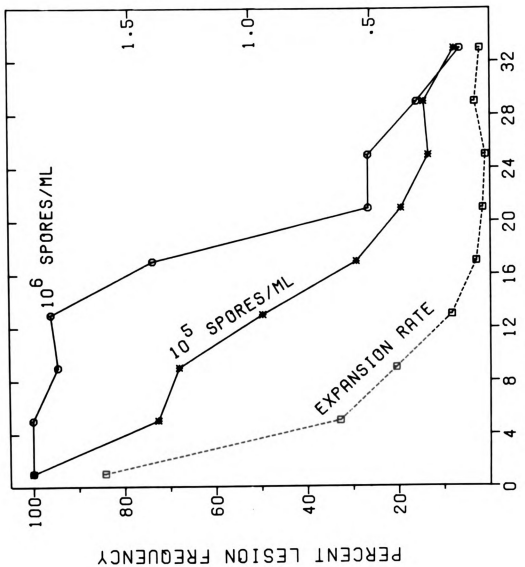
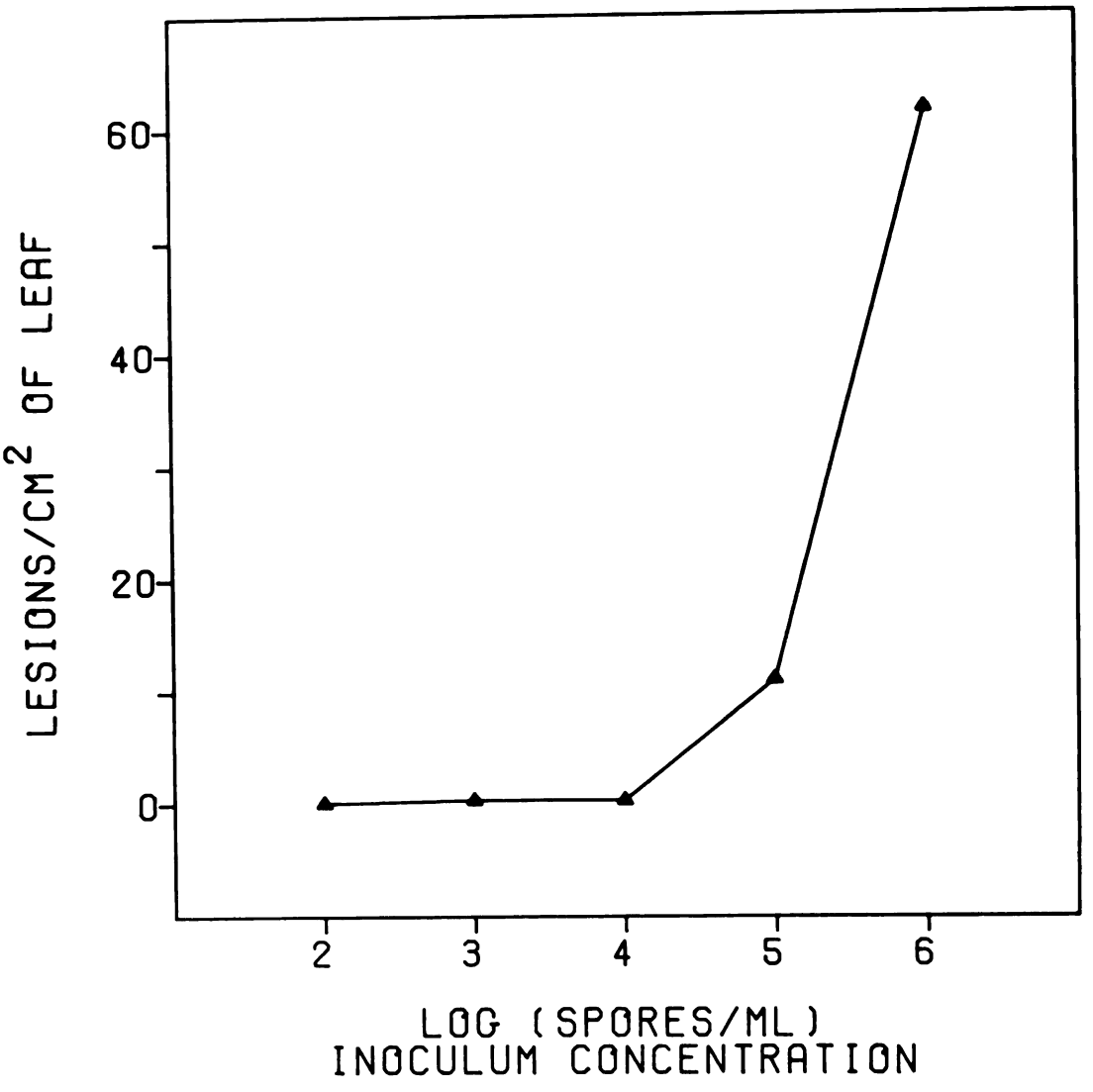

LEAF EXPANSION (CM²/DAY)
1.5
1.0
.5
10^6 SPORES/ML
10^5 SPORES/ML
EXPANSION RATE
PERCENT LESION FREQUENCY
100
80
60
40
20
0
4
8
12
16
20
24
28
32
LEAF AGE (DAYS FROM UNFOLDING)

Figure 5. Relationship of lesions per square centimeter of leaf at time of inoculation on 1- to 29-day-old Montmorency sour cherry leaves to $\log_{10}$ inoculation concentration of Coccomyces hiemalis conidia.


60
40
20
0
LESIONS/CM2 OF LEAF
2
3
4
5
6
LOG (SPORES/ML)
INOCULUM CONCENTRATION

DISCUSSION

Keitt et al (4) established that cherry leaves were resistant to the leaf spot fungus prior to unfolding and that once unfolded, leaves were susceptible and remained so through the season. The resistance of folded leaves is probably due to lack of mature stomates through which the pathogen normally penetrates. My results indicate that susceptibility of leaves decreases with age and that the decrease in susceptibility of leaves is expressed more effectively against high rather than low inoculum concentrations. The ratio of lesion number to number of spores applied decreased with increasing inoculum concentration. The nature of this decrease in infection efficiency is not known but may be limited by the concentration of stomates per square centimeter and by reduced germination at higher spore concentrations.

Results of this study can be used to develop standard techniques to assess the resistance of sour cherry selections to C. hiemalis. For accurate assessment of resistance, a range of leaf ages should be inoculated and an inoculum concentration high enough to detect leaf age effects should be used. These techniques may allow the selection of resistant plants prior to planting in the field.

My findings on the relationship of leaf age and inoculum concentration to lesion frequency should be incorporated into the cherry leaf spot prediction system. The environmental favorability index of this system could be modified by a relative susceptibility factor, e.g., the sum of the percentages of leaves in each age class that comprise the total canopy times the relative susceptibility for that age class. Determining the stage of canopy development requires good estimates of number of emerged leaves and area of those leaves. A model for predicting leaf emergence from degree-day accumulation has been validated (3) and a model for estimating leaf expansion is described in part I of this thesis.

These data suggest that leaf spot control is very important early in the season because leaves are most susceptible between the time they unfold and full expansion. Fungicide control strategies should insure good coverage during the period of leaf emergence and expansion and take advantage of the fact that older leaves are less susceptible. Growers currently do not adjust fungicide applications to account for changes in resistance during the season. In seasons where control is good during canopy development, leaf spot should be less of a problem in August and September (2). Since susceptibility decreases with age, inoculum concentration in the orchard will be the key factor in determining whether leaf spot will be a problem after terminal growth ceases.

LITERATURE CITED

1. EISENSMITH, S. P., and A. L. JONES. 1981. A model for detecting infection periods of Coccomyces hiemalis on sour cherry. Phytopathology 71:728-732.

2. EISENSMITH, S. P., and A. L. JONES. 1981. Use of an infection model for timing fungicide applications to control cherry leaf spot. Plant Disease 65:(In Press).

3. EISENSMITH, S. P., A. L. JONES, and J. A. FLORE. 1980. Predicting leaf emergence of 'Montmorency' sour cherry from degree-day accumulations. J. Amer. Soc. Hort. Sci. 105:75-78.

