

# Expression of Partial Resistance to Cherry Leaf Spot in Cultivars of Sweet, Sour, Duke, and European Ground Cherry

T. M. SJULIN, Department of Horticulture, A. L. JONES, Department of Botany and Plant Pathology and The Pesticide Research Center, and R. L. ANDERSEN, Department of Horticulture, Michigan State University, East Lansing 48824

## ABSTRACT

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Characteristics of infection and defoliation of cultivars of sweet, sour, duke, and European ground cherry by *Coccomyces hiemalis* were studied in the field and greenhouse to determine their suitability for evaluating cultivars of cherry for resistance to cherry leaf spot. Under field conditions, no cultivar was highly resistant to infection by leaf spot, but the progress of defoliation for sweet and European ground cherry was slower than that for duke and sour cherry. Among 25 cultivars tested in the field, Yellow Glass, Schmidt, and Emperor Francis sweet cherry displayed the least, and Montmorency sour cherry and Krassa Severa duke cherry the greatest, defoliation severity. In the greenhouse, inoculated leaves of sweet cherry required more days before 50% of the lesions were visible, had smaller lesions, and produced fewer conidia per lesion than inoculated leaves of sour cherry. High correlations existed between the severity of defoliation in the field and the infection characteristics of number of days for 50% of the lesions to become visible, rate of lesion appearance, lesion size, spores per lesion, and reproduction efficiency in the greenhouse. Accordingly, greenhouse studies could be useful in identifying cherry seedlings with partial resistance or tolerance to leaf spot. There was little difference in the defoliation of SHT-2 and SHT-3, two progeny with apparent resistance to leaf spot in a seedling nursery, from that of Montmorency sour cherry in the field, but lesions on SHT-2 and SHT-3 produced fewer spores than those on Montmorency in the greenhouse.

Additional keywords: *Prunus avium*, *P. cerasus*, *P. fruticosa*, *P. gondouinii*

Michigan is the major producer of cherries in the United States, with about 17,810 ha of sour (*Prunus cerasus* L. 'Montmorency') and 4,450 ha of sweet (*P. avium* L.) cherries. Cherry leaf spot, caused by *Coccomyces hiemalis* Higgins, is a major disease of cherries throughout the Great Lakes and Mid-Atlantic states and the province of Ontario, Canada. In this region, infection is closely related to the duration of wetting from rain and the temperature during the wet period (3,6). Environmental conditions favorable for infection can occur from May through September, and severe defoliation of trees is often observed in commercial sour cherry orchards during August and September following wet weather. Early defoliation from leaf spot delays acclimation of wood and flower buds in the fall, hastens deacclimation in the spring, and reduces bud survival and fruit set for at least two seasons (2,4).

Present address of first author: Driscoll Strawberry Association, Inc., 404 San Juan Road, Watsonville, CA 95076. Present address of third author: Department of Horticultural Sciences, New York State Agricultural Experiment Station, Geneva 14456.

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In Michigan cherry orchards, cultivars of sweet cherry usually show less defoliation from leaf spot infection than the sour cherry cultivar Montmorency (A. L. Jones, *unpublished*). In the Michigan State University cherry breeding program, two seedlings were considered possible sources of resistance because they were not defoliated late in the season under epidemic conditions. The objectives of this research were to evaluate cultivars of sweet, sour, duke (*P. gondouinii* Rehd.), and European ground (*P. fruticosa* Pall.) cherry for their response to inoculation with *C. hiemalis* and to determine the potential of the two selected cherry seedlings as sources of resistance to leaf spot.

## MATERIALS AND METHODS

**Field experiment.** Twenty-five cultivars and selections representing four species of cherry were increased by chip-budding onto *P. mahaleb* L. seedlings in September 1979. SHT-2 and SHT-3 were selected by R. L. Andersen as possible sources of leaf spot resistance because of their low level of disease late in the season. SHT-2 was an open-pollinated seedling of an unknown morello-type sour cherry. SHT-3 was an apparent interspecific hybrid between North Star sour cherry and an unknown cultivar of sweet cherry.

The budded trees were dug in November 1979 and stored in a cold

room at 1–4 C until they were planted in April 1980 on a 1.5 × 1.8 m spacing in a Locke sandy loam soil. The experimental design was a randomized complete block with five single-tree replications. A single vegetative shoot was forced to grow from each tree by cutting the rootstock off just above the bud union. Each tree received approximately 30 g of a 12-12-12 N-P-K fertilizer 2 wk after bud break and 33 g of urea 1 mo later. Trees were irrigated throughout the growing season with a biwall drip irrigation system buried 2–5 cm deep next to each tree. All trees were sprayed with insecticides and miticides as needed during the growing season to control insects and mites and twice within 4 wk after inoculation with a mildewicide to control powdery mildew.

Each tree was inoculated on 7 July 1980 with conidia of *C. hiemalis* washed from naturally infected leaves of Montmorency sour cherry collected from trees adjacent to the experimental plot. A misting bottle was used to spray a 2 cm<sup>2</sup> area on the lower surface of the second unfolded leaf below the shoot apex with a suspension of 10<sup>5</sup> conidia per milliliter. To increase germination and infection by the conidia, inoculations were made at dusk and each inoculated leaf was enclosed for approximately 12 hr in a plastic bag containing a wet paper napkin. Subsequent spread of inoculum and infection occurred throughout the growing season during periods of natural leaf wetness.

