Analyses of the Relationships Between Lettuce Downy Mildew and Weather Variables Using Geographic Information System Techniques

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ABSTRACT

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Previous studies in coastal California suggested that morning leaf wetness duration and temperature immediately after the prolonged leaf wetness period affect infection of lettuce by the downy mildew pathogen, *Bremia lactucae*. In this study, spatial analysis tools in a geographic information system were used to interpolate disease assessment data and then relate them to weather variables measured in 1995 and 1997 at weather stations in the Salinas Valley. Among the variables monitored at these weather stations, midday temperature (10:00 A.M. to 2:00 P.M.) was related most strongly to the interpolated downy mildew incidence in a circular area (radius = 5 km) around each station ($r = 0.52$, $P < 0.0001$); the higher the midday temperature, the lower the disease incidence. High humidity and prolonged morning leaf wetness duration also were associated with high downy mildew incidence. Cluster analysis resulted in distinct regions with different midday temperatures, which overlapped well (92.2% of the total area) with regions distinguished in previous cluster analyses of downy mildew incidence. Clusters of morning relative humidity showed similar patterns, although they overlapped less well with clusters of disease incidence. These results confirmed that midday temperature is an important determining factor for lettuce downy mildew, and its effects should be incorporated into a disease warning system for coastal California. Cluster analyses based on the effects of temperature have great potential for use in regional downy mildew risk assessment.

Additional keywords: correlation analysis, GIS, *Lactuca sativa*

In the Salinas Valley in coastal California, often called the salad bowl of the world, lettuce (*Lactuca sativa* L.) is grown year-round except for a short lettuce-free period in December. Due to the intensive lettuce production and cool weather, destructive epidemics of downy mildew, caused by *Bremia lactucae* Regel, occur in this area even though fungicides frequently are applied to protect against this disease.

To develop a spray advisory system for this disease, many essential epidemiological aspects of the disease have been characterized (19–22,26–28,31,34). Su et al. found that production of asexual spores (sporangia), which are the main propagules for spread of the disease in the field, occurs at night when high relative humidity

(RH) and low wind speeds prevail (27). Release of sporangia is associated with the onset of light (at sunrise) and is enhanced by a drop in RH (26). Sporangia of *B. lactucae* are relatively short lived and their longevity depends on ambient temperature and solar radiation (31). After deposition of spores, a film of free water on the leaf surface is required for the spores to germinate and infect. Scherm et al. (19) found that leaf wetness duration (LWD) is the most important factor limiting infection of lettuce by *B. lactucae*. The germination of *B. lactucae* sporangia at optimal temperature (10 to 15°C) decreases rapidly when LWD decreases from 4 to 2 h (19). Days when infection of lettuce by *B. lactucae* occurs typically have prolonged morning LWD (22). The effect of temperature on the latent period after infection is relatively small when temperature is fluctuating (21). However, temperature during the first few hours after penetration of leaf tissue by *B. lactucae* significantly affects the final outcome of infection (34), even though the effect is not as prominent as it is during the germination and penetration periods (19,28). As the temperature during the 8-h period immediately after penetration (during a preceding 4-h wet period) increased from 15 to 30°C, the percentage of lettuce seedlings infected decreased significantly

from >30% to about 5% (34). In addition, analyses of historical field data also revealed that, besides morning LWD, midday (10:00 A.M. to 2:00 P.M.) temperature is another factor determining infection of lettuce by *B. lactucae* (34).

Based on a series of studies (19,21,22), an infection-based disease warning system was previously developed by Scherm et al. (18,20). In this system, it was assumed that temperature was not a limiting factor for downy mildew in lettuce production areas in coastal California where morning temperature is usually <18°C, and fungicides should be applied if morning LWD persisted for ≥4 hours starting at 6:00 A.M. and if no fungicide had been applied during the past 7 days (18). Validation trials in commercial fields demonstrated that the number of fungicide applications could be significantly reduced if sprays were applied according to the warning system compared with calendar-based spray schedules (18), although unnecessary sprays still were recommended when disease pressure was very low. Sometimes, in areas where weather conditions were highly conducive to downy mildew development, the warning system did not recommend enough sprays, and the disease was not controlled very effectively, even when spore survival facilitated by overcast conditions during the daytime was taken into account (32). This system later was improved after fine-tuning the threshold of morning LWD for infection and adding the effects of temperature during the post-penetration period (34).