4. KEITT, G. W., E. C. BLODGETT, E. E. WILSON, and R. O. MAGIE. 1937. The epidemiology and control of cherry leaf spot. Wisc. Agric. Expt. Stn. Res. Bull. 132. 118 pp.

5. KRAUSE, R. A., and L. B. MASSIE. 1975. Predictive systems: Modern approaches to disease control. Annu. Rev. Phytopathol. 13:31-47.

6. POPULER, C. 1978. Changes in host susceptibility with time. Pages 239-262 in: J. G. Horsfall and E. B. Cowling, eds. Plant Disease An Advanced Treatise. Volume II. How Disease Develops in Populations. Academic Press, New York. 436 pp.

INTERRUPTED WETTING PERIODS

ABSTRACT

Montmorency sour cherry trees inoculated with conidia of Coccomyces hiemalis were subjected to interrupted wet periods (IWP) and continuous wet periods (CWP) of various durations to determine the effect of dry interruptions on infection by the leaf spot fungus. Fewer lesions/cm^2 of leaf resulted from IWP than from CWP in each of four series of experiments. A trend of decreasing infection with increasing length of dry interruption was observed when initial and final wet periods were 4 and 8 hr. Infection from IWP with an initial 4 hr wet period, 1 to 48 hr dry interruptions, and a final 8 hr wet period was greater than from a 4 hr CWP but not statistically different from an 8 hr CWP. When the dry period was 108 hr, infection was greater than from a 4 hr CWP but less than from an 8 hr CWP. Trees allowed to dry up to 16 hr after inoculation developed less infection than trees subjected to wetting immediately after inoculation. Infection on trees given initial wet periods of less than 12 hr was less than on trees with longer initial wet periods.

INTRODUCTION

A system for predicting infection of sour cherry (Prunus cerasus L. 'Montmorency') by Coccomyces hiemalis Higgins and scheduling fungicide applications to control the cherry leaf spot disease has been developed (1, 2). In this prediction system an environmental favorability index is computed using hours of continuous leaf wetness from rain and average air temperature during the wet period. In practice, wet periods are not always continuous, leading to the problem of how to interpret and predict the results of wetting periods that occur close together.

The effect of interrupted wet periods on infection of sour cherry has been studied by Keitt et al (4). Their data indicate that interrupted wet periods (IWP) result in less infection than continuous wet periods (CWP). However, these workers examined only extremely long (>96 hr) dry interruptions and did not include certain control treatments necessary for interpretation. Furthermore, the effects of leaf size, leaf age, and inoculum concentration which affect disease severity (3) were not controlled.

The objectives of this study were to confirm that IWP result in less infection than CWP and to determine if

interruptions early in a wetting period reduce infection more than interruptions late in a wetting period.

MATERIALS AND METHODS

The effects of interrupted wetting on infection by the leaf spot fungus were examined in four series of experiments performed in the greenhouse with 4-yr-old Montmorency cherry trees on *Prunus mahaleb* rootstock. Trees with three to five shoots each were maintained as previously described (3). Four to 12 fully expanded, 12- to 16-day-old leaves per tree were inoculated with conidial suspensions of *C. hiemalis* with an atomizer (3). Concentrations of conidia in the suspensions were determined with a haemocytometer and were adjusted to 3 to 7 x 10^5 spores/ml.

Inoculated trees were subjected to either CWP, or to IWP consisting of an initial wet period, a dry interruption, and a final wet period. The total duration of an IWP was the time in hours from inoculation to the end of the final wet period. Trees were placed in a mist chamber at 20 to 24 C during wet periods and in a greenhouse with relative humidities of 40 to 90% and temperatures of 18 to 28 C during dry interruptions. The leaves dried quickly after the trees were removed from the mist chamber. Following treatment, the trees were held in the greenhouse and examined for leaf spot symptoms 11 days after inoculation.

Sets of four experiments (series I) and of three

experiments (series II) were conducted to examine the effect of dry interruptions of increasing length on the level of infection. Two treatments in each series were 4 and 8 hr CWP; the remaining 12 treatments were arranged in a factorial design with the type of wet period (IWP or CWP) as one factor and length of the dry interruption as the second factor. All IWP treatments consisted of an initial 4 hr wet period separated from a final 8 hr wet period by dry interruptions of various lengths. In series I, IWP with dry interruptions of 4, 8, 12, 16, 24, and 36 hr were compared with CWP of 16, 20, 24, 28, 36, and 48 hr, respectively. In series II, IWP with dry interruptions of 1, 2, 3, 6, 48, and 108 hr were compared with CWP of 13, 14, 15, 18, 60, and 120 hr, respectively.

Experiments (series III and IV) were also conducted to determine if a dry interruption early in a wetting period reduced infection as much as an interruption late in the wet period. All experiments contained six treatments in a randomized complete block design replicated three times. In series III, trees were subjected to initial wet periods of 0, 4, 8, 12, and 16 hr; a dry interruption of 8 hr; and final wet periods of 16, 12, 8, 4, and 0 hr, respectively, to give IWP of 24 hr. A 24 hr CWP treatment served as a control. In series IV, trees were subjected to initial wet periods of 0, 8, 16, 24, and 32 hr; a dry interruption of 16 hr; and second wet periods of 32, 24, 16, 8, and 0 hr, respectively, to give IWP of 48 hr. The sixth treatment was a 48 hr CWP.

Disease severity was assessed by counting all lesions on the undersurface of inoculated leaves 11 days after inoculation. At the time of disease assessment the area of each leaf was measured with an area meter (Model LI-3000, Lambda Instrument Corp., Lincoln, NE 68504). Numbers of lesions/cm^2 of leaf were calculated and subjected to analyses of variance after a logarithmic transformation to insure homogeneity of variance (5), then converted back to the original scale for tabulation. Differences between treatment means were detected using the Least Significant Difference or Duncan's Multiple Range procedures (5).

Percent infection reduction was used to evaluate the relationship between IWP and CWP treatments and was calculated for each IWP and CWP treatment of the same duration. In cases where the IWP mean exceeded its corresponding CWP mean, percent reduction in infection was set at zero. This adjustment is possible because only nonsignificant increases over the control means were found. These data were subjected to analyses of variance after arcsine square root transformation, and differences between treatment means were detected using Duncan's Multiple Range procedure (5).

RESULTS

Interrupted wet periods resulted in significantly ($P=0.001$) fewer lesions/cm^2 of leaf area than CWP (Table 2). Mean reductions in lesions for the six IWP treatments were 8.51 and 6.25 lesions/cm^2 of leaf for series I and II, respectively. When IWP and CWP of equal lengths were compared, IWP had significantly fewer lesions than CWP except for the 4 hr dry interruption in series I and the 1 hr dry interruption in series II. Increasing the duration of the dry period between wet periods tended to reduce infection in series I, and significantly reduced infection in series II except for the 3 hr dry interruption.

Infection levels in the 4 and 8 hr CWP were compared to infection in the other 12 treatments in both series I and II to determine if infection from an IWP can be attributed to the initial or the final wet period. Log_e of the number of lesions/cm^2 from the 4 hr CWP was significantly less ($P=0.05$, range test not shown) than the log_e of the number of lesions for all other treatments within each series (Table 2). Log_e of the number of lesions from the 8 hr CWP did not differ significantly (range test not shown) from IWP treatments having dry interruptions of 1 to 48 hr in series I and from all but the 108 hr dry interruption in series II. An IWP

Table 2. Cherry leaf spot lesions per cm^2 of leaf and percent reduction in infection of sour cherry leaves inoculated with conidia of Coccomyces hiemalis and subjected to continuous wet periods (CWP) or to interrupted wet periods (IWP).

