

## Effect of Weather Variables on Strawberry Leather Rot Epidemics

K. M. Reynolds, L. V. Madden, and M. A. Ellis

Former postdoctoral research associate and associate professors, respectively, Department of Plant Pathology, The Ohio State University (OSU), Ohio Agricultural Research and Development Center (OARDC), Wooster 44691. Current address of the senior author: Forest Sciences Laboratory, USDA Forest Service, Anchorage, AK 99501.

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### ABSTRACT

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Epidemic development of strawberry leather rot, caused by *Phytophthora cactorum*, which is spread by rain splash dispersal, was monitored in six field plots in 1986 and eight in 1987. Each plot was 2 m long and three rows wide. In 1986, straw mulch was removed from the interior aisles in three plots (nonstraw plots) and left on the two exterior aisles, and no straw was removed from the remaining three plots (straw plots). In 1987, straw was removed from the interior aisles of six of the eight plots. Plots were infested in mid-May with strawberry fruit on which *P. cactorum* was sporulating. Assessments of incidence of cyme infection (i.e., proportion of tagged cymes with one or more infected fruit) on each side of each aisle were made 5 days after each rain event on the nonstraw plots, whereas assessments in the straw plots were only made on the last assessment date in both years. By early June 1986, cyme infection was

>60% in all but two of the interior aisles and <10% in both of the exterior aisles in the nonstraw plots and the straw plots. Incidence of cyme infection in 1987 in the straw and nonstraw was similar to that observed in the respective plot types in 1986. Regression analyses were used to examine the relationship between change in logit of cyme infection incidence, rainfall, and either selected weather variables or indices derived from the selected weather variables. Both the weather variables and the indices were calculated for the sporulation period immediately preceding a rain event and for the infection period immediately following a rain event. Stepwise regressions using the weather variables always yielded predictive models that differed significantly between years, whereas regressions using indices for sporulation, infection, and dispersal yielded a common model for the 2 yr.

*Additional keywords:* disease prediction, *Fragaria* × *ananassa*, quantitative epidemiology.

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Leather rot of strawberries (*Fragaria* × *ananassa* Duch.), caused by *Phytophthora cactorum* (Leb. & Cohn) Schroet, can cause major commercial crop losses under spring weather conditions that commonly occur in north central Ohio (3). Rose (23) first identified the causal organism and observed that epidemic development of leather rot was closely associated with rainfall episodes. Grove et al (12) demonstrated that propagules of *P. cactorum* were effectively dispersed by the impact of water drops on infected fruit. Epidemic development of numerous fungal and bacterial diseases is known to depend on splash dispersal (4,6,18). Field studies of splash dispersal have often established the relationship between spread of a pathogen and the occurrence of

rain episodes (7,8,13,14,20,23,25,27,28), but relatively few have attempted to predict epidemic development as a function of weather factors (4,24).

Grove et al (11) developed a model for sporulation of *P. cactorum* on infected strawberry fruit based on ambient air temperature and duration of surface wetness of fruit. A similar model was also developed to describe incidence of fruit infection in terms of the same weather variables (10). The influence of weather variables, or indices derived from these weather variables (10,11), on subsequent development of leather rot epidemics was examined in this work. The effect of applying straw mulch to crop aisles was also evaluated, because previous field observations suggested that mulch applications might be effective in limiting leather rot development (Ellis and Madden, *unpublished*).

## MATERIALS AND METHODS

**Plot establishment.** Plots were established in a commercial strawberry (cv. Early Glow) field near Wooster, OH, during early May 1986 and 1987 before flowering. Each plot was 2 m long and three rows wide. Distance between rows was 50 cm. (These areas are referred to as aisles.) Plots consisted of four aisles separated by three crop rows. On each side of a row, up to 50 flower cymes closest to the adjacent inter-row aisle were tagged, providing six sides of rows with a total of about 300 tagged cymes. Straw mulch was removed from the two interior aisles of randomly selected plots (hereafter called nonstraw plots). Additional mulch was applied to the exterior aisles of the nonstraw plots and to all aisles of the remaining plots to provide a total straw depth of 8–10 cm. Six plots were established in 1986, and the mulch treatment was randomly assigned to one plot in each of three pairs of plots. Eight plots were established in 1987, and the mulch treatment was randomly assigned to one plot in each set of four. Note that in the nonstraw plots, each internal aisle was bordered by one side of two separate rows bearing tagged cymes, but that each external aisle was bordered by only one side of a row with tagged cymes.

