Evaluation of a Mechanistic Model that Describes Potato Crop Losses Caused by Multiple Pests

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ABSTRACT

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Potato yield and foliage loss expectations for solitary and concurrent infestations of potato leafhopper (*Empoasca fabae*), early blight (*Alternaria solani*), and Verticillium wilt (*Verticillium dahliae*) were developed with a crop growth simulation model and compared to data obtained when these same organisms were studied in a factorially arranged field experiment. The principal conclusion from both the field and simulation approaches was that concurrent infestations of potato leafhopper, *A. solani*, and *V. dahliae* result in yield and foliage reductions that are less than the sum of losses caused by a solitary infestation of each organism. The simulation model provided a mechanistic framework for understanding the basis and importance of various types of pest-pest interactions. This led to the conclusion that competition between the diseases and potato leafhopper to impact photosynthetic carbon assimilation was the dominant interaction in this system. Results obtained are discussed in relation to development of empirical, regression-based models for estimating the impact of multiple pests on crop productivity. Models based on cumulative radiation interception may be one of the few empirical approaches that can provide reproducible interpretations of the effects of multiple diseases, insect pests, and other constraints on potato crop yield.

The two diseases, Verticillium wilt (caused by *Verticillium dahliae* Kleb.) and early blight (caused by *Alternaria solani* Sorauer), and the insect pest, potato leafhopper (*Empoasca fabae* Harris), often occur concurrently in potato fields of the north central United States. In factorially arranged field experiments, Johnson et al (14,17) investigated the effects of these three pests on potato yield and foliage losses. A principal conclusion from the field studies was that combined infestations resulted in yield and foliage losses that were less than the sum total of losses from solitary infestations of each organism.

In subsequent research, the effects of potato leafhopper, early blight, and Verticillium wilt were each coupled to a dynamic simulation model of potato growth (9,13,15,16). Each pest submodel was developed independently without consideration of the biology of the other organisms.

An initial objective for undertaking the previous simulation studies was to develop a research tool that could be used to describe and understand the effects of concurrent disease-insect pest infestations on crop yield. This study addresses that objective by using the potato growth model and the independently developed pest submodels to simulate potato growth in response to solitary and combined infestations of potato leafhopper, early blight, and Verticillium wilt. Results were compared with those obtained in previous field experiments (14,17). An additional objective was to discuss the simulation results in relation to yield loss assessment methods applicable to multiple disease-pest infestations.

MATERIALS AND METHODS

Potato growth model. The crop growth model (12) accumulates dry matter as the product of radiation interception (RI) and radiation use efficiency (RUE) (19). Biomass is produced on a per unit area basis (kg/m^2) and competitively partitioned into leaves, stems, tubers, and roots. Data requirements for the model include plant and row spacing, and daily inputs of solar radiation, temperature, and soil water potential. The proportion of radiation intercepted is estimated from a modeled green leaf area index (GLAI). Measurements of temperature are used to compute physiologic-age units (P_A) (i.e., P-Day's [21]); daily P_A units and soil water potential modify potential RUE. Daily additions of leaf tissue are maintained as separate cohorts (age-classes). A leaf cohort is senesced after its age exceeds a maximum P_A. Response of the model has been evaluated under several climatic and edaphic conditions in the north central United States and for its response to artificial defoliation (11).

Pest submodels. The potato leafhopper submodel requires a daily estimate of the density of nymphs on leaves in the middle of the potato canopy (13,16). Each day, this value is multiplied by a crop and leaf P_A-dependent response function to provide an estimate of feeding intensity of nymphs on all leaf cohorts (13). Nymphal feeding within a leaf cohort quantitatively reduces that cohort's RUE (16). In the field, prolonged potato leafhopper feeding results in necrosis of green leaf tissue, termed hopperburn. Within simulated leaf cohorts, hopperburn develops at a rate proportional to the product of nymphal feeding intensity and amount of green leaf tissue (16). Loss of green leaf tissue to hopperburn reduces RI.

The submodel that describes early blight is a modified logistic equation with added functions for a leaf P_A-dependent incubation period and a term for lesion expansion (4,15). Early blight affects RI by reducing green leaf tissue through new infection, lesion expansion, and by inducing premature senescence of leaf cohorts after the proportion of disease within a cohort has exceeded a crop P_A-dependent maximum severity (15). Disease-induced senescence of a cohort disables a leaf dry matter remobilization function, which results in a small reduction of RUE (15).

The Verticillium wilt submodel accelerates the aging rate of cohorts of leaf tissue by adding P_A units to each cohort daily as a function of the proportion of potato stems infected with *V. dahliae* in a plant population and the daily mean air temperature (9). Over the course of a season, the number of infected stems increases with time; this aspect of the biology is described by a Gompertz function (3). With regard to productivity, these functions result in premature senescence of leaf cohorts (reduced RI) and acceleration of a function that describes the normal age-dependent decline of RUE that occurs in leaves of noninfected crops (9,20).