Leaf spot ratings were made on 7 July 1980 and repeated every 1–2 wk until 2 October 1980. The percentage of leaves infected and the percentage defoliation were determined at each evaluation. Gompertz and logistic equations were fitted to the sigmoidal percentage infection and percentage defoliation curves, and an examination of the residuals and correlation coefficients for individual trees indicated a better fit with the Gompertz transformation ( $-\ln(-\ln(y))$ ). Linear regression of Gompertz-transformed values against time of rating was used to estimate rates of infection and defoliation for each tree (1). In addition, the days of the year corresponding to 50% infection and to 50% defoliation were estimated from the regression equations. The areas under the progress curves for percentage infection (AUIPC) and for percentage defoliation

(AUDPC) were calculated by AUIPC or  $AUDPC = \sum_{i=1}^N ((R_i + R_{i+1})/2)(t_{i+1} - t_i)$ , where  $t_i$  = day of the year at evaluation  $i$ ,  $R_i$  = percent infection or defoliation at evaluation  $i$ , and  $i$  = one to nine evaluations.

**Greenhouse experiments.** The trees used in each experiment were propagated as described for the field experiment. They were grown in 3.7-L containers in a greenhouse at 15–30 C. Trees for experiment 1 were planted in a mixture of soil and perlite (2:1, v/v) and fertilized biweekly with a 5.3 g/L solution of 20% N–20% P<sub>2</sub>O<sub>3</sub>–20% K<sub>2</sub>O fertilizer (Robert B. Peters Co., Inc., Allentown, PA). Trees for experiment 2 were planted in a mixture of sand, peat moss, and perlite (1:1:1, v/v) and fertilized once with 5.25 g of 19% N–6% P<sub>2</sub>O<sub>3</sub>–12% K<sub>2</sub>O controlled-release fertilizer (Osmocote, Sierra Chemical Co., Milpitas, CA) per container plus 0.75 g of sustained-released micronutrient mixture (Esmigran, Mallinckrodt Inc., St. Louis, MO) per container.

A single shoot was allowed to develop on each tree. Records were maintained of the age of each leaf beginning from the date of unfolding, i.e., when the laminar blades were separated by an angle greater than 90°. All leaves unfolding within a 4-day period were assigned to the same age group. The age of a leaf was the average number of days from unfolding to inoculation. Thus, each tree had a range of leaf ages present at the time of inoculation.

A single-conidial isolate of *C. hiemalis* (isolate B) obtained from naturally infected leaves of Montmorency sour cherry in a commercial orchard near Decatur, MI, was used in both experiments. The isolate was maintained by periodically inoculating young leaves of Montmorency trees grown in the greenhouse or by freezing leaves bearing sporulating lesions at –20 C for up to 6 mo.

**Experiment 1.** The resistance of sour cherry and duke cherry to leaf spot was determined with a split-plot, randomized complete block with an 8 × 4 factorial treatment design. Eight cultivars were the main plots and four leaf ages (6.5, 10.5, 14.5, and 18.5 days) were subplots. There were three single-tree replications.

Leaves were inoculated with a conidial suspension of *C. hiemalis* prepared by washing 2- to 3-wk-old lesions on leaves of Montmorency cherry with water. The concentration of the inoculum was measured with a hemacytometer and adjusted to 10<sup>5</sup> conidia per milliliter. The conidial suspension was sprayed uniformly onto the undersurface of each leaf with an atomizer (The DeVilbiss Co., Somerset, PA) operated with compressed air at a pressure of 0.7 bar. Within 5 min after inoculation, the trees were placed in a mist chamber for 48 hr at 19–21 C. Trees were then incubated at about 23 C

in a cheesecloth tent on a greenhouse bench covered with 6 cm of sand. The cheesecloth and sand were wetted daily to increase the relative humidity around the plants.

The number of lesions per leaf was counted 6 and 16 days after inoculation. Infection frequency was expressed as the number of lesions per square centimeter of leaf measured on the day of inoculation. Leaf areas were measured with an area meter (Model LI-3000, Lambda Instrument Corp., Lincoln, NE). The proportion of lesions was the number of lesions counted on day 6 divided by the number counted on day 16. The leaves were removed 20 days after inoculation and held at –20 C until they were analyzed for conidial production.

Sizes of lesions on day 20 were measured with a binocular dissecting microscope fitted with a calibrated ocular micrometer. Length by width measurements were made on five randomly selected lesions per leaf, and the lesion area was calculated as a rectangle, square, or right-angled triangle, depending on which formula

was most appropriate for the shape of the lesion. Spore production on day 20 was measured by washing conidia from each leaf into 40 ml of water. Each spore wash was counted with a hemacytometer, and spore production was expressed as the number of conidia per lesion and per square centimeter of leaf area at the time of inoculation. Log<sub>10</sub> transformations were made on lesion areas, conidia per lesion, and conidia per square centimeter of leaf area data prior to analysis of variance to eliminate proportionality between means and their standard deviations (7).

