Modeling the Influences of Plant Infection Rate and Temperature on Potato Foliage and Yield Losses Caused by *Verticillium dahliae*

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ABSTRACT

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A simple submodel was coupled to a dynamic potato growth simulation model to quantitatively describe the effects of *Verticillium dahliae* infection on loss of crop leaf area and tuber yield. This was accomplished by accelerating the leaf tissue aging rate as a function of *V. dahliae* incidence in stems and high-temperature stress. A Gompertz equation was used to describe the temporal incidence of *V. dahliae* in potato stems, and the effects of temperature were described by a linear deviation of the daily mean above 17 C. Values for the model's parameters were determined from sequential, within-season harvests of crop biomass and *V. dahliae* incidence data from five inoculated crops of Russet Burbank potato grown in three seasons. Among experiments, modeled final tuber yield, area under the tuber dry matter accumulation curve, and area under the leaf area index curve were correlated with the observed values. In two crops with similar infection rates, modeled and observed yield loss was 4.6 and 6.5%, respectively, when conditions were relatively cool (mean temperature = 20.0 C) and 17 and 15%, respectively, when conditions were warmer (mean temperature = 23.3 C). In simulation analyses, the model indicated that mean air temperature after infection, the proportion of individual stems infected by *V. dahliae*, and timing of infection are important considerations for interpreting yield losses caused by this pathogen.

Additional keywords: crop growth modeling, potato early dying, Verticillium wilt.

Potato early dying disease, caused principally by *Verticillium dahliae* Kleb., is considered to be a serious threat to potato production in most areas of the United States (7,17,21–23,25,26). Reported yield reductions in plants infected with this fungus range from very slight (17,22,26) to as high as 50% (22,23). Severity of this disease is influenced by many factors including the number of times a field has been cropped to potatoes, the presence of other organisms, cultivar, fertility, and environment (25). Given the complex etiology of potato early dying, quantitative relationships between *V. dahliae* populations, disease severity, yield, and other factors that impinge upon these relationships are not completely understood. Previous studies, however, have demonstrated that both the rate at which plants become infected (21) and tuber yield (22) can be related to the population of *V. dahliae* in soil.

Of the environmental factors that influence potato early dying and potato yield, temperature may be one of the most significant. Potatoes grow optimally within a temperature range of 18–20 C (5). The optimum range for growth of *V. dahliae* is 25–27 C (28). In controlled environment studies, net assimilation rate of potato declined by 20–25% as the temperature was increased from 20 to 25 C (5). Disease severity in potatoes (22), tomatoes (8,20), and eggplant (20) infected with *V. dahliae*, however, increased as the mean air temperature increased from 20 to 23 C to 28 C. Symptom development in potatoes infected with *V. dahliae* was arrested by reducing temperature from 20 to 13 C (13).

In the field, interactions between infection by *V. dahliae*, potato yield, and the effect of temperature have been observed by comparing seasons or locations. In a season when the average July-August temperature was 24 C, a multilocation study in Ohio (26) demonstrated yield reductions ranging from 24 to 37% in potatoes grown in fumigated microplots inoculated with *V. dahliae*; this same treatment, however, had little effect on tuber yield in a season when the average July-August temperature was 20 C. Significant relationships were obtained between yield and *V.*

dahliae soil microsclerotial density in two warm production areas of Colorado, but similar relationships could not be demonstrated in a cool growing area, though the crops were infected (22). In Oregon (23), a seed lot of Russet Burbank potatoes planted in an old production field highly infested with *V. dahliae* yielded 47% less than the same seed lot planted nearby in a field new to crop production. Mean air temperature at that site during August was 25 C (30). Similarly, in Minnesota, severe potato early dying symptoms were obtained during a season when the mean July-August temperature was 24.4 C, but, in another year, potato early dying symptoms did not develop when the time of infection by *V. dahliae* was delayed and the mean July-August temperature was 22.2 C (17).

The loss of crop productivity resulting from potato early dying is a combination of the reduced photosynthetic efficiency of tissues that remain on the plant (4,12,29) and reduced radiation interception because of shortened leaf life span and early plant and crop death (1,13). Studies of the relationships between crop productivity, plant infection by *V. dahliae*, rates of leaf senescence, and disease-influencing factors such as temperature may lead to a better understanding of potato early dying. The recent development of crop growth simulation models has provided a methodology for quantitatively evaluating hypotheses regarding the interactions between disease epidemiology, field-level physiological processes, and yield (3,11,24). These models emulate crop growth by accumulating dry matter based on an input of solar radiation and then dynamically partitioning this dry matter into the major plant tissues (24). Ideally, crop growth models are structured to be responsive to environmental variability and to common crop stresses (3,11,15,24).

The objective of this study was to investigate the potential influences of the rate of stem infection by *V. dahliae* and the mean air temperature on foliage and yield losses in potato. A simple model describing the effects of these factors on leaf aging rate is hypothesized and coupled to a model that simulates potato crop growth (16). Modeled leaf area duration and yield responses to infection are compared with those of inoculated field-grown crops.

DESCRIPTION OF THE MODEL

Potato growth model. The growth model used in this study accumulates and partitions dry matter into four plant tissue types: leaves, stems, roots, and tubers. Dry matter accumulation (g m^{-2} day^{-1}) is a multiplicative function of the following: amount of solar radiation (MJ m^{-2}) intercepted by the crop surface area, potential radiation use efficiency (g MJ^{-1} physiologic-age unit^{-1}), a moisture stress reduction factor, and a temperature-dependent phenological scale herein termed physiologic age (P_A) (27). Assimilated dry matter is partitioned competitively with four modified Michaelis-Menten equations, one for each type of tissue. Adequate plant nutrition is assumed. The model initiates at 50% emergence with inputs of seed piece size and within- and between-row plant spacing. Daily estimates of total solar radiation, minimum and maximum temperature (C), and soil matric potential (MPa) are required inputs. Details of these computations are discussed elsewhere (15,16,18).

