Weather and Downy Mildew Epidemics of Hop in Washington State

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ABSTRACT

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Relationships between weather and downy mildew epidemics of hop in the Yakima Valley of Washington State over a 38-yr period were examined with linear discriminant and logistic regression analyses. A linear discriminant function with minimum temperature in April × the total number of rainfall days in April and May, an indicator variable for the presence of an epidemic the preceding year, and the minimum temperature in May × the number of occurrences of three or more consecutive rainfall days in May correctly classified the epidemic status for 92% of the years. The percentage of years with mild epidemics correctly classified (specificity) and years with severe epidemics correctly classified (sensitivity) for a 10-yr test data set were 86 and 100%, respectively. Logistic regression, which requires fewer assumptions, had results very similar to those of the discriminant analysis.

Downy mildew of hop (*Humulus lupulus* L.), caused by *Pseudoperonospora humuli* (Miyabe & Takah.) G. W. Wils., is a serious disease of hop in the Yakima Valley of Washington and in many areas of the world where hop is grown (10,16,18). Most hop production in North America has shifted from moist to more arid areas because the disease is more severe in areas of higher rainfall (17,18). The Yakima Valley, with a semiarid environment, is the major hop-producing region in North America and the second largest in the world. However, the Yakima Valley still averages one severe epidemic every 3 yr (6). The susceptible Cluster cultivars, which comprise about 26% of the hop plantings, and the weather are important components of downy mildew epidemics of hop in the Yakima Valley (6). Such epidemics are usually of short duration because favorable weather for disease development in May is generally followed by unfavorable hot, dry conditions in June (6,18).

Sanitation practices and timely applications of fungicides before the onset of warm, wet weather are needed to manage downy mildew in hop yards in the Yakima Valley (18). Downy mildew increases very rapidly in hop yards during conditions of abundant moisture and mild temperatures, necessitating disease forecasting models to aid in scheduling disease management practices.

Fungicide applications have been scheduled by using disease forecasting models for hop-growing areas in England, Germany, Yugoslavia, Czechoslovakia, and the Yakima Valley (2,4,5,14, 16,18). The European models are empirical and include environmental variables, and some also include inoculum concentration variables to predict disease symptoms. Royle (14) accurately predicted downy mildew symptoms with a multiple regression equation that included the independent variables of rain-wetness duration, amount of rainfall, and airborne spore concentration and with a second equation that involved only relative humidity and rainfall.

A model for short-term specific forecasts for the Yakima Valley is based on the life cycle of *P. humuli* and uses initial inoculum and daily weather forecasts to predict infection (4,5,18). *P. humuli* overwinters as mycelium in the perennial crowns of hop plants, and shoots growing from infected crowns in the spring may become systemically infected by mycelium of the fungus (17). Sporangia that serve as initial sources of inoculum for a growing season are borne on the abaxial leaf surfaces of the systemically infected shoots at night when the temperature is above 5 C and the relative humidity is above 70% (5). Cool night temperatures can delay production of sporangia for several weeks in the Yakima Valley (5).

The quantity of inoculum for the specific forecasts was determined by visually monitoring hop yards for systemically infected hop shoots and by monitoring environmental conditions for production of sporangia on the systemically infected shoots. Inoculum potential was estimated from the number of infected shoots and a multiple regression equation with minimum nightly temperature $\times$ hours with relative humidity $\geq$80% and nightly mean relative humidity as independent variables (5). Rainy periods with temperatures above 8 C favor infection of healthy shoots when sporangia are present (16). Secondary infections on shoot meristems also become systemic (16). The probability of rain over a 3-day period and the expected temperatures were obtained from local weather forecasts. The quantity of inoculum and the likelihood of rain with temperatures above 8 C were then used to predict disease infection (4).

Because initial inoculum is an important component of hop downy mildew epidemics (3,6), a model using degree-day soil temperature was developed to predict the first appearance in the spring of hop shoots systemically infected with *P. humuli* (2). This model has saved considerable time in monitoring hop yards for systemically infected shoots.