Pest-pest interactions. Although each disease-insect submodel was developed independently, combining the submodels into a single program resulted in several inherent disease-disease and disease-insect interactions and the need to explicitly state one

disease-insect interaction. Two inherent interactions are attributable to the Verticillium wilt submodel. The accelerated rate of leaf aging caused by this submodel reduces the incubation period of new early blight lesions. Accelerated leaf aging also shifts the maximum feeding intensity of potato leafhopper nymphs to leaf cohorts positioned higher in the crop canopy. With respect to crop productivity losses, it was expected that effects of these interactions could range from neutral to synergistic. Other interactions are caused by the function for increasing hopperburn within the potato leafhopper submodel. Loss of green leaf tissue to hopperburn inherently reduces the amount of green leaf area available for infection by *A. solani*. In addition, because both the early blight and potato leafhopper submodels quantitatively reduce green leaf tissue within leaf cohorts, it was necessary to explicitly define their interaction. Within each leaf cohort, leaf tissue previously diseased with early blight develops hopperburn at a rate proportional to the rate of hopperburn development on healthy leaf tissue. Early blight lesions associated with hopperburn remain infectious but do not expand (in the field, hopperburn tissue is normally very dry and often dehisces from leaves). The daily calculation of the percentage of early blight on leaves excludes lesions associated with hopperburn, because field assessment of early blight on hopperburn tissues is very difficult (17). Interactions of early blight with hopperburn were considered antagonistic.

Yield and foliage loss comparisons. Expectations of yield and foliage losses for solitary and concurrent infestations of early blight, Verticillium wilt, and potato leafhopper were developed in a simulation experiment with the potato growth model. These data were then compared to a partial set of field data from a field experiment conducted in 1983 under dryland conditions at the University of Minnesota Agricultural Experiment Station in Rosemount (14). The field data were from the cultivar Russet Burbank and included yield and green leaf area ratings from a $2 \times 2 \times 2$ factorial arrangement of control (low disease or insect pressure) and moderately high levels of the two diseases and insect pest (i.e., early blight levels 1 and 3, Verticillium wilt levels 1 and 2, and potato leafhopper levels 1 and 3 in the 1983 study [14]). Crop simulations were run with environmental data (solar radiation, temperature, and soil water potential) collected in 1983 from a healthy potato crop in a field adjacent to the multiple pest study (12). The required daily inputs of potato leafhopper nymph density on midplant leaves were based on counts from the 1983 experiment (14,16). Input data required for potato growth were based on the 1983 experiment (Table 1). Parameters required to model disease-pest induced crop damage were set to values obtained when the submodels were fit to field data collected in other seasons when low (control) and moderately high infestations for each organism were obtained (9,13,15) (Table 1).

Dependent variables selected for comparison were observed and modeled final tuber dry matter yield and observed area under the proportional green leaf area curve (AUPGLAC) were compared to area under the modeled GLAI curve (AUGLAIC). Values of observed AUPGLAC were computed with the following equation:

$$\text{AUPGLAC} = \Sigma([1.0 - d] \cdot [1.0 - (e + h)]) \cdot (t_i - t_{i-1})$$
$$i = 1,9$$

in which the variables d, e, and h represent measurements of proportional crop defoliation and the proportion of crop foliage with early blight and hopperburn symptoms, respectively, assessed every week over the interval from 15 July to 13 September 1983 (i.e., cumulative crop $P_A = 257-660$); the time scale, t, is days after emergence; i is the ith assessment date. AUGLAIC was computed for each disease-pest combination by summing daily the modeled values of GLAI over the same interval used to compute AUPGLAC.

Green leaf area and symptom development. A second set of simulation experiments was conducted to evaluate effects of potato leafhopper, early blight, and Verticillium wilt on temporal

development and attrition of modeled GLAI, and on foliar early blight and hopperburn symptom development. Values for pest submodel parameters were as in Table 1, but the model was run with 1987 temperature data from Rosemount (9) and without moisture stress. Row and plant spacing in these simulations were 0.24 and 1.00 m, respectively, and length of the season was 850 P_A units (117 days after emergence) or until GLAI had been reduced below 0.5. Estimates of daily potato leafhopper nymph density on midplant leaves were based on counts from a moderately high infestation obtained in a field experiment conducted in 1986 at Rosemount (13). This infestation averaged 1.65 nymphs per midplant leaf from 27 to 117 days after emergence. Crop growth simulations were run in three groups of 2×2 factorial arrangements of control and moderately high infestations of each disease-pest combination (e.g., one group was potato leafhopper and early blight). To evaluate results, simulated GLAI was plotted over time for each pest combination. Effects of other disease-pests on early blight and hopperburn symptom expression also were evaluated with graphical plots of symptom development over time. In addition, the potential for the Verticillium wilt submodel to reduce the early blight incubation period was examined by plotting the vertical distribution of early blight symptoms within the array of leaf cohorts at the cumulative crop P_A of 675 (about 80 days after emergence) for a crop with early blight and a crop with early blight and Verticillium wilt.

