Ecology and Epidemiology

Epidemiology of Grape Powdery Mildew: A Model

Mary Ann Sall

Assistant professor, Department of Plant Pathology, University of California, Davis 95616.

ABSTRACT

SALL, M. A. 1980. Epidemiology of grape powdery mildew: a model. Phytopathology 70:338-342.

A mathematical model is formulated to describe the increase of grape powdery mildew from bud break until fruit softening on leaves and fruit of cultivar Carignane. The purpose of the model is to examine the influence of seasonal weather patterns and timing of the initial occurrence of infections on the eventual colonization of grape leaves and fruit by the fungus. The basic structure of the model is derived from Vanderplank's equation for disease development. However, in the powdery mildew model, plant growth is simulated to allow changes in susceptible tissue during the growing season and is a function of ambient temperature. The basic infection rate (r) varies as a function of ambient temperature and moisture conditions. The model is validated by the close agreement of model results with epidemics observed on cultivar Carignane grapes in 1976 and on cultivar Emerald Riesling grapes in 1977. The most severe powdery mildew is predicted for years with warm spring weather and the least when spring temperatures are coolest. The level of infection at fruit softening is significantly reduced when initial infections occurred more than 2 wk after bud break.

Additional key words: Vitis vinifera, Uncinula necator.

Grape powdery mildew, caused by *Uncinula necator* (Schw.) Burr., is a chronic problem in California vineyards (*Vitis vinifera* L.). In spite of regularly applied control measures, the disease can cause economic losses in susceptible cultivars. The seasonal weather pattern and the timing of the initial occurrence of infections each season seem largely to determine the severity of the disease.

Many reports have been made concerning the influence of environmental conditions on powdery mildew. Most agree that the disease develops rapidly between 21–30 C (4,7). Older reports based on field observations indicate that high humidity favors powdery mildew development (1,5–7). However, Delp (4) demonstrated experimentally that, although free water decreased germination, there was no significant difference in germination or growth rates over the entire range of relative humidity. In grape-growing areas, periods of high humidity often accompany the moderate temperatures which are favorable for powdery mildew development.

In many vineyards the initial appearance of infections may be delayed and often do not appear even in untreated areas until many weeks after susceptible tissue is present and favorable environmental conditions prevail. Although cleistothecia are frequently found, the role of ascospores in the epidemiology of grape powdery mildew is unclear (2). A more likely source of initial inoculum is the mycelium which survives through the winter under bud scales (10). In California, the author and other experienced observers have found these bud infections infrequently and only on grape cultivars Carignane and Thompson Seedless. Therefore, the first appearance of infections in a given location may be dependent on the presence or proximity of infected buds.

This paper presents a model of powdery mildew epidemics. The purpose of the model is to examine the influence of seasonal weather patterns and timing of the initial occurrence of infections on the colonization of grapevines by the powdery mildew fungus. The model is one of a series that will be used to evaluate potential management procedures and to define economic levels of powdery mildew control. It was formulated to describe the increase of powdery mildew on leaves and fruit for the cultivar Carignane grown near Lodi, CA.

P. megasperma f. sp. *glycinea* for isolates that infect soybean (*G. max*). The use of *glycinea* to replace *sojae* was suggested by D. P. Maxwell to be consistent with the use of the name of the genus of the host attacked and avoid the confusion which might result from the use of *sojae*.
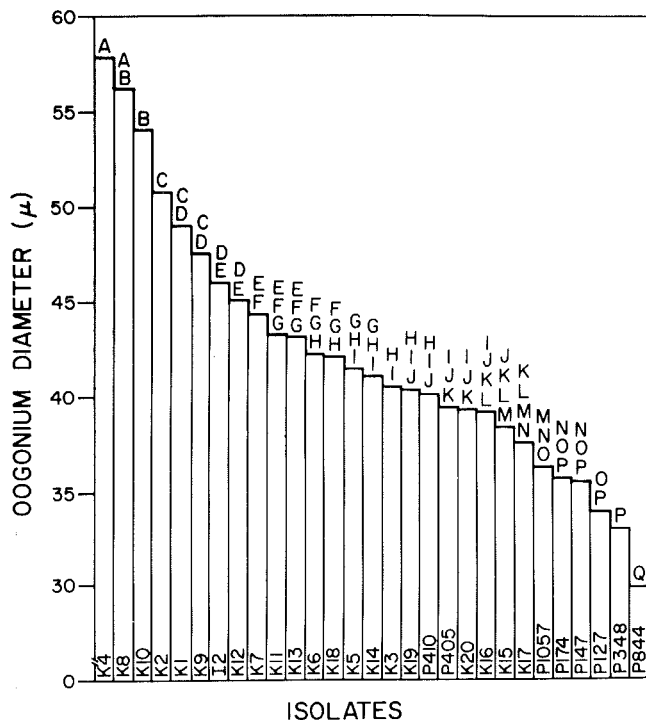

