Weather Variables Associated with Infection of Lettuce by Downy Mildew (*Bremia lactucae*) in Coastal California

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ABSTRACT

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Weather conditions and downy mildew (*Bremia lactucae*) development were monitored in 13 commercial lettuce fields in the central coast production areas of California during 1991 and 1992. Days on which infection likely had occurred were identified based on observations of the appearance of new lesions combined with quantitative information about the length of the latent period of the disease. Univariate (Kolmogorov-Smirnov tests) and multivariate (stepwise discriminant analysis) procedures were applied to statistically differentiate infection days from days on which infection had not occurred and to characterize infection days in terms of weather. With both methods of analysis and during both years, the duration of leaf surface wetness in the morning (AM-LWD) was the most important variable for infection. AM-LWD had a mean of 4.2 h (median 4.0 h) during infection days and a mean of 1.9 h (median 2.0 h) during days on which infection had not occurred. Additional weather variables did not help to differentiate between the two groups of days. Our results suggest that measured or predicted AM-LWD could be used in a decision support system for lettuce downy mildew management. The relevance of our findings is discussed within the framework of known cause-and-effect relationships regarding the infection cycle of *B. lactucae*.

Additional keywords: disease prediction, *Lactuca sativa*.

Downy mildew (causal agent *Bremia lactucae* Regel) is a major disease of lettuce (*Lactuca sativa* L.) in the coastal vegetable production areas of California (20,21). Relatively low levels of infection can downgrade the crop, cause significant trimming losses at harvest, and promote rot during postharvest transit and storage (13,38). High levels of disease can render a crop unmarketable. Although fields of diseased lettuce are present in the area during most of the growing season (March through October), disease intensities and crop losses vary greatly seasonally and annually depending, to a large extend, on climate and weather factors (12). The irregular and commonly unpredictable occurrence of downy mildew epidemics has impeded the application of integrated pest management practices in lettuce production in the past. Therefore, studies directed toward a better understanding of the factors driving downy mildew epidemics under the specific meteorological conditions in the coastal regions of California are needed. Such research could result in decision aids for improved downy mildew management.

Downy mildews are among the plant pathogens whose response to the environment has been studied in great detail (14,22). It is well established that leaf wetness duration and temperature are cardinal variables for spore germination and infection, and that sporulation is restricted to periods of darkness, high humidity, and low wind speed (15,22). The longevity of sporangia is affected by solar radiation (particularly in the UV spectrum), humidity, and temperature (3,9,24). Under constant conditions, latent period of downy mildews depend strongly on temperature (22,37). However, we found that temperature has only a small effect on the latent period of lettuce downy mildew when infected plants are exposed to fluctuating rather than constant temperatures (28).

Most of the information listed above was obtained from controlled experiments in incubators, growth chambers, and greenhouses. Such research follows a systems-approach that breaks the system (epidemic cycle) into its monocyclic components (germination, infection, latent period, sporulation, etc.) and analyzes each part separately for its response to environmental factors (16). Based on one or more of these components, models are developed that attempt to predict infection and/or disease development in the field. These models, however, sometimes fail to mimic disease development under more realistic conditions, or they need empirical adjustment to perform adequately. Evidently, substantially different conditions may be encountered in field situations compared to those tested in controlled experiments, and an epidemic in the field may be more complex than a linear combination of its monocyclic components.

Epidemiological field surveys can bridge the gap between cause-and-effect relationships demonstrated in controlled experiments and their realization under field conditions (35). In this paper, we present the results of a survey-approach to identify weather variables associated with infection of lettuce by *B. lactucae* under the meteorological conditions of coastal California. The relevance of our findings is discussed within the framework of known cause-and-effect relationships. A preliminary account of this work has been given (25).

MATERIALS AND METHODS

Sampling and data collection. The surveys were done in commercial lettuce fields in the central coast production areas of California. The region's climate is characterized by an inflow of cool, moist, and sometimes fog-laden air from the Pacific Ocean throughout the growing season. Nocturnal stratus ("high fog") occurs frequently during the summer. There are pronounced gradients of temperature (increasing) and humidity (decreasing) with increasing distance from the coast (27). Rainfall is absent during the summer.

