Characterization of Resistance to Early Blight in Three Potato Cultivars: Receptivity

J. R. Pelletier and W. E. Fry

First author: Agriculture Canada, Research Station, P.O. Box 457, St.-Jean-sur-Richelieu, Quebec, Canada J3B 6Z8. Second author: Department of Plant Pathology, Cornell University, Ithaca, NY 14853.

We thank J. S. Sweigard and A. E. Apple for helping with field work.

Supported in part by Agriculture Canada and U.S. Department of Agriculture IPM Grants 85-CRSR-2-2682, 87-CRSR-2-3007 and Cornell Hatch Project 15340. The senior author was a recipient of an F.C.A.C. postgraduate fellowship.

Contribution 335/89.11.R, Research Station, Research Branch, Agriculture Canada, St.-Jean-sur-Richelieu, Quebec, Canada.

Accepted for publication 4 October 1989.

ABSTRACT

Pelletier, J. R., and Fry, W. E. 1990. Characterization of resistance to early blight in three potato cultivars: Receptivity. Phytopathology 80: 361-366.

Receptivity of potato leaves (number of lesions per germinated conidium) to *Alternaria solani* was measured at 6- to 12-day intervals in 1984 and 1985 on detached leaves of field plot-grown potato plants, cultivars Kennebec, Norchip, and Rosa. Receptivity decreased with height in the canopy (measured in 15-cm strata) but increased over time. Changes in receptivity were described by a segmented linear function of plant physiological age, stratum, and age-stratum interaction. Physiological age was defined as the square of Pdays (minimum, optimum, and maximum temperatures: 7, 21, and 30 C, respectively) accumulated since emergence, divided by the centimeters of precipitation accumulated since planting. Dynamics of receptivity of Norchip (susceptible) were significantly different from those of Kennebec and Rosa (moderately and highly resistant, respectively). Whole-plant receptivity, calculated by weighting the receptivity of each stratum by its proportional leaf area, displayed trends over time that were similar to the receptivities of individual strata. Whole-plant receptivities of the three cultivars were significantly different. Changes in receptivity were poorly correlated with leaf area, shoot dry weights, and tuberization.

Additional keywords: infection efficiency, quantitative inoculation.

Early blight, caused by *Alternaria solani* Sorauer is prevalent wherever potatoes (*Solanum tuberosum* L.) are grown. Recently, early blight has become a more noticeable problem in the northeastern United States. Several factors probably contribute to this situation, including the greater use of susceptible cultivars, increasing use of the fungicide metalaxyl, which does not control early blight, and the application of fungicides according to decision rules designed only for late blight management. Fungicides applied to suppress late blight may not effectively control early blight (5).

Optimization of fungicide use on potatoes for management of early blight may be possible using simulation models (14). A quantitative description of the changes in host resistance that occur over time could be an important component of a model. It is generally known that younger plants are more resistant than older plants and that younger tissues are more resistant than older tissues (1,2,7,9,10). However, additional quantitative data appropriate for simulation modeling are needed.

Cultivar resistance is an important factor to be considered in fungicide use, but cultivar resistance to early blight is not yet sufficiently well characterized. Early-maturing cultivars of potato and tomato are generally more susceptible to early blight than are late-maturing cultivars (1,2,8). In addition, the disease may be more severe when the ratio of tuber to shoot fresh weight is large than when this ratio is small (10). Therefore, a rational and cost-effective approach toward fungicide use must take into account both cultivar resistance and age-related changes. The purpose of this study was to quantify the early blight resistance of three potato cultivars with reported different resistance rankings and to quantify changes in receptivity as the plants matured. Because this study deals with an attribute of different host genotypes and not of different pathogen genotypes, the term "receptivity" is used instead of "infection efficiency."

MATERIALS AND METHODS

Cultural conditions. Certified seed tubers of potato cultivars Kennebec, Norchip, and Rosa were planted on 25 May 1984 and 24 May 1985 at the Homer C. Thompson Research Farm at Freeville, NY. Investigators have reported that Norchip (early maturity) is highly susceptible, Kennebec (mid-season) has an intermediate level of resistance, and Rosa (mid-season) is highly resistant to early blight (1,3). Cultural conditions were as described previously (6). Plots were planted in areas not planted to potatoes for the two previous years. Seven plots of each cultivar were planted in a completely randomized design. Four plots were reserved for growth analysis, and three plots were reserved for the assessment of receptivity. Percent emergence was determined for 256 plants per cultivar on 13, 15, 19, and 22 June 1984 and on 15, 17, 19, 22, and 26 June 1985.