Radiation interception. Simulations were conducted to investigate the relationship between cumulative RI (MJ/m^2) by GLAI and tuber dry matter yield (kg/m^2) as affected by potato leafhopper, early blight, and Verticillium wilt. The analysis included three potato leafhopper infestations (control, intermediate, and moderately high), and six early blight and six Verticillium wilt epidemics. The intermediate and moderately high infestations of potato leafhopper nymphs were based on measurements made in field plots located at Rosemount in 1986 (13) and averaged 0.67 and 1.65 nymphs per midplant leaf, respectively, from 27 to 117 days after emergence. The early blight epidemics were created by setting the infection rate parameter (k_i) to values of 0.001, 0.002, 0.004, 0.008, or 0.016 for each of six independent simulations. Similarly, the Gompertz rate parameter (k_g) in the Verticillium wilt submodel was set to values

TABLE 1. Input data and model constants and parameters used in simulation experiments

Potato growth parameters[a]	Disease-pest submodels[b]
Seed piece size (60 g)	Potato leafhopper[c]
Row spacing (1.0 m)	Feeding effects on RUE[d]
Plant spacing (0.3 m)	parameter (k_{pr}), 0.0007
Physiologic age	Feeding threshold constant for
of leaves (P_A) (425)	hopperburn to develop (k_{th}), 4.00
Crop P_A at	Hopperburn rate
tuber initiation (210)	parameter (k_{hb}), 0.03
Maximum crop P_A (675)	Early blight[e]
Maximum RUE[d] (1.5 g/MJ)	Crop P_A at epidemic onset, 300
Partitioning constants	Initial amount of disease, 0.25%
k_1 (50.0)	Infection rate
k_2 (leaves) (1.0)	parameter (k_r), 0.015
k_3 (stems) (4.5)	Lesion expansion rate (k_{lx}), 0.20
k_4 (roots) (1.0)	Verticillium wilt[f]
k_5 (tuber) (4.5)	Crop P_A at epidemic onset, 160
	Gompertz rate parameter (k_g), 0.077
	Gompertz position constant (k_B), 6.02
	Temperature-Verticillium
	interaction constant (k_v), 1.10

[a] Seed piece size and plant and row spacing based on data of Johnson et al (14). Values of other potato growth parameters were obtained previously in model development and validation studies (11,12).
[b] Units on rate parameters k_{pr}, k_{hb}, k_r, k_{lx}, k_g are per day.
[c] Parameter values were obtained in model development and validation studies (13,16).
[d] Radiation use efficiency.
[e] Parameter values were obtained in a model development study (15).
[f] Parameter values were obtained in a model development study (9).

of 0.01, 0.02, 0.04, 0.08, or 0.16. The six early blight epidemics and the six Verticillium wilt epidemics were run as solitary epidemics with each potato leafhopper infestation. Other model input data and parameters were the same as those described above under the green leaf area experiment. Variables recorded for each

simulation were total cumulative RI and total tuber dry matter yield after 850 P_A units (117 days after emergence) or until GLAI had been reduced below 0.5. In addition, daily values of cumulative RI and cumulative tuber dry matter production were recorded for control and potato leafhopper simulations that were not
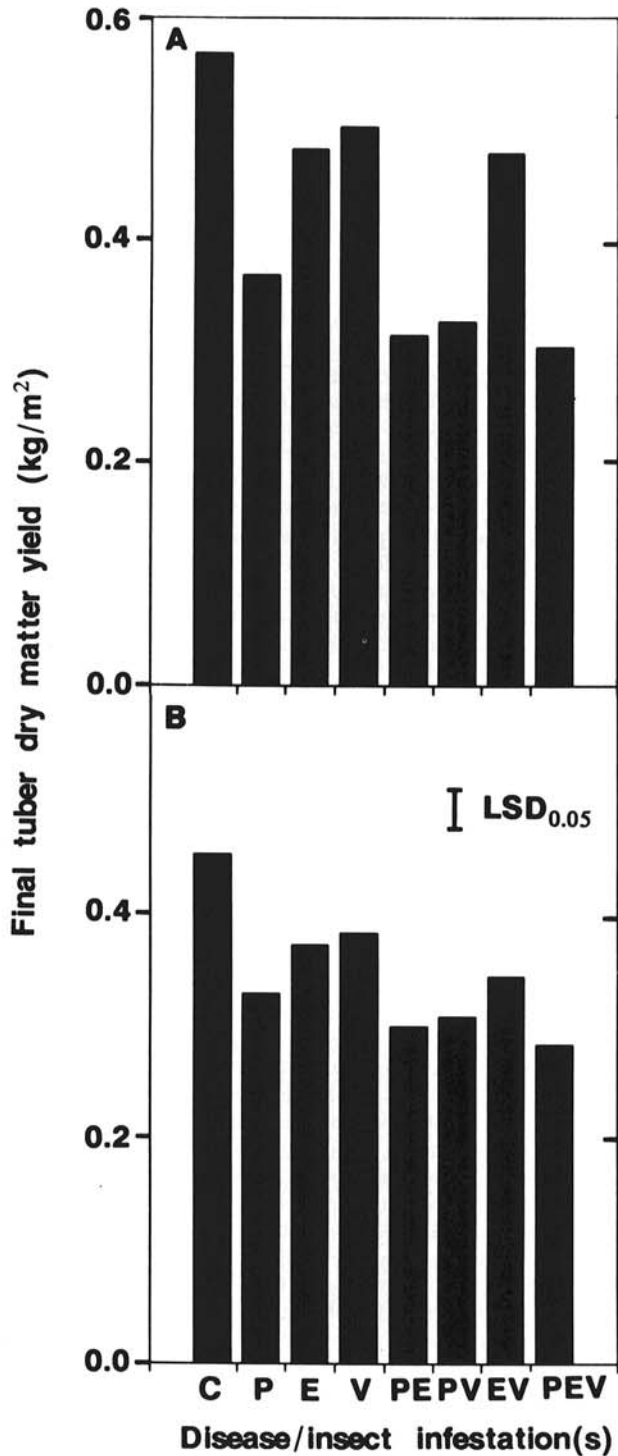