**Plot infestation.** Infected strawberry fruit on which *P. cactorum* was actively sporulating were prepared as described previously (21). Plots were infested on day 135 in 1986 and day 140 in 1987 by placing five infected fruit at the south end of each plot in each of the two interior aisles. In 1986, all three nonstraw plots showed evidence of fruit infection in the plant canopy by day 140, whereas no infection was observed in the straw plots by the same date. Because the rationale for including a straw plot treatment was to test the effectiveness of straw in limiting infection of fruit from both soil inoculum and established disease foci within the plant canopy, inoculum was reintroduced to the straw plots on day 140.

**Disease assessment.** Assessments of leather rot development were performed 5 days after the start of each rain period in the nonstraw plots, because previous studies indicated that latent periods could be expected to vary from 3 to 5 days under ambient air temperature and moisture conditions (10,11,21). Initially, straw plots in 1986 were assessed on the same schedule as the nonstraw plots. However, the very low levels of disease incidence (*DI*), and infrequent changes in *DI*, observed in the straw plots provided insufficient data for model fitting, so disease assessment on these plots was discontinued after the first three assessments. A final assessment of *DI* in the 1986 straw plots was made at the time of the final nonstraw plot assessment. Straw plots were only evaluated at the nonstraw final assessment in 1987.

At each assessment, the number of tagged cymes bearing at least one symptomatic fruit on each side of an aisle was recorded. (For brevity, we refer to cymes bearing infected fruit as infected cymes, but it should be noted that *P. cactorum* infects fruit). In 1987, none of the outer, straw-covered aisles of any plots were assessed for leather rot, because results of the 1986 study clearly indicated that disease development in these aisles did not differ from that of the straw plots. Infection data were summarized as the proportion of tagged cymes in a plot bearing at least one infected fruit that exhibited typical leather rot symptoms (23).

**Environmental monitoring.** Environmental data were collected with a micrologger (model CR-21, Campbell Scientific, Logan, UT). Air temperature and RH were monitored at 1-min intervals with a sensor (model 201, Phys-Chemical Research Corp., New York, NY) located in an aspirated shelter (2) at canopy height (30 cm) and recorded for an hourly average. Total rainfall in each 15-min period was recorded with a tipping-bucket rain gauge (model RG2501, Sierra-Misco, Inc., Berkeley, CA) placed between the strawberry rows.

The fraction of each hour that fruit were wet was estimated with a wetness sensor (model 231, Campbell Scientific), which had been coated with two layers of white latex paint (5). The wetness sensor was calibrated by spraying 10 fruit to runoff with deionized water, and the wet/dry cutoff point was selected as the sensor voltage output at which 50% water loss from fruit surfaces due to evaporation had occurred as determined by weight. The calibration procedure was repeated six times.

Weather data were summarized for each rain period. Variables derived from the weather data were categorized as primarily affecting either sporulation (*S*), dispersal (*D*), or infection (*I*), based on previous studies (10,11,21,22). Variables relevant to *S* were the number of hours in the 24-hr period immediately preceding the start of a rain event in which the leaf wetness sensor was wet (*S*<sub>1</sub>) and mean air temperature (*C*) (*S*<sub>2</sub>) during hours in which surface wetness was recorded. A sporulation index (*S*<sub>3</sub>) that incorporated *S*<sub>1</sub> and *S*<sub>2</sub> was calculated using equation 3 in Grove et al (11). Predicted sporulation from Grove et al (11) was divided by 600 to produce an index that varied from 0 to 1 (*S*<sub>3</sub>). Variables relevant to *D* were total rainfall amount (mm) in a rain period (*D*<sub>1</sub>), total length of the rain period (hr) (*D*<sub>2</sub>), mean rainfall intensity (mm hr<sup>-1</sup>) (*D*<sub>3</sub>), and maximum rainfall intensity (mm hr<sup>-1</sup>) during any 15-min interval during a rain event (*D*<sub>4</sub>). Based on previous work (22), an index of rainfall amount was also derived (*D*<sub>5</sub>) that was defined as  $D_5 = 1 - \exp(-0.07 D_1)$ . Note that *D*<sub>5</sub> equals 0.5 when *D*<sub>1</sub> equals 10 mm. Variables relevant to *I* were number of consecutive hours from the start of a rain period in which the leaf wetness sensor was wet for at least half of the hour (*I*<sub>1</sub>) and mean air temperature (*C*) during the latter time interval (*I*<sub>2</sub>). An infection index that incorporated the latter temperature and wetness data also was derived (*I*<sub>3</sub>) based on equation 7 in Grove et al (10). Codes identifying the weather and index variables are summarized in Table 1.