Understanding leaf tissue production and aging is central to the approach taken to model effects of *V. dahliae* on crop growth. Throughout the season, leaf dry matter produced on any one day is aged as an individual cohort (Fig. 1). Aging is done by accumulating daily changes in P_A. The cumulative P_A of a leaf tissue cohort determines its potential radiation use efficiency (14,18) and when it senesces from the plant (Fig. 1).

***Verticillium* submodel.** The *Verticillium* submodel uses the incidence of *V. dahliae* within stems and daily mean temperature to accelerate leaf aging:

$$dP_A\,(v)/dt = I \cdot T_V \cdot k_V$$

where $dP_A\,(v)/dt$ is the additional daily change in the physiologic age of leaf dry matter caused by *V. dahliae* infection, I is the incidence of *V. dahliae* in potato main stems, T_V is a function of temperature, and k_V is an experimentally derived constant that calibrates the effects of incidence and temperature on leaf aging. After onset of infection, $dP_A\,(v)/dt$ is added daily to the cumulative P_A of each leaf dry matter cohort (Fig. 1).

I is calculated from a Gompertz model (2) previously fitted to data:

$$I = \exp(-B \cdot \exp(-k_g \cdot t_g))$$

where B is a position parameter related to the level of disease at the epidemic onset time ($t_g = 0$), k_g is a rate parameter, and t_g is the days from disease onset.

The value for T_V is given by the following function:

$$T_V = \text{maximum } (0.0, \bar{T} - k_t)$$

T is the mean temperature computed from the daily minimum and maximum temperature by Sands et al's (27) algorithm, and k_t is a derived threshold temperature where *V. dahliae* begins to accelerate leaf aging.
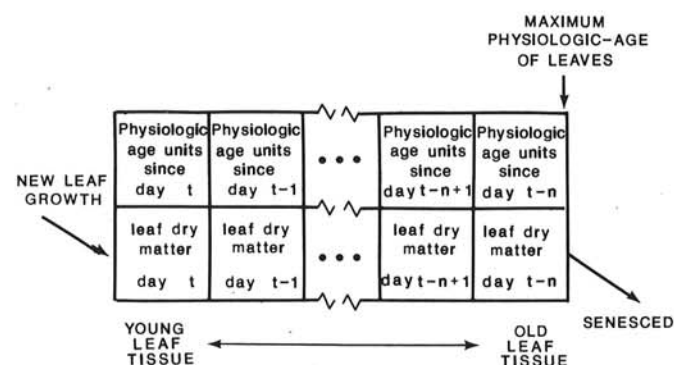
Acceleration of leaf aging affects crop growth in two ways. First, cohorts of leaf dry matter reach their maximum physiologic age more quickly, causing premature senescence of old leaf tissue (13,25) and a reduction in radiation interception (1). Second, radiation use efficiency of a cohort of leaf tissue declines more rapidly (4,12,29).

MATERIALS AND METHODS

Cultural practices. From 1985 to 1987, dry-land field plots of Russet Burbank potato were established in a Waukegan silt-loam soil located on the University of Minnesota Rosemount Agricultural Experiment Station to evaluate the *Verticillium* submodel. Sites were chosen in areas where potatoes had not been cropped for at least 2 yr. Cultural practices (including planting dates for 1985 and 1986, tillage, fertilization, herbicides, and insect and foliar disease control) have been described (15). Plot dimensions were six rows 1 m wide by 12.2 or 15.2 m long. Within each plot, rows 1, 4, and 6 were defined as borders. Rows 2 and 3 were for sequential samples of crop biomass, and row 5 was for measuring final tuber yield.

Experimental design was a randomized block with 4–6 replications. Treatments were a *V. dahliae* soil and seed tuber inoculation and an uninoculated control. Single experiments were made in 1985 and 1986, and three experiments were done in 1987. Two of the 1987 experiments were planted at the same time (24 April), but one (1987-wet) received four supplemental 2.5-cm irrigations before tuber initiation. The third experiment (1987-late) was planted 6 June at a wider than normal plant spacing (Table 1).

***Verticillium* inoculation and isolation.** A mixture of conidia, hyphal fragments, and microsclerotia of *V. dahliae* was sprayed on opened seed furrows immediately before planting and to seed pieces as they fell from the planter. Inoculum was produced by subculturing three parent isolates on Difco potato-dextrose agar (PDA) (Difco Laboratories, Detroit, MI) and then inoculating and spreading conidial suspensions made from the subcultures into 9-cm petri plates containing 8–10 ml of one-quarter strength PDA plus 7 g/L of Bacto agar. Streptomycin (200 mg/L) was added to the medium to inhibit bacterial growth. Inoculated plates were incubated 10–14 days at room temperature in the dark. Between seasons, parent cultures of the isolates were stored at 4 C.

To prepare the inoculum for field use, subcultures of the three isolates were pureed with water in a blender for 30 sec, mixed in equal proportions, strained through cheesecloth, and diluted to 20–25 plates/L. Resulting concentrations of conidia and hyphal fragments (determined by dilution plate) and microsclerotia (determined by hemacytometer) per milliliter ranged from 2 to 6 × 10^7 and 1 to 2 × 10^4, respectively. Hand-held sprayers were used to apply the inoculum at a rate of about 0.04 L/m row: one-half to seed pieces and the other half to seed furrows in a band 10–15 cm wide. Seed pieces of the control treatment were sprayed with an autoclaved and blended puree of PDA (1.0 g/L), Bacto agar (1.2

Fig. 1. How leaf dry matter is produced, stored, and aged within the potato growth model. t is the day from 50% emergence and n is the number of days the oldest leaf tissue cohort has been present on the plant.