Mean hourly temperatures were recorded with a hygrothermograph in a louvered weather shelter placed between plots at ground level. Daily precipitation was measured to the nearest 0.0254 cm with a rain gauge (Tru-Check rain gauge, Edwards Manufacturing Co., Albert Lea, MN). From the temperature data, the physiological age of the plants was expressed as Pdays accumulated from the median emergence date of each cultivar. Pdays are a measure of thermal time for potato growth based on a minimum temperature of 7 C, an optimum of 21 C, and a maximum temperature of 30 C (12). The Pdays for each day were determined by calculating the thermal time accumulated during each hour and summing over each 24-hr day (6).

Growth analysis. Four plants of each cultivar were harvested to determine leaf, stem, and tuber dry weights and to estimate the leaf area in each 15-cm canopy stratum on 2, 10, 17, 24 July, 3, 17, and 27 August 1984, and on 24 June, 1, 7, 15, 23, 30 July, 12, 24 August, and 5 September 1985. To minimize weight loss due to respiration, all tissues were placed in a microwave oven for 3 min before being placed to dry in an oven at 80 C for 2 days.

Leaf area in each stratum was quantified by estimating the area of each leaf with a cultivar-specific prediction equation and summing the individual leaf areas. A linear relationship was found between $\log_{10}$ (leaf area) measured with a planimeter and the $\log_{10}$ (length from the tip of the terminal leaflet to point of attachment of the last pair of primary leaflets to the petiole). The prediction equations were derived by linear regression using PROC REG of the SAS (13). The nonlinear form of these equations is as follows:

$$\text{Kennebec:}\quad Y = 0.90195(X^{1.71}) \qquad R^2 = 0.946 \qquad (1)$$

$$\text{Norchip:}\quad Y = 0.54419(X^{1.91}) \qquad R^2 = 0.963 \qquad (2)$$

$$\text{Rosa:}\quad Y = 0.46730(X^{2.04}) \qquad R^2 = 0.974 \qquad (3)$$

where Y = leaf area (cm^2), X = leaf length (cm), and R^2 is the coefficient of determination based on $\log_{10} Y$.

Production of inoculum. Conidia of a single field isolate of *A. solani* were used for receptivity determinations. Inoculum was prepared using a modification of a technique for conidium production by *Cochliobolus heterostrophus* (Drechs.) Drechs. (O. C. Yoder and J. Leach, *personal communication*). Mycelium-permeated mesh circles of Handi-Wipe (Colgate-Palmolive Co., New York, NY) were produced by placing mesh on inoculated V8 agar petri dishes for 7 days at 21 C in a dark incubator. Then the mesh was removed, scraped with a rubber policeman, and placed on the lid of an inverted water agar petri dish. The dishes were placed for 5 days at 18 C under cool white fluorescent tubes (F40WW, Sylvania Lighting Equipment, Fall River, MA) with a 12-hr light/dark period. The conidium-covered mesh then was stored in a desiccator at 4 C until used 2–8 wk later.

Quantification of receptivity. Six stems were harvested at random from three plants (two stems per plant) of each cultivar from within the plots on 4, 11, 19, 30 July and 7 August 1984, and on 5, 11, 20, 29 July and 5 August 1985. Each plant was harvested from a different plot. Each stem was divided into 15-cm segments, and two leaves with the node attached were selected from each segment. Alternate leaflets were inoculated with 300 ± 30 conidia by spraying an aqueous conidium suspension through the template of a quantitative inoculator. The inoculator consisted of an inverted DeVilbiss atomizer head (DeVilbiss Co., Somerset, PA) connected to a compressed air line and mounted on a ring stand. Conidial suspension (200 μl) was pipetted into the head and sprayed at about 70 kPa through an 11.3-cm^2 template which was mounted 22.5 cm from the atomizer head and 1 cm from the leaflet surface. Conidia had been vacuum collected from the dried cloth into distilled water in a test tube. After the suspension was filtered through two layers of cheesecloth, inoculum density was adjusted to about 300 conidia per application by applying conidia with the inoculator onto petri dishes containing 5% water agar, counting the number of conidia applied, and diluting the suspension accordingly. The vessel containing the spore suspension was kept in an ice bath, and the inoculum was stirred constantly on a stir plate during inoculation. Throughout the inoculation of the leaflets, 20 petri dishes were sprayed with the conidial suspension for inoculum density determination. The dishes then were placed in a dark incubator at 24 C for 24 hr. The inoculum density within the 11.3-cm^2 sprayed area was the number of conidia with at least one germ tube measuring 10 μm or greater in length.