In addition to the index variables *S*<sub>3</sub>, *D*<sub>5</sub>, and *I*<sub>3</sub> defined above, an additional index variable related to weather conditions before sporulation (*P*) was included. *P* was defined as a weighted sum of mean hourly air temperature. Weights consisted of the fraction of each hour that fruit surfaces were recorded as wet for the 72-hr period before the start of a sporulation period. To be consistent with the other index variables, the calculated values of *P* were scaled by dividing the sum of products by 1,440 degree-hr (= 72 hr of continuous surface wetness at 20 °C). Note that, from the definitions of *P* and *S* (Table 1), *P* was computed for the time interval commencing at 96 hr before a rain event and ending at 25 hr before a rain event.

**Data analyses.** A rain event was defined as any 1-hr period in which at least 1 mm of rainfall was recorded. Two or more rain events were considered to belong to a single rain period if the time between the end of one event and the start of the next was <12 hr and fruit surfaces were recorded as being continuously wet in the interim. Thus, a rain period was considered terminated if a rain event in the period was followed by either a time interval greater than 12 hr during which no rain fell (but continuous surface wetness may have been recorded) or a 12-hr interval during which

TABLE 1. Definitions of derived weather variables and indices based on weather variables

Variable name	Description
<i>D</i> <sub>1</sub>	Total amount of rainfall (mm) received during a rain event.
<i>D</i> <sub>2</sub>	Total length of a rain event (hr).
<i>D</i> <sub>3</sub>	Mean rainfall intensity for a rain event (mm hr <sup>-1</sup> ).
<i>D</i> <sub>4</sub>	Maximum rainfall intensity for any 15-min period during a rain event.
<i>D</i> <sub>5</sub>	Dispersal index derived from <i>D</i> <sub>1</sub> (22).
<i>I</i> <sub>1</sub>	Number of consecutive hr from the start of a rain event during which fruit surfaces were recorded as being wet for at least 30 min in each hour.
<i>I</i> <sub>2</sub>	Mean hourly air temperature (°C) during wetness period <i>I</i> <sub>1</sub> .
<i>I</i> <sub>3</sub>	Infection index derived from <i>I</i> <sub>1</sub> and <i>I</i> <sub>2</sub> (10).
<i>P</i>	Weighted summation of hourly air temperature (°C) in the 72-hr period preceding a sporulation period. Temperature readings were weighted by the fraction of the hr that fruit surfaces were recorded as being wet.
<i>S</i> <sub>1</sub>	Sum of wetness periods for the 24-hr period preceding a rain event (hr).
<i>S</i> <sub>2</sub>	Mean hourly air temperature (°C) during wetness periods in the 24-hr period preceding a rain event.
<i>S</i> <sub>3</sub>	Sporulation index derived from <i>S</i> <sub>1</sub> and <i>S</i> <sub>2</sub> (11), and scaled by 600, in the 24-hr period preceding a rain event.

continuous surface wetness was not recorded. Occasionally, a rain period as defined above was followed by an additional rain period within a 12-hr period, but fruit surfaces were recorded as being dry in the interim. Because the time interval between a pair of such rain periods was not sufficient for a new cycle of infection, colonization, and sporulation to be completed (10,11), only that period for which the product of  $S_3$ ,  $D_3$ , and  $I_3$  was greatest was retained for analysis. Inoculum for plot infestation was placed in the field immediately before the start of the first rain period in both years. Therefore, observations related to the first rain event in both years also were excluded from analysis, because  $S_1$ ,  $S_2$ , and  $S_3$  were computed for the 24-hr period before the start of a rain event (Table 1).

$DI$  was transformed to logits to provide an additive disease response scale and correct for multiple infections (16). In regression analyses, change in logit  $DI$  ( $CLDI$ ) was used as the dependent variable in order to describe disease increase as a function of weather variables. In addition to the variables listed in Table 1, their two- and three-way interaction products were assessed as predictors. Regressions analysis was performed using either weather variables or index variables as predictors of  $CLDI$ . Models selected from all-possible-subsets stepwise regression analysis were subsequently analyzed to test for differences in regression results between years (1,19). Selected models were evaluated by calculating residuals and deleted residuals, and plotting these versus predicted  $CLDI$ . A deleted residual is the difference between the observed and predicted dependent variable obtained if the observation (dependent and independent variables) was not used in estimating the model parameters (17,19). In addition to determining if an acceptable model was chosen, deleted residuals are used to identify highly influential observations and to partially validate model results. Residuals were used to calculate the coefficient of determination ( $R^2$ ) and  $R^2$  adjusted for degrees of freedom ( $R_a^2$ ) for each model. An additional  $R^2$ , based on the so-called PRESS statistic (17) from the deleted residuals, was calculated for each model and labeled as  $R_p^2$ .