**Experiment 2.** The disease response of 10 sweet cherry, 5 sour cherry, and 5 duke cherry cultivars to inoculation with *C. hiemalis* was determined using a split-plot design. Cultivars were the whole plots, blocked by time of inoculation with *C. hiemalis* into four single-tree replicates, and three leaf age groups were subplots. On each tree, three leaves (7.5, 19.5, and 35 days old) were inoculated at the same time for each replicate with a Schein quantitative inoculator controlled with an electronic timer (9). Two circular

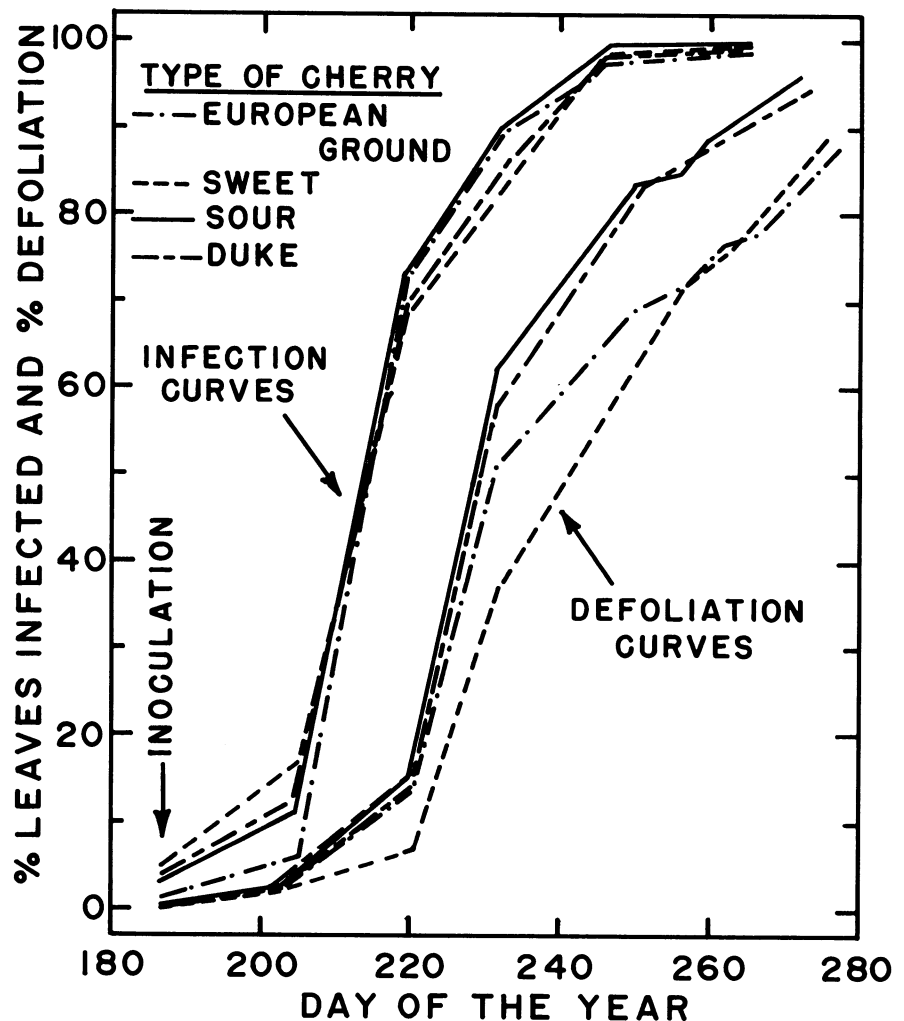


Fig. 1. Progress of mean leaf spot infection and mean defoliation of nine cultivars of sweet cherry, six of sour cherry, six of duke cherry, and four of European ground cherry following inoculation with *Coccomyces hiemalis* to a single leaf on each tree on day 189. Data are the mean severities of five replicates per cultivar and are pooled by species of cherry.

areas of 2.1 cm<sup>2</sup> were inoculated on each leaf. An atomizer containing a suspension of 10<sup>5</sup> conidia per milliliter of *C. hiemalis* was positioned 43 cm from the leaf undersurface and operated for 1 sec at 140 kPa. The number of conidia deposited on each leaf was estimated by periodically inoculating 1.5 × 1.5 cm sections of membrane filters (0.45-μm pore size). The filters were placed on 2% water agar in petri dishes and incubated in the mist chamber along with the inoculated trees for 48 hr. Germinating and total numbers of conidia were counted at ×200 in five random light microscope fields (0.88 mm diameter) for each section. An average of 4,976 conidia were deposited per square centimeter of filter. Conidial germination exceeded 90% in each replicate. Immediately after inoculation, the trees were placed in a mist chamber for 48 hr at 18–21 C. Trees were then incubated at about 17 C and

with high relative humidity as described for experiment 1.

Lesions on each leaf were counted beginning 3 days after inoculation and at 1–3 day intervals for 20 days. The total number of lesions per leaf was determined 36 days after inoculation. Infection efficiency was calculated as the number of lesions per leaf divided by the number of conidia applied to each leaf (9). Rate and time of lesion appearance were estimated from an asymptotic curve,  $Y = 1 - e^{-(bX + a)}$ , using the equivalent form,  $\ln(1/Y - 1) = bX + a$ , to fit a linear regression line where  $X$  = number of days after inoculation,  $Y$  = lesions present at day  $X$  as a proportion of the total,  $b$  = slope of the regression line, and  $a$  = intercept of the regression line. Estimates of the time when 50% of the lesions were visible and of the rate of lesion appearance (slope of the regression line) were made for each leaf and subjected to

analysis of variance, using log<sub>e</sub> transformed values for date of 50% lesion development. Lesion areas were determined 36 days after inoculation as described for experiment 1, and the data were transformed to log<sub>10</sub> prior to the analysis of variance.