Fig. 1. A, simulated tuber dry matter yield of cv. Russet Burbank potato based on 1983 environmental conditions as the result of a factorial arrangement of control (C) and moderately high infestations of potato leafhopper (P), early blight (E), and Verticillium wilt (V). B, tuber dry matter yield of Russet Burbank potato in 1983 as the result of a factorial arrangement of control and moderately high infestations of potato leafhopper, early blight, and Verticillium wilt. Data are from Johnson et al (14). Length of line labeled LSD is the least significant difference at $P = 0.05$. Multiple letters under a bar indicate disease-insect pest combinations.
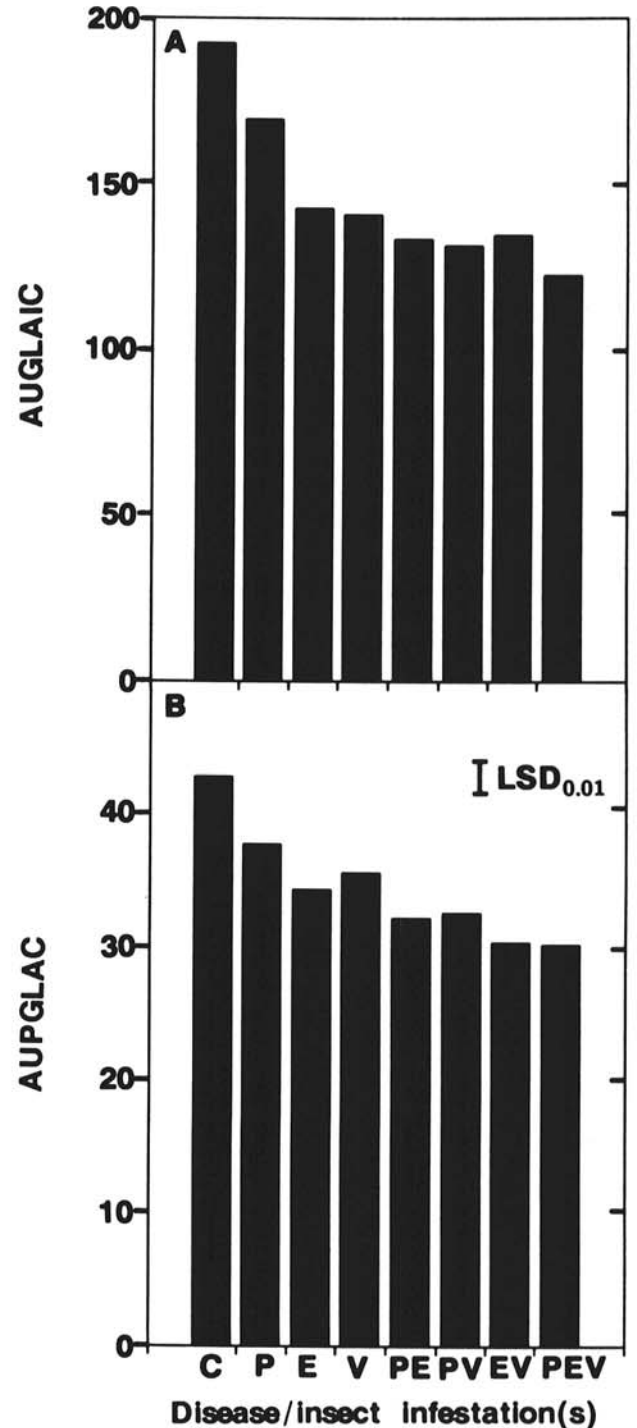
Fig. 2. A, simulated area under the green leaf area index curve (AUGLAIC) for cv. Russet Burbank potato based on 1983 environmental conditions as the result of a factorial arrangement of control (C) and moderately high infestations of potato leafhopper (P), early blight (E), and Verticillium wilt (V). B, area under the proportional green leaf area curve (AUPGLAC) for Russet Burbank potato grown in 1983 as the result of a factorial arrangement of control and moderately high infestations of potato leafhopper, early blight, and Verticillium wilt. Data are from Johnson et al (17). Length of line labeled LSD is the least significant difference at $P = 0.01$. Multiple letters under a bar indicate disease-insect pest combinations.

impacted by either disease. Simulation results were plotted in one figure to depict effects of the disease-insect submodels on the relationship between RI and tuber dry matter production.