Weather conditions and downy mildew development were monitored in 13 fields during 1991 and 1992 (Table 1). The fields had been planted to Crisphead, Romaine, or Leaf lettuce cultivars. All cultivars were susceptible to the predominant pathotypes of *B. lactucae* in California (pathotypes IIA, IIB, III, and IV [19,30]). Crop management, fertilization, and pest control followed recommended practices (2), except that fungicides to control downy mildew were not applied on an area at least 16 plant rows (8.1 m) wide and about 50 m long to permit the development of epidemics. In trial 10 (Table 1), data from unsprayed plots in a small-plot fungicide trial (H. Scherm and A. H. C. van Bruggen, *unpublished data*) were used. The plots were four plant rows (2.0 m) wide and 12.2 m long and were replicated four times. All surveys were begun after thinning.

We ascertained that inoculum of *B. lactucae* was present in the study area while our trials were done, so that weather was the chief factor governing disease development. Seven of the trials were done on organic farms where the survey plots were surrounded by areas of mixed lettuce in different growth stages, some of which always harbored inoculum. In the six remaining trials, which were done in large conventional fields in which the unsprayed area was small compared to the rest of the field, we verified that fields of lettuce infected with downy mildew were present within a distance of less than about 1 km of the survey plots.

Incidence of downy mildew (proportion of plants with at least one lesion) and severity (number of lesions per plant) were recorded at 1- to 10-day intervals, depending on crop age and disease development. Most assessments were done at 3- to 5-day intervals to provide two observations per latent period (5). At least 70 plants per field were examined for disease, but usually several hundred plants were assessed when downy mildew incidence was low or when plants were small. The sampling procedure followed an X-pattern (17), except in the first two trials during 1991 (Table 1), in which a stratified random sampling procedure (8) was applied. To summarize downy mildew development, areas under disease progress curves (AUDPC) were calculated based on disease incidence.

At two locations per field (5–20 m apart in the same plant row), canopy air temperature and relative humidity (RH) were measured at a height of 0.15 m with shielded thermistors and sulfonated polystyrene humidity transducers, respectively (Campbell Scientific Inc., Logan, UT). Vapor pressure was calculated from temperature and RH measurements by standard meteorological equations (32). Leaf wetness duration (LWD) was estimated with two to four electronic leaf wetness sensing grids (Campbell Scientific Inc.) per field. The grids were installed at a height of 0.10 m above the soil surface and were slightly tipped about their long axes toward the northwest to represent leaves exposed at night and shaded during early morning. The sensors were calibrated to record readings between 0 (completely dry) and 10 (completely wet). Leaf wetness was defined as a reading of 5.0 or greater according to a preceding calibration study on plant leaves in the laboratory. Wind speed, shortwave radiation (R_s), and precipitation (from sprinkler irrigation) were measured above the crop at a height of 0.40 m. The radiation measurements were taken with silicon pyranometers and quantum sensors (LI-COR Inc., Lincoln, NE). Outputs from quantum sensors were converted to R_s by the equations given in Britton and Dodd (6). All sensor signals were sampled at 5-min intervals with a data logger, and 60-min averages were computed for further analysis. Thus, the original weather data set consisted of hourly means of canopy air temperature, vapor pressure, wind speed, shortwave radiation, precipitation, and LWD for all fields.

Identification of infection days. Days on which infection likely had occurred were identified based on observations of the appearance of new lesions combined with quantitative information about the length of the latent period of lettuce downy mildew. We found previously that temperature has only a small effect on the latent period of *B. lactucae* over a wide range (extremes −0.7–36.4 C; means 9.5–18.2 C) of artificially and naturally fluctuating temperatures (28). Differences in latent period due to cultivar were moderate (generally less than 3 days), but the first sporulating lesions on cultivars without known field resistance occurred on average 7–9 days after inoculation. Therefore, in the present study, we assumed that infection had taken place during a 3-day period occurring 7 days before disease assessment if new lesions were found on that assessment date. (Lesions were considered fresh when they were still green or only slightly chlorotic [37]). All days that were part of such 3-day periods were considered infection days, except for days on which total LWD was less than 4 h, which was too short for infection (26,31,37). This procedure was applied to all site-days for which disease assessments were available. We estimated that 41 (of 93 site-days) and 20 (of 88 site-days) infection days occurred during the 1991 and 1992 trials, respectively (Table 1).

