Techniques

Development of a Demographic Growth Model for *Uncinula necator* by Using a Microcomputer Spreadsheet Program

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ABSTRACT

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A demographic model simulating population growth of a plant pathogenic fungus was created by using a microcomputer spreadsheet program. The model was based on the age-specific survival and fecundity rates for *Uncinula necator* and was used to examine the effects of various environmental factors and disease control strategies on population growth over a 30-day period. Simulation results are used to illustrate the potential benefits from the application of spreadsheet programs to epidemiologic modeling. Techniques were presented to enable the reader to recreate this or other simulation models based on age-specific survival and fecundity.

Additional keywords: disease management, grape powdery mildew.

Epidemiological models may facilitate studies in plant pathology in several ways. They draw attention to areas in which information on the biology of the host/pathogen system is lacking (19,22,30,31) and they serve as excellent teaching aids by displaying epidemic development under a variety of chosen conditions (5). Applications of epidemiologic models include assessing the impact of host growth and environmental factors on disease development (2,3,20,23). They may also be used to optimize disease management strategies (1,14,21,27,28).

To develop more than the most elementary model, it is necessary to be well-versed in a computer programming language. This has deterred many researchers from realizing the potential benefits of epidemiological modeling. With the advent of microcomputers and their associated software, it is now possible to develop even complex models without a significant investment of time to learn a programming language. For example, in the veterinary sciences, deterministic, stochastic, and Markov-chain epidemiologic models

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were developed and run with a microcomputer spreadsheet program (6,8,9). A management decision model for assessing the economics of pest control strategies was also developed on a microcomputer spreadsheet program (7). To date, microcomputer spreadsheet programs have not been used to develop epidemiologic models for plant diseases.

A spreadsheet-based model for grape powdery mildew, caused by the fungus *Uncinula necator* (Schwein.) Burr., was developed in this study. Powdery mildew is an economically important disease of cultivated grapevines (*Vitis vinifera* L.) in California. *U. necator* is capable of colonizing all succulent tissues on the host, while mature tissue such as older leaves and fruit with sugar levels above 12% are resistant (12,13). The infection cycle may be summarized in five phases: germination, penetration, colonization, sporulation, and dispersal.

Quantitative information on the influence of environmental and physical factors on germination, penetration, colonization, and sporulation is available. Germination is completed within 30 hr after inoculation (11). Conidia that fail to penetrate host tissue within 48 hr of inoculation do not develop further (12). Established colonies may sporulate from 5 to 35 days after inoculation (10). The daily sporulation rate depends on the age of the colonies (10). Mortality of colonies that grow in temperatures between 19 and 30 C is not observed until at least 20 days after inoculation (10). Information on dispersal of *U. necator* is unavailable.

Current disease management practices include an application of wettable sulfur immediately after budbreak, followed by applications of sulfur dust at 7- to 10-day intervals or a demethylation inhibiting fungicide at 10- to 21-day intervals (18). Fungicide applications continue until veraison (berry softening) for wine and raisin grapes or just before harvest for table grapes. In California, increasing public pressure to minimize pesticide use necessitates the evaluation of alternative disease management strategies. The spreadsheet-based simulation model developed in this study will be used to evaluate the potential impact of various disease management strategies on population growth of *U. necator*.

MATERIALS AND METHODS

Equations used in the model. The influence of temperature on germination was estimated from Delp (11) by using the polynomial regression equation:

$$GR = -2.641 + 0.256T - 0.00528T^2 \quad (1)$$

in which GR = germination rate, and T = average daily temperature. The influence of temperature on penetration was estimated from Delp (11) by using the polynomial regression equation:

$$PR = -0.639 + 0.108T - 0.00254T^2 \quad (2)$$

in which PR = penetration rate, and T = average daily temperature. The influence of temperature on daily sporulation rates was estimated from information developed by Chellemi (10). To account for differences in sporulation rates attributable to colony age, a separate polynomial regression equation was obtained for each day for colonies between the ages of 5 and 35 days (10). These equations are available from the authors upon request. The influence of liquid water on germination was estimated from Delp (11) by using the regression equation:

$$GRM = 1.155 - 0.014*T \quad (3)$$

in which GRM = reduction in the germination rate due to presence of liquid water on the host surface, and T = average daily temperature. The influence of liquid water on sporulation was estimated from Chellemi (10) by using the polynomial regression equation:

$$SRM = -10.998 + (0.939*T) - (0.019*T^2) \quad (4)$$

in which SRM = reduction in the number of conidia produced per day due to the presence of liquid water on the host surface, and T = average daily temperature. All regression procedures were performed by using SAS (25).

The probability of conidia being deposited on susceptible leaf tissue was derived by determining the ratio of susceptible leaf area to ground area occupied by the vineyard (Table 1). Measurements of total and susceptible leaf area per vine were obtained on 20-yr-old, head-trained, cane-pruned, vines of *V. vinifera* 'Chardonnay' grafted to A×R 1 rootstock and grown in Napa Valley, CA. Determination of susceptible leaf tissue was based on observations of powdery mildew development on immature and mature leaves of seven grapevine cultivars (13). A similar approach was used to estimate the maximum potential of spore release by *Botrytis squamosa* (1).

Conceptual framework for the model. The model simulated population growth of *U. necator* on *V. vinifera* 'Carignane' over time. It was based on the secondary infection cycle and was designed to follow the fate of each cohort from germination until sporulation ceased. Population size was determined by the number of viable colonies present each day.

For example, when a specified density of spores (initial inoculum) was placed on susceptible leaf tissue, the number that germinated was obtained by using the equation for germination rate in which $T1$ = the average of hourly temperatures on day 1 (Fig. 1). Of those conidia that germinated, the number successfully penetrating host tissue to establish colonies was obtained by using the equation for penetration rate in which $T2$ = the average of hourly temperatures on day 2. The number of conidia

TABLE 1. Estimates of leaf area per grapevine susceptible to *Uncinula necator*

Date	Leaf area[a]	Susceptible leaf area	Leaf area/ vine area	Susceptible leaf area/ vine area
3 April	185[b]	185	0.003	0.003
10 April	1,332	1,069	0.018	0.014
17 April	9,699	1,209	0.130	0.016
1 May	21,150	1,084	0.352	0.015

[a]Twenty-year-old, head-trained, cane-pruned *Vitis vinifera* 'Chardonnay' on A×R 1 rootstock in Napa Valley, CA.
[b]cm^2.

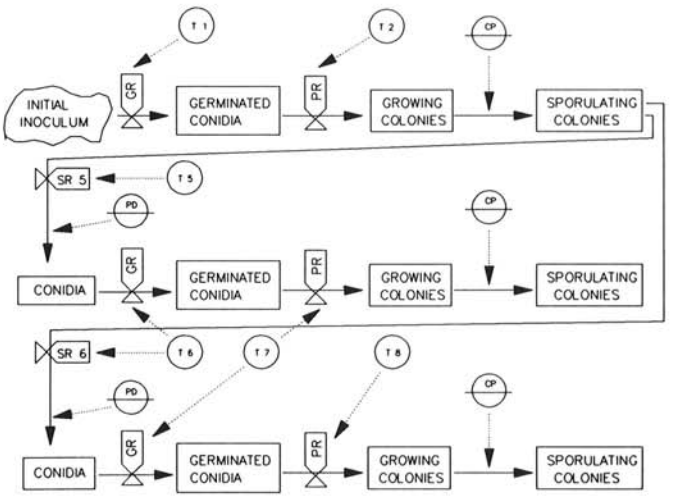

Fig. 1. Flow diagram for portion of Model I. GR = germination rate, PR = penetration rate, $SR5$ = sporulation rate for 5-day-old colonies, $SR6$ = sporulation rate for 6-day-old colonies, CP = colonization period required before colonies can begin sporulation, PD = probability of a newly produced conidium being deposited on susceptible tissue, $T1$ = temperature on day 1, $T2$ = temperature on day 2, $T5$ = temperature on day 5, $T6$ = temperature on day 6, etc.