RESULTS

Yield and foliage loss comparisons. Simulated tuber yields (Fig. 1A) in response to solitary and combined pest infestations revealed a pattern of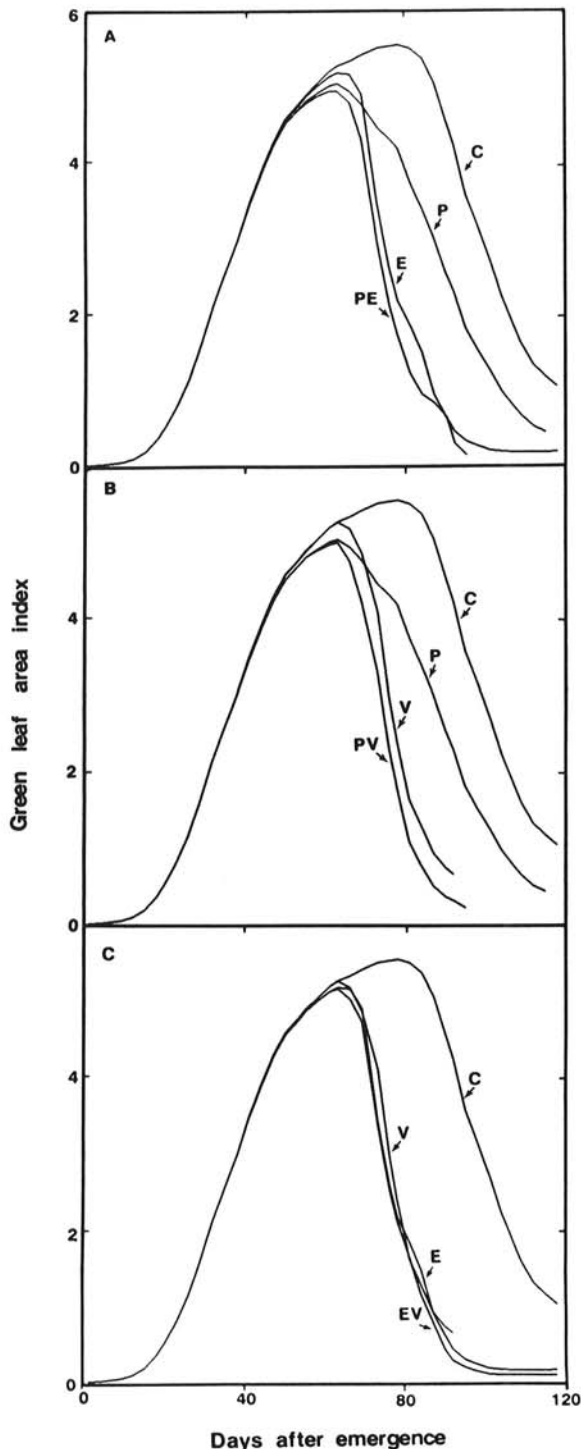 yield loss similar to that observed in the 1983 field experiment (Fig. 1B). Analysis of variance of the 1983 field data showed that each pest significantly reduced yield and that the leafhopper × early blight × Verticillium wilt and leafhopper × early blight interactions were significant ($P = 0.05$) (14). For both simulated and observed tuber yields, losses attributable to one pest were greatest when other pests were at low levels. For example, simulated and observed tuber dry matter losses attributable to early blight were 0.086 and 0.081 kg/m^2, respectively, when potato leafhopper and Verticillium wilt were controlled (i.e, the difference between bars labeled C and E in Fig. 1); however, effects of early blight were reduced to a simulated loss of 0.022 and an observed loss of 0.025 kg/m^2 when both potato leafhopper and Verticillium wilt were present (PV–PVE in Fig. 1).

Similarly, for observed potato foliage losses, variation in AUPGLAC was attributed to several significant ($P = 0.01$) less-than-additive interactions that resulted from the pest combination treatments (17) (Fig. 2B). Simulated reductions in the AUGLAIC curve also resulted in less-than-additive responses when pest infestations were combined (Fig. 2A). To illustrate, early blight and Verticillium wilt each individually reduced the AUGLAIC by 50 and 52, respectively (C–E and C–V in Fig. 2A); the combined reduction in AUGLAIC by the two diseases was 58 (C–EV in Fig. 2A). Compared to tuber losses, the impact of potato leafhopper on potato foliage was less apparent in both the field and simulation experiments (Fig. 2), because most leaf area affected by this pest is green but has reduced RUE.

Green leaf area and symptom development. Temporal development and attrition of simulated GLAI in 2 × 2 factorial arrangements of each pest combination demonstrated nonadditivity of disease-pest induced foliage losses. For instance, in solitary potato leafhopper infestations, reductions of green leaf area attributable to this insect were solely due to hopperburn and occurred after midseason (i.e., the difference in area under lines labeled C and P in Fig. 3A from 50 to 117 days after emergence). When potato leafhopper was combined with either early blight or Verticillium wilt, however, the amount of green leaf area loss attributable to hopperburn was reduced compared to the nondiseased crop simulations (i.e., the difference in area under curves labeled E and PE in Fig. 3A and V and PV in Fig. 3B, respectively, compared to the difference in area under curves labeled C and P in Fig. 3A or B). Reduced loss of green leaf area to hopperburn was caused by premature, early blight or Verticillium wilt induced defoliation of older leaf cohorts. Similarly, competition between the early blight and Verticillium wilt to induce premature senescence of leaf cohorts was apparent when these two diseases were combined (Fig. 3C). For the model parameters used, the simulation results predicted that addition of either disease to a crop already infested with the other would have little if any additional impact on the temporal distribution of green leaf area.