Statistical analyses. Before statistical analyses, each day (infection day or day on which infection had not occurred) was further divided into three 8-h periods, namely 0601-1400 h (Pacific standard time; morning), 1401-2200 h (afternoon), and 2201-0600 h (night). To match the biology of *B. lactucae*, each day was defined as beginning at 1401 h and ending at 1400 h the next day (Fig. 1). Infection was assumed to occur as the last link of the sequences: sporulation (night) → dispersal (morning) → infection (morning), or sporulation (night) → dispersal (morning) → survival (afternoon) → infection (night or morning).

Summary statistics (means, maxima, minima, sums, and durations) of the original weather variables were calculated for each of the three periods. This resulted in 14 new variables (Table 2) that were used in all subsequent analyses. Simple correlation coefficients were computed to determine associations among these variables and to check for multicollinearity (highly intercorrelated independent variables).

TABLE 1. Description of the study sites in coastal California

Trial	Location	Cropping season	Duration (days)	Cultivar	Irrigation method	AUDPC[a] (proportion days)	No. of infection days[b]
1	Watsonville	Spring 1991	27	Parris Island Cos	Sprinkler	3.04	3
2	Watsonville	Spring 1991	28	Parris Island Cos	Sprinkler	0.48	3
3	Santa Cruz	Spring 1991	24	Tanja	Sprinkler	5.82	6
4	Santa Cruz	Spring 1991	19	Tanja	Sprinkler	1.81	3
5	Santa Maria	Summer 1991	50	Salinas	Furrow	10.39	7
6	Castroville	Summer 1991	52	Salinas	Furrow	11.64	14
7	Watsonville	Summer 1991	33	Tanja	Sprinkler	4.24	5
8	Watsonville	Spring 1992	30	Parris Island Cos	Sprinkler	17.39	3
9	Santa Cruz	Spring 1992	31	Parris Island Cos	Sprinkler	4.87	6
10	Castroville	Summer 1992	36	Salinas	Sprinkler	3.05	6
11	Castroville	Fall 1992	54	Coastal 105	Subsurface-drip	2.73	5
12	Salinas	Fall 1992	28	Clemente/Darkland	Subsurface-drip	0	0
13	Salinas	Fall 1992	21	Darkland	Furrow	0	0

[a] Area under disease progress curve.

[b] Days on which infection likely had occurred were identified based on observations of the appearance of new lesions combined with quantitative information about the length of the latent period of lettuce downy mildew (described in text).

Box-plots were constructed to compare distributions of the weather variables during infection days and days without infection. The similarity of the distributions of each variable among the two groups of days was estimated with the Kolmogorov-Smirnov test (SAS Institute Inc., Cary, NC). This nonparametric test evaluates the hypothesis that two samples come from identical distributions (34). Because the distributions of 14 variables, all of which were intercorrelated, were tested at the same time, a significance level, $P = 0.0036$ ($=0.05/14$), was used to decide which distributions were significantly different (Bonferroni correction). Using this level ensured that the overall probability of declaring differences significant by chance alone was about 0.05 (18).

To confirm the results of these univariate tests, the weather variables were used as predictors in stepwise discriminant analysis (1) to statistically classify each day into the two groups, infection days or days without infection. All variables were subjected to the Box-Cox transformation procedure (10) to achieve homogeneity of variance among groups and then standardized to zero mean and unit variance before discriminant analysis. The analysis was done with a singularity (tolerance) option of 0.10 to bypass multicollinearity. The degree of differentiation between the two groups obtained by entering the selected variables was interpreted in terms of the magnitude and significance level of the average squared canonical correlation (ASCC), which estimates the amount of variance accounted for by classifying the observations into the two groups. Discriminant analyses were performed for the 1991 and 1992 data sets separately, using procedures within the Statistical Analysis System Library (SAS Institute, Inc.).