Recently, the growing demands for localized predictions and forecasts over large regions have prompted the application of geographic information systems (GIS) in plant protection (23). GIS has been used most extensively for mapping distributions of insects (4–6), disease (7,9), or specific genotypes of plant pathogens (11,12). Because localized disease and pest prediction requires high-resolution weather data, GIS techniques also have been used to interpolate or extrapolate weather data before feeding these into the prediction models, such as a temperature-based prediction of the development of gypsy moth (*Lymantria dispar*) (16). Interpolation tools in GIS also have been used to predict disease risk from observed or predicted disease intensity in the vicinity based on spatial

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autocorrelation. Gage et al. (8) developed interpolated maps of gypsy moth population density based on the counts of male gypsy moths from traps throughout Michigan, using a distance-weighting algorithm. Luo et al. (13) used GIS to generate interpolated disease risk maps for rice leaf blast based on the predicted disease risk at several locations. Moreover, GIS techniques have been widely used for relating disease or insect risks to biological and physiographic features of landscape. For example, Shepherd et al. (24) overlaid digitized historical maps of defoliation caused by the Douglas fir tussock moth in British Columbia from 1924 to 1986 to obtain a map of defoliation frequency. This outbreak-frequency map then was overlaid with forest type and biogeoclimatic maps to determine how forest type and climate were related to outbreak frequency. Similar work also has been done on plant diseases. Nelson et al. (14) related the risk of virus diseases in tomato fields to prevalence of diseased hosts and insect vectors in the neighborhood. Wilds (29) identified the factors affecting dogwood anthracnose (*Discula destructiva*) in the southern Appalachian Mountains as the abundance of the host, elevation, slope, and potential soil moisture. Wilson et al. (30) developed a model using altitude and sun-index to predict the presence of *Phytophthora cinnamomi* in sclerophyll vegetation communities in southeastern Australia.

In a previous geostatistical and GIS analysis of lettuce downy mildew in the Salinas Valley in 1995 and 1997 (33), we found that the spread of the disease was localized. No significant spatial autocorrelation was detected beyond a distance of 5 km. Meanwhile, significant seasonal changes and spatial trends were found in disease incidence. Lettuce downy mildew generally tended to be more severe in cool and wet seasons (spring and fall), and in north end of the Salinas Valley, which is closer to the Pacific Ocean. However, the relationship between incidence of lettuce downy mildew and weather variables had not been analyzed.

The objectives of this study were to identify major weather factors affecting lettuce downy mildew in the Salinas Valley, and to assess the possibility of estimating the regional risk of lettuce downy mildew based on these weather variables using GIS.

MATERIALS AND METHODS

Study area. The study area covered the lettuce production regions in the Salinas Valley, an area of about 104 km in length and 10 to 20 km in width. The study area lies mostly at elevations <100 m above sea level and generally is characterized by intensively cultivated soils covered with cool-season vegetable crops and strawberries. There also are several cities and towns located in this area, including Watsonville,

Castroville, Salinas, Gonzales, Soledad, Greenfield, and King City.

Disease surveys. Six surveys were conducted monthly from April to September 1995. During each survey, 32 to 55 fields were visited throughout the study area. In each field, 100 plants were assessed in a "V" pattern, and incidence of lettuce downy mildew was evaluated as described previously (33). Longitude and latitude were measured using a global positioning system (Trailblazer, model no. 62001; Magellan System Corporation, San Dimas, CA) to locate individual fields (error ≤100 m). In the summer of 1997, 50 to 71 fields were surveyed four times at weekly intervals. The survey covered only the north and middle portions of the valley from Castroville to Soledad. The same fields were surveyed every week from 16 June to 7 July, except when they were inaccessible due to application of chemicals or irrigation.

Weather data collection. During 1995, hourly weather data from eight California Irrigation Management Information System (CIMIS) weather stations in the study area were downloaded via the Internet. The weather station sites were located in such a way that they represented the weather characteristics in their vicinity while topographic depressions, obstructions, roads, rivers, and abrupt crop or vegetation changes were avoided. The weather variables selected included hourly mean air temperature, RH, wind speed, and solar radiation. Fenwall Thermistor/HUMICAP RH sensors (model Hmp35C; made by Vaisala Inc., Irvine, CA and modified by Campbell Scientific, Inc., Logan, UT), enclosed in a naturally aspirated radiation shield (R. M. Young Company, Traverse, MI) and located at a height of 1.5 m, were used for measurement of air temperature and RH. Wind speed was measured with three-cup anemometers (model 014A; Met-One Instruments Inc., Grants Pass, OR) placed at a height of 2 m. Total solar radiation was measured with pyranometers (model LI200S; Li-Cor Inc., Lincoln, NE) located at a height of 2 m.

