

Population dynamics of the plant pathogenic fungus *Uncinula necator*¹

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Cohort life tables were constructed and population parameters determined for *Uncinula necator* (Schw.) Burr. parasitizing the foliage of *Vitis vinifera* L. cv. Carignane at various temperatures. The net reproductive rate per individual conidium at 19, 22, 26, and 30°C was 577, 2272, 1300, and 157 conidia per generation, respectively. Mean generation times ranged from 22.84 days at 19°C to 13.60 days at 30°C. Intrinsic growth rates (r) varied from 0.43 per day at 19°C to 1.24 per day at 26°C. Doubling times ranged from 0.56 days at 26°C to 1.63 days at 19°C. Matrix population models were used to project population growth. Stable age distributions at 19, 22, 26, and 30°C were reached after 70, 50, 45, and 45 days, respectively. At a stable age distribution, greater than 96% of the population was contained in the first age-class (days 1–5).

Key words: demography, cohort life table, grape powdery mildew, net reproductive rate, population growth rate.

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Les auteurs ont construit des tables de chronoséquence des du cycle de reproduction et ont déterminé les paramètres des populations de l'*Uncinula necator* (Schw.) Burr. parasite du feuillage du *Vitis vinifera* L. cv. carignane, à diverses températures. Le taux net de reproduction par conidie individuelle à 19, 22, 26 et 30°C est respectivement de 577, 2272, 1300, et 157 conidies par génération. Les temps moyens de génération varient entre 22,84 j à 19°C à 13,60 j à 30°C. Les taux intrinsèques de croissance (r) varient de 0,43 par jour à 19°C à 1,24 par j à 26°C. Le temps de duplication va de 0,56 j à 26°C à 1,63 j à 19°C. Des modèles matriciels de population ont été utilisés pour projeter la croissance des populations. On atteint des âges de distribution stables à 19, 22, 26, et 30°C après 70, 50, 45 et 45 j, respectivement. À un âge de distribution stable, plus de 96% de la population se retrouve dans la première classe d'âge (j 1–5).

Mots clés : démographie, chronoséquences des poussées de croissance, mildiou poudreux du raisin, taux net de reproduction, taux de croissance des populations.

[Traduit par la rédaction]

Introduction

Epidemics of plant disease result from interactions between populations of pathogens and hosts as influenced by the environment (Zadoks and Schein 1979). Considerable attention has been applied towards understanding the population dynamics of diseased plants through the analysis of disease progress curves (Berger 1981; Pennypacker et al. 1980; Vanderplank 1963). Analysis of disease progress curves have also been used to indirectly ascertain the population dynamics of the pathogen, e.g., use of logistic or monomolecular model to indicate presence or absence of secondary infection cycles during epidemics. Inherent in this approach are several limiting assumptions which must be considered when deriving biological interpretations (Williams 1972). A single mathematical function may represent multiple mechanisms. Thus, the biological relevance of the parameters and final form of the function are not always apparent. Another critical assumption is that all members of the population are of the same age.

Less attention has been applied to direct studies of the population dynamics of plant pathogens even though they are instrumental in determining the rate at which epidemics of plant disease may proceed. Vital rates (i.e., growth, reproductive, and mortality rates) describe the development of individuals through the life cycle, and the response of these rates to the environment will determine population dynamics (Caswell

1989). Because vital rates are age dependent, the demographic structure of populations should be considered when investigating population dynamics. The limiting assumptions associated with growth curve analysis restrict their application to the population dynamics of plant pathogens.

In classical demographic analysis the life table is used for tabulating age-specific survival and reproduction. Life tables can be used for summarizing age-specific life-history information and determining various population parameters such as the intrinsic rate of increase (Birch 1948). They also are used to develop demographic models for the projection of population growth and determination of stable age distributions (Caswell 1989; Leslie 1945) and to address problems in tephritid ecology and management (Carey 1986).

The intrinsic rate of increase (r), defined as the rate of increase per individual under specified physical conditions in an unlimited environment, can be used to compare population growth potentials (Birch 1948). For example, r can be used to compare the growth of different species in the same environment (Tanigoshi and McMurty 1977), the same species in different environments (Messenger 1964), or to measure effects of toxic materials on potential population growth (Gentile et al. 1982).