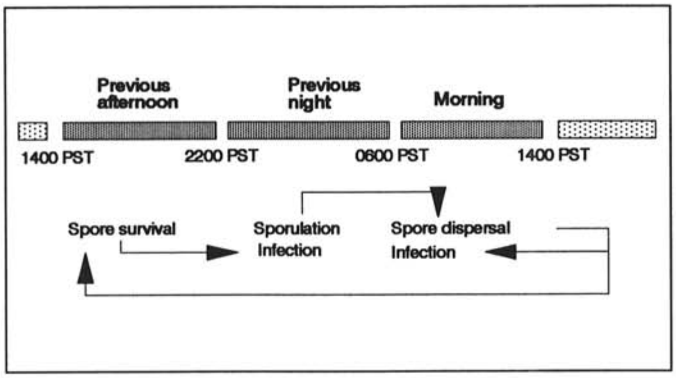

Fig. 1. Schematic representation of the infection cycle of lettuce downy mildew. Weather variables were summarized separately for the periods afternoon, night, and morning to match the biology of the pathogen. PST = Pacific standard time.

A series of permutation tests (18) was done to estimate the probability of obtaining a significant differentiation between infection days and days without infection by chance alone. For the 1991 data set, 41 of 93 days were randomly assigned to infection days, with the constraint that total leaf wetness duration (DAY-LWD) during infection days needed to be at least 4 h. The same procedure was applied to the 1992 data set in which 20 of 88 days were randomly assigned to infection days. For each year, 150 random permutations were obtained using the SAS pseudorandom number generator. Stepwise discriminant analyses were performed on each of the 150 permutations, and the weather variables that were statistically most important in each analysis were recorded.

RESULTS

Disease development. Disease progress curves (not shown) displayed erratic behavior on a per plant or per field basis because lesions on older leaves were removed when the leaves senesced. For the same reason, new lesions frequently did not result in increases in disease intensity. AUDPC values ranged from 0 to 17.4 proportion-days (Table 1), with a mean of 5.0 proportion-days. In two fields (trials 12 and 13), disease did not develop, but data were included because downy mildew inoculum was present in adjacent fields while the studies were done.

Weather variables. Based on pooled data from both years (181 site-days), correlations among the 14 weather variables were generally low to moderate (Table 3). However, DAY-LWD correlated strongly with LWD at night (NI-LWD; $r = 0.867$) and LWD in the morning (AM-LWD; $r = 0.720$). Correlation coefficients this high are potentially troublesome for multivariate analyses unless options to bypass multicollinearity, such as appropriate tolerance values, are used in further computations (1).

There was considerable overlap between the distributions of

TABLE 2. Definition of variables used for summarizing weather conditions at the study sites in coastal California

	Variable			
Measurement	Afternoon (1401-2200 hours)[a]	Night (2201-0600 hours)	Morning (0601-1400 hours)	Day (1401-1400 hours)
Mean wind speed (m s^{-1})	PM-WIND	NI-WIND	AM-WIND	. . .
Mean temperature (C)	PM-TEMP	NI-TEMP	AM-TEMP	. . .
Mean vapor pressure deficit (mbar)	PM-VPD	NI-VPD	AM-VPD	. . .
Solar irradiance (MJ m^{-2})	PM-SOLAR	. . .	AM-SOLAR	. . .
Leaf wetness duration (h)	. . .	NI-LWD	AM-LWD	DAY-LWD

[a] Pacific standard time.

TABLE 3. Simple correlations among weather variables at the study sites in coastal California during 1991 and 1992 ($n = 181$)