Fig. 3. Oogonia diameters of 29 isolates of *Phytophthora megasperma*. Each isolate was grown on V-8 juice agar at 24 C for 1 mo. Value represents mean of 30 measurements of each isolate. Mean values followed by same letter are not significantly different (*P* = 0.01) according to Duncan's multiple range test.
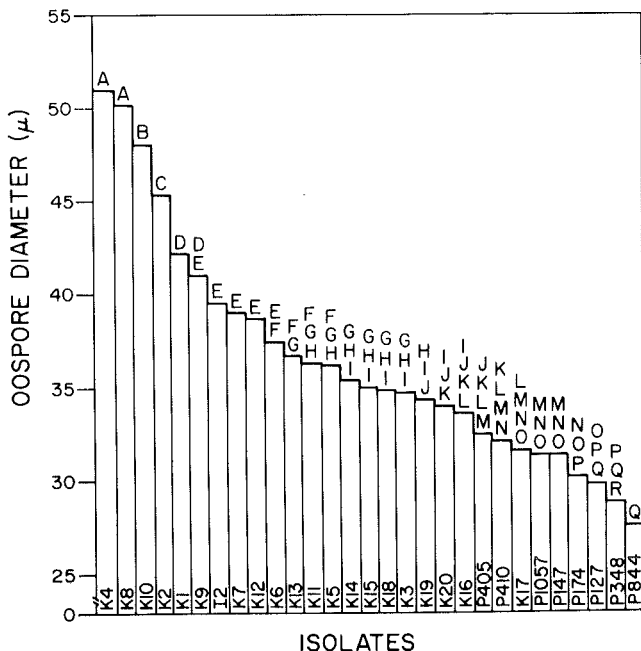

Fig. 4. Oospore diameters of 29 isolates of *Phytophthora megasperma*. Each isolate was grown on V-8 juice agar at 24 C for 1 mo. Value represents mean of 30 measurements of each isolate. Mean values followed by same letter are not significantly different (*P* = 0.01) according to Duncan's multiple range test.
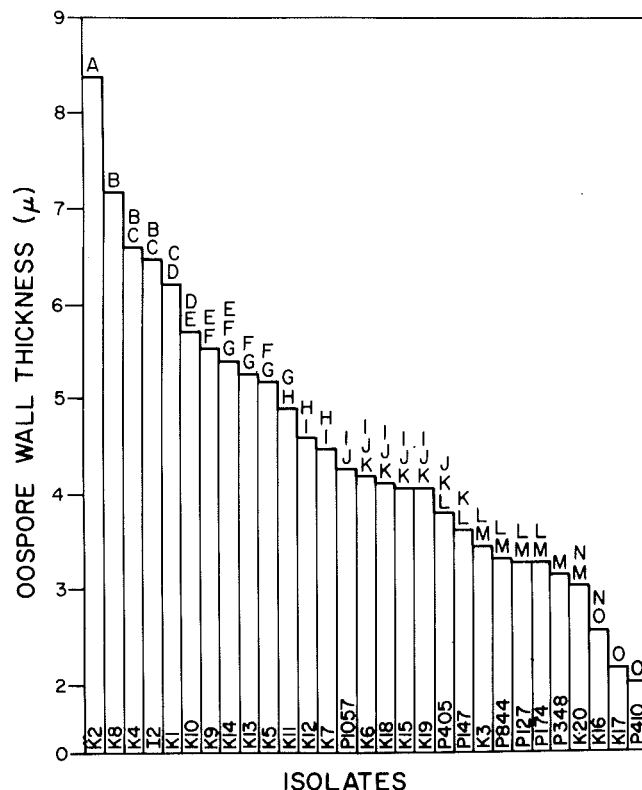

Fig. 5. Oospore wall thicknesses of 29 isolates of *Phytophthora megasperma*. Each isolate was grown on V-8 juice agar at 24 C for 1 mo. Value represents mean of 30 measurements of each isolate. Mean values followed by same letter are not significantly different (*P* = 0.01) according to Duncan's multiple range test.