Conidial production was measured 9, 18, and 36 days after inoculation. At 9 and 18 days, conidia were washed from each inoculated leaf into 9 ml of distilled deionized water with a DeVilbiss atomizer operated at 70 kPa. To preserve the conidia and to minimize their adherence to glass surfaces, 1 ml of 2% (w/v) formaldehyde plus 1% (v/v) polyoxyethylene sorbitan monolaurate (Tween 20, Sigma Chemical Co., St. Louis, MO) in distilled deionized water were added to each spore suspension. At 36 days, conidia were removed by immersing the inoculated area of each leaf into the formaldehyde-Tween 20

**Table 1.** Development of leaf spot and defoliation of cultivars within four species of cherry in an orchard at the Michigan State University Horticultural Research Farm, East Lansing, and single degree-of-freedom comparisons between species groups

Cultivar <sup>u</sup> or comparison	Infection rate <sup>v</sup>	Date of 50% infection (day of year) <sup>w</sup>	Infection severity (AUIPC) <sup>x</sup>	Defoliation rate <sup>v</sup>	Date of 50% defoliation (day of year) <sup>w</sup>	Defoliation severity (AUDPC) <sup>x</sup>
Sweet cherry						
Black Tartarian	0.086 cdefg <sup>y</sup>	211.9 bcdefgh	6251 abcdef	0.064 abcdefg	234.2 abcd	4045 cdef
Emperor Francis	0.089 bcdefg	212.2 bcdefgh	6191 bcdef	0.052 efgh	246.5 defg	2828 h
Governor Wood	0.085 cdefg	214.8 defgh	5981 defg	0.057 defgh	236.7 bcde	3724 def
Hedelfingen	0.062 g	210.7 abcde	6451 abc	0.038 ghi	246.8 defg	2874 gh
Lambert	0.071 fg	212.5 bcdefgh	6202 bcdef	0.088 ab	238.9 cdefg	3471 fg
Napoleon	0.073 efg	211.5 abcdefg	6269 abcde	0.064 abcdefg	234.4 abcd	3755 def
Schmidt	0.079 cdefg	208.9 abc	6679 a	0.034 hi	247.4 efg	2803 h
Windsor	0.075 defg	213.9 cdefgh	6038 cdefg	0.055 defgh	246.6 defg	2879 gh
Yellow Glass	0.083 cdefg	216.6 h	5754 g	0.049 fghi	249.3 fg	2716 h
Sour cherry						
Early Richmond	0.085 cdefg	210.3 abcd	6424 abc	0.064 abcdefg	228.0 abc	4551 abc
English Morello	0.078 cdefg	210.2 abcd	6312 abcd	0.077 abcde	227.4 abc	4644 abc
Meteor	0.108 abcd	210.5 abcde	6327 abcd	0.060 cdefgh	228.7 abc	4377 abcd
Montmorency	0.107 abcde	208.6 ab	6560 ab	0.090 a	224.5 ab	4936 ab
North Star	0.126 a	215.0 defgh	6011 cdefg	0.044 fghi	237.5 cdef	3736 def
SHT-2	0.112 abc	215.4 efgh	5924 defg	0.055 defgh	235.2 abcde	3623 ef
Duke cherry						
Brassington Duke	0.082 cdefg	216.2 gh	5848 efg	0.063 abcdefg	237.9 cdefg	3686 ef
Kansas Sweet	0.091 bcdefg	216.0 fgh	5905 defg	0.067 abcdef	238.0 cdefg	3542 f
Krassa Severa	0.104 abcdef	206.9 a	6655 ab	0.085 abc	222.8 a	4994 a
May Duke	0.082 cdefg	208.9 abc	6421 abc	0.065 abcdefg	230.1 abc	4378 abcd
SHT-3	0.085 cdefg	216.2 gh	5818 fg	0.062 bcdefg	231.3 abc	4219 cde
Wezesna Z Prin	0.100 abcdef	212.0 bcdefgh	6219 bcdef	0.082 abcd	227.5 abc	4594 abc
European ground cherry						
Dwarf Rich	0.109 abcd	213.2 bcdefgh	6095 cdefg	0.058 cdefgh	240.0 cdefg	3555 f
IR 323-2	0.105 abcdef	215.4 efgh	5926 defg	0.066 abcdef	229.4 abc	4342 bcd
IR 586-3	0.121 ab	211.1 abcdef	6315 abcd	0.062 bcdefg	234.5 abcd	3996 cdef
IR 587-1	0.086 cdefg	214.4 defgh	5958 defg	0.025 i	250.3 g	2934 gh
Sweet cherry/9 cultivars	0.078	212.6	6202	0.056	242.3	3233
Sour cherry/6 cultivars	0.103	211.6	6260	0.065	230.2	4311
Duke cherry/6 cultivars	0.091	212.7	6144	0.071	231.3	4235
European cherry/4 cultivars	0.105	213.5	6073	0.052	238.6	3707
Sour vs. sweet	0.01 <sup>z</sup>	ns	ns	0.05	0.01	0.01
Sour vs. duke	0.05	ns	ns	ns	ns	ns
Sour vs. European	ns	ns	0.05	0.05	0.01	0.01
Duke vs. sweet	0.05	ns	ns	0.01	0.01	0.01
European vs. sweet	0.01	ns	ns	ns	ns	0.01

<sup>u</sup> Each value is the mean of five single-tree replications.