Although their potential contributions were discussed in some detail by Zadoks and Schein (1979), life tables and their associated population models have not been developed for plant pathogenic fungi. The limited application of these techniques stem from difficulties involved in ascertaining vital rates

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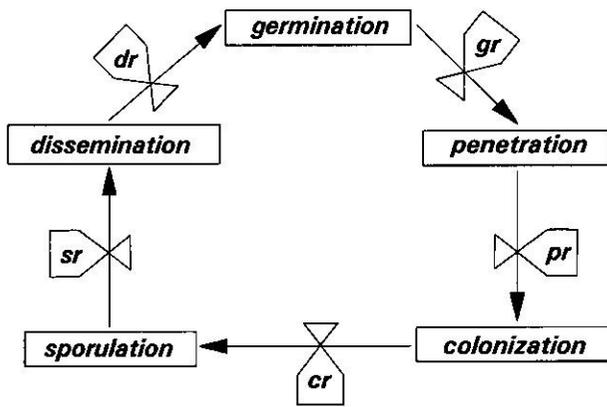


FIG. 1. Infection cycle for *Uncinula necator*. *gr*, germination rate; *pr*, penetration rate; *cr*, colonization rate; *sr*, sporulation rate; and *dr*, dispersal rate.

for plant pathogens. Plant pathologists often use less reliable, indirect methods for estimating rates. For example, in the development of a simulation model for barley powdery mildew, sporulation rates were estimated by spore catches on trap plants as an indirect measure of sporulation (Aust et al. 1982).

Grape powdery mildew, caused by the fungus *Uncinula necator* (Schw.) Burr., is an economically important disease of cultivated grape (*Vitis vinifera* L.). *Uncinula necator* is capable of colonizing all succulent host tissues while mature tissue including older leaves and fruit with sugar levels above 12% are resistant (Delp 1954; Doster and Schnathorst 1985a). The infection cycle can be separated into five phases: germination, penetration, colonization, sporulation, and dispersal (Fig. 1).

Quantitative data on the influence of environmental and physical parameters on germination, penetration, colonization, and sporulation are available (Chellemi 1990; Delp 1954; Doster and Schnathorst 1985a, 1985b). Delp (1954) showed that germination is completed within 30 h after inoculation at temperatures between 12 and 30°C. Conidia that fail to germinate or penetrate host tissue within 48 h of inoculation are no longer viable (Doster and Schnathorst 1985a). Germination and penetration do not occur above 33°C (Delp 1954). Established colonies begin sporulating at 5 days and continue sporulating up to 35 days after inoculation (Chellemi 1990). The daily sporulation rate is dependent on age of the colonies (Chellemi 1990). Once successful penetration has occurred, mortality of colonies growing between 19 and 30°C is not observed until at least 20 days after inoculation (Chellemi 1990). Information on dispersal of *U. necator* is unavailable.

The purpose of this research was to ascertain population attributes of the plant pathogenic fungus *U. necator* (Burr) Schw. under different temperature regimes. Life table analysis and matrix population models were used to derive various population parameters, and their application to studies in plant disease epidemiology and fungal ecology are discussed.

Methods

In this study, we assume that an unlimited supply of susceptible host tissue is available and all newly produced conidia reach susceptible host tissue.

Cohort life tables were constructed for a single spore isolate of *U. necator* growing on *V. vinifera* cv. Carignane at 19, 22, 26, and 30°C. Parameters included in the tables were the median age (in days) of each age-class x (t), the proportion of individuals dying between

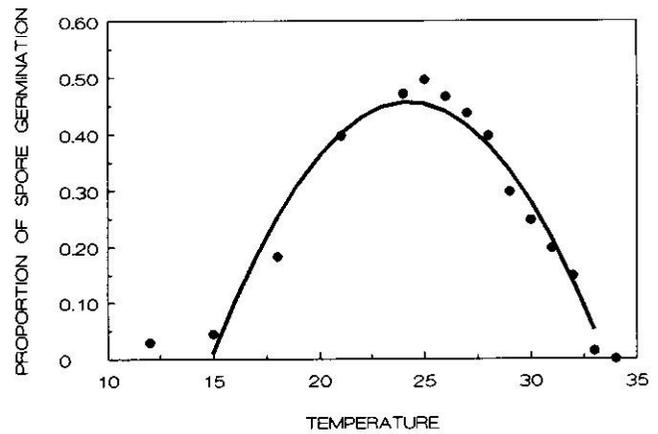


FIG. 2. Observed and predicted values for estimating temperature effects on germination with the equation $G = -2.641 + 0.256T - 0.00528T^2$ where G is the proportion of conidia that germinate and T is temperature. Solid line represents estimated values. Observed values are from Delp (1954).