LITERATURE CITED

1. BHELWA, P. W. 1975. Physiology of two isolates of alfalfa *Phytophthora*. Botanique 5:19-24.
2. DRECHSLER, C. 1931. A crown rot of hollyhocks caused by *Phytophthora. megasperma* n. sp. J. Wash. Acad. Sci. 21:513-516.
3. ERWIN, D. C. 1965. Reclassification of the causal agent of root rot of alfalfa from *Phytophthora cryptogea* to *P. megasperma*. Phytopathology 55:1139-1143.
4. ERWIN, D. C. 1966. Varietal reaction of alfalfa to *Phytophthora megasperma* and variation in virulence of the causal fungus. Phytopathology 56:653-657.
5. HILDEBRAND, A. A. 1959. A root and stalk rot of soybean caused by *Phytophthora megasperma* Drechsler var. *sojae*. Can. J. Bot. 37:927-957.
6. IRWIN, J. A. G. 1974. Reaction of lucerne cultivars to *Phytophthora megasperma*, the cause of a root rot in Queensland. Austr. J. Exp. Agric. Anim. Husb. 14:561-565.
7. IRWIN, J. A. G., S. A. MILLER, and D. P. MAXWELL. 1979. Alfalfa seedling resistance to *Phytophthora megasperma*. Phytopathology 69:1051-1055.
8. JOHNSON, T. 1968. Host specialization as a taxonomic criterion. Pages 534-546 in: G. C. Ainsworth, and A. S. Sussman, eds. The Fungi. An Advanced Treatise. Vol. 3. Academic Press, New York, and London. 738 pp.
9. JONES, J. P., and H. W. JOHNSON. 1969. Lupine, a new host for *Phytophthora megasperma* var. *sojae*. Phytopathology 59:504-507.
10. KAUFMANN, M. J., and J. W. GERDEMANN. 1958. Root and stem rot of soybean caused by *Phytophthora sojae* n. sp. Phytopathology 48:201-208.
11. KEELING, B. L. 1976. A comparison of methods used to test soybean for resistance to *Phytophthora megasperma* var. *sojae*. Plant Dis. Rep. 60:800-802.
12. LUTTRELL, E. S. 1974. Parasitism of fungi on vascular plants. Mycologia 66:1-15.
13. MATSUMOTO, N., and T. ARAKI. 1978. Alfalfa root rot caused by *Phytophthora megasperma* Drechsler in Japan. Ann. Phytopathol. Soc. Jpn. 44:214-217.

THE MODEL

The basic structure of the model is derived from Vanderplank's (9) compound interest equation for disease development:

$$dx/dt = r \, x_{t-p} \, (1 - x_t) \tag{1}$$

in which: r = basic infection rate; x_{t-p} = proportion of tissue infected and producing inoculum at time t; $(1-x_t)$ = proportion of tissue not infected at time t; and p = length of the latent period.

However, in this powdery mildew model, changes in the equation are made on each simulated day to reflect changing conditions. The apparent infection rate is not assumed to be constant, but varies as a function of temperature and moisture conditions. Also, the susceptible tissue increases through the growing season to simulate vine growth. The model is made up of a series of submodels which compute vine growth, the diurnal temperature pattern, and infection rate. It produces an average daily increase in infected and uninfected leaf and berry surface area per cane from bud break until about fruit softening (150 days).

Model predictions do not extend beyond fruit softening when fruit has about 8% sugar because at this time the fruit becomes resistant to further infection (4). Subsequent leaf infections are infrequent and occur only on shaded leaves until temperatures drop in the autumn after harvest.

Vine growth submodel. This submodel describes the increase in the surface area of the susceptible parts of the vine. It is based on the assumption that when other factors are constant or not limiting, variations in temperature largely account for variations in vine growth rate.

The temperature effect (TE) on surface area expansion is not known. However, the relationship with photosynthesis rate of grapevines was derived from published data (8):

$$TE = -0.35968 + 0.10789 \, T - 0.00214 \, T^2 \tag{2}$$

in which: TE = effect of temperature on modifying the maximum rate ($0 \leqslant TE \leqslant 1$); and T = air temperature, C. The effect of temperature on photosynthesis also was assumed to be proportional to the rate of surface area increase.

The surface area of berries and leaves were periodically measured on field-grown, 15-yr-old, head-trained vines of cultivar Carignane. The leaves quickly expanded after bud break and growth rates did not slow down until after the beginning of fruit softening. Growth of the berries followed an S-shaped curve (Fig. 1).