TABLE 1. Input data used in model runs

			Experiment		
				1987[a]	
Input	1985	1986	Wet	Dry	Late
Seed piece size (g)[b]	69	56	51	51	51
Plant spacing (m)	0.33	0.35	0.24	0.24	0.44
Physiologic age[c] at tuber initiation	210	210	210	260	210
Cumulative physiologic age of the crop at harvest	785	800	850	850	710

[a] The wet experiment received supplemental irrigation the first few weeks after emergence, whereas the dry experiment did not. The late experiment was planted about 5 wk after the wet and dry experiments.
[b] Average grams fresh weight.
[c] P_A, after Sands et al (27). .

g/L), and streptomycin (40 mg/L).

Isolations for *V. dahliae* were made four to eight times in each experiment from segments of potato main stems sampled 5–15 cm above the soil surface. On each isolation date, 32–60 stems from each treatment (8–15 from each replication) were randomly sampled from the outside and inside border rows. The stem segments were surface disinfected, and the sap was squeezed onto ethanol-water agar and incubated as described earlier (17).

Nematode assays. In mid-August of each season, soil samples were taken in the fibrous root zone 0–15 cm below the potato hill and assayed for nematodes. In 1985 and 1986, each plot was subsampled in 10 areas and the subsamples were bulked for analysis. Five similar subsamples were taken in each plot in 1987 and then bulked by replication. Soils and roots within the samples were assayed together according to standard procedures at the Michigan State University Nematode Diagnostic Lab in 1985 and 1986, and the University of Minnesota Plant Disease Clinic in 1986 and 1987.

Environmental monitoring. A portable weather station equipped with a CR-21 micrologger (Campbell Scientific, Logan, UT) was located in or near the experimental sites and used to collect daily measurements of minimum and maximum temperature, solar radiation, and rainfall. Soil moisture content was measured gravimetrically twice a week in each replication at depths of 0–15 and 16–30 cm below the hill.

Biomass sampling. Throughout the season, plant samples were harvested every 2 (1985 and 1986) or 3 (1987) wk to determine crop biomass. On each harvest date, four or five plants (that is, hills) were sampled from each plot and separated into green leaf tissue, stems, and tubers. Dead and chlorotic leaves were discarded; roots were not sampled. Each biomass sample contained about 16–20 main stems. Tuber fresh weights were recorded immediately and dry weights of the other tissues were recorded after desiccation at 60 C for 1–2 wk. Leaf dry weight was transformed to leaf area index (LAI) and tuber dry weight was estimated from the fresh-weight values with procedures previously described (15).

Data analysis. Gompertz model B and k_g parameters were estimated for the inoculated treatment of each experiment by regressing transformed infected stem incidence data on days from onset (2). Only the first date with incidence values greater than 90% was used in each regression analysis. In all experiments, the onset time of infection was defined as the day from emergence corresponding to a cumulative P_A of 160 (6).

Environment was summarized by computing the mean seasonal temperature from the daily minimums and maximums for the period of crop growth from the onset of infection ($P_A = 160$) to the cumulative P_A of 700. Mean weekly temperatures for the entire season were similarly calculated. Daily soil matric potentials for the 1985 and 1986 experiments have been published (15), and soil matric potentials for 1987 were estimated by using the same procedure (15).

Model simulations were run with partitioning parameters determined earlier for Russet Burbank potato (15). Because potato early dying also causes premature senescence of stem tissue, the model was modified to eliminate from both control and infected crops the relatively small component of stem surface area in the radiation interception function (16) after the cumulative P_A of 400. Other input information used in model analyses is in Table 1.

Estimates of k_V first were made using the environment and biomass data and the derived Gompertz parameters from 1985 and 1986 experiments. This was done by iteratively running the model with different values of k_V and, after each iteration, comparing the modeled crop response with the observed field data. Values of k_V were estimated using different integer values of k_t ranging from 15 to 20 C. Sets of k_V and k_t were then evaluated on the three 1987 experiments, and the best set was used in further analysis.

Within experiments, observed differences among the treatments were compared by paired *t*-tests. Among all experiments, modeled and observed crop data were compared by plotting temporal development of LAI and tuber dry matter accumulation, and by examining correlation coefficients from the following variables: area under the LAI curve, area under the tuber dry matter

accumulation curve, individual values of LAI, and final tuber yield. Correlations among control crops, infected crops, and the difference between the control and infected crops were compared separately. A simple correlation matrix between the observed percent yield loss, infection rate (k_g), and mean seasonal temperature (as calculated above) also was computed.

Simulation experiments. To see what effect accelerating leaf aging had on modeled radiation use efficiency (14), a comparison was made between the computed daily radiation use efficiencies of the 1986 control crops and the infected crops.

Three factorial simulation experiments were done to further examine the interacting effects of the *V. dahliae* infection rate (k_g) and mean air temperature on modeled leaf area duration and tuber yield. First, the effect of mean air temperature on development and duration of leaf area index was compared in infected and uninfected crops by simulating potato growth at three different mean temperatures (19, 22, and 25 C) with values of k_g equal to 0.0 and 0.12. Second, mean daily temperature was varied from 17 to 25 C and simulations were run for 100 days with values of k_g equal to 0.00, 0.07, 0.12, and 0.17. Final tuber yield (MT/ha) was the dependent variable. Last, using mean temperatures of 19, 22, and 25 C, simulations were run for 830 P_A units and the value of k_g was varied from 0.02 to 0.20. Percent yield of each infected crop was computed by dividing final tuber yield into that of the appropriate uninfected control.