Inoculated leaves were misted with distilled water, placed in plastic bags lined with moist paper towels, and put into an incubator at 18 C for a 12-hr light/dark period. The leaves were removed from the bags and placed upright in trays of distilled water for 4 days in the incubator. By this time, infection sites appeared as small black flecks. Leaflets were placed on a light table, and the number of infection sites within the inoculated area was determined. Receptivity for each leaflet was calculated as the number of infection sites within the inoculated area divided by the mean number of conidia that had germinated on the 20 petri dishes. A total of 3,720 leaflets was inoculated over both growing seasons.

Statistical analysis. Median emergence dates were estimated from percent emergence as a function of days after planting with PROC PROBIT of the SAS (13).

Two types of "time" variables were evaluated to account for different receptivities in the two seasons. The first type included plant growth components: shoot (stem and leaf) dry weight, leaf area (cm^2), leaf dry weight, tuber dry weight, and the ratio of tuber to shoot dry weight (which was used as a measure of the ratio of strength of sink for photosynthate to source strength). The second type of time variable was based on physiological age of the potato plant, expressed as the physiological days in Pdays accumulated from the median emergence date of each cultivar. The variables evaluated were Pdays, Pdays divided by the precipitation (cm) accumulated since planting, and Pdays squared divided by precipitation (Pday*).

Model selection. Preliminary analysis revealed that Pday* best accounted for the difference in rate of receptivity increase between 1984 and 1985 (see below). The trend of receptivity over Pday* was nonlinear and was characterized by a period of little or no increase in receptivity early in the growing season, followed by a period of rapid increase. To linearize the trend, three data transformations were evaluated: 1) $\log_{10}$ (receptivity) versus Pday*, 2) receptivity versus $\log_{10}$ (Pday*), and 3) $\log_{10}$ (receptivity) versus $\log_{10}$ (Pday*). Inspection of R^2 and residual plots suggested that none of these transformations provided a satisfactory linear fit. Therefore, a segmented regression model was used, which consisted of two linear phases:

$$r_i = A + B(P) + C(\text{stratum}) + D(P \times \text{stratum}) \quad \text{if Pday*} < P \qquad (4)$$

$$r_i = A + B(\text{Pday*}) + C(\text{stratum}) + D(\text{Pday*} \times \text{stratum}) \quad \text{if Pday*} \geq P \qquad (5)$$

where r_i is the receptivity of the ith stratum, P is the intersection point in units of Pday* between the two linear segments, and A, B, C, and D are regression coefficients. Stratum values of 1, 2, 3...n designated strata that were 0–15, 15–30, and 30–45 cm from the soil, and so on. Plots of receptivity against strata did not show any marked deviation from linearity. The segmented