Equations which represent the rate of surface area expansion under optimum temperature conditions were derived from these data, the known temperature record, and equation 2:

$$DBO = 172.4 \, BSA - 21.2 \, BSA^2 \tag{3}$$

$$DVO = 1.33 \, YD \tag{4}$$

in which: DBO = daily increase in berry surface area (cm^2) per cane under optimum temperature conditions; BSA = berry surface area (cm^2); DVO = daily increase in (upper and lower) leaf surface area (cm^2) per cane under optimum temperature conditions; and YD = days of crop growth from 1 April. The expansion of surface area under suboptimal conditions is assumed to be related to the median daily temperature:

$$DBSA = DBO \cdot TE \tag{5}$$

$$DVSA = DVO \cdot TE \tag{6}$$

$$BSA_i = BSA_{i-1} + DBSA_i \tag{7}$$

$$VSA_i = VSA_{i-1} + DBSA_i \tag{8}$$

in which: DBSA = daily increase in berry surface area (cm^2) per cane; DVSA = daily increase in leaf surface area (cm^2) per cane;

VSA = vine surface area (cm^2) per cane; and TE = temperature effect computed according to equation 2 with T = the median daily temperature. These submodels have not been independently validated. However, the curves they describe (Fig. 1) are similar to published patterns of fresh weight growth (11).

The first iteration of the model is assumed to represent the first day of shoot growth, and thus leaf surface expansion begins (DVSA, equation 6). When the median temperature exceeds 20 C, fruit development begins (11) (DBSA, equation 5). For day i, the total susceptible surface area (TSA$_i$) is found:

$$TSA_i = DVSA + DBSA + TSA_{i-1} \tag{9}$$

Diurnal temperature submodel. The purpose of this model is to describe a diurnal temperature pattern when provided with the daily high (T$_{max}$) and low (T$_{min}$) temperatures. It was derived from data recorded on 20 strip charts with a Model H311 Weathermeasure Hygrothermograph, (Weather Measure Co., Sacramento, CA 95841) in a vineyard near Lodi, CA. The recording thermograph was located in a standard weather shelter between vines and should represent the ambient air temperature near the vines. The selected charts were chosen systematically from those recorded from 1 April to 31 August 1976.

Temperature forms a modified sine-wave pattern (Fig. 2):

$$T_h = A \sin (15 \, H + 210) + M \tag{10}$$

in which: T$_h$ = air temperature at time H; A = (T$_{max}$ − T$_{min}$)/2; H = time by the 24-hour clock; and M = daily median air temperature. The simulated daily low occurs at 0400 hours and the high at 1600 hours.

Infection submodel. This submodel relates ambient air temperature and rainfall to the rate of colonization of the vine surface by powdery mildew.

Colonization of the vine surface by powdery mildew involves the processes of germination, infection, and growth. An equation relating the effects of air temperature on these processes was derived from growth chamber experiments (3) (Fig. 3):
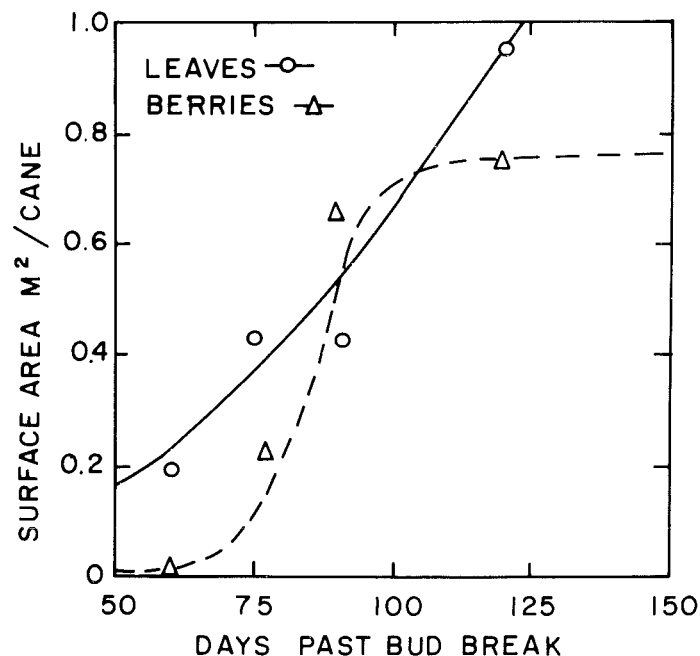

Fig. 1. Observed (Δ, o) and predicted (———) (equations 5 and 6) patterns of surface area expansion for berries and leaves, respectively, from 15-yr-old Carignane grapevines grown near Lodi, CA.

$$PT = 0 \qquad\qquad ; T \leqslant 0 \qquad (11)$$

$$PT = 0.000241 \; T_h^{\,2.06737} \, (35-T_h)^{\,0.72859} \quad ; 0 < T < 35$$

$$PT = 0 \qquad\qquad ; T \geqslant 35$$

in which: PT = effect of air temperature on the rate of colonization.