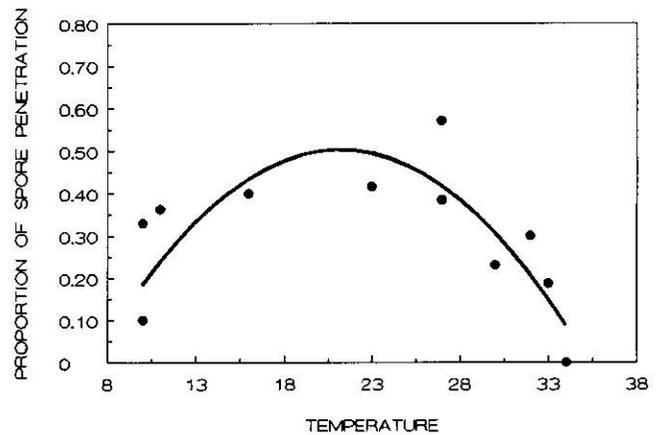


FIG. 3. Observed versus predicted values for estimating temperature effects on penetration with the equation $P = -0.639 + 0.108T - 0.00254T^2$ where P is the proportion of conidia that penetrate the host and T is the temperature. Solid line represents estimated values. Observed values are from Delp (1953).

age-class x and $x + 1$ (q_x), the proportion of survivors between x and $x + 1$ ($1 - q_x$), the proportion of individuals surviving from birth to the beginning of age-class x (l_x), and the number of offspring provided by an individual between age x and $x + 1$ (m_x).

The effect of temperature on germination of conidia was derived from observations by Delp (1954) of germination on glass slides and leaf surfaces of several *V. vinifera* cultivars. The effect of temperature on penetration was derived from observations by Delp (1953) of developing mildew colonies of leaf surfaces of *V. vinifera* cultivars Carignane and Emperor. A quadratic function was used to estimate the proportion of inoculated conidia that survive to germinate and penetrate host tissue at various temperatures from the data collected by Delp (Figs. 2, 3).

Information on sporulation and mortality of established colonies was obtained from studies by Chellemi (1990). Using a single spore isolate, individual conidia were transferred to pre-designated locations on the foliage of *V. vinifera* cv. Carignane via a single camel hair attached to a dissecting needle. Sporulation and mortality of established colonies were quantified over time at four temperatures by harvesting colonies at periodic intervals and enumerating the number of conidia produced. The number of offspring per individual per day

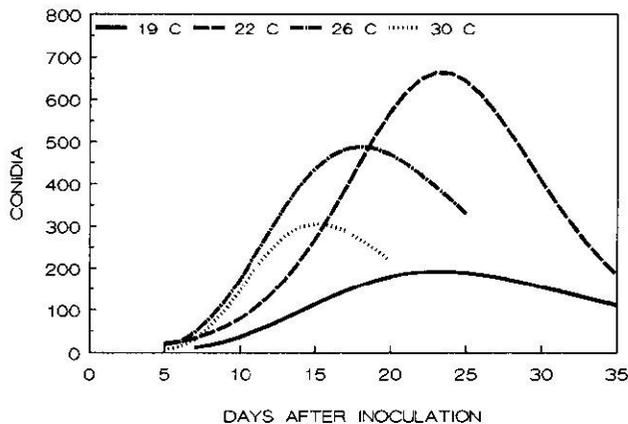


FIG. 4. Effect of temperature on the number of offspring (conidia) produced per individual per day. Curves are derived from cumulative sporulation total obtained by Chellemi (1990).

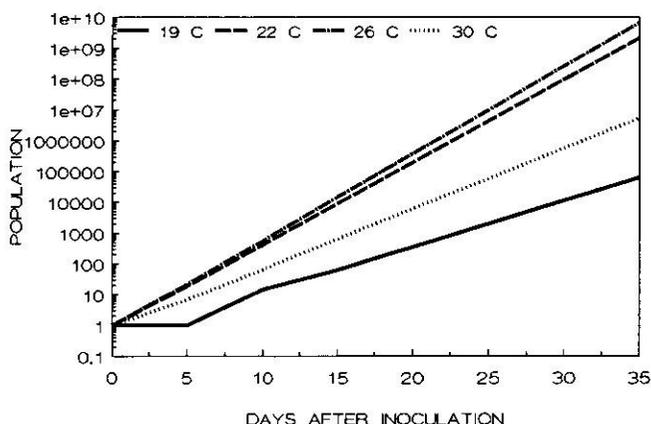


FIG. 5. Numerical projection of total population size as affected by temperature, based upon an initial population consisting of a single individual in age-class 1.

was obtained from measurements of the cumulative production of conidia per day (Fig. 4).