RESULTS

Observed incidence of *V. dahliae*. In the inoculated treatments, *V. dahliae* was first recovered from potato stems within the cumulative P_A range of 176 to 247 (23 to 31 days after emergence).
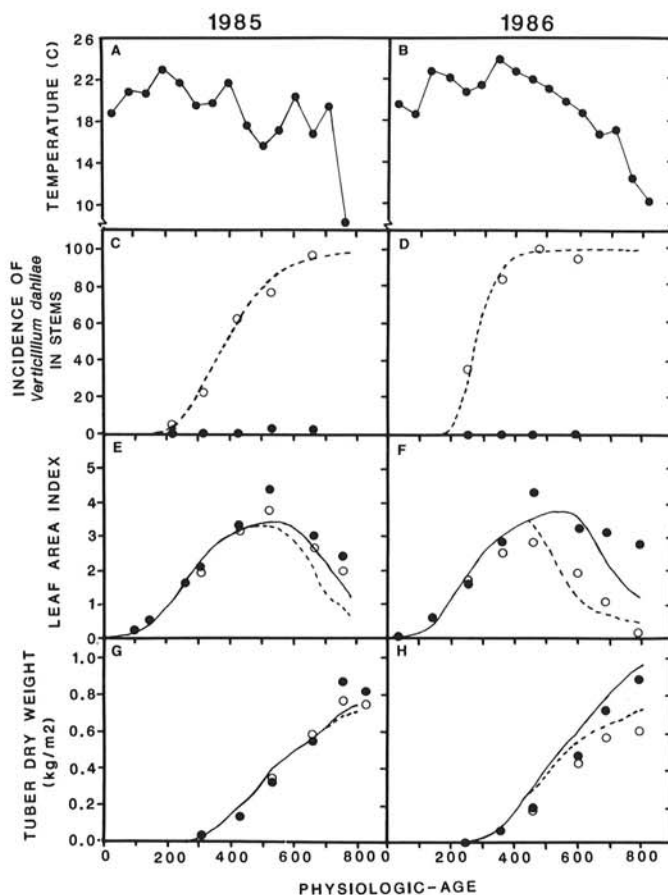

Fig. 2. Observed mean weekly temperature (A and B), the estimated Gompertz function (---) compared with observed (o) increase in incidence of *Verticillium dahliae* in potato stems (C and D), and modeled (———) and observed (o) leaf area index (E and F) and tuber dry weight (G and H) from inoculated (o —) and control (● ———) crops of Russet Burbank potatoes grown in 1985 and 1986.

Incidence in stems increased with subsequent sampling dates, always reaching levels greater than 95% (Fig. 2C and D and Fig. 3D, E, and F). The Gompertz model accurately described the observed increase in incidence of stem infection by *V. dahliae* (Table 2, Fig. 2C and D and Fig. 3D, E, and F). Based on the estimated values of k_g and their standard errors (Table 2), rates of stem infection were similar for the 1985, 1987-wet, and 1987-dry experiments but higher infection rates were obtained in 1986 and 1987-late. Incidence of *V. dahliae* in stems of the control treatments never exceeded 4% except for the 1987-dry experiment, which reached 20% late in the season (Fig. 2C and D and Fig. 3D, E, and F).

Nematode assays. *Paratylenchus* (pin nematode) was the only plant parasitic genus recovered in 1985 and 1986 and densities were considered low, averaging 1 and 69 nematodes/100 cm³ soil for 1985 and 1986, respectively. In 1987, the density of *Paratylenchus* was intermediate to that found previously, and a low density of a monosexual *Pratylenchus* sp. (39 nematodes/100 cm³) also was present.

Environment. Mean temperatures from onset of *V. dahliae* infection ($P_A = 160$) to $P_A = 700$ were 20.0, 21.3, 23.3, and 20.4 for the 1985, 1986, 1987-wet and -dry, and 1987-late experiments, respectively (Fig. 2A and B and Fig. 3A, B, and C). Mean temperature was below normal in August 1985, averaging 18.0 C; in contrast, July 1987 was warm, averaging 24.1 C.

Frequent rainfall occurred in 1986 and soil matric potentials were always greater than −0.14 MPa (15). Dry periods occurred in July 1985 (15) and May-June 1987 and the estimated soil matric potential reached lows of −0.20 and −0.38 MPa, respectively. In 1987, the supplemental irrigations applied to the wet experiment significantly increased ($P < 0.05$) soil matric potential over that measured in the dry experiment (Fig. 4).