## RESULTS

The general pattern of disease progress was similar both among plots within years and between years (Figs. 1 and 2). In 1986, mean disease incidence in the interior aisles of the three nonstraw plots was 90.9, 72.0, and 61.5% by the final assessment on day 159. In contrast, leather rot development in the exterior (straw-covered) aisles in these same plots only averaged 8.1, 6.0, and 6.3%, respectively, on the same date. Final mean disease incidence values for the interior aisles in the 1987 nonstraw plots were 83.0, 73.3, 80.2, 85.2, 79.5, and 65.7% on day 159 (Fig. 2). Disease incidence at the final assessment was very low in all straw plots in both years and never exceeded 10%. In the straw plots of 1987, final disease incidence was 1.3 and 6.2%. The straw plot data were not analyzed further because of the low levels of  $DI$  and infrequent changes in  $DI$  that resulted in a predominance of zero-valued observations in terms of  $CLDI$ . For subsequent regression analyses of disease progress in the nonstraw plots, mean plot  $DI$  was calculated for each assessment using only  $DI$  values for the four sides of rows adjacent to the interior aisles of a plot (Figs. 1 and 2).

A total of 16 rain events was recorded in 1986, and these occurred in 10 distinct periods (Table 2). Only eight rain events were recorded in 1987, representing six distinct periods (Table 3). A total of 126 mm of rain was received in 1986 (mean = 12.6 mm per rain period) compared with a total of 45 mm in 1987 (mean = 7.5 mm per rain period). Despite these substantial differences in rainfall history, disease progress was similar between years (Figs. 1 and 2).

Diurnal patterns of mean hourly air temperature fluctuation were also similar between years, but daily maxima were slightly higher in 1987 (Figs. 1 and 2). The latter differences in air temperature between years were reflected in generally higher values for both  $S_2$  and  $I_2$  in 1987 (Table 3) compared with 1986 (Table 2).  $S_3$  never approached its maximum value of 1 (which

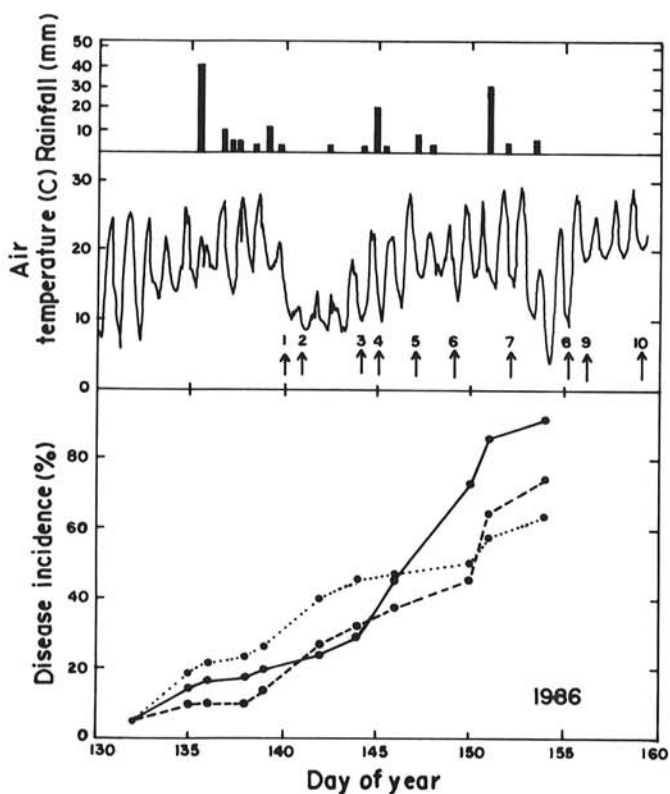


Fig. 1. Leather rot epidemic development in plots from which straw had been removed, total rainfall recorded per rain period, and mean hourly air temperature in 1986. Numbered arrows indicate the date and order of disease assessment, 5 days after the start of a rain period. Disease incidence means are positioned at the start of the rain events, not at the time of assessment.