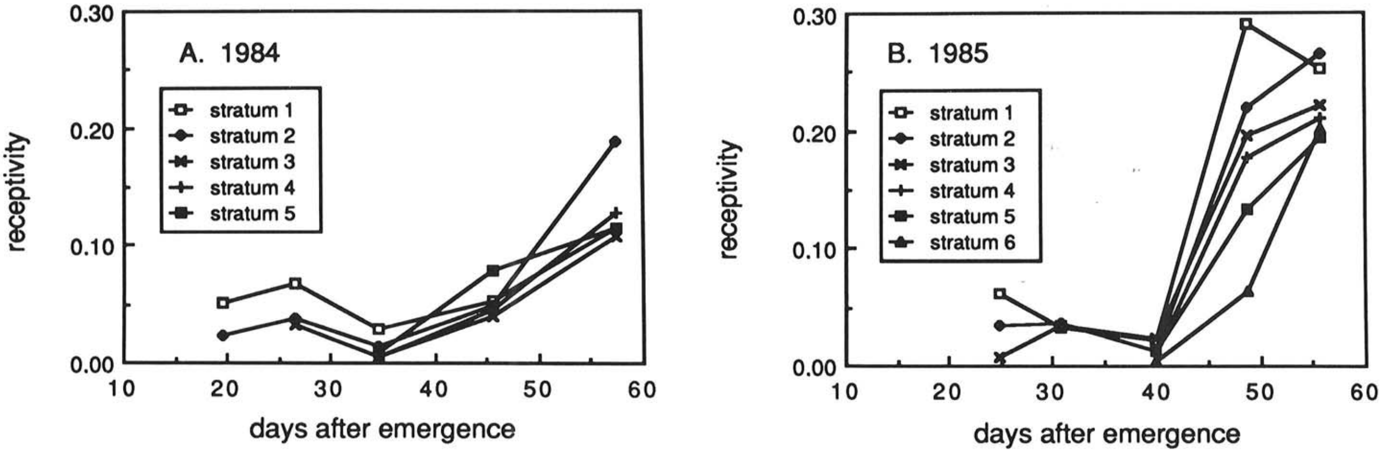

Fig. 1. Receptivity (number of lesions per germinated conidium) of foliage of the potato cultivar Kennebec to *Alternaria solani* plotted against days after emergence in **A,** 1984, and **B,** 1985.

regression model was fit by nonlinear regression with the false secant method of PROC NLIN of the SAS (13). The intersection point P was estimated iteratively for each cultivar by minimizing the residual sum of squares.

Whole-plant receptivity. The change in receptivity in the canopy as a whole over Pday* was investigated by summarizing the receptivities for individual strata into whole-plant receptivity (R), which was calculated as follows:

$$R = \sum_{i=1}^{n} r_i \times PL_i \qquad (6)$$

in which r_i = mean receptivity of the ith stratum, and PL_i = proportion of total plant leaf area that is in the ith stratum. A segmented regression model was used to describe the change in R as a function of Pday*:

$$R = A + B(P) \quad \text{if Pday}^* < P \qquad (7)$$
$$R = A + B(\text{Pday}^*) \quad \text{if Pday}^* \geq P \qquad (8)$$

where terms are the same as those described above. The regression model was fit using R calculated for each stem by nonlinear regression as outlined for receptivity of individual strata.

RESULTS

Plant emergence. Probit analysis revealed that, in 1984, Norchip emerged at a median of 18.7 days after planting, followed by Kennebec at 20.5 days and Rosa at 23.0 days after planting. The median emergence dates in 1985 were 16.3, 17.2, and 17.6 days after planting for Norchip, Kennebec, and Rosa, respectively.

Selection of time variable. Several plant growth variables were evaluated as a basis for explaining the difference in receptivities between the 1984 and 1985 seasons. Receptivity increased at a faster rate in 1985 than in 1984 (Fig. 1). An attempt was made to identify an independent variable (time) which could account for the different receptivities in the two growing seasons. The time variable was selected by inspecting plots of receptivity against potential variables and looking for superimposition of the receptivity data from 1984 and 1985. In contrast to receptivity, tuber dry weight and shoot dry weight over days after median emergence tended to increase earlier in 1984 than in 1985 (Figs. 2 and 3). When the average receptivity was plotted against tuber or shoot dry weight, the separation between the receptivity curves for the different growing seasons was greater than when receptivity was plotted against days after emergence. A similar trend was observed when average receptivity was plotted against tuber to shoot dry weight and is illustrated with data from the cultivar Kennebec (Fig. 4). There was no apparent relationship between average receptivity and total leaf dry weight, as illustrated by data for the cultivar Norchip (Fig. 5). Leaf area was similar to leaf dry weight as a predictor and therefore is not shown here. In summary, a satisfactory relationship was not found between receptivity and plant growth components.