Wet treatment				Lesion numbers observed from		Reduction in infection[u]	
IWP		CWP					
Wet (hr)	Dry (hr)	Wet (hr)	Wet (hr)	IWP (lesions/cm^2)	CWP (lesions/cm^2)	(%)	
Series I							
-	-	-	4	---	0.3[v]	---	
-	-	-	8	---	2.7	---	
4	4	8	16	4.8[v]	6.8	20.5[v]	ns
4	8	8	20	6.2	14.0***[w]	50.9	ns
4	12	8	24	8.4	14.0***	32.0	ns
4	16	8	28	5.2	14.0***	60.5	ns
4	24	8	36	3.9	14.5***	73.1	ns
4	36	8	48	1.6	17.5***	84.9	ns
		Mean response		4.45	12.96[x]		
Series II							
-	-	-	4	---	0.2[y]	---	
-	-	-	8	---	3.6	---	
4	1	8	13	2.8[y]	4.6	31.8[y]	a[z]
4	2	8	14	1.5	7.2***[w]	75.5	b
4	3	8	15	3.1	6.4*	35.2	a
4	6	8	16	2.1	7.8***	72.0	b
4	48	8	60	1.5	12.7***	87.6	bc
4	108	8	120	0.5	11.3***	97.3	c

Table 2. (con't)

Mean response	1.64	7.89[x]

[u]Calculated by dividing the difference between CWP and IWP lesion numbers by the lesions/cm^2 of leaf from CWP times 100 for each dry interruption.

[v]Means of four nonreplicated experiments.

[w]Mean values between IWP and CWP columns differ significantly (P=0.05, *; P=0.001, ***) according to the Least Significant Difference test performed on log_e transformed data.

[x]Values differ significantly (P=0.001) as determined by analysis of variance of disease data subjected to log_e transformation before analysis.

[y]Means of three experiments with each experiment replicated twice.

[z]Values followed by the same letter do not differ significantly (P=0.05) according to Duncan's Multiple Range test performed on arcsine square root transformed data.

with an initial 4 hr wet period, a 108 hr dry interruption, and a final 8 hr wet period had significantly more (P=0.05) lesions than a 4 hr CWP and significantly fewer (P=0.05) lesions than an 8 hr CWP.

Data from experiments where the length of the initial and final wet periods were varied but the dry period was maintained at 8 or 16 hr are presented in Table 3. The ranking of IWP treatment means for lesions/cm^2 of leaf and for percent reduction in infection were not consistent among experiments in series III and IV. However, an increase in infection with increased length of the initial wet period was noted in series III but not series IV. Initial wet periods of 4, 8, and 12 hr in series III resulted in means of 1.8, 2.1, and 2.6 lesions/cm^2 of leaf, respectively. Sixteen and 24 hr CWP in series III and 32 and 48 hr CWP in series IV resulted in more infection than IWP treatments of 24 and 48 hr, respectively. Trees allowed to dry 8 or 16 hr after inoculation and subjected to wet periods of 16 or 32 hr, respectively, had less disease than trees subjected to initial wet periods of 16 or 32 hr immediately after inoculation.

Table 3. Cherry leaf spot lesions per cm^2 of leaf and percent reduction in infection of leaves of sour cherry inoculated with conidia of Coccomyces hiemalis and subjected to various wetting regimes.

Wet treatment			Lesions/cm^2 of leaf area				Reduction in infection[w]			
			Experiment number			Mean	Experiment number			Mean
Wet (hr)	Dry (hr)	Wet (hr)	1 (no.)	2 (no.)	3 (no.)	response (no.)	1 (%)	2 (%)	3 (%)	response (%)
Series III experiments										
24	0	0	2.7[x] c[y]	6.7[x] c[y]	2.4[x] b[y]	3.5 d[y]	---	---	---	---
0	8	16	2.1 bc	3.3 ab	1.5 a	2.2 ab	38.8[x] ab[y]	56.0[x] ns	67.2[x] b[y]	54.1 b[y]
4	8	12	1.3 a	2.8 a	1.4 a	1.8 a	81.3 c	64.6 ns	67.2 b	71.4 b
8	8	8	1.7 ab	3.9 ab	1.4 a	2.1 ab	54.5 bc	46.4 ns	70.0 b	57.2 b
12	8	4	2.6 c	4.4 b	1.5 a	2.6 bc	14.5 a	32.4 ns	60.1 b	34.5 a
16	8	0	2.7 c	4.4 b	2.6 b	3.2 cd	18.9 ab	33.0 ns	12.4 a	20.9 a

Table 3. (con't)

Series IV experiments

48 + 0 + 0	7.1[z]	b[y]	6.1[z]	b[y]	59.7[z]	ns	13.7	b[y]	---		---		---		---	
0 + 16 + 32	0.9	a	4.2	b	24.8	ns	4.6	a	82.7[z]	b[y]	23.8[z]	ns	57.1[z]	b[y]	55.1	bc[y]
8 + 16 + 24	0.8	a	3.1	ab	30.7	ns	4.1	a	88.7	b	52.3	ns	47.5	b	64.5	c
16 + 16 + 16	1.2	a	1.5	a	27.8	ns	3.7	a	76.1	b	74.4	ns	37.8	ab	63.4	c
24 + 16 + 8	1.4	a	3.1	b	48.7	ns	6.0	a	74.4	b	51.0	ns	9.1	a	42.9	b
32 + 16 + 0	18.7	b	3.4	b	39.5	ns	13.6	b	2.9	a	45.8	ns	31.7	ab	23.3	a

[w]Calculated by dividing the difference between lesion numbers from the first treatment in each series and the remaining five treatments by the lesions/cm^2 of leaf from the first treatment times 100.

[x]Means of four replications.

[y]Values in a column followed by the same letter do not differ significantly (P=0.05) according to Duncan's Multiple Range test performed on transformed data.

[z]Means of three replications.

DISCUSSION

Although the four series of experiments used shorter dry durations than those employed by Keitt et al (4), my results support their conclusion that IWP result in less infection than CWP. Because of this, an improved predictive system is needed to account for reduced cherry leaf spot infection from IWP. In the existing predictive system (1), IWP with dry interruptions < 8 hr were arbitrarily treated as a CWP and IWP with dry interruptions > 8 hr were treated as separate CWP. My study indicates that when IWP are treated as a CWP, infection predictions are too severe.

My data indicate that early ($\leq$8 hr) dry interruptions result in fewer lesions than dry interruptions after a long (8-16 hr) initial wet period. Moist chamber experiments by Keitt et al (4) indicate light infection from a 4 hr wet period and increased infection with longer wet periods. The increase in infection; however, is not linear, and about one-half of the infection obtained from a 70 hr CWP occurs in the first 12 hr. Dry periods during the first 12 hr of a wet period should be more disrupting than dry periods after 12 hr of continuous wetting.

When wet periods are not continuous, the question arises as to how much each wet period contributes to the final

incidence of infection. In my studies, trees subjected to an 8 hr final wet period 1 to 48 hr after a 4 hr initial wet period had levels of infection not different from a CWP of 8 hr. However, when Keitt et al (4) subjected trees to a 30 hr final wet period 96 to 192 hr after a 16 hr initial wet period, the infection level was equivalent to that from a 16 hr CWP. Thus, the final wet period appears to be most important when the initial wet period is 4 to 12 hr.

The variability of my data is great. Dry interruptions of 1, 3, or 4 hr should not be expected to reduce infection by half as much as 2, 6, or 8 hr dry interruptions (Table 2), and a tenfold increase in infection frequency among experiments should not occur (Table 3). Some of the variability can be attributed to the low levels of infection which result from CWP of 4 or 8 hr. A 4 hr CWP is the minimal wet period for infection under the conditions of my experiments. Fluctuating temperatures and relative humidities during the dry interruption and incubation period may have contributed to the variability between experiments. Other sources of variation are inoculum quality and the amount of inoculum deposited on a leaf.

To predict infection severity from IWP requires an understanding of the underlying mechanism of spore germination and penetration during interrupted wetting. Keitt et al (4) found that cherry leaf spot conidia on glass slides subjected to dry periods show reduced germination; and after a 12 hr wet period and 12 hr dry period, no additional

germination or germ tube extension occurred upon rewetting. If the second wet period does not promote germination or germ tube extension, it may increase survival of infections initiated during the first wet period. Because leaves might be expected to provide a much better substrate than glass for spore survival, spore germination and development should be monitored on the leaf surface during IWP and CWP to establish the mechanism for increased infection upon rewetting.

LITERATURE CITED

1. EISENSMITH, S. P, and A. L. JONES. 1981. A model for detecting infection periods of Coccomyces hiemalis on sour cherry. Phytopathology 71:728-732.

2. EISENSMITH, S. P., and A. L. JONES. 1981. Use of an infection model for timing fungicide applications to control cherry leaf spot. Plant Dis. 65:(In press).