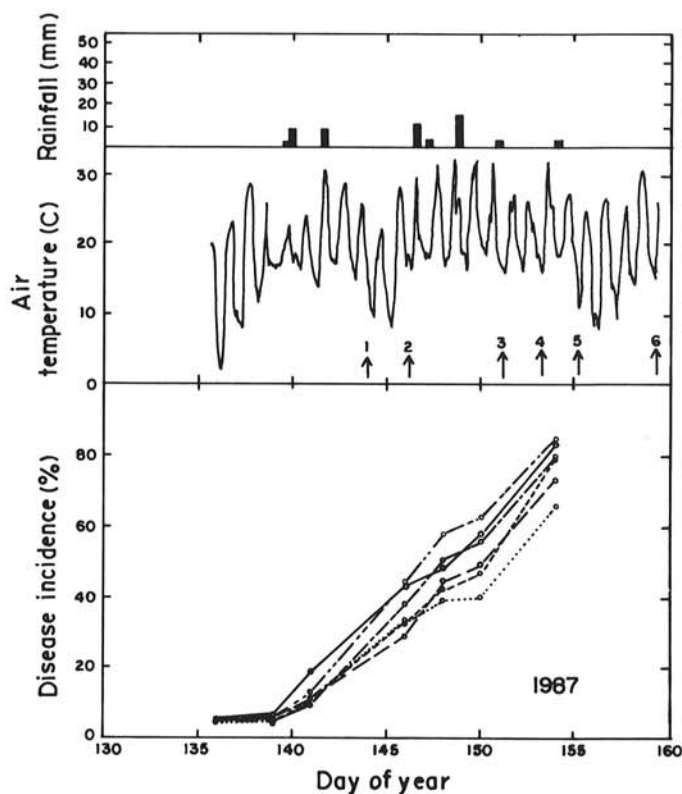


Fig. 2. Leather rot epidemic development in plots from which straw had been removed, total rainfall recorded per rain period, and mean hourly air temperature in 1987. Numbered arrows indicate the date and order of disease assessment, 5 days after the start of a rain period. Disease incidence means are positioned at the start of the rain events, not at the time of assessment.



represents ideal conditions for sporulation), attaining maxima of 0.27 and 0.32 in 1986 and 1987, respectively (Tables 2 and 3). In contrast, weather conditions for infection by *P. cactorum*, as indicated by  $I_3$ , were almost always optimal in both years (Tables 2 and 3). In fact,  $I_3$  was  $<1$  for only one of the 14 rain events that were included in subsequent analyses.

An analysis using all weather and index variables simultaneously could not be performed, because inclusion of both sets of variables in a single analysis resulted in an overspecified (singular) correlation matrix. In the stepwise regression of *CLDI* on the weather variables, the best combination of predictors included  $S_1$ ,  $D_1$ ,  $I_1$ ,  $I_2$ , and the square of  $I_2$  (Tables 2 and 3). The model for combined years accounted for 48% of the experimental variation ( $P[F=11.86] < 0.0001$ ). All estimated parameters were significant

( $P=0.01$ ). However, in the regression procedure used to assess the significance of a difference in models between years, the above set of variables proved unsatisfactory. Tolerance conditions in the regression procedure forced the automatic elimination of one variable in both the reduced model (one equation for both years) and the full model (separate equations by year). Moreover, the model for each year contained a different subset of the independent variables, with frequent differences among signs for the regression coefficients that were common to any given pair of the three models. Various alternative sets of independent variables were tried subsequently with the same result.

The regression of *CLDI* on index variables (Tables 2 and 3) proved to be far superior to that based on weather variables. Because  $I_3$  was virtually constant in this study, it was excluded

TABLE 2. Summary of selected weather and index variables<sup>a</sup> for each rain period in 1986<sup>b</sup>