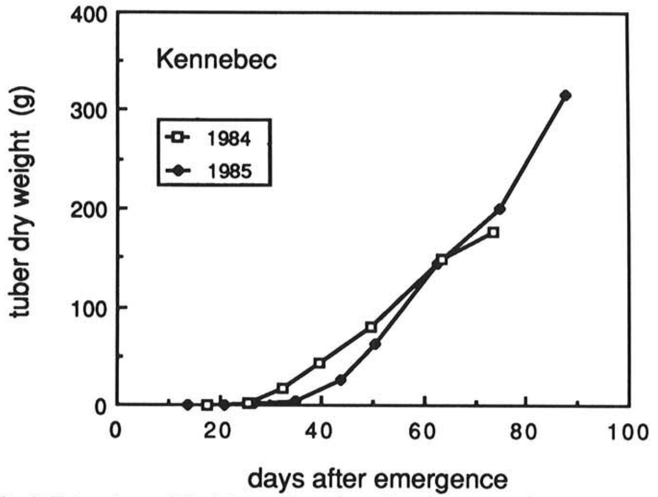

Fig. 2. Tuber dry weight (g) per plant plotted against days after emergence for the potato cultivar Kennebec in 1984 and 1985.

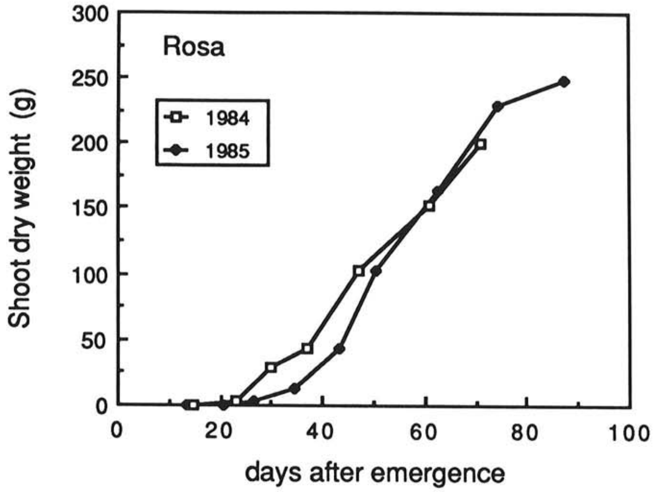

Fig. 3. Shoot (leaf and stem) dry weight (g) per plant plotted against days after emergence for the potato cultivar Rosa in 1984 and 1985.

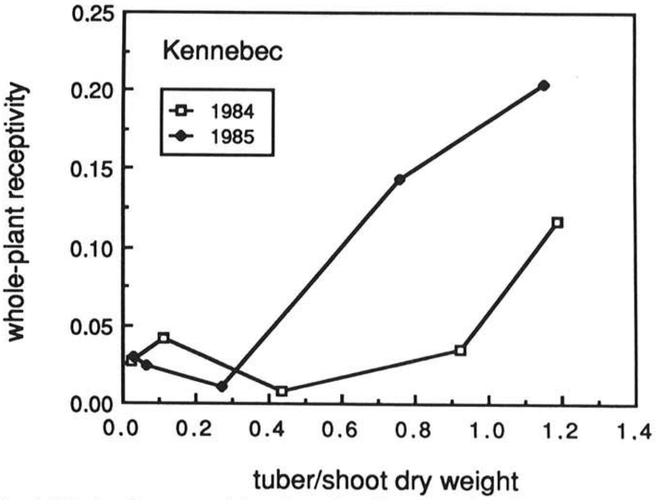

Fig. 4. Whole-plant receptivity plotted against the ratio of tuber to shoot dry weight for the cultivar Kennebec in 1984 and 1985.

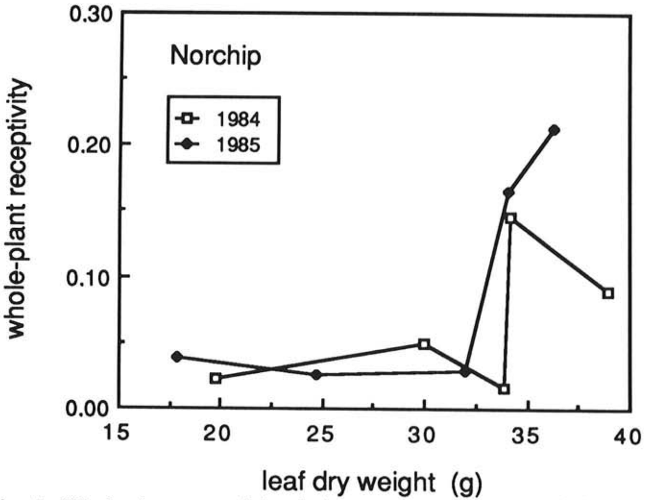

Fig. 5. Whole-plant receptivity (lesions per germinated conidium) of Norchip foliage to *Alternaria solani* plotted against leaf dry weight (g) per plant in 1984 and 1985.