	Weather variable[a]												
	PM-WIND	PM-TEMP	PM-VPD	PM-SOLAR	NI-WIND	NI-TEMP	NI-VPD	NI-LWD	AM-WIND	AM-TEMP	AM-VPD	AM-SOLAR	AM-LWD
PM-TEMP	−0.100	1.000											
PM-VPD	−0.268	0.611	1.000										
PM-SOLAR	−0.115	0.416	0.495	1.000									
NI-WIND	0.649	−0.036	−0.167	−0.232	1.000								
NI-TEMP	0.316	0.241	−0.477	−0.362	0.356	1.000							
NI-VPD	0.191	−0.035	0.169	−0.085	0.283	0.090	1.000						
NI-LWD	−0.121	0.079	0.019	−0.096	−0.120	−0.109	−0.406	1.000					
AM-WIND	0.548	0.045	−0.116	−0.106	0.577	0.237	0.294	−0.069	1.000				
AM-TEMP	0.153	0.613	0.085	−0.045	0.103	0.550	0.010	0.115	0.281	1.000			
AM-VPD	−0.122	0.390	0.612	0.200	−0.029	−0.302	0.263	0.031	0.224	0.480	1.000		
AM-SOLAR	−0.229	0.310	0.474	0.469	−0.184	−0.428	−0.091	0.144	0.092	0.270	0.612	1.000	
AM-LWD	−0.161	0.063	−0.027	−0.078	−0.089	−0.013	−0.108	0.420	−0.136	−0.128	−0.232	−0.093	1.000
DAY-LWD	−0.165	0.002	−0.105	−0.216	−0.129	−0.002	−0.290	0.867	−0.111	0.027	−0.138	0.002	0.720

[a] Table 2 explains variable names.

most weather variables during infection days and days on which infection had not occurred (Fig. 2), indicating that no distinct separation between the two groups could be expected based on single variables. It is visually evident that the best separation was obtained with AM-LWD and DAY-LWD. Based on data from both years, AM-LWD had a mean of 4.2 h (median 4.0 h) on infection days, and a mean of 1.9 h (median 2.0 h) on days without infection. According to the Kolmogorov-Smirnov tests (Fig. 2), only AM-LWD and DAY-LWD had significantly different distributions during infection days and days without infection at $P = 0.0036$ (equivalent to $P = 0.05$ for the overall test). In contrast, PM-TEMP ($P \leq 0.1231$), PM-VPD ($P \leq 0.4334$), PM-SOLAR ($P \leq 0.3555$), NI-TEMP ($P \leq 0.5090$), NI-VPD ($P \leq 0.3831$), and AM-SOLAR ($P \leq 0.2853$) had very similar distributions in the two groups. NI-VPD was ≤1.0 mbar on more than 75% of all nights, indicating that conditions were generally conducive to sporulation (23).

In 1991, AM-LWD was the only variable entered into the solution of stepwise discriminant analysis (Table 4), resulting in an ASCC of 0.3616 ($P \leq 0.0001$). In 1992, six variables were selected (ASCC = 0.4353; $P \leq 0.0001$). However, only the first three variables (AM-LWD, AM-WIND, and PM-WIND) were significant at $P = 0.05$, and AM-LWD (partial ASCC = 0.2960) was statistically more important than the other five variables together (Table 4). When the data from both years were combined, the analysis resulted in a model with the variables AM-LWD, NI-WIND, NI-LWD, DAY-LWD, AM-WIND, and PM-WIND. Again, AM-LWD (partial ASCC = 0.3063) was more important than the other five variables together, and only two additional variables (NI-WIND and DAY-LWD) were significant at the 0.05 level (Table 4). Multicollinearity was not a problem in any of these analyses, as indicated by tolerance values >0.10 (data not shown).

Permutation tests. When infection days were assigned randomly during the season, a statistically significant differentiation between infection days and days without infection was observed in 292 of 300 discriminant analyses (using a very liberal significance level of $P = 0.20$ [7]). Most frequently, DAY-LWD and NI-LWD were selected as the most important variables (Fig. 3). This was expected because the constraint that DAY-LWD during infection days needed to be at least 4 h resulted in a systematic bias in the "random" assignment of days to the two groups. This pattern