Rain period sequence <sup>c</sup>	Day of year	$D_1$ (mm)	$D_5$	$P$ (C-hr)	$S_1$ (hr)	$S_2$ (C)	$S_3$	$I_1$ (hr)	$I_2$ (C)	$I_3$
1	135	41	0.94	0.60	...	...	...	12.0	18.4	1.00
*2a	136	10	0.50	0.44	13.5	20.8	0.20	10.9	15.9	1.00
2b	136	5	0.29	0.56	2.6	18.2	0.03	12.4	20.0	1.00
2c	137	5	0.29	0.56	13.5	20.0	0.20	1.3	22.7	0.77
3a	138	1	0.07	0.57	3.1	22.8	0.04	12.2	22.1	1.00
*3b	138	12	0.57	0.57	14.7	21.4	0.23	8.7	17.4	1.00
*4	139	2	0.13	0.53	12.0	12.7	0.02	13.7	18.4	1.00
*5	142	2	0.13	0.50	15.3	10.3	0.01	8.3	10.9	1.00
6a	144	1	0.07	0.39	18.3	13.2	0.07	2.0	13.4	0.67
*6b	144	19	0.74	0.38	15.3	15.1	0.10	11.2	12.8	1.00
6c	145	1	0.07	0.40	14.5	16.1	0.12	1.9	14.4	0.72
7a	146	8	0.43	0.36	8.1	19.5	0.08	12.9	16.3	1.00
*7b	146	3	0.19	0.30	16.5	18.3	0.27	12.0	17.3	1.00
*8	150	30	0.88	0.57	12.4	20.8	0.17	10.2	16.9	1.00
*9	151	4	0.24	0.56	13.9	21.0	0.21	11.6	16.7	1.00
*10	154	5	0.29	0.44	3.6	11.7	0.00	6.8	7.0	0.76

<sup>a</sup> Weather variables and indices are defined in Table 1.

<sup>b</sup> Assessments of disease incidence were performed 5 days after a rain period.

<sup>c</sup> The event in a sequence preceded by \* was included in analysis based on the product  $S_3D_5I_3$ .

TABLE 3. Summary of selected weather and index variables<sup>a</sup> for each rain period in 1987<sup>b</sup>

Rain event sequence <sup>c</sup>	Day of year	$D_1$ (mm)	$D_5$	$P$	$S_1$ (hr)	$S_2$ (C)	$S_3$	$I_1$ (hr)	$I_2$ (C)	$I_3$
1a	139	1	0.07	0.07	...	...	...	1.0	20.9	0.68
1b	139	8	0.43	0.13	...	...	...	10.6	18.2	1.00
*2	141	8	0.43	0.48	8.4	21.3	0.09	11.2	17.9	1.00
*3a	146	10	0.50	0.08	3.6	21.6	0.04	11.5	19.8	1.00
3b	146	1	0.07	0.05	16.6	20.7	0.32	1.0	18.1	0.62
*4	148	16	0.67	0.32	9.0	23.1	0.08	10.9	18.8	1.00
*5	150	1	0.07	0.48	15.2	22.8	0.21	12.0	17.0	1.00
*6	153	2	0.13	0.34	12.4	22.4	0.15	9.8	18.5	1.00

<sup>a</sup> Weather variables and indices are defined in Table 1.

<sup>b</sup> Assessments of disease incidence were performed 5 days after a rain period.

<sup>c</sup> The event in a sequence preceded by \* was included in analysis based on the product  $S_3D_5I_3$ .

TABLE 4. Regression results for predicting increase in logit of leather rot incidence in 1986 and 1987

Year	Observations	Coefficient for: <sup>a</sup>			$MSE^b$	$R^2^b$	$R_a^2^c$	$R_p^2^d$	$F^e$	df <sup>f</sup>	Significance
		$D_5$	$S_3D_5$	$S_3P$							
1986	27	1.4	-13.2	8.4	0.06	0.69	0.66	0.63	17.7	3,24	$<0.001$
1987	30	3.3	-29.5	8.2	0.31	0.70	0.67	0.65	21.2	3,27	$<0.001$
Both	57	2.2	-15.8	7.2	0.22	0.65	0.63	0.60	33.2	3,54	$<0.001$
Difference					0.21				1.8	3,51	0.16

<sup>a</sup> Mean square error.

<sup>b</sup> Coefficient of determination.

<sup>c</sup> Coefficient of determination adjusted for degrees of freedom.

<sup>d</sup> Coefficient of determination based on deleted residuals.

<sup>e</sup> F-statistic for significance of regression equation.

<sup>f</sup> Degrees of freedom.

<sup>g</sup> See Table 1 for description of variables.

from consideration in the stepwise regression analysis. The reduced model for combined years had an  $R^2$  of 0.65 and an  $R_a^2$  of 0.63 (Table 4). Moreover, results from the regression procedure used to assess the significance of a difference in models between years indicated that the separate equations by year did not differ significantly from one another (Table 4).

Plots of deleted residuals (1,19) for the reduced model (both years combined) (Fig. 3C), and for the full model (Fig. 3A and 3B) revealed no highly influential or unusual observations. In this partial validation (19), predictions did not deteriorate when observations were individually removed from the analysis. Although the equation that was fit to the 1987 epidemic had an  $R^2$  about equal to that for the 1986 data (Table 4), the residual plot for 1987 exhibited a quadratic trend in the errors (Fig. 3B). However, this lack of fit in the 1987 data was not apparent in the reduced model (Fig. 3C), indicating that the selected model was acceptable. The coefficient of determination based on the deleted residuals ( $R_p^2$ ) equaled 0.60, which was close to the  $R^2$  of 0.65 (Table 4).