Crop response. Crop responses to infection by *V. dahliae* varied among experiments. Observed yield losses were 6.5, 28, 14, 16, and
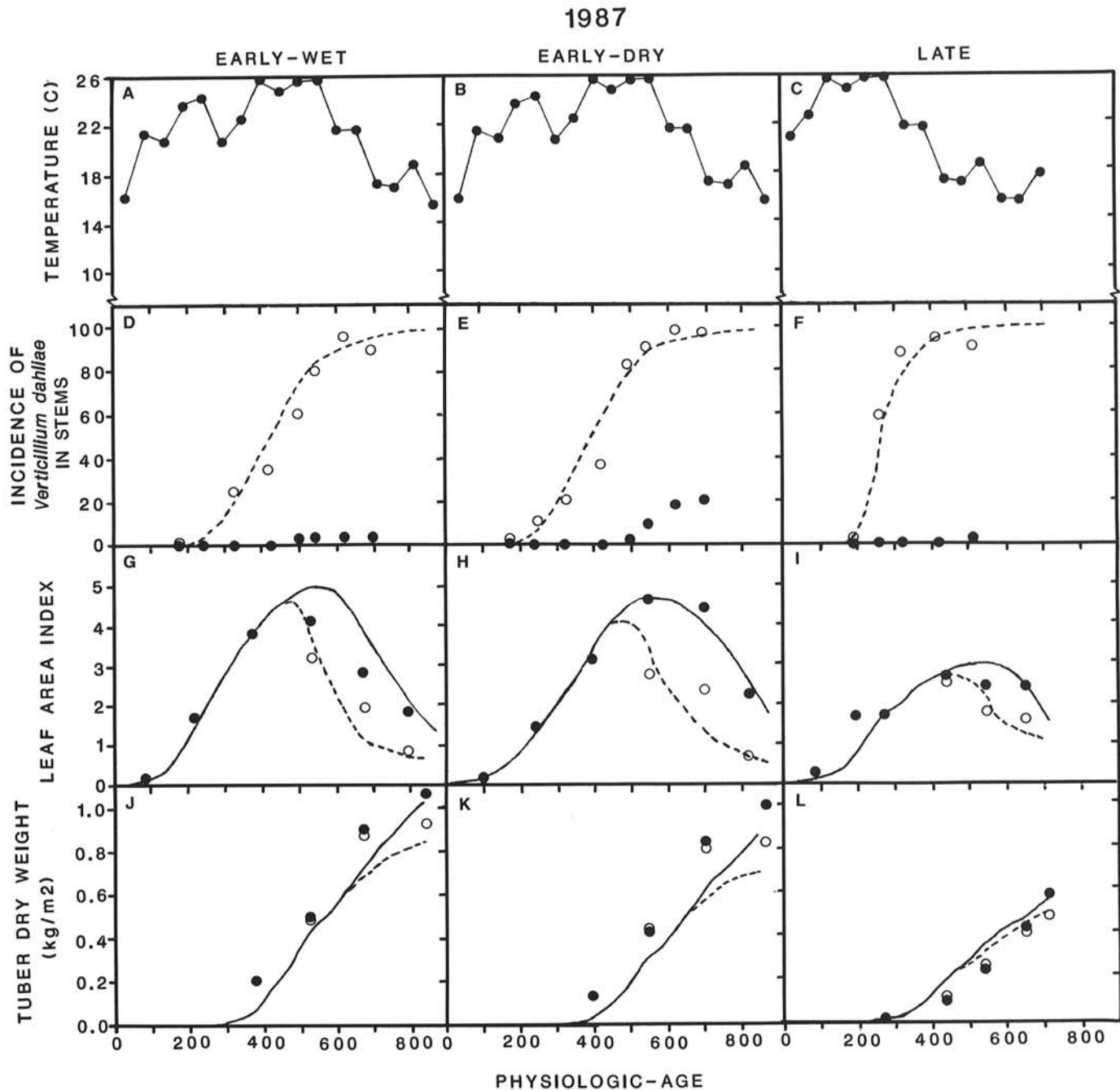
1987

Fig. 3. Observed mean weekly temperature (A–C), the estimated Gompertz function (---) compared with observed (o) increase in incidence of *Verticillium dahliae* in potato stems (D–F), and modeled (——) and observed (o) leaf area index (G–I) and tuber dry weight (J–L) from inoculated (o ---) and control (● ——) crops of Russet Burbank potatoes from three experiments grown in 1987.

TABLE 2. Fit of the linear Gompertz model $(-\ln(-\ln(y)) = -\ln(B) + k_g \cdot t_g)^a$ to the temporal incidence of *Verticillium dahliae* in the basal portion of Russet Burbank potato stems for five inoculated crops grown in 1985, 1986, and 1987

	Estimate			
Crop/treatment	$k_g \pm$ standard error	$-\ln(B) \pm$ standard error	y_0^b ($t_g = 0$)	r^2
1985	0.077 ± 0.009	-1.79 ± 0.41	0.0025	0.96
1986	0.172 ± 0.021	-2.10 ± 0.41	0.0003	0.98
1987-wet	0.067 ± 0.009	-1.93 ± 0.40	0.0010	0.92
1987-dry	0.075 ± 0.008	-1.87 ± 0.48	0.0016	0.95
1987-late	0.130 ± 0.016	-1.78 ± 0.37	0.0027	0.97

[a] y = proportional recovery of *V. dahliae* in sample sizes ranging from 32 to 60 stems. Four to eight dates were sampled in each crop. t_g = days from onset of the epidemic. B is a position parameter related to the amount of disease at onset, and k_g is the infection rate parameter. Onset ($t_g = 0$) was assumed to be the day from 50% emergence corresponding to the cumulative physiologic age of 160.

[b] y_0 = back transformed initial incidence of *V. dahliae* in stems.
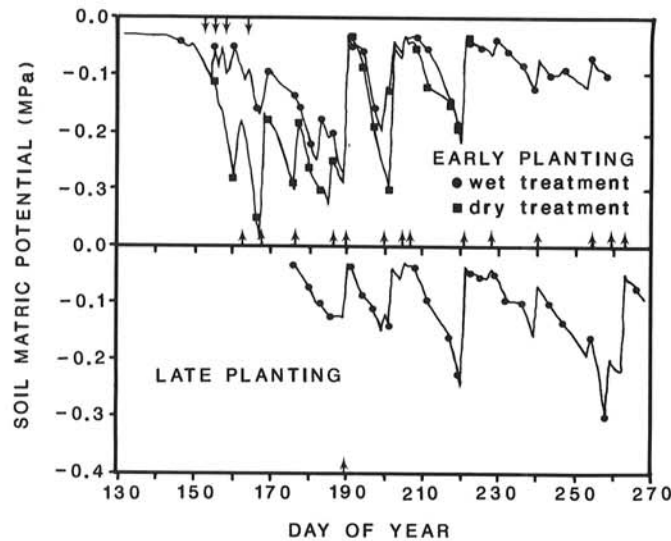

Fig. 4. Average soil matric potential in the upper 30 cm of soil by day of year for the three experiments in 1987. Arrows along the top line indicate irrigations applied to the early planted wet experiment. Arrows on the middle line indicate rainfall events greater than 5 mm, and along the bottom, the arrow represents a 3-cm irrigation applied to all experiments.

TABLE 3. Correlations between observed and simulated final tuber yield and observed and simulated areas under the leaf area index curve and tuber dry matter bulking curve from five experiments of paired control and *Verticillium dahliae*-infected potato crops grown in 1985, 1986, and 1987

Variable	Control crop (r)	*V. dahliae*-infected crop (r)	Control crop minus the *V. dahliae*-infected crop (r)
Final tuber dry matter yield	0.94^{**a}	0.85^*	0.81^*
Area under the tuber dry matter bulking curve	0.89^{**}	0.89^{**}	0.91^{**}
Area under leaf area index curve	0.92^{**}	0.99^{***}	0.69

[a] * Significant at $P = 0.10$ (3 df). ** Significant at $P = 0.05$ (3 df). *** Significant at $P = 0.01$ (3 df).