produced by colonies on day 5 was obtained by using the equation for the sporulation rate of 5-day-old colonies:

$$SR5 = C(-386.144 + 32.870T - 0.659T^2) \quad (5)$$

in which $SR5$ = the number of conidia produced per colony, C = the number of 5-day-old colonies present, and T = the average of hourly temperatures on day 5. The number of conidia germinating on day 6 was determined after multiplying the probability of conidia being deposited onto susceptible tissue by the equation for germination rate.

If water was present on the host surface on day 5 then the number of conidia produced by 5-day-old colonies was modified by using equation 4. If water was present on day 6 then the number of conidia that germinated on day 6 was modified by using equation 3. The contribution of individual colonies to population growth is followed for up to 35 days. Thus, age-structure and changes in environmental conditions were included in projections of population growth.

Software program. A spreadsheet program, SuperCalc 5.0, (Computer Associates, San Jose, CA) was used for construction and simulation of the model. A spreadsheet provides the user with a worksheet in which text, data, and mathematical functions can be entered. The information is stored in cells identified as the intersection of a row and column, e.g., $A1$ refers to the cell located in the first row of column A. The equation $A1 + B1$ entered in cell $C1$ will add $A1 + B1$ and report the results in cell $C1$. Calculations are performed as indicated; given any change in information, the spreadsheet will automatically recalculate. Other beneficial features of a spreadsheet are that equations may be modified without retyping the entire equation and are easily copied to other cells by using a copy command. The spreadsheet can run on an IBM or IBM-compatible computer with at least 640K of random access memory, a math coprocessor, and DOS 2.1 or greater.

Simulations. Two models were constructed. Model I contained information about temperature effects on population growth, while Model II contained information about the effects of temperature in the presence of liquid moisture on the foliage. Formulas used in the first five columns and six rows of Model I are presented in Figure 2. Formulas and cell locations used to construct the model are available from the authors upon request. The models were used to examine population growth over a 30-day period. The influence of initial inoculum levels on subsequent population growth was investigated by using various quantities of initial inoculum levels and by changing the time at which initial inoculum was introduced. Finally, the sensitivity of population growth to changes in the probability of conidia being deposited onto susceptible tissue was examined by varying the probability over a range of temperatures.

RESULTS

Temperature significantly affected population growth (Fig. 3A). Optimum temperature for population growth was between 22 and 26 C. Growth was greatest at 24 C, at which an initial population of 100 conidia on day 1 resulted in 3,188 colonies after 30 days. When the same initial population size was used at 30 C, only 144 colonies were produced after 30 days.

A reduction in population growth occurred in the presence of liquid water on the foliage (Fig. 3B). At 24 C, population size was reduced by 49% after 30 days when compared to growth in the absence of moisture. Water narrowed the optimum temperature range from 22–26 to 22–25 C. At 20 and 29 C, an initial population of 100 conidia resulted in only 110 and 101 colonies, respectively, after 30 days. At 30 C, population size declined to 77 colonies after 30 days.

Reducing the amount of initial inoculum also affected population size (Fig. 4). However, at 25 C an 80% reduction in initial inoculum, from 100 to 20 conidia, still allowed the population

	A	B	C	D	E
1					
2			INITIAL INOCULUM=	PROBABILITY OF DEPOSITION=	
3			100	.01	
4					
5			1	2	3
6	DAY	TEMP	GERMINATION	PENETRATION	COLONIZATION
7	1	24	IF(OR(B7<15,B7>33),0, C3*(-2.6+(.3*B7)-(.005*B7 ^ 2)))	IF(OR(B8<15,B8>33),0, C7*(-.6+(.1*B8)-(.002*B8 ^ 2)))	IF(B9>35,0,D7)
8	2	24	IF(OR(B8<15,B8>33),0, AL7*D3*(-2.6+(.3*B8)-(.005*B8 ^ 2)))	IF(OR(B9<15,B9>33),0, C8*(-.6+.1*B9)-(.002*B9 ^ 2)))	IF(B10>35,0,D8)
9	3	24	IF(OR(B9<15,B9>33),0, AL8*D3*(-2.6+(.3*B9)-(.005*B9 ^ 2)))	IF(OR(B10<15,B10>33),0, C9*(-.6+.1*B10)-(.002*B10 ^ 2)))	IF(B11>35,0,D9)
10	4	24			
11	5	24			