3. EISENSMITH, S. P., T. M. SJULIN, A. L. JONES, and C. E. CRESS. 1981. Effects of leaf age and inoculum concentration on infection of sour cherry by Coccomyces hiemalis. Phytopathology 71:(In press).

4. KEITT, G. W., E. C. BLODGETT, E. E. WILSON, and R. O. MAGIE. 1937. The epidemiology and control of cherry leaf spot. Wisc. Agric. Expt. Stn. Bull. 132. 118 pp.

5. STEEL, R. G. D., and J. H. TORRIE. 1980. Principles and procedures of statistics. 2nd Ed. McGraw-Hill Book Co., New York. 633 pp.

APPENDIX A

DESCRIPTION OF METHOD AND FORTRAN PROGRAM USED TO CALCULATE AND ACCUMULATE DEGREE-DAYS

Accumulated growing degree-days (GDD) can be used to relate temperature to phenological development of plants because rates of physiological processes are regulated to a considerable extent by temperature. The degree-day concept has been used to predict insect development (8,9,11,15,17, 19), optimum dates for planting and harvest (7,13,16,18,20), phenological stages of tree fruit (4,5), and development times for cotton (14), alfalfa (10), and corn (3). Such use of GDD is based on three assumptions: 1) the relationship between temperature and rate of development is linear and constant over a growth period, 2) temperature is the major environmental factor governing growth and is measured in the plant canopy, and 3) there exists a constant GDD value for the development of any phenological state of the organism.

Three commonly used methods for calculating degree-days, once a suitable base temperature has been determined (1), will be described. Method 1 is to subtract a base temperature from the daily mean temperature. If the daily mean is equal to or below the base temperature a value of zero is used (2). Method 2 is to subtract a base temperature from the daily maximum temperature. Again, a value of zero is used if the maximum temperature is equal to or less than the base temperature (12). Method 3 and the one used in this thesis is based on a sine wave approximation of the diurnal temperature fluctuation, and makes use of horizontal and vertical cutoffs (6). A horizontal cutoff implies that heat is accumulated at a constant rate for the period when the

temperature exceeds the cutoff and a vertical cutoff implies that no heat is accumulated for the period when the temperature exceeds the cutoff. Four situations are possible when using this method of accumulating GDD and have been described (6); however, only two cases were used to calculate degree-days in Part I of this thesis and will be described below:

Case 1. The base temperature (K1) is below the daily minimum temperature and no horizontal or vertical threshold is used.

$$GDD = (MAX - MIN)/2 - K1$$

Case 2. The base temperature (K1) is above the daily minimum temperature and no horizontal or vertical threshold is used.

$$GDD = [(MAX - MIN) \cos \phi - (2K1 - MAX - MIN)(\pi/2 - \phi)]/2\pi$$

where $\phi = \arcsin [(2K1 - MAX - MIN)/(MAX - MIN)]$

The following FORTRAN computer program was used to accumulate GDD for construction of the leaf emergence and leaf expansion models in Part I of this thesis.

LITERATURE CITED

1. ARNOLD, C. Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Amer. Soc. Hort. Sci. 74:430-445.

2. _____. 1960. Maximum-minimum temperatures as a basis for computing heat units. Proc. Amer. Soc. Hort. Sci. 76:682-692.

3. _____. 1974. Predicting stages of sweet corn development. J. Amer. Soc. Hort. Sci. 99:501-505.

4. ASHCROFT, G. L., E. A. RICHARDSON, and S. D. SEELEY. 1976. A statistical method for determining chill requirements of fruit buds. Appendix D in: "Reducing fruit losses caused by low spring temperatures", Final report of the Utah Agric. Expt. Stn. to the Four Corners Regional Commission, Project No. 562-366-084. Document No. 10550101.

5. BAKER, G. A., and R. M. BROOKS. 1944. Climate in relation to deciduous fruit production in California. III. Effect of temperature on number of days from full bloom to harvest of apricot and prune fruits. Proc. Amer. Soc. Hort. Sci. 45:95-103.

6. BASKERVILLE, G. L., and P. EMIN. 1969. Rapid estimation of heat accumulated from maximum and minimum temperatures. Ecology 50:514-517.

7. BOMALSKI, H. H. 1948. Growing degree-days. Food Packer 29:51-59.

8. ECKENRODE, C. J., and R. K. CHAPMAN. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal-unit accumulation. Ann. Entomol. Soc. Amer. 65:151-156.

9. FOSTER, J. E., and P. L. TAYLOR. 1975. Thermal-unit requirement for development of the Hessian fly under controlled environment. Environ. Entomol. 4:195-202.

10. GIESE, R. L., R. M. PEART, and R. T. HUBER. 1975. Pest management. Science 187:1045-1052.

11. GILBERT, N., and A. P. GUTIERREZ. 1973. A plant-aphid-parasite relationship. J. Animal Ecol. 42:323-340.

12. GILMORE, C. E., Jr., and J. S. ROGERS. 1958. Heat units for measuring maturity in corn. Agron. J. 50:611-615.

13. GOULD, W. A. 1950. Here's heat guide for 47 varieties of snap beans. Food Packer 110:35-37.

14. GUITERREZ, A. P., L. A. FALCON, W. LOEW, P. A. LEIPZIG, and R. VAN DEN BOSCH. 1975. An analysis of cotton production in California: A model for Acala cotton and the effects of defoliation on its yields. Environ. Entomol. 4:125-136.

15. IVES, W. G. H. 1973. Heat units and outbreaks of the forest tent caterpillar, Malacosoma disstria (Lepidoptera:Lasiocampidae). Can. Entomol. 105:529-543.

16. LANA, E. P., and E. S. HABER. 1952. Seasonal variability as indicated by cumulative degree hours with sweet corn. Proc. Amer. Soc. Hort. Sci. 59:389-392.

17. MILES, G. E., T. R. HINTS, A. L. PRITSKER, M. C. WILSON, and R. M. PEART. 1974. SIMAWEV II: Simulation of the alfalfa weevil using GASP IV. pp. 1157-1161 in Proc. 5th Annu. Pittsburgh Modeling and Simulation Conf. University of Pittsburgh, Pittsburgh, PA.

18. PHILLIPS, E. E. 1950. Heat units summation theory as applied to cannery crops. The Canner 110:10.

19. TUMMULA, R. L., W. G. RUESINK, and D. L. HAYNES. 1975. A discrete component approach to the management of the cereal leaf beetle ecosystem. Environ. Entomol. 4:175-186.