14% in the 1985, 1986, 1987-wet, 1987-dry, and 1987-late experiments, respectively. Final tuber yields were significantly ($P < 0.05$) reduced by the *V. dahliae* treatment in each of the 1986-1987 experiments, and a significant reduction ($P < 0.05$) in leaf area index also occurred on at least one sampling date in the same four experiments when compared to the uninoculated treatments. In all experiments, stem dry weights were similar between the inoculated and uninoculated treatments up to the cumulative P_A range of 300 to 400. After this time, stem dry weights from infected crops averaged 14% less than the control crops owing to attrition from senescence and to slight reductions in stem length.

The values of k_V and k_t that best described the observed crop response were 1.1 and 17 C, respectively. The simulated crops generally described the observed points, although the model overestimated maximum values of LAI and tuber dry matter in some cases (Figs. 2H and 3G) and underestimated them in others (Fig. 2E; F, G and Fig. 3J and K). Response of the *Verticillium* submodel to the 1985 and 1987-late input data was relatively small (Fig. 2E and G and Fig. 3I and L), but greater responses occurred using the data from the 1986 and early planted 1987 experiments (Fig. 2F and H and Fig. 3G, H, J, K).

Among experiments, significant correlations ($P < 0.10$) were found between modeled and observed final tuber yields and areas under the tuber dry matter accumulation curves from the control treatments, the *V. dahliae* inoculated treatments, and the difference between the two treatments (Table 3). Modeled differences in final tuber dry matter yield were 24, 201, 189, 189, and 53 g/m², and observed differences and standard errors were 58 ± 49, 261 ± 43, 149 ± 29, 164 ± 29, and 97 ± 22 g/m² for the 1985,

1986, and 1987-wet, 1987-dry, and 1987-late experiments, respectively.

Modeled and observed areas under the LAI curve were significantly correlated among experiments for both the control treatment and the *V. dahliae* treatment (Table 3). The correlation between the modeled and observed treatment difference for area under the LAI curve was positive ($r = 0.69$) but not significant. However, for all sampling dates where both treatments were harvested, the observed differences in LAI between the inoculated and uninoculated treatments were correlated with the modeled differences ($r = 0.55$, $n = 18$, $P < 0.05$).

Neither mean seasonal temperature nor the Gompertz infection rate parameter were significantly correlated at $P \geqslant 0.10$ with the observed percentage yield reduction ($r = 0.22$ and 0.77, respectively). Mean seasonal temperature and infection rate were not correlated ($r = -0.42$).

Simulation experiments. Differences between infected and control crops in modeled radiation use efficiency were evident within the cumulative P_A range of 300 to P_A 600 where the accelerated leaf aging rate of the *V. dahliae* infected crop reduced radiation use efficiency an average of 8.8% compared to the control. A maximum reduction of 17% occurred at the cumulative P_A of 450. Before this interval, modeled net growth rates were similar in both crops.

Modeled LAI and tuber yield responded differentially to varying temperature and *V. dahliae* infection rate (Figs. 5–7). Increasing temperature from 19 to 25 C greatly accelerated leaf aging rate and reduced LAI (Fig. 5). When crop growth was modeled over a 100-day growing season, tuber yields of both the control and infected crops declined as the mean temperature increased (Fig. 6). Accumulation of 830 P_A units required 98 days at a mean temperature of 20 C but required 119 days at 25 C. Over a period of 830 P_A units, percent yield of the infected crops compared to uninfected controls showed a sigmoid response with increasing infection rate (Fig. 7).

To add perspective to Figure 7, after 100 days, a value of $k_g = 0.02$ results in 24% of the stems infected with $B = 7.0$ and an onset P_A of 160 (about 18–20 days after emergence). Using similar onset conditions, values of $k_g = 0.05, 0.09, 0.12,$ and 0.17 would result in 90% incidence at approximately 102, 65, 53, and 43 days after emergence, respectively.