In 1997, in addition to hourly weather data from five CIMIS weather stations located between Castroville and Soledad, 15-min interval data from 14 weather stations in the same area, provided by Adcon Telemetry Company (Adcon Telemetry Inc., Santa Rosa, CA) also were used. The weather stations of Adcon were located near lettuce fields. The wind speed, air temperature and RH, and solar radiation sensors were located at heights of 2.75, 0.30, and 3 m, respectively. In addition to these weather variables, leaf wetness measurements at a height of 0.4 m (on top of the temperature and RH sensors) also were included in Adcon's data.

Weather data summary. To cover all the epidemiological components of lettuce downy mildew (sporulation, spore release,

survival, germination, and infection), each day was divided into several periods. Among them, four periods were considered: night (8:00 P.M. to 5:00 A.M., sporulation), morning (6:00 to 10:00 a.m., infection), midday (10:00 A.M. to 2:00 P.M., post infection and survival), and afternoon (2:00 to 6:00 P.M., survival). Average solar radiation, temperature, RH, and wind speed were calculated for each of the four periods per day. Assuming that the height of the lettuce crop was 0.20 m, the wind speed (U) measured at a particular height (H) was used to estimate the wind speed (ws) at the lettuce canopy with a power law profile: $ws = U \times [(0.2 - 0.2 \times 0.64)/(H - 0.2 \times 0.64)]^{1/2}$ (19). The total number of sporulation hours (SPH) during which weather conditions were suitable for sporulation of *B. lactucae* (e.g., when solar radiation = 0, wind speed <0.5 ms⁻¹, and RH >80%) (27) was calculated. In 1997, the ending time of morning LWD also was determined based on the 15-min data from Adcon weather stations. A leaf surface was considered wet if the sensor's value was above a threshold of 1.0. The weekly means and coefficients of variation of all weather variables were summarized for all 4 weeks before each survey in 1995, and for a 7-week period in 1997 (from 4 weeks before the first survey to the day before the fourth survey). Pearson correlation coefficients between weather variables at each station were calculated in SAS (version 6.12; SAS Institute Inc., Cary, NC) for all days in 1995 and 1997 together.

Correlation analysis of disease incidence and weather variables. Previously, disease incidence was interpolated into grids for each survey in 1995 and 1997 (33) and the Salinas Valley was divided into two clusters based on downy mildew data (33), one with higher incidence close to the coast and the other with lower disease incidence inland. In this study, a point coverage first was generated based on the latitude and longitude of the weather stations using ArcInfo (rev. 7.1.2, Environmental Systems Research Institute, Inc., Redlands, CA). A circle with a radius of 5 km then was drawn around each weather station in GIS (Fig. 1). Mean disease incidence was calculated for the area within each circle based on the interpolated incidence grids for each of the surveys in 1995 and 1997 (33) using ArcGrid (3). Weekly averages of the above weather variables were calculated for each of the 4 weeks prior to each disease survey. Pearson correlation coefficients were calculated in SAS for disease incidence and the weekly mean weather variables for 1995, 1997, and the combined data set. A linear multiple regression model then was developed to relate disease incidence to the weather variables using combined data sets with backward and stepwise methods in SAS.

Cluster analysis of weather variables. This analysis was done only for 1997

weather data because there were only up to eight weather stations available in 1995. For the variables that had significant correlation coefficients with lettuce downy mildew, weekly means (from 4 weeks before the first of the four weekly disease surveys to the day before the last survey) were summarized for each weather variable per weather station for 1997. A point coverage was generated in ArcInfo based on the geographic position of the weather stations, and the weekly weather summaries were associated with it as an attribute table. Then, for each weekly weather summary, a grid (grid size = 200 m) was interpolated from the point coverage using the inverse distance weighting method with a power of 2. After smoothening and standardization, cluster analysis was conducted on the stack consisting of these grids

(seven grids for each variable) to classify the Salinas Valley into several weather clusters. Because cluster analysis does not have a theoretical distribution assumption, one cannot use common statistical tests to determine the appropriate number of clusters (25). A pseudo *F* test, which tests the ratio of variance between clusters and pooled variance within individual clusters, was used to determine the quality of the clustering (1). The separability of the clusters also was examined by drawing an ellipse for each cluster with a radius of 2σ (standard deviation for each individual weather variable for the cluster) around the cluster mean vector in ArcGrid (3). Both approaches indicated that two was an appropriate number of clusters, providing a good separation for most of the weather variables; therefore, we used two clusters,

low versus high, in all of the cluster analyses.