Temporal development of simulated hopperburn and early blight also reflected competitive foliage loss interactions among the diseases and insect pest. The most hopperburn occurred when potato leafhopper was the only pest in the simulation (Fig. 4A). Premature, early blight or Verticillium wilt induced senescence removed hopperburn symptoms that were disproportionately higher in older leaf cohorts. The rate of increase of early blight symptom development over time was delayed if potato leafhopper was included as a pest in the simulated crop (Fig. 4B). This reduction resulted mostly from removal of expanding early blight lesions by hopperburn and to a very small degree to loss of green leaf area available for new infections. Inclusion of Verticillium wilt with early blight had the effect of slightly accelerating early blight disease progress late in the season (about 85 days after emergence, crop $P_A = 675$, [Fig. 4B]). The vertical distribution of early blight on foliage at the cumulative crop P_A of 675 showed that this effect of Verticillium wilt submodel occurred in most leaf cohorts (Fig. 5).

Radiation interception. In simulation of the healthy potato crop, cumulative tuber dry matter production was linearly related to cumulative RI over the range from 400 to 1,600 MJ/m^2

Fig. 3. Simulated green leaf area index over time for cv. Russet Burbank potato as the result of 2 × 2 factorial arrangements of control (C) and moderately high infestations of potato leafhopper (P), early blight (E), and Verticillium wilt (V). Multiple letters labeling a curve indicate disease-insect pest combinations. **A,** potato leafhopper and early blight. **B,** potato leafhopper and Verticillium wilt. **C,** early blight and Verticillium wilt.

(this is shown in Fig. 6 by the line labeled C). Previous to 400 MJ/m^2 of cumulative RI, most captured sunlight was directed to development of the crop canopy. Potato leafhopper infestations greatly reduced RUE, which is indicated in Figure 6 by the reduction in the slopes of lines labeled P_i and P_h compared to the line labeled C. In addition, potato leafhopper, because of hopperburn, also had a small effect on cumulative RI. Final cumulative RI for the control, and intermediate and moderately high potato leafhopper infestations were 1,646, 1,588, and 1,485 MJ/m^2, respectively (this is indicated by the stars in Fig. 6).

The simulated early blight and Verticillium wilt epidemics impacted final tuber dry matter production mostly through effects on RI (points other than stars in Fig. 6). The disease epidemics also had slight effects on RUE; this is shown in Figure 6 by the final yield points for disease epidemics that fall slightly below the lines that represent the relationship between cumulative tuber dry matter production and cumulative RI in healthy and potato leafhopper infested crops. When potato leafhopper was absent from simulations, the maximum reduction of tuber dry matter caused by either disease was about 0.47 kg/m^2 (Fig. 6). Addition of the high potato leafhopper infestation to the disease epidemic simulations reduced the yield loss attributable to either early blight or Verticillium wilt to about 0.14 kg/m^2.
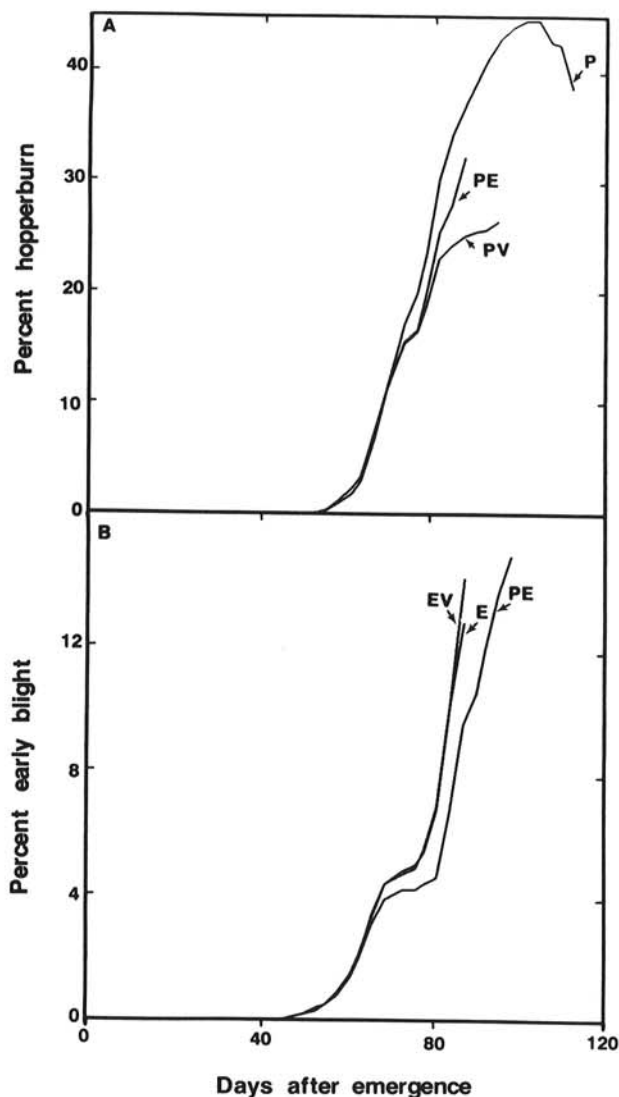
DISCUSSION