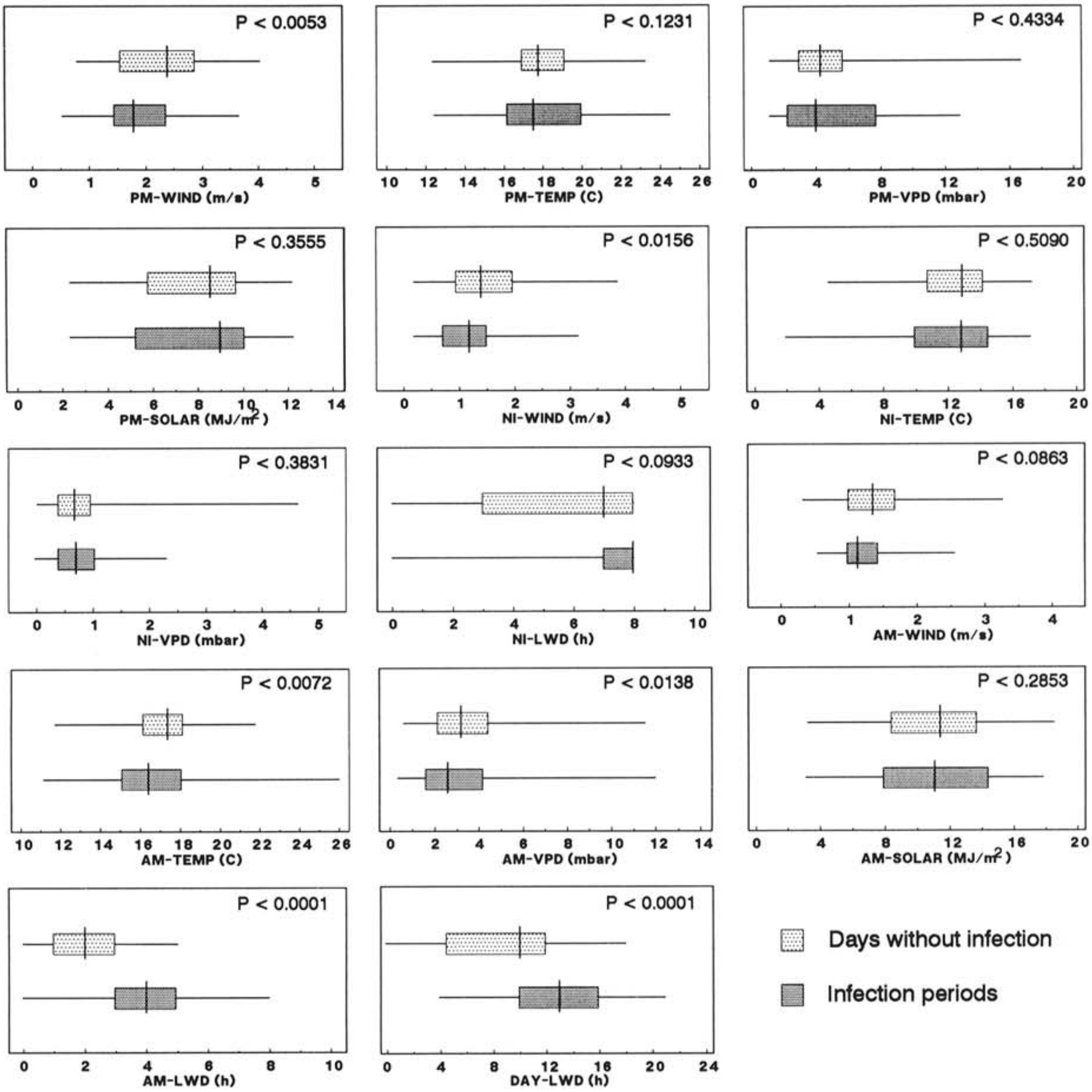

Fig. 2. Distributions of weather variables during infection days of lettuce downy mildew and days on which infection had not occurred. The data are presented as box-plots. The rectangles show the values below which 25% (left side of the box), 50% (center line), and 75% (right side of the box) of the observations fall. The horizontal lines extending from the boxes represent the extremes of the distributions. Distributions with $P \leq 0.0036$ (=0.05/14) were considered significantly different (Kolmogorov-Smirnov test). Table 2 explains the variable names.

was less apparent in 1992 than in 1991 (Fig. 3). AM-LWD was selected with frequencies of 0.180 (permutations on 1991 data) and 0.067 (permutations on 1992 data). Thus, the probability of obtaining AM-LWD as the most important variable in both years by chance alone (i.e., with random latent periods) was about 0.012 (=0.067 × 0.180).