Comparison of clusters of disease incidence and weather variables. The cluster grid based on interpolated disease incidence was overlaid with the cluster grids based on interpolation of temperature, RH, and the combination. To determine the relation between the clusters of weather and clusters of disease, the numbers of cells classified into four groups were summarized, and the percentage of each group was calculated. The groups consisted of low RH (or high temperature, or both) and low disease incidence, low RH (or high temperature or both) and high disease incidence, high RH (or low temperature or both) and low disease incidence, and high RH (or low temperature or both) and high disease incidence.

RESULTS

Weather data summary. Among the 2,583 potential 4-h (or 9-h) means from all of the stations and all of the days within the 4 weeks before the disease surveys in 1995 and 1997, solar radiation data was available for 2,202 records; temperature, RH, and wind speed data were available for 2,550 to 2,561 records; and leaf wetness data was available for only 686 records (Table 1). Generally, morning (6:00 to 10:00 A.M.) temperature was relatively cool (with a mean of 15.2°C), almost optimal for infection by *B. lactucae*. Temperatures during midday (20.7°C) and afternoon (19.9°C) were slightly higher than optimal for infection, but not for survival (Table 1). Wind speed usually was low during night and morning, reaching the highest value in the afternoon. In contrast to wind speed, RH was highest at night and lowest during the afternoon. The average duration suitable for sporulation of *B. lactucae* in a night was long

Fig. 1. Distribution of weather stations in the Salinas Valley (the Pacific Ocean is located at its north end) in 1995 and 1997, showing the circles (radius = 5 km) around each station; mean downy mildew incidence of lettuce was calculated within each circle.

Table 1. Simple statistics of weather variables used in correlation analysis with lettuce downy mildew incidence in 1995 (10 March through 30 September) and 1997 (19 May through 6 July)

Name	Weather variables ^a	No. of observations ^b	Mean	Coefficient of variation (%) ^c
SRm (W m ⁻²)	Solar radiation, morning (m) 06:00–10:00 A.M.	2,202	333.18	41.61
SRd (W m ⁻²)	Solar radiation, midday (d) 10:00 A.M.–2:00 P.M.	2,202	780.36	23.14
SRa (W m ⁻²)	Solar radiation, afternoon (a) 2:00 P.M.–6:00 P.M.	2,202	442.09	28.87
Tm (°C)	Temperature 06:00–10:00 A.M.	2,559	15.18	19.09
Td (°C)	Temperature 10:00 A.M.–2:00 P.M.	2,560	20.73	20.57
Ta (°C)	Temperature 2:00 P.M.–6:00 P.M.	2,560	19.93	19.31
Tn (°C)	Temperature, night (n) 8:00 P.M.–05:00 A.M.	2,558	12.47	18.85
RHm (%)	Relative humidity (RH) 06:00–10:00 A.M.	2,559	82.01	13.09
RHd (%)	RH 10:00 A.M.–2:00 P.M.	2,560	62.62	24.09
RHa (%)	RH 2:00 P.M.–6:00 P.M.	2,560	64.27	22.43
RHn (%)	RH 8:00 P.M.–05:00 A.M.	2,558	89.87	9.72
WSm (m s ⁻¹)	Wind speed 06:00–10:00 A.M.	2,553	0.36	59.33
WSd (m s ⁻¹)	Wind speed 10:00 A.M.–2:00 P.M.	2,559	0.76	39.63
WSa (m s ⁻¹)	Wind speed 2:00 P.M.–6:00 P.M.	2,559	0.91	42.37
WSn (m s ⁻¹)	Wind speed 8:00 P.M.–05:00 A.M.	2,551	0.34	56.05
SPH (h) ^d	Sporulation hours	2,552	6.23	51.01
ELWD ^e	End of morning leaf wetness	686	9.84	13.87

^a Calculated from hourly (California Irrigation Management Information System) or 15-min (Adcon) data.