DISCUSSION

The objective of this study was to develop a model that enhances understanding of factors influencing the variability of yield reductions caused by *V. dahliae*. Because a population parameter (infection rate) was used as an input to accelerate leaf aging, interpretation of the model must be made at the population (crop) level of biological hierarchy. Also, the potato growth model is deterministic; thus, the results are only meaningful when infection of stems occurs randomly or systematically in a crop, and not when disease has a patchy distribution.
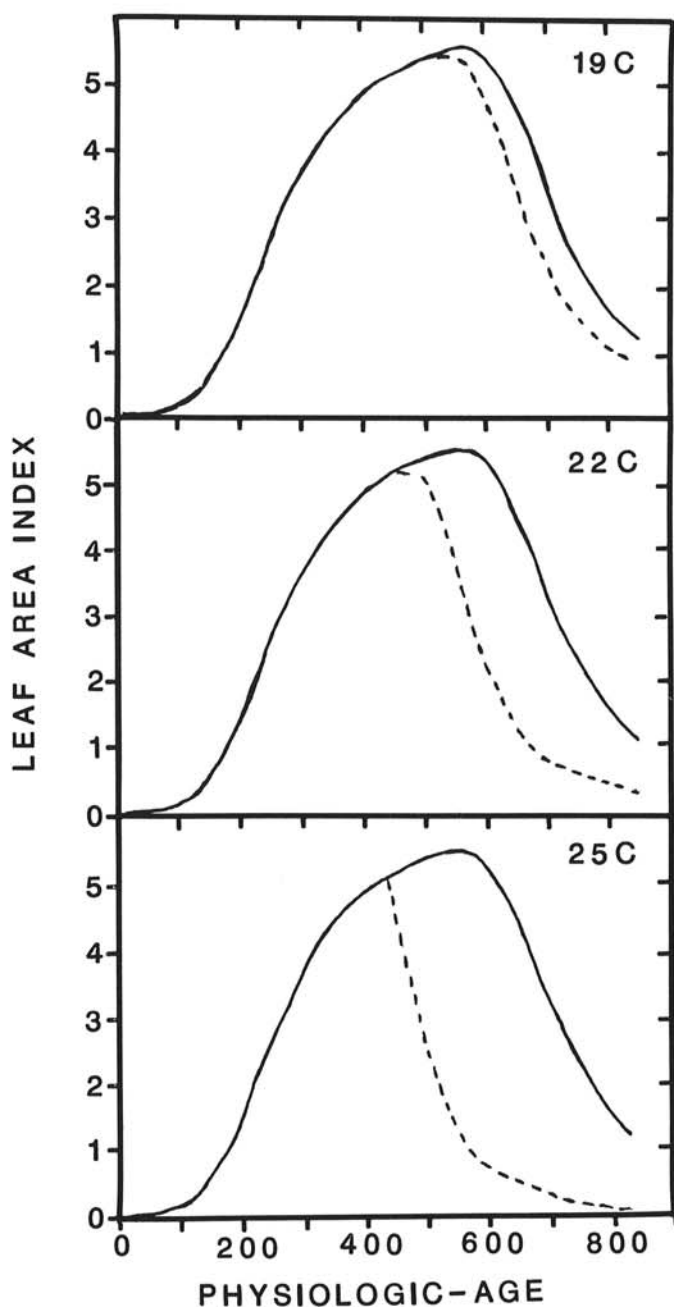
The major assumption of the *Verticillium* submodel is that the degree to which the leaf aging rate is accelerated is a proportional constant of the product of *V. dahliae* incidence in stems and high-temperature stress. This assumption is based on the idea that, once a stem becomes systemically infected, the pathogen and other influencing factors (in this case temperature) can act in concert to produce disease, resulting in an accelerated rate of leaf aging and shortened leaf life spans. Percent incidence of *V. dahliae* in stems is included because, in a population of plants, disease-induced acceleration of the mean leaf aging rate also must be dependent on the number of individuals (stems) that are infected. Undoubtedly, further research could improve on this relationship, particularly as to how it relates to potato physiology, extremes of inoculum density and temperature, and other factors influencing potato early dying. Few studies, however, have studied leaf life spans in crop populations, and information is lacking to formulate alternatives. When one uses simulation analysis to address a problem, construction of a simple one- or two-variable linear model to test a hypothesis usually is a valid beginning approach. Moreover, the submodel reasonably described the data presented,

Fig. 5. Effect of mean temperature on modeled leaf area index over time in *Verticillium dahliae* infected (---) and uninfected (———) Russet Burbank potatoes. The *V. dahliae* infection rate parameters were as follows: onset P_A = 160, Gompertz B = 7.0, and k_g = 0.12.
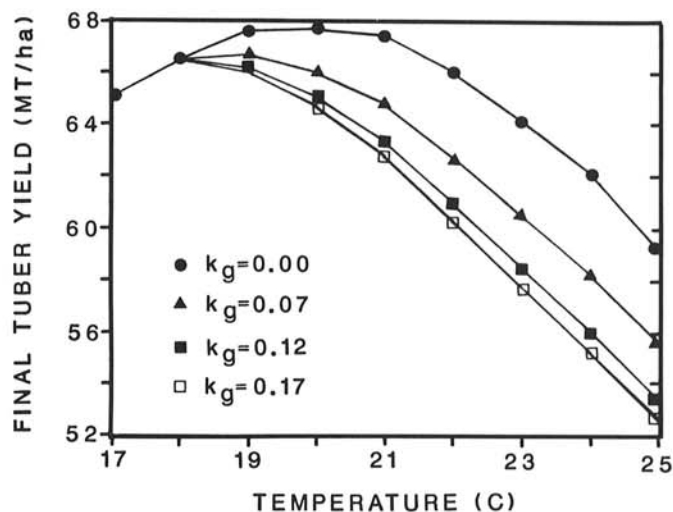

Fig. 6. Effect of mean temperature on simulated yield of Russet Burbank potatoes infected with *Verticillium dahliae* at different rates and grown for a period of 100 days. k_g is the Gompertz infection rate parameter. The *V. dahliae* infection rate parameters were as follows: onset P_A = 160, Gompertz B = 7.0, and k_g = 0.12.
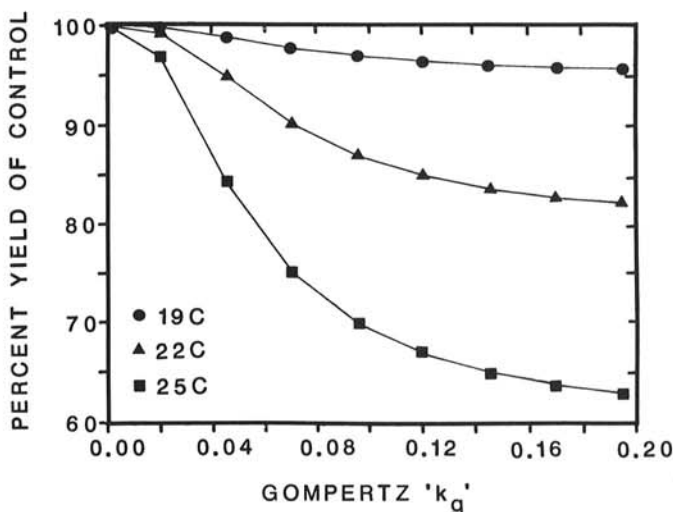

Fig. 7. Effect of the *Verticillium dahliae* stem infection rate (k_g) on percent reductions of simulated final tuber yield of Russet Burbank potatoes grown at three different mean temperatures for a period of 830 physiologic-age units (25). The *V. dahliae* infection rate parameters were as follows: onset P_A = 160, Gompertz B = 7.0, and k_g = 0.12.

and it now may serve as a framework for adding greater complexity.