The use of cumulative physiological age (Pdays) as a basis for explaining the difference in receptivity between the 1984 and 1985 growing seasons was investigated. Cumulative Pdays increased linearly with time in both 1984 and 1985. The regression equation for 1984 was $Y = -4.535 + 7.663(X)$ ($R^2 > 0.999$) and $Y = -2.743 + 7.814(X)$ ($R^2 = 0.998$) for 1985, where Y is Pdays and X is days after emergence. Comparison of the regression lines (4) revealed that Pdays increased at a faster rate in 1984 than in 1985 ($P = 0.001$).

Plots of cumulative precipitation (cm) since planting indicated that 1984 was wetter than 1985 (Fig. 6). Plots of average receptivity against Pdays divided by precipitation suggested erroneously that receptivity increased more quickly in 1984 than in 1985. The variable that best accounted for the receptivity difference between 1984 and 1985 was squared Pdays divided by cumulative precipitation (Fig. 7), referred to in the remainder of this paper as Pday*. Pdays* increased faster in 1985 than in 1984. The occasional drops in value for cumulative Pdays* are explained by sporadic rainfall events.

Effect of cultivar, stratum, and Pday* on receptivity. Pairwise comparisons of the regression equations (4) of receptivity on Pdays* (equations 4 and 5) for each cultivar revealed that Norchip and Rosa were significantly different ($P < 0.001$) and that Norchip and Kennebec were significantly different ($0.001 < P < 0.005$). Kennebec and Rosa were not significantly different ($0.1 < P < 0.5$). Therefore, regression coefficients were calculated from data for Norchip and from pooled data of Kennebec and Rosa (Table 1). The intersection point between the two linear segments was 2,580 Pday* for Norchip and 3,305 Pday* for Kennebec and Rosa. Thus, the increase in receptivity occurred earlier in Norchip than in Kennebec and Rosa.

Comparison of the signs of the multiple regression coefficients in Table 1 revealed that, after the intersection, receptivity increased with Pday* in all three cultivars. After the intersection, receptivity increased more rapidly with Pday* in Kennebec and Rosa than in Norchip. Receptivity was significantly greater in the lowest strata (which contained the oldest leaves) for Norchip, as shown by the significant negative coefficient for stratum effect in Table 1. The difference between strata in Norchip tended to increase with Pday*, as revealed by the positive stratum-Pday* interaction term. The coefficient for stratum effect was not significant in Kennebec and Rosa, but when the stratum-Pday* interaction term was considered, receptivity was highest in the lower strata. The difference between strata decreased with Pday*, as indicated by the negative interaction coefficient.

Whole-plant receptivity. Pairwise comparisons of the regression

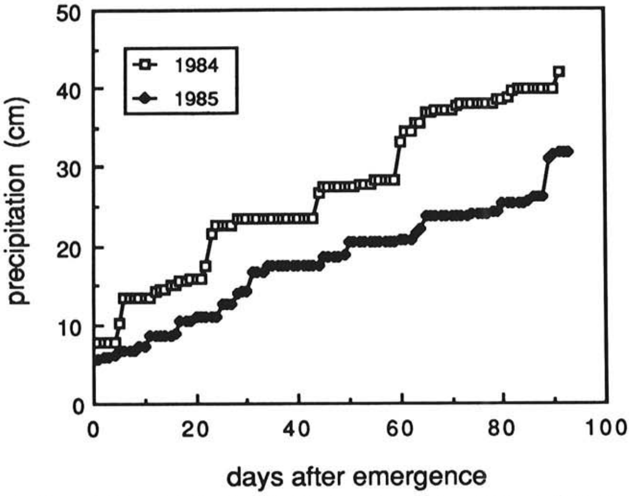

Fig. 6. Cumulative precipitation (cm) since planting plotted against days after emergence in 1984 and 1985.