20. WINKLER, A. J., and W. O. WILLIAMS. 1940. The heat required to bring Tokay grapes to maturity. Proc. Amer. Soc. Hort. Sci. 37:650-652.

```
      PROGRAM DDSPE(INPUT,OUTPUT,TAPE60,TAPE70,TAPE1=INPUT,TAPE2=OUTPUT)

C  CALCULATES DEGREE DAYS FROM START DATE TO STOP DATE

      DIMENSION CV(5,10), SD(5,10), XBAR(5,10)
      DIMENSION TABLE(5,10,15), IDDAY(12,31)
      INTEGER DA1,DA2,DA3,YR1,YR2,YR3,SC,D,Y
      LOGICAL FLAG
      COMMON /MONTH/ NAME(12), MNDAY(12)
      COMMON /DATES/ MO1,DA1,YR1,MO2,DA2,YR2
      COMMON /TEMPS/ MAX(366), MIN(366)
      COMMON /OUTP/ TITLE(10), IHEAD(31), IYEAR(15)
C
C          ARRAY                PURPOSE
C
C        NAME       STORES NAMES OF MONTHS FOR OUTPUT
C        MNDAY      STORES NUMBER OF DAYS IN EACH MONTH
C        MAX        HOLDS MAXIMUM TEMPERATURES FOR UP TO ONE YEAR
C        MIN        HOLDS MINIMUM TEMPERATURES FOR UP TO ONE YEAR
C        TITLE           THESE THREE ARRAYS ARE USED
C        IHEAD           FOR LABELLING THE OUTPUT
C        IYEAR           PRODUCED IN ITS VARIOUS FORMS
C        CV         STORES THE CALCULATED COEFFICIENTS OF VARIANCE
C        SD         STORES THE STANDARD DEVIATIONS FOR LATER OUTPUT
C        XBAR       STORES THE MEANS FOR LATER OUTPUT
C        TABLE      STORES THE TOTAL DD ACCUMULATION FOR LATER USE
C        IDDAY      STORES THE DAILY DD ACCUMULATIONS FOR LATER OUTPUT
C
C  INITIALIZE HORIZONTAL AND VERTICAL CUTOFFS

      R2 = 0.0
      R3 = 0.0
      R1INCR = 0.0
      X = FECMD ("RMARGIN,140")

C  READ IN DD CALCULATION METHOD AND PARAMETER VALUES

      WRITE (2,200)
200   FORMAT (33HOWHICH METHOD OF DD CALCULATIONS?/
     +42H (1=MAX/MIN,2=MAX/BASE,3=BASKERVILLE/EMIN)/2H *)
      READ (1,100) KEY
100   FORMAT(I1)
      IF (KEY.LT.3) GO TO 1
      WRITE (2,201)
201   FORMAT(27H ENTER VERTICAL CUTOFF (K2)/2H *)
      READ*, R2
      WRITE (2,202)
202   FORMAT(29H ENTER HORIZONTAL CUTOFF (K3)/2H *)
      READ*, R3
1     WRITE (2,203)
203   FORMAT(56H ENTER NUMBER OF START DATES WITHIN A YEAR, BASES, YEARS
     +/14H (MAX=5,10,15)/2H *)
      READ*, IEND1,IEND2,IEND3
      IF (IEND1.LE.5.AND.IEND2.LE.10.AND.IEND3.LE.15) GO TO 2
```

```
      WRITE (2,204)
204   FORMAT(48H ERROR -- EXCEEDED MAX NUMBER ALLOWED. TRY AGAIN)
      GO TO 1
2     WRITE (2,205)
205   FORMAT(16H ENTER BASE (K1)/2H *)
      READ*, R1
      IF (IEND2.GT.1) WRITE (2,212)
212   FORMAT(35H ENTER INCREMENT FOR MULTIPLE BASES/2H *)
      IF (IEND2.GT.1) READ*, R1INCR

C  SET UP OUTPUT HEADING

      DO 1001 I=1,31
1001  IHEAD(I) = I
      DO 1010 NB=1,IEND2
1010  TITLE(NB) = FLOAT(NB-1)*R1INCR + R1

C  THIS LOOP IS FOR DIFFERENT YEARS

      DO 2000 KK=1, IEND3
      IF (KK.GT.1) WRITE (2,206)
206   FORMAT(16H FOR NEXT YEAR--)
4     WRITE (2,207)
207   FORMAT(28H ENTER START DATE (MO/DA/YR)/2H *)
      READ (1,101) MO1,DA1,YR1
101   FORMAT(3(I2,1X))

C  TEST FOR LEAP YEAR

      MNDAY(2) = 28
      IF (YR1/4*4.EQ.YR1.AND.MO1.LT.3) MNDAY(2) = 29

C  SAVE YEAR FOR OUTPUT

      IYEAR(KK) = 1900 + YR1
      IF (MO1.LE.12.AND.DA1.LE.MNDAY(MO1)) GO TO 6
5     WRITE (2,208)
208   FORMAT(27H ERROR IN DATE -- TRY AGAIN)
      GO TO 4
6     WRITE (2,209)
209   FORMAT(27H ENTER STOP DATE (MO/DA/YR)/2H *)
      READ (1,101) MO2,DA2,YR2

C  TEST FOR LEAP YEAR

      IF (YR2/4*4.EQ.YR2) MNDAY(2) = 29
      IF (MO2.LE.12.AND.DA2.LE.MNDAY(MO2)) GO TO 7
      WRITE (2,208)
      GO TO 6

C  CALCULATE NUMBER OF DAYS BETWEEN START AND STOP DATES

7     NDAYS = JUL(YR2,MO2,DA2) - JUL(YR1,MO1,DA1) + 1
      IF (NDAYS.LT.1) GO TO 5
```

```
      ISTOP = NDAYS
      ISTART = 1

C  INPUT TEMPERATURE DATA

      CALL TEMPIO(NDAYS,KK)

C  SAVE START DATE FOR USE AS A PRINT CONTROL

      IDA = DA1
      IMO = MO1
      IYR = YR1
      IF (KK.NE.1) GO TO 8

C  DETERMINE TYPE OF OUTPUT AND WHERE TO WRITE IT

      WRITE (2,210)
210   FORMAT(33H-WHICH OUTPUT? (1=DAILY, 2=TOTAL)/2H *)
      READ (1,100) IANSW
      WRITE (2,211)
211   FORMAT(38H OUTPUT DEVICE? (1=TERMINAL, 2=TAPE70)/2H *)
      READ (1,100) IFLAG
      FLAG = IFLAG.EQ.2

C  THIS LOOP IS FOR DIFFERENT START DATES

      DO 2000 II=1,IEND1

C  FOR FIRST TIME USE DATA START DATE

      IF (II.EQ.1) GO TO 18
15    WRITE (2,207)
      READ (1,101) MO3,DA3,YR3
      IF (MO3.LE.12.AND.DA3.LE.MNDAY(MO3)) GO TO 17
16    WRITE (2,208)
      GO TO 15

C  TEST FOR DIFFERENT ERROR POSSIBILITIES

16    ITEST1 = JUL(YR3,MO3,DA3) - JUL(YR2,MO2,DA2)
      ITEST2 = JUL(YR1,MO1,DA1) - JUL (YR3,MO3,DA3)
      IF (ITEST1.GT.0.OR.ITEST2.GT.0) GO TO 16
      ISTART = 1-ITEST2

C  SAVE START DATE FOR USE AS A PRINT CONTROL

      IDA = DA3
      IMO = MO3
      IYR = YR3

C  THIS LOOP IS FOR DIFFERENT BASES

18    DO 2000 JJ=1,IEND2
      BASE = FLOAT(JJ-1)*R1INCR + R1
```

```
      IF (IANSW.EQ.2) GO TO 19

C  INITIALIZE DAILY ACCUMULATION ARRAY

      DO 70 ND=1,31
      DO 70 NM=1,12
70    IDDAY(NM,ND) = 0

C  USE PRINT CONTROLS FOR PROPER DATA PLACEMENT

      M = IMO
      D = IDA
      Y = IYR
19    DD = 0.0

C  IF OUTPUT IS TO GO ON FILE WRITE TITLE

      IF (FLAG) WRITE (70,700) IMO, IDA, IYR, BASE, R2, R3
700   FORMAT(/T11,12HSTARTING ON:,I3,2(1H/,I2),4X,3HK1=,F5.1,
     +4X,3HK2=,F5.1,4X,3HK3=,F5.1)

C  THIS LOOP IS FOR DEGREE DAY CALCULATIONS VIA PROPER METHOD

      DO 1000 LL=ISTART,ISTOP

C  DETERMINE WHICH METHOD TO USE AND CALCULATE DEGREE-DAYS

      ITEST1 = KEY - 2
      IF (ITEST1) 20,21,22
20    HEAT=AMAX1(FLOAT(MAX(LL)+MIN(LL))/2.0-BASE,0.0)
      GO TO 24
21    HEAT=AMAX1(FLOAT(MAX(LL))-BASE,0.0)
      GO TO 24
22    IF (R3.GT.0.0.OR.R2.LE.0.0) GO TO 23
      CALL DDAY1(MAX(LL),MIN(LL),BASE,R2,HEAT)
      GO TO 24
23    CALL DDAY2(MAX(LL),MIN(LL),BASE,R3,HEAT)
24    DD = DD + HEAT
      IF (IANSW.EQ.2) GO TO 1000

C  FIGURE OUT THE DAY OF THE YEAR FOR OUTPUT

      I1 = 1
      IF (FLAG) IDATE = JUL(Y,M,D) - JUL(Y,I1,I1) + 1

C  IF OUTPUT IS TO GO ON FILE WRITE IT ON TAPE70

      IF (FLAG) WRITE (70,701) IDATE, M, D, Y, HEAT, DD
701   FORMAT(I5,1X,3I3,2F10.3)
      IDDAY(M,D) = DD + .5
      D = D + 1
      IF (D.LE.MNDAY(M)) GO TO 1000
      D = 1
      M = M + 1
```

```
      IF (M.GT.12) Y = Y + 1
      IF (M.GT.12) M = 1
1000  CONTINUE
      IF (IANSW.EQ.2) GO TO 26
      IF (FLAG) GO TO 2000