Two different approaches to understanding effects of combined infestations of potato leafhopper, early blight, and Verticillium wilt in potato (i.e., crop growth simulation and field factorial experimentation) have led to similar conclusions as to how these two diseases and an insect pest impact potato foliage and tuber yield. While neither approach can be considered rigorous proof of the conclusions of the other, the similar responses obtained by both approaches are indicative that the major main effects and interactions in this multiple pest-potato yield system have been described. Consequently, this analysis, which builds on results of several studies (8,10,14,17), can be used as a base for
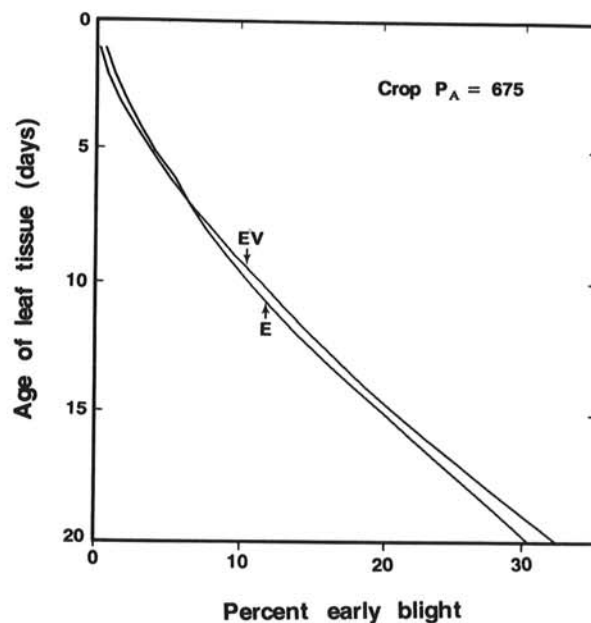
Fig. 5. Simulated vertical distribution of early blight disease at the cumulative crop physiologic-age units (P_A) of 675 resulting from a solitary epidemic (E) and for an epidemic combined with Verticillium wilt (EV).
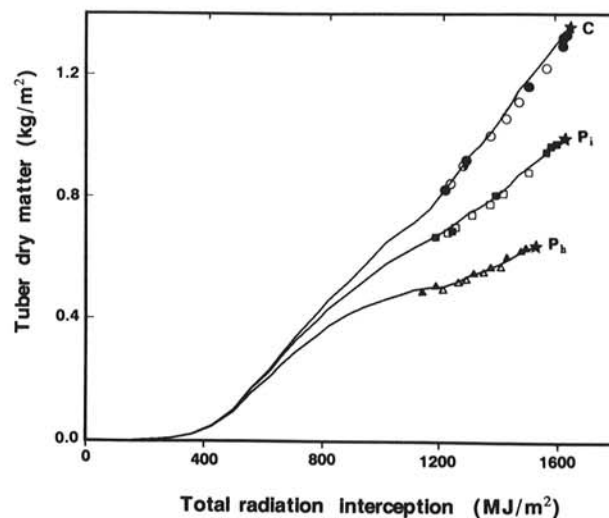
Fig. 4. Simulated foliar hopperburn and early blight symptom development over time on cv. Russet Burbank potato. **A**, percentage of hopperburn resulting from a solitary potato leafhopper infestation (P) and for potato leafhopper combined with early blight (PE), and Verticillium wilt (PV). **B**, percentage of early blight resulting from a solitary epidemic (E) and for epidemics combined with potato leafhopper and Verticillium wilt.

Fig. 6. Simulated cumulative (lines) and final (stars) tuber dry matter yields for control (C) and intermediate (P_i) and moderately high (P_h) potato leafhopper infestations in relation to cumulative solar radiation interception by the simulated crop canopy. Plotted symbols other than stars are final tuber yields for six independent early blight epidemics (open symbols) and six independent Verticillium wilt epidemics (solid symbols) simulated as solitary infestations in the upper control curve (circles) and in combination with intermediate and moderately high potato leafhopper infestations in the lower curves (squares and triangles, respectively).

several broader points of discussion that are important in multiple pest-yield loss assessment. These points include the importance of various types of disease-pest interactions in yield development, the utility of empirical, symptom-based crop loss models for predicting yield losses caused by multiple pests, and the potential for Monteith's (19) RI/RUE hypothesis to serve as a bridge between regression-based crop loss models and simulation-based approaches to understanding effects of pests on crop productivity.