## DISCUSSION

The influence of straw mulch on leather rot development was striking. Previous field observations indicated that mulch effectively limits disease development (Ellis and Madden, unpublished), but the effectiveness of mulching had not been

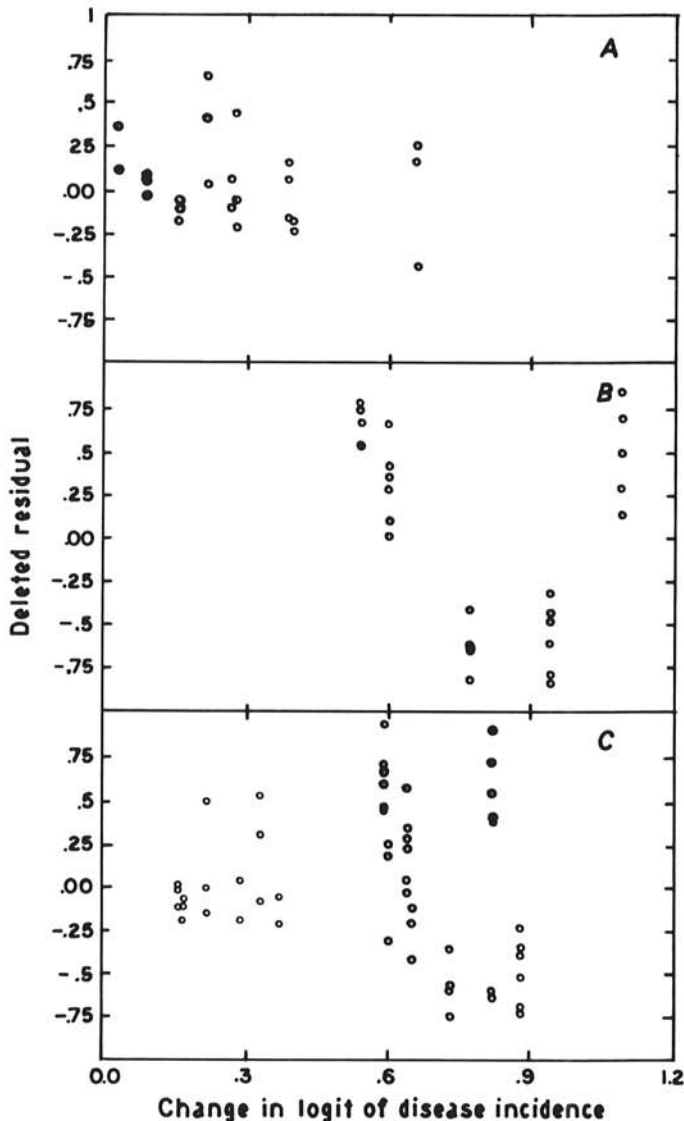


Fig. 3. Deleted residuals for regressions of change in logit of leather rot incidence on selected index variables. A, 1986 data. B, 1987 data. C, combined 1986 and 1987 data (reduced model).

quantified. Reynolds et al (21) were not able to demonstrate a statistically significant effect of mulch on strawberry fruit infection by *P. cactorum* in rain simulation experiments. However, mulch layer depth was only 2 cm in the latter study (21), whereas in the present one, depth was 8–10 cm. The presence of a sufficiently thick mulch layer probably limits disease development by inhibiting infection from inoculum in soil under natural field conditions. Results from 1986 and 1987 straw plots clearly indicate that the application of straw mulch was highly effective in preventing the establishment of an inoculum reservoir in the plant canopy. The comparative results for infection incidence in interior versus exterior aisles in the 1986 nonstraw plots further indicate that mulch also limits spread of disease once it has become established in the plant canopy, probably by preventing the repeated splashing of inoculum that has been dispersed from infected fruit.