^b Due to missing values, the number of observations varied.

^c Coefficient of variation = 100% × standard deviation/mean.

^d Total number of sporulation hours during which solar radiation is zero, wind speed <0.5 m s⁻¹, and RH > 80%.

^e The ending time of morning leaf wetness duration; time (Pacific Standard Time) when the 15-min leaf wetness value first decreased to <1.0 in the morning.

enough (average SPH = 6.23 h) to allow sporangia of *B. lactucae* to mature. Pearson correlation coefficients between weather variables varied widely (*data not shown*). Temperature during midday (10:00 A.M. to 2:00 P.M.) correlated strongly with solar radiation, temperature during all other periods, and RH. Both SPH and ending time of morning LWD (eLWD) were closely related to morning RH (*data not shown*).

Correlation between weather variables and disease incidence. Although the results were obtained from separate data sets in 1995 and 1997, only the results from the combined data set are presented (Table 2) because they all were very similar (*data not shown*). Generally, disease incidence was more strongly related to the weather variables during the fourth, third, and second week prior to the survey dates (–4, –3, and –2 weeks), than to the weather variables during the week just before the surveys (–1 week). Among the different weather variables, midday temperature (between 10:00 A.M. and 2:00 P.M., which is assumed to affect the post-penetration stage of the disease cycle) had the strongest and most consistent relationship with downy mildew incidence, followed by afternoon temperature, midday RH, and morning temperature. Temperature always had negative correlation coefficients, whereas RH always had positive correlation coefficients with downy mildew incidence. The signs of correlation coefficients between wind speed or solar radiation and downy mildew incidence were not consistent, and most of them were not significant ($P = 0.05$). The analysis did not show any significant association between downy mildew incidence and SPH. Only during the fourth week before the surveys did ending time of eLWD have a significant positive correlation coefficient to downy mildew incidence. Although the absolute values of correlation coefficients for eLWD were high compared with other weather variables, they were not significant due to fewer data points. The available observations of leaf wetness termination time were 14 for –1 week and 56 for the rest of the weeks, whereas solar radiation had 93 or 94 observations and the other variables had 122 or 123 observations.

Regardless of the methods used in multiple regression (stepwise or backward), the analysis selected the same variables: midday and afternoon temperatures during the third week before the disease surveys, and morning and night RH during the fourth week before the disease surveys (Table 3). Ending time of eLWD and solar radiation were not included in the multiple regression analysis because of the inconsistent correlation coefficients and missing data.

Interpolation of weather variables. Interpolation was done in GIS only for the

1997 survey data because the number of available weather stations in 1995 was too low to carry out interpolation. Although multiple regression selected four variables (midday and afternoon temperatures, and RH during night and morning), we interpolated only midday temperature (Td) and morning RH (RHm) because of the high correlations between Td and afternoon temperature, and between RHm and night RH (*data not shown*). As with downy mildew incidence (33), the inverse distance weighting method with a power of 2 provided reasonable interpolation for 7 weekly averages (starting from 4 weeks before the first survey to the day before the last survey) of both weather variables. All the interpolated maps showed lower temperature and higher morning RH in the northern region of the Salinas Valley, and higher temperature and lower RH in the southern part of the valley, but only first and fourth weekly means were presented (Fig. 2).

Cluster analysis of weather variables. The two clusters that resulted from the analysis based on seven weekly mean midday temperatures, on seven weekly mean morning RH values, or on the combined data set were distributed similarly in the Salinas Valley (Fig. 3). The north portion of the research area was classified into a

cluster with high morning RH and low midday temperature whereas the south portion was classified into a cluster with low morning RH and high temperature. The division of the Salinas Valley based on midday temperature, morning RH, or combined data sets was very similar to the previous division based on incidence of lettuce downy mildew, in which the northern part of the valley was classified as a high disease region and the southern part as an area with low disease incidence (33).

Comparison of the clusters of weather variables and disease incidence. Overlay of the distribution map of downy mildew incidence clusters with those of the weather variables showed that most of the points that were classified into the cluster with high disease incidence were typical of high morning RH and low midday temperature, whereas low disease areas were characterized by high midday temperature and low morning RH (Table 4). Using seven weekly mean midday temperatures, 90% of the high-disease areas were classified into the low-temperature cluster and 93% of the low-disease areas into the high-temperature cluster. The sum of these two accounted for 92.2% of total research area. These percentages were 85, 90, and 89%, respectively, for morning RH.