Fig. 2. An example of the spreadsheet formulas and cell addresses used in construction of the model. Letters **A–E** at the top represent spreadsheet columns and numbers 1–11 at the left represent spreadsheet rows.

to increase to 624 colonies after 30 days.

A delay in the introduction of initial inoculum significantly affected population size after 30 days (Fig. 5). A 5-day delay in the introduction of 100 conidia resulted in 1,416 colonies after 30 days while a 10-day delay resulted in 500 colonies. Modification of the initial inoculum load of 100 conidia to reflect a daily influx of 20 conidia per day over a 5-day period or 10 conidia per day over a 10-day period resulted in population sizes of 2,167 and 1,473 colonies, respectively.

Sensitivity of population growth to changes in the probability of a spore being deposited on susceptible tissue was evident at 20, 25, and 30 C (Fig. 6). A decrease in the probability of conidia being deposited onto susceptible tissue from 0.02 to 0.01 resulted in 62, 73, and 69% reduction in population size at 20, 25, and 30 C, respectively. A decrease in the population size 30 days after inoculation was evident at 30 C. The decrease was due to colonies that cease sporulating after 20 days at 30 C (10).

DISCUSSION

In this study, the model revealed the influence of environmental parameters on the growth potential of *U. necator*. After 30 days of growth, population sizes at 20 and 30 C were reduced by 83 and 95%, respectively, when compared to growth at 24 C. The sensitivity of population growth to changes in temperature indicates the potential for a temperature-based spray forecasting system. Several systems that use the relationship between temperature and the infection potential of *U. necator* have been proposed (24,26,32). In the cooler, coastal areas of California, the number of spray applications did not decrease nor did the level of disease control increase (24). Inclusion of sporulation parameters may enhance their sensitivity to temperature changes. We have initiated investigations of a spray-forecasting system that includes a sporulation parameter.

The model confirmed an interaction between moisture and temperature. The effect of moisture was greater at the extreme temperatures used in this study than at the optimal temperatures for growth. This may explain conflicting reports by earlier researchers on the influence of moisture on development of grape powdery mildew (4,15,16,29). A constant 60% reduction in the infection rate by free moisture was assumed in a previous model developed for epidemics of grape powdery mildew (23). In this study, growth of populations at 27 C was reduced by 58%. However, similar reductions did not occur at other temperatures.

In field studies in which a dormant application of lime sulfur was used to reduce overwintering ascospores, initial levels of disease incidence were reduced from 67 to 29%, when compared to an unsprayed control (17). However, even with the dormant sprays, early season levels of disease incidence ranged from 0 to 30%. Simulation results indicated that despite an 80% reduction in initial inoculum, a substantial population size can be obtained after 30 days at 25 C. Thus, efficacy of dormant sprays must be improved if they are to be used to suppress epidemics of grape powdery mildew in California.

A 10-day delay in the introduction of inoculum had a greater effect on population growth than an 80% reduction in initial inoculum. This suggests that disease management programs for delaying the onset of epidemics, such as an early season fungicide application, when used in combination with other disease management tactics may contribute more towards reducing the overall fungicide use in a growing season. This strategy is now being evaluated by several growers in California.