When the dispersal index,  $D_5$ , was used as the sole predictor of  $CLDI$ , it accounted for 41% of the variation in  $CLDI$ . The regression of  $CLDI$  on the selected index variables (Table 4) improved the proportion of variation accounted for, indicating that weather conditions during fruit colonization and sporulation were also important factors determining increase in leather rot following rain. The two indices  $P$  and  $S_3$  (Table 1) were constructed in order to at least partially distinguish between weather conditions that affect colonization of infected fruit and subsequent sporulation of *P. cactorum* on that fruit, respectively. Grove et al (11) described the effect of temperature and wetness on sporulation of *P. cactorum* on strawberry fruit, and this work provided the basis for derivation of the sporulation index  $S_3$ . Preliminary work related to the latter study described optimal temperature and wetness conditions for colonization that provided the basis for the derivation of  $P$ . However, both  $P$  and  $S_3$  may well play a multiple role in our model (Table 4). For instance, it is quite possible that weather conditions summarized by  $P$  and  $S_3$  also influence susceptibility of fruit to infection by *P. cactorum*. Development of a strawberry fruit following pollination is very rapid, with full development being accomplished in 3–4 wk, so that the 4-day weather history represented by  $P$  and  $S_3$  includes a major portion of the developmental history of the fruit. Thus, parameter estimates (Table 4) may be affected not only by pathogen genotype, but by host variety as well.

The relationship between  $CLDI$  and the aggregate of significant disease index variables is expressed in Table 4, but the relationships of the index variables to each other is best expressed in a rearranged version of the reduced model:

$$CLDI = 7.2 S_3 P + D_5(2.2 - 15.8 S_3).$$

The effects of  $S_3$  and  $P$  on  $CLDI$  only enter the relationship in interaction terms. Of particular interest is the fact that the total effect of  $D_5$  is negative for  $S_3 > 0.14$ . Inclusion of the term  $S_3 D_5$  in the model compensates for the co-occurrence of high values of  $D_5$ ,  $S_3$ , and  $P$ , which were relatively highly correlated with one another. Correlations between  $D_5$  and  $S_3$ ,  $D_5$  and  $P$ , and  $S_3$  and  $P$  were 0.67, 0.74, and 0.85, respectively (unpublished). Related to the latter observation, Reynolds et al (21) observed that infection of strawberry fruit by *P. cactorum* was higher for low-intensity rains (15 mm hr<sup>-1</sup>) than moderate-intensity rains (30 mm hr<sup>-1</sup>). It was suggested that higher absolute rates of inoculum retention may occur in low- as opposed to moderate-intensity rains due to higher rates of inoculum removal by wash off in the latter rain type (21).

As our results clearly showed, index variables were much more consistent in predicting  $CLDI$ . At least part of the better performance of index variables may be attributed to the fact that they include important nonlinear effects that have been well demonstrated (10,11). At least some of the indices incorporate information obtained from controlled-environment studies (10,11) on infection and sporulation by *P. cactorum*. The indices, unlike the less-restricted weather variables ( $S_1$ ,  $S_2$ ,  $D_1$ ,  $D_2$ ,  $D_3$ ,  $D_4$ ,  $I_1$ , and  $I_2$ ), have bounds of 0 and 1. Unusual weather conditions that produce uncharacteristically large or small weather variables would be avoided by using weather indices  $S_3$ ,  $D_5$ , and  $I_3$ . Observations substantially removed from the majority of the data

points have an unreasonably large influence on regression results (19). A additional advantage of the use of index variables was illustrated by our analysis. Whereas the stepwise regression analysis based on weather variables included  $I_1$  and  $I_2$ , examination of the index variable data before regression analysis revealed that  $I_3$  was essentially constant for those rain events selected for inclusion in analysis (Tables 2 and 3) and that this variable should not be included in the set of possible independent variables. The near-constancy of  $I_3$  for leather rot epidemics in north central Ohio contrasts with other host-pathogen systems in which forecasting is based primarily on weather conditions that are conducive to infection (15,26). The optimum temperature for infection of strawberry fruit by *P. cactorum* was previously found to be approximately 20 C (10). However, even at 13.4 C, which is far from ideal, 67% fruit infection is predicted with a 2-hr period of wetness (Table 2, rain period 6a). For many other pathogens, weather conditions for infection may not be a limiting factor in epidemic progress, so that the approach to disease forecasting may need to be developed along lines similar to those described here.

Results from the present study suggest that indices derived from temperature and surface wetness conditions associated with the 96-hr period before a rain event as well as rainfall amount can be used to predict subsequent increase in leather rot. Further studies are warranted both for improving the accuracy of predictions and to provide a more rigorous validation of the model (17). At present, no systemic fungicides have been registered for control of strawberry leather rot, so that a forecasting system based on our models cannot be used to prevent a predicted increase in disease. However, knowledge of recent infection history can be used to adjust the standard spray program in order to minimize subsequent inoculum production (9).

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