Table 2. Pearson correlation coefficients between downy mildew incidence and weather variables during different weeks prior to surveys in 1995 and 1997 combined

Variables ^b	Correlation coefficients during different weekly periods ^a			
	–1 Week	–2 Week	–3 Week	–4 Week
SRm	0.027	0.132	0.111	–0.165
SRd	0.013	–0.017	–0.098	–0.283
Sra	–0.010	–0.045	0.010	–0.315
Tm	–0.125	–0.286	–0.394	–0.181
Td	–0.252	–0.359	–0.516	–0.321
Ta	–0.180	–0.300	–0.464	–0.345
Tn	–0.060	–0.290	–0.229	–0.101
RHm	0.112	0.127	0.337	0.230
RHd	0.235	0.236	0.428	0.356
Rha	0.186	0.199	0.357	0.418
RHn	0.034	0.079	0.172	0.218
WSm	–0.060	0.125	0.295	0.275
WSd	0.038	0.146	0.210	0.130
WSa	–0.079	–0.002	0.120	0.042
WSn	–0.173	–0.060	0.205	0.136
SPH	0.122	0.060	–0.084	0.029
ELWD	0.338	0.171	0.226	0.269

^a Values that were significant at $P = 0.05$ are indicated in bold.

^b SR = solar radiation, m = morning, d = midday, a = afternoon, T = temperature, n = night, RH = relative humidity, WS = wind speed, SPH = sporulation hours, and eLWD = the ending time of morning leaf wetness duration.

Table 3. Summary of stepwise selection in multiple regression analysis of lettuce downy mildew incidence to weather variables for combined data from 1995 and 1997

Step	Variable entered ^a	Partial R^2	Model R^2	F value	Pr>F
1	Td3	0.268	0.268	43.99	<0.001
2	RHn4	0.027	0.295	4.56	0.035
3	Ta3	0.032	0.327	5.54	0.020
4	RHm4	0.023	0.350	4.10	0.045

^a Td3 and Ta3 are mean midday and afternoon temperature, respectively, for the third week before disease surveys, and RHn4 and RHm4 are mean night and morning relative humidity, respectively, for the fourth week before disease surveys.

DISCUSSION

A major impediment to studying effects of weather variables on plant diseases is the lack of observations in space, with disease records and associated weather variables at exactly the same location. However, the interpolation and spatial analysis tools in GIS have made these kinds of analyses possible and convenient. After interpolation of disease and weather variables, correlation and cluster analyses can be performed. Furthermore, by using the interpolation and spatial analysis tools in GIS, we were able to use the average disease incidence around a weather station instead of the disease incidence at a single point in the correlation and regression analyses. This made the detection of consistent relationships between disease incidence and weather variables more likely, and the results were affected less by a few abnormal observations.

A significant correlation was revealed between incidence of lettuce downy mildew and temperature during morning, midday, and afternoon. Association of morning temperature with lettuce downy mildew was consistent with the results of

growth-chamber experiments on spore germination and infection (19). However, both midday and afternoon temperature had much stronger associations with downy mildew incidence than morning temperature in this study. Infection occurs mostly during the morning; therefore, the midday and afternoon temperatures were unlikely to affect the germination of sporangia and the penetration of lettuce leaves by the pathogen. Moreover, solar radiation plays a much greater role in killing sporangia of *B. lactucae* than high temperature in coastal California (31), but only a weak correlation between solar radiation and disease incidence was found in this study. Therefore, the effects of high temperatures on survival of sporangia could not, by itself, explain the very strong association of high temperature with low disease incidence. This is different from the results obtained by Scherm et al. (21) for effects of temperature on latent period, in which fluctuating temperature was found to play a relatively small role in affecting latent period of lettuce downy mildew, and high temperature rarely affected the development of downy mildew symptoms once the

pathogen had infected lettuce. However, temperature treatments were started from 12 or 24 h after inoculation in all these experiments to ensure that temperature did not interfere with the infection process (21). That was actually 8 to 9 h after germination and penetration, which took only 3 to 4 h in most studies (15,17,19,28). Little attention has been paid to this 8- to 9-h period after penetration of the host by the pathogen in epidemiological studies (10,34). However, this period may be very important in determining if infection is successful for obligate parasitic pathogens such as *B. lactucae*. Because the parasitic relationship is not likely to be fully established during this interval, and the pathogen has used up a large proportion of its energy reserves for germination and penetration, the pathogen is likely to be more susceptible to environmental stresses during this stage. It is a reasonable deduction that the high midday temperature may affect the establishment of the parasitic relationship between lettuce and *B. lactucae* after germination and penetration, and this is consistent with the results from growth-chamber experiments (34).