<sup>v</sup> Slope of linear regression of Gompertz-transformed percent infection or percent defoliation data against time.

<sup>w</sup> Estimated from the linear regression of Gompertz-transformed percent infection or percent defoliation data.

<sup>x</sup> AUIPC = area under infection progress curve, AUDPC = area under defoliation progress curve.

<sup>y</sup> Mean separation by Duncan's multiple range test ( $P = 0.05$ ).

<sup>z</sup> Level of significance ( $P$ ), ns = not significant.

solution. Samples were stored at 2 C until counted within 2 wk.

The number of conidia in each sample was estimated by measuring absorbance of the spore suspensions at 700 nm with a dual-beam spectrophotometer (model DB-G, Beckman Instruments, Inc., Fullerton, CA). A standard curve relating absorbance to conidial concentration as determined by hemacytometer counts was developed for each set of samples measured on a given day. Conidial concentrations were estimated from absorbance by a power curve,  $Y = bA^m$ , using the equivalent form,  $\log_{10} b + m(\log_{10} A)$ , to fit a linear regression line where  $A$  = absorbance at 700 nm,  $Y$  = conidial concentration,  $b$  = intercept, and  $m$  = slope of linear regression line. Conidial production was expressed as conidia per lesion and as reproductive efficiency (defined as the number of conidia produced divided by the number of viable conidia applied as inoculum).

Simple correlations between resistance factors measured in the greenhouse and infection and defoliation severities measured in the field were determined for 19 of the 20 cultivars evaluated in experiment 2.

## RESULTS

**Field experiments.** Leaf spot increased rapidly on all cultivars following inoculation (Fig. 1). Less than 5% of the leaves were infected on the day of inoculation (day 189), but about 70% were infected 4 wk after inoculation (day 219) and over 98% were infected 8 wk after inoculation (day 248). Defoliation progressed faster on sour and duke cherry then on sweet cherry (Fig. 1). Defoliation of European ground cherry was rapid initially but slowed later in the season.

All cultivars were susceptible to infection by *C. hiemalis*. Infection rates varied twofold among the 25 cultivars, from 0.062 for Hedelfingen to 0.126 for North Star (Table 1). The average infection rate for cultivars of sweet cherry (0.078 lesions per day) was significantly lower (Table 1) than that for cultivars of duke (0.091), sour (0.103), and European ground (1.05) cherry. The date of 50% infection differed by less than 10 days among the cultivars, and early dates of 50% infection were not always associated with high infection rates. For example, Yellow Glass and Schmidt had similar infection rates, but the date of 50% infection for Yellow Glass was 7 days later. Similarly, the infection rates for North Star and Montmorency were similar, but the date of 50% infection for North Star was 6 days later. The AUIPCs ranged from 5754 for Yellow Glass to 6679 for Schmidt. The estimated date of 50% infection and the AUIPCs did not differ significantly among the four cherry species.

Defoliation rates differed by more

than threefold among the 25 cultivars, from 0.025 for IR 587-1 to 0.090 for Montmorency (Table 1). The date of 50% defoliation ranged from day 223 for Krassa Severa to day 250 for IR 587-1. AUDPC was highest for Krassa Severa (4994) and lowest for Yellow Glass (2716). Most cultivars with low AUDPCs also had low defoliation rates and later dates of 50% defoliation. Simple correlations between AUDPCs and defoliation rate ( $r = 0.743$ ) or date of 50% defoliation ( $r = -0.986$ ) were highly significant ( $P = <0.01$ ). Infection rate and AUIPC were poorly correlated but the date of 50% infection was significantly correlated with AUDPC ( $r = -0.426$ ,  $P = 0.05$ ). Some cultivars that were highly susceptible to infection were among the most resistant to defoliation, and vice versa (Table 1). For example, Schmidt had the highest AUIPC but one of the lowest AUDPCs.

**Greenhouse experiments.** In experiment 1, analysis of variance revealed that the infection frequency 6 days after inoculation, lesion size, and number of conidia per lesion (and per square centimeter of leaf area at inoculation) differed significantly among the eight cultivars (Table 2). Montmorency and English Morello sour cherry had about 2.8 times more lesions per square centimeter of leaf tissue than Kansas Sweet and SHT-3 duke cherry. Lesions on Meteor, Montmorency, English Morello, and Early Richmond sour cherry were 5.3, 2.5, 2.3, and 2.2 times larger, respectively, than lesions on Kansas Sweet duke cherry. Twenty days after inoculation, each lesion on Meteor contained 1.15 times and each lesion on Early Richmond and Montmorency contained 1.08 times

the number of conidia produced per lesion on SHT-2. The number of spores per lesion and lesion size were correlated ( $r = 0.76$ ,  $P = 0.01$ ).