The expected number of conidia by which a single conidium is replaced with by the end of its life (net reproductive rate (R_0)) was calculated as $\sum l_x m_x$. The mean age of the parents of the offspring produced by a cohort (mean generation time (T_g)) was calculated as $\sum t l_x m_x / \sum l_x m_x$. The intrinsic rate of growth (r) was calculated from Lotka's (1925) renewal equation

$$[1] \quad 1 = \sum_0^{\infty} e^{-rt} l_x m_x$$

The solution of r was computed using the iterative equation

$$[2] \quad r_1 = r_0 - \frac{(\sum e^{-r_0 t} l_x m_x) - 1}{\sum x e^{-r_0 t} l_x m_x}$$

where r_0 is the initial guess and r_1 is the next approximation (Carey 1989). The iterative process was terminated when $r_1 - r_0 < 0.001$.

Projection matrices for population growth at 19, 22, 26, and 30°C were constructed from the life tables. Convergence of populations to a stable age distribution was determined after repeated multiplications by the population vector.

Results

Using observations of colony mortality by Chellemi (1990), cohort life tables were developed for a 35-day period for colonies growing at 19 and 22°C, a 25-day period for colonies

TABLE 1. Cohort life tables for individual colonies of *U. necator* growing on *V. vinifera* cv. Carignane at various temperatures

x	t	q_x	$1-q_x$	l_x	m_x
19°C					
0	2.5	0.85	0.15	1	0
1	7.5	0	1	0.15	99
2	12.5	0	1	0.15	405
3	17.5	0	1	0.15	786
4	22.5	0	1	0.15	951
5	27.5	0	1	0.15	857
6	32.5	1	0	0.15	646
22°C					
0	2.5	0.78	0.22	1	19
1	7.5	0	1	0.22	247
2	12.5	0	1	0.22	891
3	17.5	0	1	0.22	2246
4	22.5	0	1	0.22	3236
5	27.5	0	1	0.22	2572
6	32.5	1	0	0.22	1325
26°C					
0	2.5	0.80	0.20	1	22
1	7.5	0	1	0.20	445
2	12.5	0	1	0.20	1690
3	17.5	0	1	0.20	2390
4	22.5	1	0	0.20	1960
30°C					
0	2.5	0.95	0.05	1	7
1	7.5	0	1	0.05	350
2	12.5	0	1	0.05	1317
3	17.5	1	0	0.05	1325

NOTE: Symbols are as follows: x , age-class; t , median age (days) of individuals in age class; q_x , proportion of individuals dying between x and $x + 1$; $1-q_x$, proportion surviving between x and $x + 1$; l_x , proportion of individuals surviving from birth to age x ; and m_x , number of offspring by an individual between x and $x + 1$.

growing at 26°C, and a 20-day period for colonies growing at 30°C (Table 1). Age-classes were grouped in 5-day intervals. Mortality of individuals was high during the first age-class. After the first age-class, subsequent mortality did not occur until the last age-class.

Similar mean generation times of 22.72 and 22.84 days were observed at 19 and 22°C, respectively (Table 2). Mean generation times were shortened by 6 days at 26°C and 9 days at 30°C. Net reproductive rates varied from 157 conidia at 30°C to 2272 at 22°C and were lowest at the two extreme temperatures used in this study. Values of r varied from 0.42 per day at 19°C to 1.24 per day at 26°C. As with the net reproductive rates, intrinsic growth rates were lowest at the two extreme temperatures used in this study. Doubling times varied from 1.63 days at 19°C to 0.56 days at 26°C.

Projection matrices were multiplied by an initial population vector consisting of a single individual in the first age-class (Table 3). At 26 and 30°C, stable age distributions were reached after 45 days. At 22°C, a stable age distribution was reached after 50 days. At 19°C, populations required 70 days to converge to a stable age distribution. Once a stable age distribution was reached, the majority of individuals were in the first age-class (Table 3).

Projected population growth at 19 and 30°C was several

TABLE 2. Estimated population parameters of *Uncinula necator* under several environmental regimes

	19°C	22°C	26°C	30°C
Mean generation time (days)	22.84	22.72	16.78	13.61
Net reproductive rate ^a	577	2272	1300	157
Intrinsic growth rate (per day)	0.43	1.12	1.24	0.84
Doubling time (days)	1.63	0.58	0.56	0.82

^aConidia per generation.TABLE 3. Matrices used for projecting population growth of *Uncinula necator* at various temperatures