A second assumption, which was not addressed by the sequentially harvested crop biomass data, is that the differences in LAI between the infected and control treatments are largely due to premature senescence of old leaf tissue and not to differences in development of new leaf tissue. In 1986, the number of leaves per plant was intensively monitored and both treatments were similar up to a cumulative P_A of 500 when senescence of older leaves became apparent in the inoculated treatment. Similarly, Harrison and Issac (13) found that infection by *V. dahliae* did not affect the total number of leaves produced on a plant or the rate of new leaf initiation; but they also stated that leaves produced on infected field-grown plants may be slightly stunted. For the Russet Burbank cultivar, rate of new leaf initiation slows and nearly ceases within the P_A range of 500 to 600 (19), whereas, in this study, the greatest differences in LAI (leaf biomass) between infected and control treatments were found in the latter half of the season (Figs. 2 and 3).

Biological interpretation of the *V. dahliae* incidence component of the model is twofold. First, time of stem infection is very important. Compared to late infection, early infections give the pathogen more time to colonize the vascular system (7) and to affect the productivity and life spans of relatively younger leaves. In addition, with early infection, there is an increased likelihood that the crop will experience a coinciding period of high-temperature stress resulting in a greater rate of leaf aging and more severe early dying. The second important consideration is the percentage of stems infected. Because the relationship between radiation interception and LAI is a nonlinear saturation curve (14), low levels of infection probably will not greatly influence crop productivity, although foliage losses on some stems may be severe. Coupled to the growth model, the Gompertz disease progress curve integrates the above argument by modeling from the population perspective both the timing of infection and number of infected individuals in the epidemic. With regard to crop productivity, these conclusions are very similar to those found when a model of Verticillium wilt was coupled to a model of cotton growth (11).

The temperature component of the submodel equation describes the increasingly favorable conditions for growth and activity of *V. dahliae* in host tissue as temperature increases from the threshold of 17 C to its optimum of 25–27 C (28). Temperature-dependent interactions between disease and host physiology also may be summarized (4,12). The value of the threshold was chosen because it resulted in the best fit of the data; however, with different strains of the fungus or in different production areas, it is likely that the threshold value could be slightly different. Relative to appropriate values of the other parameters, greater values of k_t increased the sensitivity of the model to high temperature and lower values of k_t resulted in increased sensitivity to infection rate. Another component of temperature influencing disease severity is modeled within Sands et al's P_A phenological scale (27). As temperature increases above 20 C, the accumulation of P_A units in a healthy crop slows and the tuber yield declines when to compared to crops grown under cooler conditions for the same period of time (Fig. 6). In general, similar yields can be obtained for healthy crops grown to the same cumulative P_A, but at higher temperatures, the slower daily net crop growth rate allows more time for the disease to impact yield.

Justification of the temperature component is based on observations in the literature (8,9,13,17,20,22,23,25,26) and the data presented here. In controlled environments, the influence of temperature on potato growth and diseases caused by *V. dahliae* has been readily demonstrated (8,13,20,22), but understanding the problem in the field is a correlative problem, usually done with very few degrees of freedom. Considering that every effort was made in this study to standardize the methods used each season, the observed differences in crop response and yield between the similarly infected 1985 and 1987 early planted experiments are some of the most indicative field data demonstrating a role for temperature in potato early dying (Figs. 2 and 3).

Nematode populations were monitored because of their potential to interact with *V. dahliae* causing greater expression of potato early dying symptoms (25). However, *Pratylenchus penetrans*, a bisexual nematode species viewed as the primary interactant in potato early dying (25,26), was not found in the experimental sites in any of the three seasons. Other nematodes that are considered plant pathogens were present in low populations. Bacterial pathogens also are considered a potential interactant in potato early dying (25); but, probably because these experiments were located on dry-land sites, bacterial disease symptoms were only very rarely observed.

In cotton, slight to moderate moisture stress early in the season has been suggested as a way to manage the severity of Verticillium wilt (10). In this study, the 1987 experiment was designed to evaluate this condition with the use of supplemental irrigation on one treatment. Early in the season, significant differences in soil matric potential were attained between the treatments, but the resulting rates of stem infection and percentage reductions in yield caused by *V. dahliae* were similar ($k_g = 0.067$ and 0.075, and yield loss = 14 and 16% for the wet and dry treatments, respectively).

The simulation analyses provided a more complete picture of how temperature and infection rate interact within the model to accelerate leaf aging and reduce tuber yield. Extrapolation of the model was limited to the left (increasing) side of *V. dahliae* temperature optimum curve and to onset times and infection rates similar to those observed. For a given temperature, yield reductions appear to be asymptotic with increasing infection rate (Fig. 7). The range of yield reductions shown in Figure 7 (0–37%) is similar to that reported in the literature (7,9,13,17,22,23,26).

Although the model still requires further validation, two implications of this study may lead to better understanding and management of potato early dying disease. First, the model provides a framework for further studies on the effects of *V. dahliae* and other potato-disease-influencing factors on crop growth and productivity. For example, the model may be particularly applicable to studies on the interaction of nitrogen nutrition, *V. dahliae* infection, and rate of leaf senescence (7). Also, recent results of Nicot and Rouse (21) showed that the presence of *P. penetrans* may increase the rate of stem infection. Consequently, the model may be a useful tool for elucidating the mechanisms of this interaction (26). Second, the knowledge that yield reductions can be related to the combined effects of infection rate and mean air temperature may lead to better survey designs to evaluate the impact of this disease, or to a current season prognosis for the potential of severe potato early dying within a crop. To illustrate, stems could be sampled near midseason (approximate P_A = 350–400), and by assuming an onset time, an infection rate could be estimated. This information may be useful to producers for timing harvest and aiding other crop-management decisions.

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