In experiment 2, the infection efficiency for the 20 cultivars ranged from 0.48% for Brassington Duke to 1.51% for Governor Wood (Table 3). Differences among cultivars and among species in the number of days required for 50% of the lesions to develop were highly significant (Table 3). Depending on the age of the leaves at inoculation, lesions developed 2-4 days later on sweet cherry than on sour cherry (Fig. 2). Also, the rate of lesion appearance was significantly slower ( $P = 0.01$ ) for cultivars of sweet cherry (0.44 lesions per day) than for cultivars of sour and duke cherry (0.75 and 0.65 lesions per day, respectively). The rate of lesion appearance decreased linearly with increasing leaf age when averaged over all cultivars. Lesions developed sooner on Early Richmond, English Morello, Meteor, and Montmorency sour cherries than on North Star sour cherry or on any of the sweet cherry varieties. Lesion size 36 days after inoculation was significantly smaller ( $P = 0.01$ ) on leaves of sweet cherry (0.22 mm<sup>2</sup>) than on leaves of duke (0.88 mm<sup>2</sup>) and sour (1.24 mm<sup>2</sup>) cherry, and lesions on duke cherry were significantly smaller than those on sour cherry.

Large differences were observed among cultivars in conidial production per lesion on each sampling date (Table 3). Conidial production per lesion was significantly lower ( $P = 0.01$ ) on cultivars of sweet cherry than on cultivars of duke and sour cherry, and it was lower on cultivars of duke cherry than on cultivars of sour cherry (Fig. 3). North Star was an

**Table 2.** Reaction of sour and duke cherry cultivars to infection by *Coccomyces hiemalis* isolate B in the greenhouse, experiment 1

Cultivar <sup>u</sup> or source	Infection frequency <sup>v</sup>				Sporulation	
	6 Days (lesions per cm <sup>2</sup> )	16 Days (lesions per cm <sup>2</sup> )	Proportion of lesions <sup>w</sup> (no.)	Lesion size (mm <sup>2</sup> )	Conidia per lesion (log)	Conidia per cm <sup>2</sup> (log) <sup>x</sup>
Sour cherry						
Early Richmond	1.86 bc <sup>y</sup>	2.58	0.774 a	0.62 b	4.77 ab	5.08 abc
English Morello	3.76 a	5.44	0.673 a	0.64 b	4.68 bc	5.37 ab
Meteor	1.76 bc	2.45	0.703 a	1.49 a	5.05 a	5.41 a
Montmorency	3.77 a	5.00	0.807 a	0.70 b	4.77 ab	5.37 ab
North Star	3.36 ab	5.29	0.624 a	0.33 cd	4.44 bc	5.07 abc
SHT-2	2.44 abc	5.37	0.345 b	0.30 cd	4.38 c	4.95 bc
Duke cherry						
Kansas Sweet	1.15 c	1.96	0.563 ab	0.28 d	4.47 bc	4.68 c
SHT-3	1.32 c	2.25	0.546 ab	0.46 bc	4.55 bc	4.76 c
<b>Significance of F test from analysis of variance</b>						
Cultivar (C)	0.01	ns <sup>z</sup>	0.05	0.01	0.01	0.01
Leaf age (LA)	ns	ns	ns	0.05	0.01	ns
C × LA	ns	ns	ns	0.05	0.01	0.01

<sup>u</sup> Mean of three single-tree replications averaged over four leaf ages.

<sup>v</sup> Lesions 6 and 16 days after inoculation per square centimeter of leaf area measured at inoculation. Differences in lesion frequency among cultivars on day 16 were not significant at  $P = 0.05$ .

<sup>w</sup> Number of lesions 6 days after inoculation divided by the number 16 days after inoculation.

<sup>x</sup> Conidia per square centimeter of leaf area measured at inoculation.

<sup>y</sup> Mean separation within columns by Duncan's multiple range test,  $P = 0.05$ .

<sup>z</sup> ns = Not significant.

**Table 3.** Reaction of sweet, sour, and duke cherry cultivars to infection by *Coccomyces hiemalis* isolate B in the greenhouse, experiment 2