The use of the spreadsheet program allowed the models for grape powdery mildew to be computerized, with the user having only a cursory knowledge of computers and no knowledge of a formal programming language. After construction, the model was easily modified by making changes in the desired cells; this allows the effects of various environmental factors and disease management strategies on subsequent population growth to be

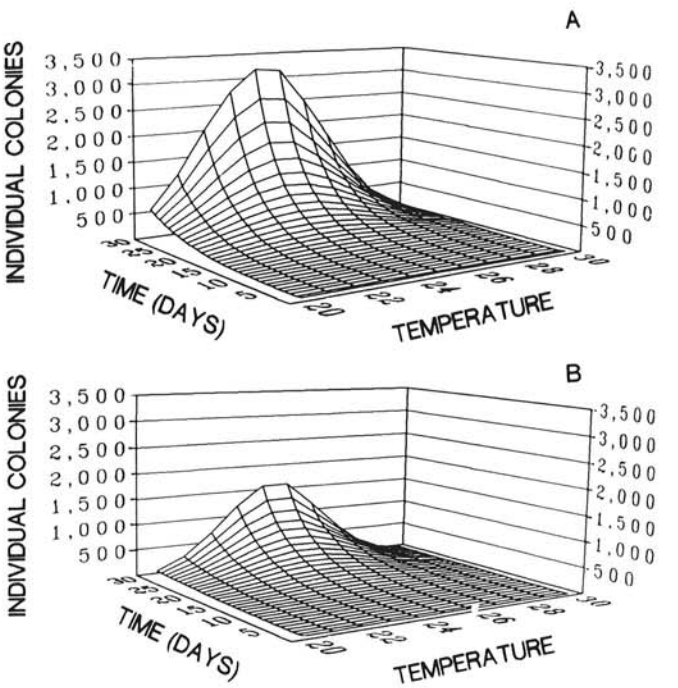

Fig. 3. Influence of temperature and moisture on simulated population growth of *Uncinula necator* over a 30-day period. Initial inoculum levels consist of 100 conidia. **A,** influence of temperature; **B,** influence of temperature in the presence of moisture.

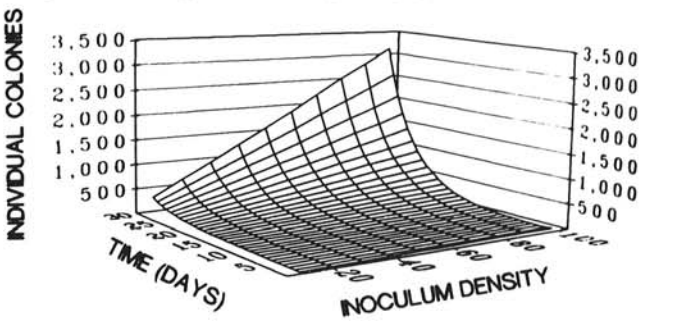

Fig. 4. Influence of initial inoculum levels on simulated population growth of *Uncinula necator* over a 30-day period at a constant temperature of 25 C.