C  PRINT OUT DAILY ACCUMULATION TABLE

      WRITE (2,226)
      WRITE (2,401) NAME(IMO),IDA,IYR,BASE,R2,R3
401   FORMAT(19X,A3,I3,I5,20X,3HK1=,F5.1,5X,3HK2=,F5.1,
     +5X,3HK3=,F5.1)

C  DETERMINE IF YEAR BOUNDARY IS CROSSED

      IF (YR.NE.YR2) GO TO 25
      WRITE (2,402) (NAME(I),I=IMO,MO2)
402   FORMAT(5HO DAY,12(7X,A3))
      I2 = 31

C  DETERMINE IF MONTH BOUNDARY IS CROSSED

      IF (IMO.EQ.MO2) I1 = IDA
      IF (IMO.EQ.MO2) I2 = DA2
      DO 5050 L=I1,I2
      WRITE (2,403) L,(IDDAY(K,L),K=IMO,MO2)
403   FORMAT(I5,12(5X,I5))
5050  CONTINUE
      GO TO 2000
25    WRITE (2,402) (NAME(I),I=1,12)
      WRITE (2,404) (L,(IDDAY(K,L),K=1,12),L=1,31)
404   FORMAT(13(I5,5X))
      GO TO 2000

C  STORE THE DEGREE DAY ACCUMULATIONS

26    TABLE(II,JJ,KK) = DD
      IF (FLAG) WRITE (70,702) MO2,DA2,YR2,DD
702   FORMAT(1X,3I3,F10.3)
2000  CONTINUE
      IF (FLAG) STOP1
      IF (IANSW.EQ.1) STOP1

C  WRITE TABLE OF BASES AND DD ACCUMULATIONS

      DO 3000 I=1,IEND1
      WRITE (2,226)
      WRITE (2,225) IEND2,(TITLE(NB),NB=1,IEND2),I,R2,R3
225   FORMAT(2X,3HK1=,5X, =(F5.1,5X)/11H START DATE,I2,5X,3HK2=,F5.1
     +,5X,3HK3=,F5.1)
      WRITE (2,227) (IYEAR(K),IEND2,(TABLE(I,J,K),J=1,IEND2),K=1,IEND3)
      WRITE (2,226)
226   FORMAT(1H-)
227   FORMAT(I6,4X, =F10.4)
```

```
3000  CONTINUE
      IF (IEND3.EQ.1) STOP2

C  TEST FOR WHICH STATS TO DO

      WRITE (2,233)
223   FORMAT(26H STATISTICS? (0=NO, 1=YES)/2H *)
      READ (1,100) IANSWR
      IF (IANSWR.EQ.0) STOP3
      WRITE (2,234)
234   FORMAT(21H WHICH? (0=NO, 1=YES)/
     +26H COEFFICIENTS OF VARIANCE?/2H *)
      READ (1,100) KEY1
      WRITE (2,235)
235   FORMAT(21H STANDARD DEVIATIONS?/2H *)
      READ (1,100) KEY2
      WRITE (2,236)
236   FORMAT(7H MEANS?/2H *)
      READ (1,100) KEY3

C  CALCULATE STATS FOR ALL START DATES

      WRITE (2,226)
      DO 4000 I=1,IEND1
      DO 4000 J=1,IEND2
      SUMSS = 0.0
      SUM = 0.0
      NUM = 0

C  THIS LOOP IS FOR DIFFERENT YEARS

      DO 3500 K=1,IEND3
      NUM = NUM + 1
      SUM = SUM + TABLE(I,J,K)
3500  SUMSS = SUMMS + TABLE(I,J,K)**2

C  THE MEAN, VARIANCE, STANDARD DEVIATION, AND COEFFICIENT
C  OF VARIANCE ARE CALCULATED

      IF (SUM.LT.1.) GO TO 4000
      XBAR(I,J) = SUM/FLOAT(NUM)
      S2 = (SUMSS-SUM**2/FLOAT(NUM))/FLOAT(NUM-1)
      SD(I,J) = SQRT(S2)
      CV(I,J) = 100.*SD(I,J)/XBAR(I,J)
4000  CONTINUE

C  PRINT DESIRED STATISTIC TABLES

      WRITE (2,228) IEND2, (TITLE(NB), NB=1,IEND2)
228   FORMAT(13X, =(F5.1,5X))
      IF (KEY1.NE.1) GO TO 27
      WRITE (2,229)
229   FORMAT(25HOCOEFFICIENTS OF VARIANCE/)
      WRITE (2,230) (IEND2,(CV(I,J),J=1,IEND2),I=1,IEND1)
```

```
230   FORMAT(10X, =F10.4)
27    IF (KEY2.NE.1) GO TO 28
      WRITE (2,231)
231   FORMAT(20HOSTANDARD DEVIATIONS/)
      WRITE (2,230) (IEND2, (SD(I,J),J=1,IEND2),I=1,IEND1)
28    IF (KEY3.NE.1) STOP4
      WRITE (2,232)
232   FORMAT (6HOMEANS/)
      WRITE (2,230) (IEND2,(XBAR(I,J),J=1,IEND2),I=1,IEND1)
      STOP5
      END
C*************************************************************
C                    J U L
C*************************************************************
      FUNCTION JUL(IYE,MON,IDAY)

C  THIS FUNCTION RETURNS THE JULIAN DATE

      L1 = 365*IYE +IYE/4
      C=30.6*FLOAT(MON) - 32.3
      IF (MON.GE.3) GO TO 1
      IF (MOD(IYE,4).EQ.0) L1 = L1-1
      C=C + 2.3
1     JUL = L1 + INT(C) + IDAY
      RETURN
      END
C*************************************************************
C                    D D A Y 1
C*************************************************************
      SUBROUTINE DDAY1(MAX,MIN,R1,R2,HEAT)
      DATA TWOPI/6.283185308/,PIOVR2/1.570796327/
      ANG(FK) = ATAN(FK/SQRT(DIF**2-FK**2))
      HEAT = 0.0
      IF (FLOAT(MAX).LE.R1) RETURN
      SUM = MAX + MIN
      DIF = MAX - MIN
      FR1 = 2.*R1 - SUM
      IF (FLOAT(MAX).GT.R2) GO TO 1
      HEAT = SUM/2. - R1
      IF (FLOAT(MIN).GE.R1) RETURN
      TH1 = ANG(FR1)
      HEAT = (DIF*COS(TH1)-FR1*(PIOVR2-TH1))/TWOPI
      RETURN
1     FR2 = 2.*R2 - SUM
      TH2 = ANG(FR2)
      IF (FLOAT(MIN).LT.R1) GO TO 2
      HEAT = (-DIF*COS(TH2)-FR1*(TH2+PIOVR2))/TWOPI
      RETURN
2     TH1 = ANG(FR1)
      HEAT = (-DIF*(COS(TH2)-COS(TH1))-FR1*(TH2-TH1)/TWOPI
      RETURN
      END
C*************************************************************
C                    D D A Y 2
C*************************************************************
```

```
      SUBROUTINE DDAY2(MAX,MIN,R1,R3, HEAT)
      DATA TWOPI/6.283185308/,PIOVR2/1.570796327/
      HEAT = 0.0
      IF (FLOAT(MAX).LE.R1) RETURN
      J = R3
      FR1 = 2.*R1
1     SUM = MAX + MIN
      DIF = MAX - MIN
      HEAT = (SUM-FR1)/2.
      IF (FLOAT(MIN).GE.R1) GO TO 2
      THETA = ATAN((FR1-SUM)/SQRT(DIF**2-(FR1-SUM)**2))
      HEAT = (DIF*COS(THETA)-(FR1-SUM)*PIOVR2-THETA))/TWOPI
2     IF (R3.LE.0.0.OR.FLOAT(MAX).LE.R3) RETURN
      IF (J.LE.0) GO TO 3
      FR1 = 2.*R3
      J = 0
      ZHEAT = HEAT
      GO TO 1
3     HEAT = ZHEAT - HEAT
      RETURN
      END
C*************************************************************
C                    G E T P F
C*************************************************************
      SUBROUTINE GETPF
C
C     PURPOSE:
C        THIS ROUTINE GETS THE PERMANENT FILE NAME OF THE DATA
C        AND ATTACHES IT AS TAPE60.  ALSO CHECKS FOR ERRORS IN
C        THE ATTACH PROCESS AND TELLS USER.
C
C     KEY VARIABLES OR ROUTINES USED:
C
C        RETURNF - CDC SYSTEM ROUTINE TO RETURN LOCAL FILES
C        PFFDB - CDC SYSTEM ROUTINE TO DEFINE FILE DEF. BLOCK
C        PFATT - CDC SYSTEM ROUTINE TO ATTACH PERMANENT FILES
C        CKPFERR - CDC SYSTEM ROUTINE TO CHECK PF ERRORS
C        IRETCD - THE CODE RETURNED BY PFATT -- USED BY CKPFERR
C        LUN - LOGICAL UNIT NUMBER
C        IFDB - ARRAY WHICH HOLDS THE PERMANENT FILE NAME
C        IPFBUF - ARRAY USED BY SYSTEM TO HOLD FILE INFORMATION
C
      DIMENSION IFDB(4), IPFBUF(12)
      COMMON /IO/ IN, IOUT
      DATA LUN/60/, IN/1/, IOUT/2/

C  RETURN LOCAL FILE TAPE60

1     CALL RETURNF(LUN)

C  INITIALIZE PERMANENT FILE NAME ARRAY

      DO 10 I=1,4
10    IFDB(I) = 0
```

```
      WRITE (IOUT,100)
100   FORMAT (50H PLEASE ENTER THE PERMANENT FILE NAME FOR THE DATA