Cultivar <sup>1</sup>	Infection efficiency <sup>2</sup> (%)	Development of 50% of lesions <sup>3</sup> (days)	Rate of lesion appearance <sup>4</sup>	Lesion size (mm <sup>2</sup> )	Conidia per lesion (log)			Reproductive efficiency (log) <sup>7</sup>
					9 Days <sup>5</sup>	18 Days	36 Days	
<b>Sweet cherry</b>								
Angela	0.67 de <sup>2</sup>	9.88 g	0.37 de	0.20 hijk	2.05 de	2.63 fg	3.14 ghi	0.74 hi
Black Tartarian	0.89 cde	7.34 ef	0.43 de	0.18 ijk	2.27 bcd	2.62 fg	2.77 hi	0.55 ij
Emperor Francis	0.72 de	7.56 f	0.43 de	0.14 jk	2.52 abcd	2.88 ef	2.96 hi	0.57 ij
Governor Wood	1.51 a	7.56 f	0.47 de	0.27 hij	2.24 bcde	2.71 fg	2.87 hi	0.84 hi
Hedelfingen	0.71 de	5.93 cde	0.53 cd	0.26 hij	2.60 abcd	3.17 de	3.46 fg	0.83 hi
Lambert	0.83 cde	6.67 def	0.51 cd	0.33 ghi	2.62 abcd	3.15 def	3.46 fg	1.15 gh
Napoleon	1.10 abcd	7.16 ef	0.54 cd	0.31 ghi	2.43 abcd	3.24 cde	3.48 fg	1.18 gh
Schmidt	0.68 de	9.96 g	0.24 e	0.13 k	1.57 ef	2.34 g	2.69 i	0.20 j
Windsor	1.10 abcd	7.03 ef	0.35 de	0.18 ijk	2.17 cde	2.58 fg	2.80 hi	0.74 hi
Yellow Glass	0.87 cde	6.46 def	0.49 de	0.28 ghi	2.22 bcde	2.87 ef	3.19 gh	0.88 hi
<b>Sour cherry</b>								
Early Richmond	0.92 bcde	4.32 a	0.88 a	1.81 ab	2.89 ab	3.88 a	4.99 a	2.79 ab
English Morello	0.93 bcde	5.03 abc	0.83 a	1.01 bcd	2.98 a	3.61 abc	4.52 bcd	2.27 cd
Meteor	1.40 ab	4.23 a	0.82 a	2.36 a	2.91 ab	3.67 ab	4.81 abc	2.90 a
Montmorency	0.95 bcde	4.63 ab	0.74 abc	1.32 abc	2.90 ab	3.86 a	4.86 ab	2.57 abc
North Star	0.88 cde	5.43 bcd	0.49 de	0.51 efg	1.98 de	3.17 de	3.91 e	1.75 ef
<b>Duke cherry</b>								
Brassington Duke	0.48 e	6.59 def	0.57 bcd	0.68 def	2.17 cde	3.42 bcd	4.33 d	1.89 def
Kansas Sweet	0.77 cde	5.84 cde	0.57 bcd	0.78 cde	2.05 de	3.45 bcd	4.41 cd	2.16 cde
Krassa Severa	1.24 abc	4.30 a	0.88 a	1.95 a	3.08 a	3.81 ab	4.97 a	2.84 ab
May Duke	0.89 cde	6.76 def	0.42 de	0.39 fgh	1.25 f	2.76 f	3.69 ef	1.48 fg
Wczesna Z Prin	0.69 de	4.77 ab	0.79 ab	0.90 cde	2.80 abc	3.85 a	4.80 abc	2.41 bc

<sup>1</sup> Mean of four single-tree replications averaged over three leaf ages.

<sup>2</sup> Number of lesions per leaf 36 days after inoculation divided by number of viable conidia applied to each per leaf ( $\times 100$ ).

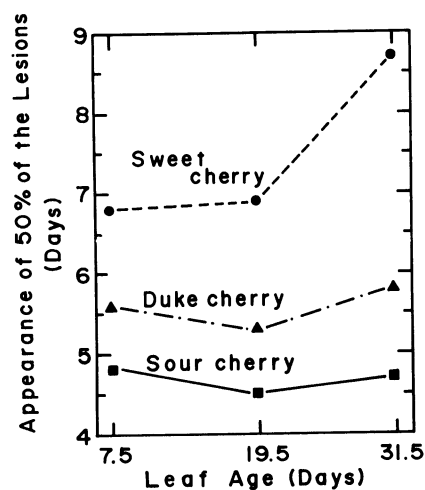
<sup>3</sup> Estimated from asymptotic regression of proportion of total lesions against days after inoculation.

<sup>4</sup> Slope of asymptotic regression.

<sup>5</sup> Number of days after inoculation.

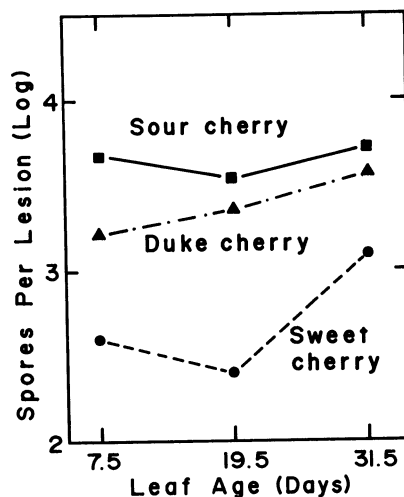
<sup>6</sup> Ratio of total number of conidia per leaf 36 days after inoculation compared with number of conidia applied at inoculation.

<sup>7</sup> Mean separation within columns by Duncan's multiple range test,  $P = 0.05$ .



**Fig. 2.** The number of days after inoculation required for 50% of the lesions to appear in relation to the age of the leaves when inoculated with conidia of *Coccomyces hiemalis* isolate B. The data are the mean of four single tree replicates per cultivar and are pooled across 10 sweet, 5 sour, and 5 duke cherry cultivars.

exception to this relationship. Regardless of leaf age, the number of conidia per lesion was significantly less for North Star than those for the other cultivars of sour cherry (Table 3). Reproductive efficiency (ratio of conidia produced to conidia applied as inoculum) differed greatly among the three species 36 days after inoculation. The average repro-



**Fig. 3.** Relationship of spores produced per lesion to days after inoculation for three leaf ages in groups of cultivars of three *Prunus* spp. inoculated with *Coccomyces hiemalis*.

ductive efficiency for sweet cherries (5.84) was significantly less ( $P = 0.01$ ) than that for sour and duke cherries, and the average reproductive efficiency for sour cherries (285.23) was significantly greater ( $P = 0.01$ ) than that for duke cherries (142.25). Among sour cherries, the reproductive efficiency was much less for North Star than for other cultivars.

There was a high correlation between the AUDPCs measured in the field and five of the six factors measured in

greenhouse experiment 2 (Table 4). Infection efficiency was the only factor that was not correlated with AUDPC. None of the correlations between AUIPC measured in the field and six factors measured in the greenhouse was significant.