DISCUSSION

Our 2-yr study confirmed earlier reports (12) that lettuce downy mildew occurs irregularly in the coastal regions of California. In several fields, symptoms appeared at early stages of crop development, but subsequently, no disease progress was observed for several weeks, despite the presence of sporulating lesions in these fields. At other locations, high levels of disease developed within less than 2 wk. These observations indicated that weather factors are important in limiting or favoring the disease.

Our statistical analyses were aimed at identifying weather variables significantly different during infection days versus days on which infection had not occurred. They showed that the best differentiation between the two groups was obtained with the variable AM-LWD. Additional variables did not help to differentiate between the two groups. This was consistent for both years (1991 and 1992) and with different methods of analyses (univariate and multivariate procedures). A preliminary analysis of the 1991 data set, in which a degree-day model for latent period was used to identify infection days, also resulted in AM-LWD as the most important factor for discrimination (25). The consistency of these results suggests that measured or predicted AM-LWD could be used in a decision support system for lettuce downy mildew management.

One possible explanation for the importance of AM-LWD for infection is that AM-LWD correlates well ($r = 0.720$) with DAY-LWD. In other words, the significance of AM-LWD in our analyses could have been an artifact arising from the division of each day into three separate periods for summarizing daily weather conditions. However, there are several arguments against this explanation. First, DAY-LWD was ≥4 h (the minimum required for infection by *B. lactucae*) on more than 75% of the days without infection (Fig. 2), suggesting that total leaf wetness duration was generally not limiting. Second, in the coastal areas of California, there are situations during which AM-LWD can occur without preceding leaf wetness at night. One of these is sprinkler irrigation, which is commonly applied in the morning. Similarly, coastal fog can result in AM-LWD without leaf wetness during the preceding night. Due to the cold waters off the central California coast and the persistent marine inversion, stratus clouds occur frequently in the study area. Daytime heating over the interior of California draws the clouds into the coastal valleys during the early evening, thus inhibiting the formation of dew at night (27). They usually dissipate during midmorning without causing leaf wetness on crops. Occasionally, however, the stratus develops into heavy, persistent fog with drizzle and prolonged AM-LWD. Third, there may be a biological explanation for the importance of AM-LWD. It has been hypothesized for other downy mildews that infection occurs primarily in the morning because spore dispersal and infection can occur concurrently during this period (4,11,33) and because relatively short periods of exposure to bright sunlight and low humidity (similar to those encountered during sunny afternoons in the study area) can be sufficient to inactivate downy mildew conidia (3,9,24). In semicontrolled experiments (done on potted plants outdoors), we found that spore dispersal and infection by *B. lactucae* can occur during the same morning if AM-LWD is long enough (29).

Although statistically highly significant, the discrimination between infection days and days without infection was less than perfect. The total amount of variance among the two groups of days explained by the analysis was less than 50% (Table 4). This suggests that factors other than the presence of inoculum and weather conditions conducive to infection are important for epidemics of lettuce downy mildew in coastal California. It has already been pointed out that the environment in the study area is generally favorable for sporulation of the fungus because advection of moist air from the ocean supplies consistently high humidity at night. However, spore survival could be an important factor, as discussed above, because afternoons are mostly clear with high incidence of solar radiation (latitude ~36 N). But we cannot make assertions regarding this hypothesis without data about the survival of *B. lactucae* conidia under the specific meteorological conditions of coastal California.

In our analyses, we related observations of the appearance of new lesions to weather events occurring one latent period earlier to identify weather conditions conducive to infection. This approach is based on several key assumptions. First, we assumed that inoculum was not limiting. In our trials, we ascertained that *B. lactucae* was present in the area while the studies were done. This assumption seems to hold generally for most of the coastal areas, because lettuce is grown as an extensive monocrop from March through October in successive, overlapping plantings, and the coastal fog belt may provide a reservoir of inoculum throughout the cropping season. However, there may be periods when inoculum is absent regionally, for example during early spring

TABLE 4. Weather variables selected by stepwise discriminant analysis for differentiating between infection days[a] of lettuce downy mildew and days on which infection had not occurred, based on field surveys in coastal California