The temperature experienced by the powdery mildew fungus changes throughout the day, but how it reacts to these changes is not known. In this model, it is assumed that the growth rate of the fungus changes instantly in response to temperature changes and that past temperatures do not influence the growth rate at any time. Thus, the effect of the diurnal pattern can be found by combining equations 10 and 11 and applying the intermediate value theorem of calculus. A good estimation of the intermediate value is:

$$MPT = \left[\sum_{h=1}^{24} P\,T_h \right] \Big/ \; 24 \qquad (12)$$

in which: PT_h = value of PT from equation 11 computed with hourly temperatures derived from equation 10; and MPT = mean value of PT_h. This estimator is not equivalent to computing PT based on the mean temperature for the day. For example, the MPT computed for the day illustrated in Fig. 2 is 0.59, while PT based on the mean temperature (25.5 C) is 1.00.

Humidity is reported to have little effect on germination or development. However, free water causes poor germination (4) and may cause colony death (3). At all temperatures, the depression in germination caused by the presence of free water was about 60% of the maximum rate. It was assumed that the influence of moisture on germination would be the same as its influence on the rate of colonization. Thus,

$$PW = 0.4; \text{ if free water present,} \qquad (13)$$

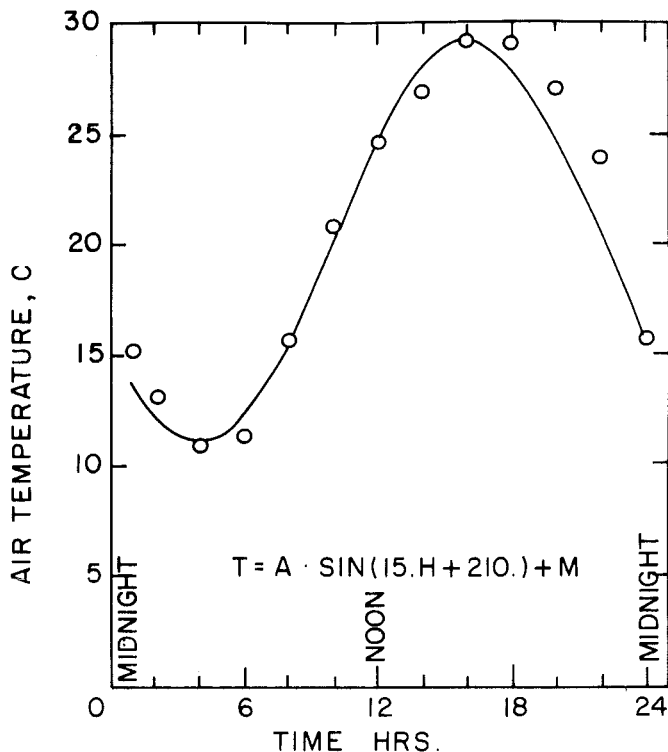$$= 1.0; \text{ if no water present,}$$

in which: PW = effect of free water on maximum rate of colonization. Free water was assumed to be present on days when recorded rainfall exceeded trace (0.01 in.) amounts.

The rate of colonization of powdery mildew on Carignane vines under optimum temperature conditions and in the absence of free water was derived from greenhouse experiments. Fifty rooted cuttings with from 10–52 leaves per shoot were inoculated on the first fully expanded leaf. The extent of the surface area which was colonized was evaluated weekly for 6 wk. The basic infection rate under optimal conditions (R_{max}) was derived from the colonization data, using Vanderplank's (9) estimation method.

The influence of temperature and moisture conditions on the infection rate may be represented by:

$$R = R_{max} \; MPT \quad PW \qquad (14)$$

in which: R = apparent infection rate; R_{max} = 0.35, for cultivar Carignane; MPT = temperature effect, eq. 12; and PW = moisture effect, eq. 13.