## DISCUSSION

Although earlier researchers established that cultivated cherry was susceptible to cherry leaf spot (5,6), little information was available on the relative susceptibility of the main cherry cultivars grown in the Great Lakes region. Evaluations in both field and greenhouse conditions have demonstrated the partial resistance of sweet cherry, compared with sour cherry, to leaf spot. Most cultivars of sweet cherry had lower AUDPCs in the field and longer latent periods, smaller lesions, and reduced sporulation in the greenhouse than cultivars of sour cherry. The partial resistance of sweet cherry to leaf spot may be why it is easier for growers to control leaf spot with fungicides on sweet cherries than on Montmorency sour cherry (A. L. Jones, unpublished). Furthermore, this study indicates that Schmidt, and possibly Hedelfingen and Yellow Glass, may be useful as standards for judging the resistance of cherry selections to leaf spot. Selections with smaller lesions, longer latent periods, and slight sporulation 36 days after inoculation may be useful as sources of resistance to cherry leaf spot.

**Table 4.** Correlations of resistance factors measured in the greenhouse following inoculation with *Coccomyces hiemalis* with resistance factors measured in the field for 19 cherry cultivars<sup>u</sup>

Greenhouse resistance factors <sup>v</sup>	Field resistance factors <sup>w</sup>	
	Infection severity (AUIPC)	Defoliation severity (AUDPC)
Infection efficiency	0.099 ns <sup>x</sup>	0.313 ns
Days to 50% of lesions visible	0.091 ns	0.704**
Rate of lesion appearance	0.261 ns	0.789**
Log <sub>10</sub> (lesion size)	0.359 ns	0.808**
Log <sub>10</sub> (conidia per lesion) <sup>y</sup>	0.231 ns	0.782**
Log <sub>10</sub> (reproductive efficiency) <sup>z</sup>	0.191 ns	0.815**

<sup>u</sup>Correlations included each cultivar in experiment 2 except Angela.

<sup>v</sup>Mean of four replications over three leaf ages for each cultivar.

<sup>w</sup>Mean of five replications for each cultivar.

<sup>x</sup>Correlation coefficient (*r*): ns = not significant at *P* = 0.05, \*\* = significant at *P* = 0.01.

<sup>y</sup>Total number of conidia per lesion 36 days after inoculation.

<sup>z</sup>Thirty-six days after inoculation.

The susceptibility of cherry cultivars to *C. hiemalis* may differ between regions. Isolates from other species of *Prunus* have varied in host range in cross-inoculation tests (5,8). More information is needed on possible physiological specialization in *C. hiemalis*.

The failure of a few seedlings in a seedling nursery to defoliate in an epidemic year was not a reliable indicator of inherent resistance to leaf spot. Two selections (SHT-2 and SHT-3) showed apparent resistance to defoliation in a seedling block, but the selections were susceptible when propagated on mahaleb rootstocks and inoculated with *C.*

*hiemalis*. This illustrates that seedlings should be retested to verify possible resistance. The apparent resistance of these two seedlings may be related to their low vigor as seedlings vs. their high vigor when propagated on rootstocks.

The need for increased resistance to *C. hiemalis* is especially important in sour cherry. The sour cherry industry in the Great Lakes region is based almost exclusively on the cultivar Montmorency. Montmorency was very susceptible to defoliation in this study, but the sour cherry cultivar North Star was much less susceptible to leaf spot. Although North Star was readily infected by *C. hiemalis*,

the fungus did not sporulate as profusely and defoliation was less severe than in the other sour cherries. Sour cherry cultivars with partial resistance to leaf spot would need fewer protective fungicide treatments to minimize leaf spot infection and subsequent defoliation.

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#### LITERATURE CITED

- Berger, R. D. 1981. Comparison of the Gompertz and logistic equations to describe plant disease progress. *Phytopathology* 71:716-719.
- Dutton, W. C., and Wells, H. M. 1925. Cherry leaf spot residual effects and control. *Mich. State Univ. Agric. Exp. Stn. Spec. Bull.* 147. 15 pp.
- Eisensmith, S. P., and Jones, A. L. 1981. A model for detecting infection periods of *Coccomyces hiemalis* on sour cherry. *Phytopathology* 71:728-732.
- Howell, G. S., and Stackhouse, S. S. 1973. The effect of defoliation time on acclimation and dehardening in tart cherry (*Prunus cerasus* L.). *J. Am. Soc. Hortic. Sci.* 98:132-136.
- Keitt, G. W. 1918. Inoculation experiments with species of *Coccomyces* from stone fruits. *J. Agric. Res.* 13:539-569.
- Keitt, G. W., Blodgett, E. C., Wilson, E. E., and Magie, R. O. 1937. The epidemiology and control of cherry leaf spot. *Univ. Wisc. Agric. Exp. Stn. Res. Bull.* 132. 117 pp.
- Little, T. M., and Hills, F. J. 1978. *Agricultural Experimentation*. John Wiley & Sons, New York. 350 pp.
- Magie, R. O. 1935. Variability of monosporic cultures of *Coccomyces hiemalis*. *Phytopathology* 25:131-159.
- Schein, R. D. 1964. Design, performance and use of a quantitative inoculator. *Phytopathology* 54:509-513.