Year	Variable[b]	$P > F$	Cumulative ASCC[c]	$P >$ ASCC
1991	AM-LWD	0.0001	0.3616	0.0001
1992	AM-LWD	0.0001	0.2960	0.0001
	PM-WIND	0.0118	0.3469	0.0001
	AM-WIND	0.0296	0.3829	0.0001
	NI-VPD	0.0992	0.4029	0.0001
	DAY-LWD	0.1375	0.4189	0.0001
	NI-LWD	0.1279	0.4353	0.0001
Combined years	AM-LWD	0.0001	0.3063	0.0001
	NI-WIND	0.0132	0.3299	0.0001
	NI-LWD	0.1456	0.3509	0.0001
	DAY-LWD	0.0053	0.3792	0.0001
	AM-WIND	0.1006	0.3846	0.0001
	PM-WIND	0.1674	0.3913	0.0001

[a] Days on which infection likely had occurred were identified based on observations of the appearance of new lesions combined with quantitative information about the length of the latent period of the disease (described in text).

[b] Table 2 explains variable names.

[c] Average squared canonical correlation.

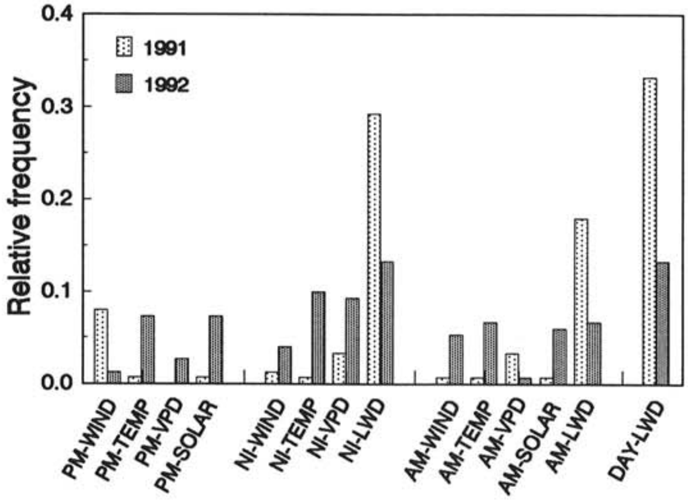

Fig. 3. Relative frequencies with which weather variables were selected by stepwise discriminant analysis for differentiating between infection days of lettuce downy mildew and days without infection when infection days were assigned randomly during the season (permutation tests). Each year 150 permutations were performed. Table 2 explains the variable names.

or after a persistent hot spell. Such situations need to be considered in the development of decision aids for downy mildew management. Second, we assumed that we could identify new lesions 1 or 2 days after they had appeared. Fresh downy mildew lesions are green or slightly chlorotic, and they turn yellow and necrotic after a few days (37). Thus, it is not difficult to distinguish between different age classes of lesions. However, there may be periods during which conditions are not conducive to sporulation, and chlorosis may occur as the first symptom of the disease in such situations. Moreover, a staggering in lesion appearance over a period of several days (22) may sometimes make the identification of distinct age classes impossible. Third, we assumed that latent periods were approximately constant (between 7 and 9 days in length), i.e., independent of temperature and other factors. This assumption contradicts results from constant-temperature experiments (37) in which strong interactions between temperature and latent period were observed. However, we found that temperature has only a small effect on the latent period of lettuce downy mildew when infected plants were exposed to fluctuating rather than constant temperatures (28). Based on these data, the assumption of a 7- to 9-day latent period seems realistic. This also is supported by our permutation tests, which showed no consistent pattern in the importance of weather variables for infection when latent periods were random.

Due to the restrictions posed by some of the underlying assumptions, the analyses should be regarded as an exploratory description rather than as a rigorous test. They are presented here with that understanding. Further work is currently under way to identify a mechanistic basis for the association between morning wetness period and infection (29), to quantify the importance of different sources of morning leaf wetness (sprinkler irrigation, coastal fog, and prolonged dew) for infection (27), and to determine the effects of different types and frequencies of irrigation on disease development (36).

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