The rate of colonization of the vine surface by powdery mildew for day i (DXT_i) is found by using a difference equation approximation of equation 1:

$$DXT_i = R \; XT_{i-p}\,(1 - XT_i) \qquad (15)$$

in which: XT_i = proportion of surface area already colonized by day i; p = length of the latent period, estimated to average 9 days, and the amount of infected surface area (ISA_i) is found by:

$$ISA_i = DXT_i \; TSA_i + ISA_{i-1} \qquad (16)$$

Note that XT_i is equal to zero until the day of initial infection. To begin the simulation of disease spread, the day and amount of initial infection must be specified.
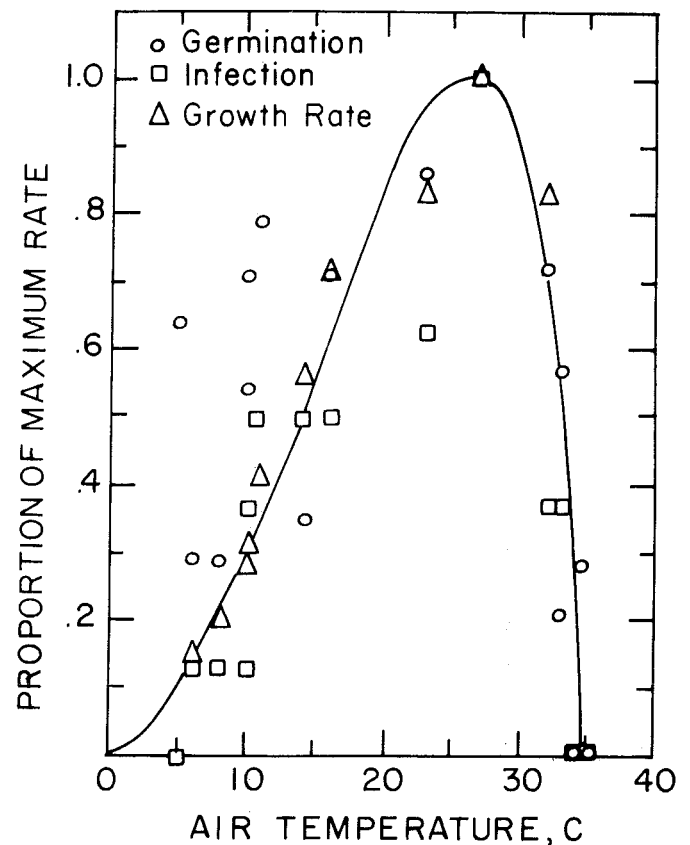

Fig. 2. Observed (o) and predicted (———) (equation 10) diurnal temperature pattern for 13 May 1976 in a vineyard near Lodi, CA.

Fig. 3. Observed (o, □, △) (from C. J. Delp. 1953 Ph. D. Thesis, Univ. California, Davis) and predicted (equation 11) temperature response curve for the germination, infection, and growth of *Uncinula necator*.

VALIDATION

To establish prima facie validity of the model structure, predicted values were compared to observed powdery mildew levels in a Carignane vineyard near Lodi, CA in 1976. Data from this vineyard were used to develop the vine growth and diurnal temperature submodels, so the comparison was not an independent test for these submodels. Each week 15 vines were observed and the percentage of the surface area of leaves and fruit colonized by the fungus was estimated. The level of surface colonization of the fruit was estimated by visual examination of 200 clusters in the field and by dissecting 10 clusters, counting the infected berries, and measuring berry diameters to estimate surface area. Leaf colonization was estimated by visually estimating infection level on upper and lower surface of leaves on 150 canes and by planimeter measurements of leaves from five canes. The comparison (Fig. 4) shows a remarkably close fit in which predicted values are not significantly different from observations based on χ^2 test ($P \leqslant 0.05$).

A further test of the model structure was made by comparing predicted values to observations made in an Emerald Riesling vineyard near Soledad, CA in 1977. The vine growth submodel was adjusted to reflect differences in the two grape cultivars. Again, approximately weekly observations of mildew level were made and the predicted values appear to be fairly close (Fig. 5) (χ^2 test, $P \leqslant 0.10$).