Projection matrix					Initial pop.	Eigenvector		
19°C								
0	99	405	786	951	857	646	1	0.968
0.15	0	0	0	0	0	0	0	0.027
0	1	0	0	0	0	0	0	0.005
0	0	1	0	0	0	0	0	<0.001
0	0	0	1	0	0	0	0	<0.001
0	0	0	0	1	0	0	0	<0.001
0	0	0	0	0	1	0	0	<0.001
22°C								
19	247	891	2246	3236	2572	1325	1	0.989
0.22	0	0	0	0	0	0	0	0.010
0	1	0	0	0	0	0	0	<0.001
0	0	1	0	0	0	0	0	<0.001
0	0	0	1	0	0	0	0	<0.001
0	0	0	0	1	0	0	0	<0.001
0	0	0	0	0	1	0	0	<0.001
26°C								
22	445	1690	2390	1690			1	0.992
0.20	0	0	0	0			0	0.007
0	1	0	0	0			0	<0.001
0	0	1	0	0			0	<0.001
0	0	0	1	0			0	<0.001
30°C								
7	350	1317	1325				1	0.994
0.05	0	0	0				0	0.005
0	1	0	0				0	<0.001
0	0	1	0				0	<0.001

NOTE: Age-classes are divided into 5-day intervals.

orders of magnitude lower than growth at 22 and 26°C (Fig. 5). After 35 days, up to 6.7 billion conidia were projected from an initial population of 1 conidium at 26°C.

Discussion

Uncinula necator has a tremendous potential for rapid population growth. Intrinsic growth rates greater than one are rarely reported in the literature. An intrinsic growth rate of 1.14 per day was reported for the free-living nematode *Caenorhabditis briggsae* (Schiemer 1982). Growth rates between 0.24 and 0.82 per day were reported for eight species of planktonic rotifers (Stemberger and Gilbert 1985).

A few reports of demographically derived growth rates for fungi are available. An estimated maximum growth rate (r_{max}) of 0.59 per day was reported for the plant pathogenic fungus *Puccinia recondita* (Zadoks and Schein 1979). This estimate

was obtained by substituting values of T_g and R_0 into the equation

$$[3] N(t) = N(o) e^{rt}$$

where $R_0 = N(t)/N(o)$ and $T_g = t$. Problems associated with this derivation of r have been documented (Birch 1948). When the authors used the iterative solution for Lotka's equation, an intrinsic growth rate of 0.70 per day was obtained for *P. recondita*. This value falls in between the range of intrinsic growth rates estimated for *U. necator*. Because temperatures fluctuated when the data were collected for *P. recondita* (Mehta and Zakoks 1970), it can be concluded that the growth potential of these two fungi are similar.

The population parameters developed in this study are useful in evaluating the logic of interventive disease management strategies on populations of the target pathogen. For example,

when a population of *U. necator* has reached stable age distribution, over 96% of the individuals are in the first age-class (0–5 days). In nature, this group is composed of ungerminated and recently germinated conidia. Current disease management practices in California consist of applying protectant fungicides on a calendar schedule (Gubler et al. 1989). Hence, the current pest management strategy is focused on the age-class containing the largest proportion of individuals.

Population parameters estimated in this study, such as net reproductive rate and intrinsic growth rate, have direct application in the estimation of parasitic fitness. As defined by Groth and Barrett (1980), fitness of an organism is determined by the number of offspring left by, and the survival rate of, individuals per interval of time. Prior attempts to estimate parasitic fitness of plant pathogenic fungi relied on use of the apparent infection rate as derived from analysis of disease progress curves (Vanderplank 1963; MacKenzie 1977). In addition to the limitations previously mentioned, microclimate differences between various epidemics and the accuracy with which disease intensity can be measured preclude comparison of growth rates estimated from disease progress curves.

Fitness of *U. necator* isolates has not been studied. Differences in pathogenicity were examined for 35 isolates of *U. necator* obtained from various *Vitis* and *Parthenocissus* sp. (Gadoury and Pearson 1991). No differences in the rate of colony expansion on seedlings of *V. vinifera* was observed among isolates obtained from *Vitis* sp. Slight differences in latent periods were obtained. However, omission of individual reproduction and mortality of individuals from the study prevent the determination of variability in fitness among isolates.

The population generated for *U. necator* in this study contain the assumption that all spores are capable of reaching susceptible host tissue. Because many variables including meteorologic phenomena and host phenology influence dispersal, it is doubtful this assumption holds true in nature. However, the parameters do provide an estimate of the maximum reproductive potential under ideal conditions. This establishes a basis for statistical comparison of population growth potentials of different fungi and provides quantitative indication of the reproductive potential of fungi in relation to other organisms.

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