A long-range forecasting model based on the amount of initial inoculum, previous weather records, and 30-day weather forecasts early in the season was developed for the Yakima Valley region (6). A stepwise linear discriminant analysis program selected April precipitation and the number of days with precipitation >0.3 mm in May as predictors of downy mildew epidemics. May is usually the critical time to manage hop downy mildew. Therefore, on 1 May, April precipitation was obtained from weather records, and the number of rainy days needed in May for a severe epidemic to occur was determined by solving for this function in the linear discriminant equations (6). Long-term (30-day) weather forecasts were consulted to determine whether precipitation was expected to be normal, below normal, or above normal. The mean number of rainy days in May since 1954 is four, and this was considered to be the number of rainy days when precipitation was normal. A forecast for downy mildew was then made for the month of May, which took into account the amount of initial inoculum in hop yards and the likelihood of exceeding the number of rainy days in May required for a severe epidemic. For example, in 1986, seven rainy days were calculated as being needed in May for a severe epidemic to occur, and normal precipitation was expected for May. Therefore, growers were correctly advised that downy mildew would probably not be a threat.

Understanding the effect of weather on disease development is important in managing hop downy mildew. Above-normal temperatures in April and wet weather in April and May were previously found to favor development of downy mildew in the Yakima Valley, but wet weather with low minimum temperatures did not (6). The stepwise linear discriminant model that used April precipitation and the number of days with precipitation >0.3 mm in May as disease predictors was developed for data from 1954 to 1981. The purpose of this work was to validate the previous prediction models with data from 1982 to 1991 and to further investigate the effect of weather on development of downy mildew epidemics by discriminant and logistic regression analyses on a more extensive data set.

MATERIALS AND METHODS

Years with severe downy mildew epidemics from 1954 to 1981 were identified from Washington Hop Commission newsletters, which described crop conditions in each year. Years with no mention of downy mildew epidemics were classified as having none or only mild epidemics, and those for which epidemics were mentioned were classified as having severe epidemics.

The severity of epidemics was quantified from 1980 to 1991. Disease incidence was monitored from mid-April to mid-July in hop yards of the Cluster cultivars that had not been treated with fungicides. The percentage of hop hills with systemically infected shoots (from primary and secondary infections) was determined along at least four transects in each yard. Transects usually ran the length of rectangular, 4- to 10-ha yards. Six to eight yards were monitored in 1980–1987 and 1989, five in 1988 and 1990, and two in 1991.

Air temperature at a height of 1.5 m and rainfall were measured at Prosser from 1954 to 1987 with a hygrothermograph and a rain gauge, respectively, and from 1988 to 1991 with a probe thermistor (model XN217, Campbell Scientific, Logan, UT) and a tipping bucket rain gauge (Qualimetrix, Oakland, CA), respectively. Weather data were not used from Sunnyside as in a previous study (6), because electronic monitoring equipment was added at Prosser and data were more accessible. Weather data from 1954 to 1991 were analyzed from April through June because this is the time of year when epidemics develop (6). Precipitation for a day was counted only when it equaled or exceeded 0.30 mm.

Linear discriminant analyses (i.e., methods for classifying an observation into one of several populations) were used to identify weather variables that could be useful for predicting epidemics (7). The performance of previously selected models (6) was also evaluated for weather data collected at Prosser. For new model development, the data were split into two sets: the years 1954–1981, which were used previously for model development (6), constituted the training data while 1982–1991 comprised the test data. Linear discriminant analysis was used to identify combinations of weather variables with good sensitivity (years with severe epidemics classified correctly) and specificity (years with mild epidemics classified correctly) for training data. These discriminant functions were applied to test data to select models that performed well at classifying additional years as having severe epidemics or mild epidemics. Reclassification of years that were used to create the discriminant function may overestimate model performance. Therefore, as an additional means of model evaluation, cross-validation was used in which each observation in the data set was classified by using a discriminant function computed from the other observations in the data set, excluding the observation being classified. Logistic regression analyses were used as an alternative method to identify weather variables that could be used for predicting epidemics. Logistic regression involves relating qualitative variables, such as epidemic status, to other variables through a logistic cumulative distribution function. The assumptions of multivariate normality and homogeneity of covariance matrices required for linear discriminant analyses are not necessary for logistic regression to be valid (9).