Simulation results and discussion. The model has been used to evaluate the effect of various weather patterns on the course of mildew development. To do this, a generalized temperature pattern for Lodi, CA, was derived using the weather records 1957-1977:

$$T_{max} = 20.953 + 0.202 \ YD - 0.001 \ YD^2, \qquad (17)$$

$$T_{min} = 5.147 + 0.162 \ YD - 0.001 \ YD^2. \qquad (18)$$

This was considered normal, and adjustment factors (TA) were multiplied by equations 17 and 18 to create various sequences:

Cold spring, TA $= 0.85 + 0.002 \ YD, \ YD < 75,$ (19)
$\qquad\qquad\qquad = 1.0 \qquad\qquad , YD \geqslant 75;$

Warm spring, TA $= 1.15 - 0.002 \ YD, \ YD < 75,$ (20)
$\qquad\qquad\qquad = 1.0 \qquad\qquad , YD \geqslant 75;$

Cold summer, TA $= 1.0 \qquad\qquad , YD < 75;$ (21)
$\qquad\qquad\qquad = 1.15 - 0.002 \ YD, \ YD \geqslant 75;$

Warm summer, TA $= 1.0 \qquad\qquad , YD < 75;$ (22)
$\qquad\qquad\qquad = 0.85 + 0.002 \ YD \ , YD \geqslant 75.$

Scattered spring or summer rain patterns were formed by assuming measurable rain fell every 14 days during the season.

The model results predict that the seasonal weather patterns will have marked effects on powdery mildew incidence (Table 1). The most severe mildew is predicted for years with warm spring weather, whereas the least is predicted when the spring temperatures are coolest. The rain patterns had almost no effect. Support of these results was found in 1978, when the powdery mildew was severe in most grape-growing regions of California and

the early spring temperatures averaged ~2.2 C above normal.

The influence of the timing of initial infections on subsequent colonization also was examined (Fig. 6). The level of infection at fruit softening is less than half as great when initial infection is delayed more than 2 wk after bud break. The model results indicate that early prevention of powdery mildew is essential for good control of the disease.
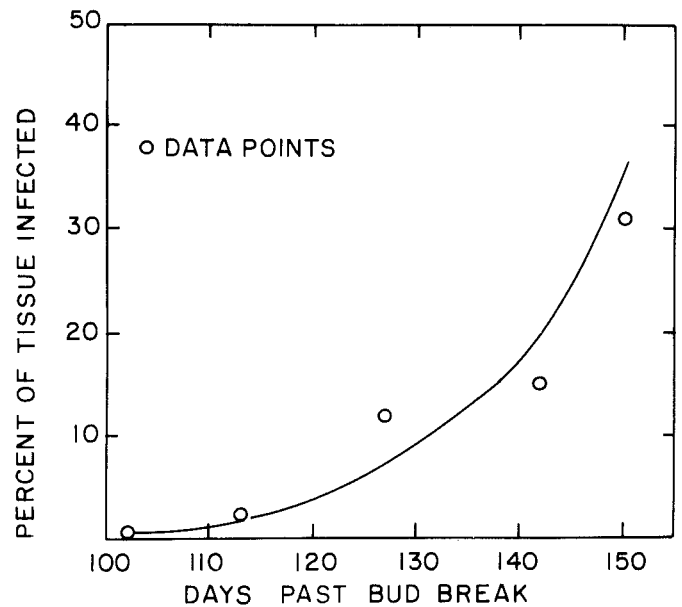
Fig. 4. Model validation–comparison of powdery mildew epidemic which occurred in an untreated Carignane vineyard near Lodi, CA in 1976 (o) and the epidemic curve predicted (——) by the powdery mildew model using the temperature and rainfall records and the date when powdery mildew was first observed from the comparison vineyard.

TABLE 1. Epidemiological model prediction of grape leaf and fruit colonization by *Uncinula necator* at the fruit softening stage for various temperature and rainfall patterns (see text) at Lodi, CA

Temperature pattern	Surface area colonized (%)		
	Scattered spring rain	Scattered summer rain	No rain
Normal Lodi, CA[a]	54.4	53.3	59.4
Cool spring	46.5	45.4	51.4
Warm spring	61.1	59.9	66.0
Cool summer	48.3	47.2	53.2
Warm summer	56.8	55.7	61.8

[a] Normal temperature pattern for Lodi, CA, was derived from weather data for 1957–1977.