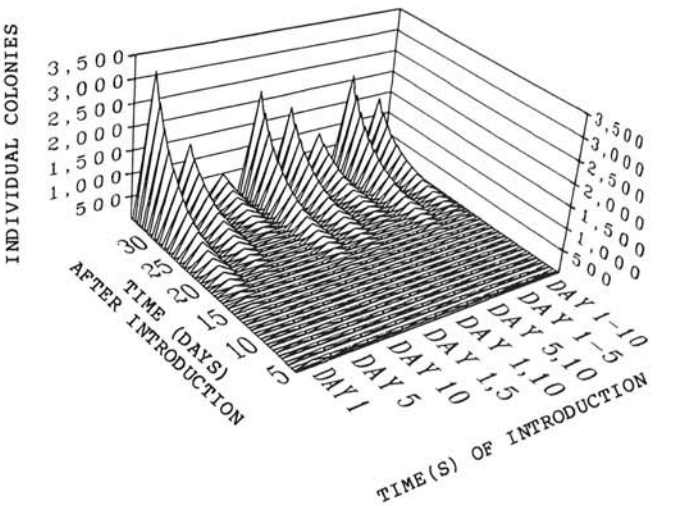

Fig. 5. Influence of a delay in the introduction of inoculum on subsequent population growth of *Uncinula necator* over a 30-day period. Temperature was constant at 25 C and the total amount of initial inoculum introduced for each treatment was 100 conidia. Day 1 = inoculum introduced on day 1, day 5 = inoculum introduced on day 5, day 10 = inoculum introduced on day 10, day 1,5 = inoculum introduced on days 1 and 5, day 1,10 = inoculum introduced on days 1 and 10, day 5,10 = inoculum introduced on days 5 and 10, day 1–5 = inoculum introduced on days 1–5, and day 1–10 = inoculum introduced on days 1–10.

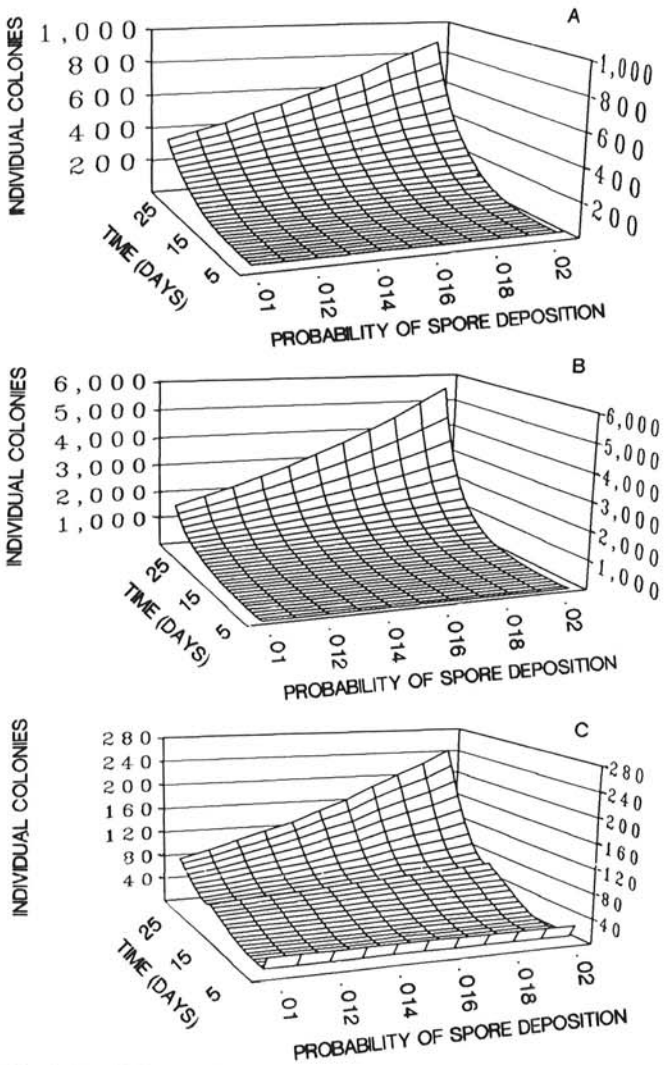

Fig. 6. Sensitivity of simulated population growth of *Uncinula necator* to changes in the dispersal rate. Initial population consists of 100 conidia. **A,** population growth at 20 C; **B,** population growth at 25 C; and **C,** population growth at 30 C.

studied. One can use the information available on the biology of a plant pathogen to make informed choices as to the direction of future investigations on disease management. By eliminating dependence on mainframe computers and their associated networks, user-friendly software such as the spreadsheet program used in this study should enhance the accessibility of epidemiologic models to growers, extension agents, pest-control advisors, and other field-oriented professionals.

Spreadsheet programs are also useful for sensitivity analyses, i.e., for evaluating the effect of changing parameter values in a model. Because a simulation run requires only a few seconds, sensitivity analysis could be used more frequently to access the reliability of estimated parameters or key assumptions in the model. This, in turn, will hasten model development. With the increasing availability of spreadsheet programs, epidemiologic models should be used by more plant pathologists to understand the underlying principles that govern epidemics of plant disease.

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