RESULTS

Severe hop downy mildew epidemics occurred in 9 of 28 yr during the period 1954–1981 (6). During the period 1982–1991, the highest mean incidence of downy mildew in sampled hop yards was 3.9, 5.8, 3.0, 0.7, 1.5, 1.5, 43, 1.3, 44, and 21%, respectively. The years 1988, 1990, and 1991 had the highest disease incidences and were classified as having severe epidemics, and the other 7 yr were classified as having mild epidemics.

On the basis of linear discriminant and logistic regression analyses, the product of minimum temperature in April (*Min TA*) and the total number of days in April and May with rainfall (*T Day RAM*), the product of minimum temperature in May (*Min TM*) and the number of occurrences of three or more consecutive days in May with rainfall (*C3 Day R*), and an indicator variable for presence of a severe epidemic the preceding year (*P Yr*) were selected as predictors of downy mildew epidemics.

Classification functions obtained from the discriminant analysis were severe: $-9.40 + 0.31\,(\mathit{Min\ TA} \times \mathit{T\ Day\ RAM}) + 0.58\,(\mathit{Min\ TM} \times \mathit{C\ 3\ Day\ R}) + 5.15\,(\mathit{P\ Yr},\ 1 = \text{yes},\ 0 = \text{no})$ and mild: $-1.57 + 0.14\,(\mathit{Min\ TA} \times \mathit{T\ Day\ RAM}) + 0.11\,(\mathit{Min\ TM} \times \mathit{C\ 3\ Day\ R}) + 2.02\,(\mathit{P\ Yr},\ 1 = \text{yes},\ 0 = \text{no})$. Positive coefficients in the discriminant function indicate a positive relationship between the likelihood of an epidemic and model variables.

The epidemic in each year was classified as severe or mild on the basis of which function had the largest calculated value. These classification functions correctly classified 92% of the years with respect to severity of downy mildew epidemic. Specificity and sensitivity of the test data were 86 and 100%, respectively (Table 1). Misclassified years for the training data were 1978 and 1981 (both severe epidemic years), and the misclassified year for the test data was 1989 (mild epidemic year). Homogeneity of within covariance matrices was not rejected ($P = 0.1414$).

The cross-validation analysis also correctly classified 92% of the years with respect to severity of downy mildew epidemic. Specificity and sensitivity were 96 and 83%, respectively, for all 38 yr.

The logistic regression was used for classification in the following manner: If PROB < 0.5, then classify as mild epidemic; if PROB ≥ 0.5, then classify as severe epidemic, where PROB $= 1/[1 + \exp(\mathit{lf})]$, and $\mathit{lf} = 12.1854 - 0.28\,(\mathit{Min\ TA} \times \mathit{T\ Day\ RAM}) - 0.75\,(\mathit{Min\ TM} \times \mathit{C\ 3\ Day\ R}) - 6.59\,(\mathit{P\ Yr},\ 1 = \text{yes},\ 0 = \text{no})$. The likelihood ratio chi-square for the model was 24.469 with three degrees of freedom. Negative coefficients in the logistic regression model indicated a positive relationship between the likelihood of an epidemic and model variables.

The logistic regression function correctly classified 89% of the years with respect to severity of a downy mildew epidemic. Sensitivity for the test data was 100% (Table 1). Misclassified years for the training data were 1978 and 1981 and 1984 and 1989 for the test years.