     +/2H *)

C  READ IN PERMANENT FILE NAME

      READ (IN,200) (IFDB(K),K=1,4)
200   FORMAT (4A10)

C  INITIALIZE FILE DEFINITION BLOCK

      CALL PFFDB(LUN,IFDB,IPFBUF,12)

C  ATTACH FILE AS TAPE60

      IRETCD = PFATT(IPFBUF)
      IF (IRETCD.EQ.0) RETURN

C  CHECK FOR WHICH ERROR WAS COMMITTED AND TRY AGAIN

      CALL CKPFERR(IRETCD,0)
      GO TO 1
      END
C*************************************************************
C                    T E M P I O
C*************************************************************
      SUBROUTINE TEMPIO(NDAYS,KK)

C  THIS ROUTINE INPUTS MAX & MIN TEMPS FROM USER AND WRITES
C  THEM IN STANDARD FORM ON TAPE60, OR JUST READS FROM TAPE60
C  WITH OPTIONAL ECHO PRINT.  NDAYS DETERMINES NUMBER OF DAYS READ

      DIMENSION LABEL(2)
      INTEGER BEGIN,END,YR,TEMP(31),DA1,YR1,SC,ANSW,DUMYR,DUMMO
      LOGICAL FLAG
      COMMON /MONTH/ NAME(12), MNDAY(12)
      COMMON /DATES/ MO1,DA1,YR1,MO2,DA2,YR2
      COMMON /TEMPS/ MAX(366),MIN(366)
      COMMON /OUTP/ TITLE(10), IHEAD(31), IYEAR(15)
C
C          ARRAY                PURPOSE
C
C        LABEL     HOLDS TITLE WHICH DESCRIBES THE TEMPERATURE DATA
C        TEMP      USED FOR TEMPERATURE I/O AND REFORMATTING
C
C  DETERMINE MODE OF TEMPERATURE INPUT

      IF (KK.EQ.1) WRITE (2,250)
250   FORMAT(37H INPUT DEVICE? (1=TERMINAL, 2=TAPE60)/2H *)
      IF (KK.EQ.1) READ (1,150) ANSW
      IF (ANSW.EQ.2.AND.KK.EQ.1) CALL GETPF
      IF (ANSW.EQ.2) GO TO 3

C  CALCULATE SKIP CONTROL FOR I/O
```

```
      SC = DA1*3

C  STORE MONTH AND YEAR FOR USE AS FILE READ CONTROLS

      MON = MO1
      YR = YR1

C  FIGURE OUT HEADING FLAG FOR I/O

      WRITE (2,248)
248   FORMAT(36H ENTER A TITLE TO DESCRIBE YOUR DATA/2H *)
      READ (1,149) LABEL(1), LABEL(2)
149   FORMAT(2A10)
      IOY = YR1
      IOM = MO1 - 1
      IF (IOM.EQ.0) IOY = IOY - 1
      IF (IOY.NE.YR1) IOM = 12
      WRITE (60,649) LABEL(1), LABEL(2), IOY, IOM
649   FORMAT(T11,2A10/2I2)

C  CALCULATE NUMBER OF DAYS TO BE READ

      NUML = NDAYS
      NUMR = MINO(MNDAY(MO1)+1-DA1,NUML)
      I1 = DA1
      I2 = NUMR + DA1 - 1

C  PROMPT USER FOR TEMP ENTRY

      WRITE (2,247)
247   FORMAT(51HOENTER TEMPERATURES AS INTEGERS SEPARATED BY COMMAS/)
1     WRITE (2,249) SC, I2, (IHEAD(I), I=I1,I2)
249   FORMAT(1HO,T8, =X, =I3)
      WRITE (2,251) NAME(MON),YR,SC
251   FORMAT(1X,A3,I2,1X,3HMAX,T8, =X,1H*)

C  READ MAX TEMPS

      READ*, (TEMP(I),I=1,NUMR)

C  PUT INTO STANDARD FORM ON TAPE60

      WRITE (60,650) YR,MON,SC,NUMR,(TEMP(I),I=1,NUMR)
650   FORMAT(2I2,1X,3HMAX,T8, =X, =I3)

C  REPEAT FOR MINS

      WRITE (2,252) NAME(MON),YR,SC
252   FORMAT(1X,A3,I2,1X,3HMIN,T8, =X,1H*)
      READ*, (TEMP(I),I=1,NUMR)
      WRITE (60,651) YR,MON,SC,NUMR,(TEMP(I),I=1,NUMR)
651   FORMAT(2I2,1X,3HMIN,T8, =X, =I3)

C  CALCULATE NUMBER OF DAYS LEFT TO BE READ AND TEST
```

```
C  FOR END OF TEMPERATURE INPUT

      NUML = NUML - NUMR
      IF (NUML.EQ.0) GO TO 3

C  UPDATE MONTH AND TEST FOR END OF YEAR

      MON = MON + 1
      IF (MON.LT.13) GO TO 2
      MON = 1
      YR = YR + 1

C  CALCULATE NUMBER OF DAYS THAT WILL BE READ

2     NUMR = MINO(MNDAY(MON),NUML)
      SC = 3
      I1 = 1
      I2 = NUMR
      GO TO 1
3     REWIND 60

C  CALCULATE SKIP CONTROLS FOR I/O

      SC = DA1*3

C  STORE MONTH AND YEAR FOR USE AS FILE READ CONTROLS

      MON = MO1
      YR = YR1

C  SEARCH TEMPERATURE FILE FOR DATA RIGHT BEFORE START DATE

4     READ (60,652) DUMYR,DUMMO
      IF(EOF(60)) 7,5
652   FORMAT(/2I2)

C  LOOK AT SPECIAL CASE OF JANUARY

5     IF (MON.NE.1) GO TO 6
      DUMYR = DUMYR + 1
      DUMMO = DUMMO - 12
6     IF (DUMYR.EQ.YR.AND.DUMMO.EQ.(MON-1)) GO TO 8
      GO TO 4

C  DID NOT FIND DATE -- ISSUE ERROR MESSAGE

7     WRITE (2,259)
259   FORMAT(27H-DATA FILE STRUCTURE IS BAD)
      STOP6
8     WRITE (2,253)
253   FORMAT(37HO PRINT TEMPERATURE DATA?  (0=NO,1=YES)/2H *)
      READ (1,150) IFLAG
150   FORMAT(I1)
```

```
C  SET FLAG FOR PRINTING OUTPUT

      FLAG = IFLAG.EQ.1

C  CALCULATE NUMBER OF DAYS TO BE READ

      NUML = NDAYS
      NUMR = MINO(MNDAY(MO1)+1-DA1,NUML)
      END = NUMR
      IF (FLAG) WRITE (2,254) (IHEAD(I),I=1,31)
254   FORMAT(1H-,9X,31I3)

C  READ AND WRITE TEMPERATURE DATA

      READ (60,653) YR,SC,NUMR,(MAX(I),I=1,END)
      IF (FLAG) WRITE (2,255) NAME(MON),YR,SC,NUMR,(MAX(I),I=1,END)
653   FORMAT(I2,3X, =X, =I3)
255   FORMAT(1X,A3,I2,1X,3HMAX,T8, =X, =I3)
      READ (60,653) YR,SC,NUMR,(MIN(I),I=1,END)
      IF (FLAG) WRITE (2,256) NAME(MON),YR,SC,NUMR,(MIN(I),I=1,END)
256   FORMAT(1X,A3,I2,1X,3HMIN,T8, =X, =I3)

C  TEST FOR MIN GREATER THAN MAX TEMPERATURE

      DO 1000 IA=1,END
      IF (MIN(IA).GT.MAX(IA)) GO TO 11
1000  CONTINUE

C  TEST FOR END OF DATA I/O

9     IF (NDAYS.EQ.END) RETURN

C  UPDATE  MONTH AND TEST FOR YEAR CHANGE

      MON = MON + 1
      IF (MON.LT.13) GO TO 10
      MON = 1
      YR = YR + 1
10    BEGIN = END + 1

C  CALCULATE NUMBER OF DAYS LEFT TO BE READ

      NUML = NUML - NUMR

C  CALCULATE NUMBER OF DAYS THAT WILL BE READ

      NUMR = MINO(MNDAY(MON),NUML)
      END = NUMR + BEGIN - 1

C  READ AND WRITE REST OF TEMPERATURE DATA

      READ (60,654) YR,NUMR,(MAX(I),I=BEGIN,END)
      IF (FLAG) WRITE (2,257) NAME(MON),YR,NUMR,(MAX(I),I=BEGIN,END)
654   FORMAT(I2,6X, =I3)
```

```
257   FORMAT(1X,A3,I2,1X,3HMAX, =I3)
      READ (60,654) YR,NUMR,(MIN(I),I=BEGIN,END)
      IF (FLAG) WRITE (2,258) NAME(MON),YR,NUMR,(MIN(I),I=BEGIN,END)
258   FORMAT(1X,A3,I2,1X,3HMIN, =I3)

C  TEST FOR MIN GREATER THAN MAX TEMPERATURE

      DO 1010 IA=BEGIN,END
      IF (MIN(IA).GT.MAX(IA)) GO TO 11
1010  CONTINUE

C  LOOP AROUND UNTIL ALL DATA IS READ

      GO TO 9
11    WRITE (2,260) MIN(IA), MAX(IA)
260   FORMAT(25HOTHE MINIMUM TEMPERATURE ,I3,
     +41H IS GREATER THAN THE MAXIMUM TEMPERATURE ,I3)
      STOP7
      END
C*************************************************************
C                    B  L  K  D  A  T
C*************************************************************
      BLOCK DATA
      COMMON /MONTH/ NAME(12),MNDAY(12)
      DATA NAME/3HJAN,3HFEB,3HMAR,3HAPR,3HMAY,3HJUN,3HJUL,3HAUG,
     +3HSEP,3HOCT,3HNOV,3HDEC/
      DATA MNDAY/31,28,31,30,31,30,31,31,30,31,30,31/
      END
```