A day with high morning solar radiation usually is preceded by a clear night that provides heavy dew formation for sporulation and germination. High morning solar radiation itself, however, dries the leaf surface more quickly. Therefore, the effects of high morning solar radiation on downy mildew may be multiple and mixed. This may explain why no consistent correlation between morning solar radiation and downy mildew incidence was observed. Midday and afternoon solar radiation were significantly related to downy mildew incidence only at the beginning of the epidemics (~4 weeks), although high midday solar radiation generally is very effective in killing sporangia of *B. lactucae* in coastal California during the summer (31). A possible explanation is that, after a lettuce crop reaches the rosette stage, the shading effects of its canopy become more important, and the actual solar radiation dose received by *B. lactucae* depends more on the conditions within the lettuce canopy than on the solar radiation level outside the canopy.

During this research, wind speed data from two different sources were measured at two different heights. Although the data were standardized to crop height before conducting correlation analysis, wind speeds from two sources might still have been incompatible. This might partly account for the inconsistent association between downy mildew incidence and wind speed.

No consistent association was found between ending time of eLWD and incidence of lettuce downy mildew in this study, although it was demonstrated that LWD was a dominant factor affecting infection of downy mildew in growth-chamber ex-

Fig. 2. The first and fourth interpolated weekly mean midday (10:00 A.M. to 2:00 P.M.) temperatures and morning relative humidities (6:00 A.M. to 10:00 A.M.) during the 7-week period before and during the lettuce downy mildew surveys in 1997.

periments (19) and observations in commercial fields (22). The difference between measured leaf wetness and the actual leaf wetness inside the lettuce canopy might have contributed to the weak correlation because the leaf wetness we used was measured by sensors located outside of lettuce canopy, on top of the RH and air temperature sensors, which were set up at a level higher than most lettuce leaves. The inconsistent results also might have been due to the large number of missing data, because the number of available observations was

much lower for leaf wetness than for the other weather variables.

Cluster analysis was first used in a previous article to classify the epidemic types of lettuce downy mildew in the Salinas Valley (33), and was used again in the classification of the areas based on weather variables in this study. According to the results of correlation analyses and cluster analyses in GIS, the epidemics of lettuce downy mildew were closely associated with weather variables. The consistent results from GIS analyses and growth-chamber and field experiments (34) dem-

onstrated that the methods we employed are useful in the investigation of association between plant diseases and environmental factors.

Although the value of R^2 for the regression model was relatively low (0.35), the overlap areas between clusters of weather and disease incidence was more than 92% of the total area in the Salinas Valley. This indicated that this method has great potential for use in regional risk assessment where there are only a few categories of output. In addition to confirming the effect of midday temperature, which previously had been incorporated into the disease warning (34), the results from this study suggested other applications in the decision-making for management of the disease. Farmers can calibrate their spray regimes based on the risk their fields encounter. For fields located in a region of high risk, the farmer can adapt a more conservative fungicide advisory system; whereas, for fields located in a region of low risk, they can be more aggressive in cutting production costs via fewer fungicide applications.

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Fig. 3. Comparison of clusters of lettuce downy mildew incidence for four weekly surveys in 1997 with clusters of seven weekly (before and during the surveys) midday temperature, morning relative humidity, and midday temperature and morning relative humidity combined.

Table 4. Percentages of high and low disease incidence areas (based on cluster analysis of downy mildew survey) classified into each cluster of weather variables in 1997

Disease clusters	Percentage in total area	Weather clusters ^b	Percentage of areas by weather variables ^a		
			RHm	Td	Td & RHm
Low disease	74	A	90	93	93
	...	B	10	7	7
High disease	26	A	15	10	11
	...	B	85	90	89

^a A = cluster with high midday temperature, low morning relative humidity, or both; B = cluster with low temperature, high relative humidity, or both.

^b RHm = morning relative humidity and Td = midday (10:00 A.M. to 2:00 P.M.) temperature.

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