TABLE 1. Specificity and sensitivity of years with mild and severe downy mildew epidemics when weather variables were analyzed by linear discriminant analysis and logistic regression analysis

Analysis[a]	Training data 1954–1981 (%)	Test data 1982–1991 (%)
Discriminant analysis		
Specificity	100	86
Sensitivity	78	100
Logistic regression analysis		
Specificity	100	71
Sensitivity	78	100

[a] Specificity = year with mild epidemic classified correctly, and sensitivity = year with severe epidemic classified correctly.

The discriminant function model with April precipitation and number of days with precipitation in May, the predictors used previously (6), correctly classified 86% of the years of the training data and 60% of the years of the test data. A cross-validation assessment of this model resulted in 76% of the 38 yr being correctly classified. These two variables correctly classified 82% of the training data and 70% of the test data when used in logistic regression analysis.

DISCUSSION

Weather data from April and May successfully described the occurrence of downy mildew epidemics in Yakima Valley. In this and a previous study (6), precipitation and above-normal temperatures in April and May were identified as weather variables favoring downy mildew epidemics. Both linear discriminant analysis and logistic regression yielded similar results, providing increased confidence in the models.

In this study, the product of minimum temperature in April and number of rainy days in April and May and the product of minimum temperature in May and number of occurrences of three or more consecutive rainy days in May were good indicators of downy mildew epidemics. On the basis of these interactions, minimum temperature and rainfall are important factors in downy mildew development, and a favorable level of one may compensate for a marginal level in the other. Rotem et al (12) reported a similar phenomenon for infection of potato with *Phytophthora infestans*. They demonstrated that a favorable level of either temperature, inoculum concentration, or wetting duration (or a favorable combination of two of these factors) may compensate for a certain deficiency in the third factor. Hypotheses of compensation were proposed by Rotem to explain such phenomena (11).

Downy mildew infections in England were not correlated with temperatures (13), and the temperature range for sporulation of *P. humuli* is quite large (20). However, we found that warm minimum daily temperatures in April and May favor disease development. An explanation is that temperatures in England were not sufficiently low to restrict disease development (13), whereas in Washington, low temperatures frequently restrict sporulation and infection in April and May when rain usually occurs (5). Night temperatures lower than 5 C inhibit sporangial formation on systemically infected hop shoots (5). The thresholds for local infections on leaves and for systemic shoot infections have been reported to be 5 and 8 C, respectively (15).

Rainfall was expected to be an important factor in the development of hop downy mildew because a high relative humidity promotes formation of sporangia and because free water is needed for infection (5,16,20). The rate of liberation of sporangia is also increased during and immediately after rain (8). The total number of days with rainfall in April and May and three consecutive days with rainfall in May influenced downy mildew epidemics in the Yakima Valley.

Initial inoculum was demonstrated to be an important factor in downy mildew epidemics. Large amounts of inoculum have compensated for unfavorable or marginal environmental conditions during the development of epidemics (11). Initial inoculum is an important component of disease epidemics of polycyclic diseases such as hop downy mildew, especially when the epidemic is relatively short or when the level of initial inoculum is relatively high. Severe epidemics of hop downy mildew in the semiarid environment of the Yakima Valley in Washington rarely endure longer than 4 or 5 wk, and relatively high levels of inoculum have existed in some yards and years (3,6).

A severe downy mildew epidemic of hop in one year favored an epidemic the next year. In Washington State, one, several, or no systemically infected shoots may arise from an infected hop crown in the spring (19). More systemically infected shoots arise in a yard during the spring following a severe epidemic (3,6). This is probably because more of the perennial crowns are infected during a severe than during mild epidemic, which would give rise to more systemically infected shoots (3).

A severe epidemic occurred in 1981, but this year was classified as a mild epidemic by the classification functions. A severe epidemic occurred the preceding year, and a relatively high number of systemically infected shoots were observed early in the growing season (6). April and May were drier than other years having severe downy mildew epidemics; however, an above-normal amount of rainfall occurred in June 1981. The number of days with rainfall was seven, which was the third highest, and total precipitation was 20.1 mm, which was the eighth highest for a June in the 38-yr period. Sufficient moisture occurred in May (four rainy days and 24.9 mm of precipitation) to carry inoculum over until June, when additional moisture was available for the epidemic to continue and increase on the susceptible cultivars. Therefore, weather conditions in June may be favorable for an epidemic to continue to develop.