With regard to the types of disease-pest interactions important to understanding yield losses, the results obtained indicated that indirect population level interactions that are mediated through the crop were very important. Most commonly, these interactions are antagonistic and involve competition between diseases or insect pests to damage the processes of photosynthetic carbon assimilation and/or utilization. Two examples of this kind of interaction in this study were the competitive defoliation interaction that occurred between early blight and Verticillium wilt (Fig. 3C) and the reduced impact of disease-induced defoliation in crops already damaged by potato leafhopper feeding (Fig. 6). Of lesser importance in this system were interactions that were mediated at the tissue level of biological organization. For example, early blight disease progress within leaf cohorts was reduced by loss of leaf area to hopperburn, but not nearly to the extent that early blight effects on yield were diminished when combined with potato leafhopper. Similarly, modeling effects of Verticillium wilt as an acceleration of the aging rate of leaf cohorts caused a reduction in the simulated incubation period of early blight. This resulted in a slight synergistic acceleration in the rate of early blight disease progress within individual leaf cohorts of *V. dahliae* infected crops (Figs. 4 and 5). When viewed in an isolated context, an observation of this type of interaction could lead to a hypothesis that combined infestations of these two diseases could result in yield reductions that were greater than the sum of each disease alone. The field and simulation results showed that such a synergistic tissue level interaction would have to be relatively strong to override the antagonistic competition these two diseases undergo when defoliating a potato canopy.

Most empirical models developed for prediction of disease effects on crop yield use disease severity as an input to regression-based, yield loss equations (6,23). A common assumption of these models is that proportional lesion area (or some arithmetic transformation of the data) is linearly correlated to reduced crop yield. An initial objective when we began this project was to investigate the possibility that symptom-based regression models could be extended to the situation that involves multiple diseases-pests. Results presented in Figure 4 demonstrated some of the inherent problems that should be expected if data like that obtained in this study were used as inputs for development of symptom-based yield loss models. First, the simulations predicted that early blight disease progress curves would show relatively little change when combined with either Verticillium wilt or potato leafhopper. In contrast, the yield losses attributed to early blight were greatly diminished by the addition of the other disease or insect pest. In addition, for the six early epidemics that were modeled in Figure 6, proportional lesion area on leaves was much less variable among epidemics than was the amount of disease-induced defoliation (see Fig. 5 in reference 15). Poor correlation between the percentage of hopperburn and yield also occurred when potato leafhopper was combined with the two diseases. These insects can reduce photosynthesis in leaves after a few hours of feeding but, typically, hopperburn does not develop until after nymphs have fed on leaves for 1 or 2 wk. Consequently, when early blight and Verticillium wilt reduce the amount of hopperburn through defoliation (Fig. 4), the visual symptoms of potato leafhopper damage are reduced, but the past and potential impact of the insects on crop growth has not been lessened. For the three organisms examined in this study, the data suggest that several disease-pest or disease-disease interaction terms would be needed within a symptom-based regression model to accurately describe effects of combined infestations on potato yield. In other experiences with regression models for multiple yield constraints

(18,25), it was difficult to develop models suitable for accurate prediction of crop losses over a wide range of crop and pest conditions.

A contribution of this study is development of the idea that Monteith's RI/RUE hypothesis (19) can be used as a basis for coupling the effects of disease and insect pests to a crop-growth simulator. A principal advantage of the RI/RUE approach is that physiologic detail can be minimized while at the same time maintaining mechanistic integrity. This advantage also allows for closer ties to theoretical approaches (7) and for more effort to be directed towards epidemiologic considerations of integrating and understanding disease and insect effects on crop growth dynamics (22).

Monteith's RI/RUE hypothesis also leads to simple and testable yield loss models that can be developed from field and growth chamber experimentation (1,2,5,24). For example, Allen and Scott (1) measured RI and tuber dry matter production over time in field-grown potatoes and obtained relationships very similar to those presented in Figure 6. In field experiments, Haverkort and Bicamumpaka (5) concluded that late blight of potato (caused by *Phytophthora infestans* de Bary) affects RI but not RUE. Recently, Bowden and Rouse (2) concluded that Verticillium wilt may have a greater impact on RUE than shown in the simulation results presented in this study.

Johnson et al (17) applied the RI/RUE concept to the potato yields from the 1983 factorial experiment described previously but with AUPGLAC substituted for RI. For three different cultivars, the resulting models all had a highly significant term for AUPGLAC and an additional significant term for area under the hopperburn curve. Because leaf area lost to hopperburn was accounted for by AUPGLAC, we concluded that the additional hopperburn term described the effect of potato leafhopper on RUE. Coefficients of variation in these models for 1983 ranged from 0.75 to 0.83 if all plots were regressed and from 0.88 to 0.92 if identically treated plots were averaged across replications. It is this author's opinion that yield plotted as a function of RI (or a related variable) represents the only approach that will provide reproducible interpretations of the crop losses induced by complex multiple disease-pest infestations. Consequently, for regional crop loss assessment projects, the objective of the project should be to focus on understanding how diseases, insects, and weeds impact RI and RUE within the region. This would lead to relatively simple, mechanistic models with a higher probability of adaptation to other areas or regions compared to symptom-based or pest density-based regression models. In addition, crop physiologists and agronomists could potentially make further use of data obtained in an RI/RUE approach. One drawback of an RI/RUE approach for multiple pest assessment is the difficulty of exactly partitioning yield losses into specific diseases or insect pests; however, given the complexity of the interactions that affect the visual record of crop damage, anything more than relative ranking of the specific pests involved is probably an unrealistic expectation of any approach.

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