Fig. 5. Model validation—comparison of powdery mildew epidemic which occurred in an untreated Emerald Riesling vineyard near Soledad, CA in 1977 (o) and the epidemic curve predicted (———) by the powdery mildew model using the temperature and rainfall records and the date when powdery mildew was first observed from the comparison vineyard.
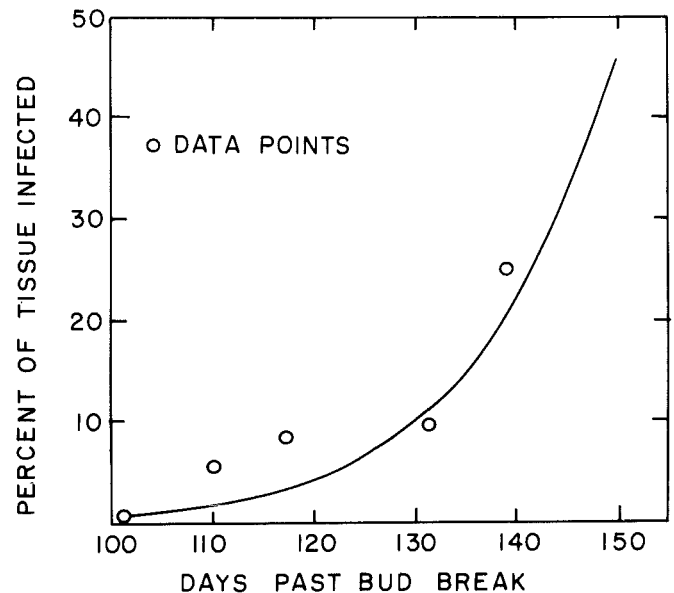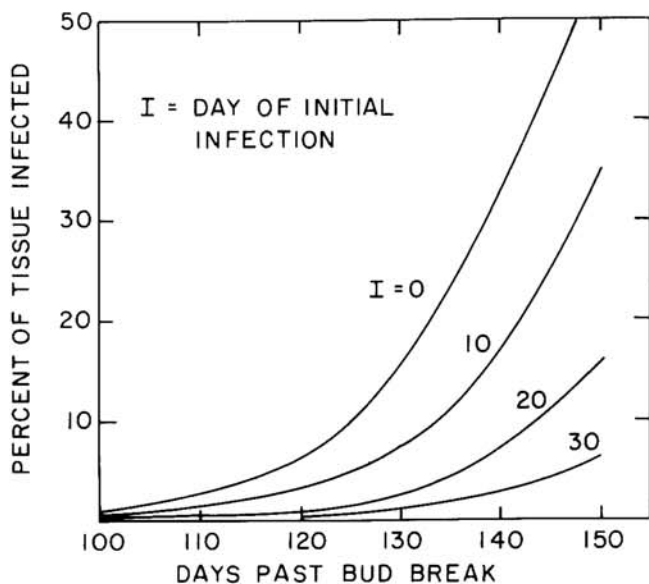
Fig. 6. Model predictions—the influence of the timing of initial infections on subsequent development of powdery mildew.

LITERATURE CITED

1. BIOLETTI, F. T., and F. CH. H. FLOSSFEDER. 1915. Oidium or powdery mildew of the vine. Calif. Agric. Exp. Stn. Circ. 114. 12 pp.
2. BLUMER, S. 1967. Echte Mehltaupilze (Erysiphaceae) ein Bestimmungsbuch für die in Europa vorkommenden Arten. G. Fischer, Jena. 436 pp.
3. DELP, C. J. 1953. Some environmental factors which influence the development of the grape powdery mildew fungus, *Uncinula necator* (Schw.) Burr. Ph.D. Thesis. University of California, Davis. 133 pp.
4. DELP, C. J. 1954. Effect of temperature and humidity on the grape powdery mildew fungus. Phytopathology 44:615-626.
5. DuPLESSIS, S. J. 1944. Powdery mildew of the vine and its control. S. Afr. Dep. Agric., Sci. Bull. 238. 24 pp.
6. GLADWIN, F. E. 1928. Downy and powdery mildew of the grape and their control. N.Y. Agric. Exp. Stn. Bull. 560. 14 pp.
7. JACOB, H. E. 1929. Powdery mildew of the grape and its control in California. Calif. Agric. Ext. Serv. Circ. 31. 17 pp.
8. KRIEDEMANN, P. E. 1968. Photosynthesis in vine leaves as a function of light intensity, temperature, and leaf age. Vitis 7:213-220.
9. VANDERPLANK, J. E. 1963. Plant Diseases: Epidemics and Control. Academic Press, New York. 349 pp.
10. VAN DER SPUY, J. E., and F. N. MATTHEE. 1977. Overwintering of the Oidium stage of *Uncinula necator* in the buds of the grapevine. Plant Dis. Rep. 61:612-615.
11. WINKLER, A. J., J. A. COOK, W. M. KLIEWER, and L. A. LIDER. 1974. General Viticulture. University of California Press, Berkeley. 710 pp.