The year 1978, when a severe epidemic occurred, was incorrectly classified in this study but not in the previous one (6). The difference is likely due to the location where the weather data were collected. Mean minimum temperatures were 1.0 and 1.3 degrees centigrade lower at Prosser than at Sunnyside in April and May 1978, respectively. Only one rainy day occurred in May at Prosser, whereas four occurred in Sunnyside. This illustrates the importance of collecting weather data close to the disease-rating location when analyzing the effects of weather on disease development for an area.

The mild epidemic year 1989 was incorrectly classified by the classification function. In this year, minimum temperature and rainfall in April were sufficient for disease infection; but only 2 days with precipitation occurred in May, and minimum temperatures during both wet periods were lower than 7 C. Wet periods with minimum temperatures below 7 C were previously associated with mild epidemics (6).

The nonepidemic year 1984 was correctly classified with linear discriminant analysis but not with logistic regression analysis. In this year, nine rainy days occurred in April and six in May, which generally would be sufficient moisture to promote a severe epidemic. However, minimum temperatures were lower than 7 C during or just before all the wet periods in April and before five of the six wet periods in May. Hop yards were monitored for systemically infected shoots with sporangia in 1984, and sporulation was found to be inhibited by low night temperatures (5).

The long-range forecasting model developed in the previous study (6) was used to forecast downy mildew epidemics in the Yakima Valley from 1982 through 1989. The advanced warnings proved useful for growers because fungicides needed to be applied over large areas and coordinated with irrigation. Growers were correctly advised in early May for 7 of the 8 yr. A severe epidemic was expected in 1987, but only a mild epidemic occurred. Two rainy days in May of that year were needed for a severe epidemic, but only 1 day with rain occurred.

The actual forecasts had a higher percentage of correct forecasts than did the model (6 of 10 yr were correctly classified), in which weather data for the entire season were used. This is because initial inoculum was quantified throughout the region and was considered in making the actual forecast. This proved to be a reliable factor and is probably the most single important variable in forecasting hop downy mildew epidemics in the Yakima Valley. A disadvantage of the long-range disease forecasts was obtaining reliable 30-day weather forecasts. An advantage of the long-range disease model was that when coupled with the short-term specific forecasts, growers became more familiar with weather variables that promoted severe disease epidemics and were therefore more prepared to manage downy mildew when conditions were favorable. This can be considered a benefit of a forecasting model (1).

The long-range forecasting model developed in the previous study (6) when coupled with amount of initial inoculum is probably more suited to making disease predictions than the model developed in this study because it is less complex and only one weather variable (number of rainy days in May) in the functions needs to be determined early in the season. However, the model in this study helped to more fully describe the interacting effects of weather variables on the development of hop downy mildew epidemics. It also showed the importance of three or more consecutive rainy days for the development of severe epidemics.

Logistic regression, which does not depend on the multivariate normality assumption, and discriminant analysis, which does depend on this assumption, yielded similar results. Both methods are reported here to assess potential effects of possible violation of the multivariate normality assumption and to relate our results with discriminant analysis to our previous study (6). The models developed in Washington indicate which environmental conditions favor downy mildew epidemics and the importance of initial inoculum in the development of downy mildew in hop yards.

Disease forecasting models, which are useful in disease management, can be built when predictor variables are available. Sanitation practices and fungicide applications can be scheduled when conditions favor disease development. However, reliable weather forecasts are needed if infection is to be predicted. Otherwise, past infections, disease symptoms, and additional inoculum production can only be predicted for hop downy mildew. The disadvantage of the latter is that the first infection period of the season is ignored. This can be costly where cultivars very susceptible to infection are grown and when initial inoculum levels are high.

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