APPENDIX B

DATA FROM DR. J. D. MOORE USED TO CONSTRUCT ENVIRONMENTAL FAVORABILITY MODEL

Table B1. Original data of Figure 22 in the Epidemiology and Control of Cherry Leaf Spot, Wisconsin Agric. Expt. Stn. Res. Bull. 132 by G.W. Keitt, E.C. Blodgett, E.E. Wilson, and R.O. Magie, 1937 obtained from Dr. J.D. Moore at the University of Wisconsin at Madison, Wisconsin.

Number of hours in inoculation chamber	Air temperature °C in inoculation chamber	Average number lesions on maximally infected inch^2/leaf
4	8	0.0
4	12	2.3
4	16	4.3
4	20	7.7
4	24	1.7
4	28	0.0
6	8	0.0
6	12	2.5
6	16	11.5
6	20	17.0
6	24	10.6
6	28	2.3
8	8	0.3
8	12	5.2
8	16	18.8
8	20	36.2
8	24	21.9
8	28	3.0
12	8	8.4
12	12	25.0
12	16	47.5
12	20	59.6
12	24	35.9
12	28	5.3
20	8	12.8
20	12	48.4
20	16	69.0
20	20	95.8
20	24	49.4
20	28	12.8
30	8	21.4
30	12	60.4
30	16	102.4
30	20	100.6
30	24	56.4
30	28	13.6
40	8	37.1
40	12	86.2
40	16	110.4
40	20	107.8
40	24	46.9
40	28	13.3

Table B1. (cont'd.)

50	8	49.7
50	12	105.0
50	16	131.9
50	20	119.2
50	24	70.4
50	28	22.8
70	8	64.0
70	12	131.1
70	16	144.8
70	20	124.3
70	24	74.3
70	28	34.2

APPENDIX C

ALTERNATIVE FORMS OF ENVIRONMENTAL FAVORABILITY MODEL AND CALCULATED WETTING DURATIONS FOR SELECTED EFI AND TEMPERATURE VALUES

Table C1. Alternative forms of environmental favorability model equation.

Equation 1. If W and T are known:

$$EFI = [a + bW + cT + dW^2 + eT^2 + fWT]^2$$

Equation 2. If EFI and T are known:

$$W = \frac{-(b + fT) + \sqrt{(b + fT)^2 - 4d(cT + eT^2 + a - EFI^{0.5})}}{2d}$$

Equation 3. If EFI and W are known:

$$T = \frac{-(c + fW) + \sqrt{(c + fW)^2 - 4e(a + bW + dW^2 - EFI^{0.5})}}{2e}$$

where:

a = -11.0
b = 0.2858
c = 1.464
d = -0.0019
e = -0.0389
f = -0.003
T = average air temperature (°C)
W = length of wetting period (hrs)
EFI = environmental favorability index

Table C2. Hours of leaf wetness required for conidial infection calculated for selected environmental favorability index and temperature values with equation 2 of table C1.

Average air temperature		Environmental favorability index		
		14	28	42
(°F)	(°C)	(hr.)	(hr.)	(hr.)
82	27.78	27.12	--	--
81	27.22	23.24	43.08	--
80	26.67	20.08	35.57	--
79	26.11	17.43	30.82	--
78	25.56	15.17	27.23	42.90
77	25.00	13.23	24.35	36.96
76	24.44	11.56	21.97	32.98
75	23.89	10.11	19.98	29.95
74	23.33	8.86	18.30	27.54
73	22.78	7.79	16.88	25.57
72	22.22	6.89	15.69	23.96
71	21.67	6.15	14.70	22.63
70	21.11	5.54	13.89	21.56
69	20.56	5.07	13.25	20.70
68	20.00	4.72	12.77	20.05
67	19.44	4.50	12.43	19.57
66	18.89	4.39	12.24	19.26
65	18.33	4.40	12.17	19.11
64	17.78	4.52	12.24	19.12
63	17.22	4.74	12.44	19.28
62	16.67	5.08	12.76	19.58
61	16.11	5.52	13.20	20.02
60	15.56	6.08	13.77	20.61
59	15.00	6.74	14.46	21.35
58	14.44	7.50	15.29	22.23
57	13.89	8.39	16.24	23.27
56	13.33	9.38	17.33	24.47
55	12.78	10.49	18.55	25.84
54	12.22	11.73	19.93	27.40
53	11.67	13.09	21.46	29.15
52	11.11	14.59	23.16	31.13
51	10.56	16.23	25.05	33.35
50	10.00	18.02	27.14	35.88
49	9.44	19.98	29.46	38.76
48	8.89	22.12	32.04	42.10
47	8.33	24.47	34.95	46.08
46	7.78	27.05	38.24	51.06