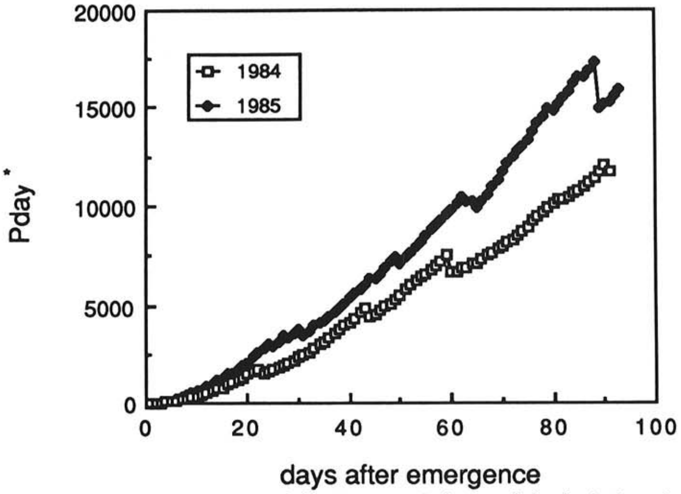

Fig. 7. Pdays* (squared Pdays divided by cumulative precipitation) plotted against days after emergence in 1984 and 1985.

TABLE 1. Regression results for the effect of Pday* and stratum on receptivity for Kennebec, Norchip, and Rosa

Cultivar	Source	df[a]	SS[b]	R^2_{adj}[c]	
Kennebec and Rosa	Model	4	5.4437	0.628	
	Error	449	1.2902		
	Variable	Coefficient	ASE[d]		Significance
	Intercept	−0.1801	0.02025		$P < 0.001$
	Pday*	0.00006644	0.000004603		$P < 0.001$
	Stratum	0.005176	0.006475		$0.2 < P < 0.3$
	Pday* × stratum	−0.000003146	0.000001313		$0.01 < P < 0.02$
Cultivar	Source	df	SS	R^2_{adj}	
Norchip	Model	4	3.4639	0.519	
	Error	191	0.9194		
	Variable	Coefficient	ASE[d]		Significance
	Intercept	−0.002778	0.03154		$P > 0.5$
	Pday*	0.00003580	0.000007170		$P < 0.001$
	Stratum	−0.03051	0.01309		$0.01 < P < 0.02$
	Pday* × stratum	0.00000359	0.000002768		$0.1 < P < 0.2$

[a] Degrees of freedom

[b] Sum of squares.

[c] Coefficient of determination (adjusted for degrees of freedom).

[d] Asymptotic standard error.

equations revealed that all cultivars were significantly different from each other ($P < 0.05$). The intersection point between the linear segments was 3,085, 3,050, and 3,000 Pday* for Kennebec, Norchip, and Rosa, respectively. Whole-plant receptivity increased with Pday*, as indicated by the positive coefficient for Pday* in Table 2. The increase in R with Pday* was most rapid in Kennebec, followed by Norchip, then Rosa. The y-intercept was lowest in Kennebec (Fig. 8). From these results, R from 0 Pdays* up to the intersection point was calculated as 0.0310, 0.0395, and 0.0233 lesions per germinated conidium for Kennebec, Norchip, and Rosa, respectively.

DISCUSSION

These experiments revealed that receptivity increased as the plants grew older. This provided a basis for identifying a model to describe the dynamics of receptivity over time. Our work is qualitatively similar to other work conducted concurrently with four potato cultivars using a floating leaf disk assay (7). The lower strata, which contained the oldest leaves, had higher receptivities than upper portions of plant. These findings are consistent with laboratory studies in which older leaves were found to be more susceptible than younger leaves (8,10,11).

We had expected to identify a mechanistic basis for increased susceptibility by viewing tubers as a sink for metabolites and relating size of sink to susceptibility. However, the relationship between receptivity and leaf dry weight, shoot dry weight, leaf area per plant, the strength of the sink for metabolites (tuber dry weight), or the sink-to-source ratio (tuber dry weight to stem dry weight) was inconsistent over the two growing seasons. Furthermore, tuberization occurred earlier in 1984 than in 1985, yet receptivity increased more slowly in 1984. These findings are inconsistent with a previous study in which a high positive correlation was found between the ratio of tuber fresh weight to shoot fresh weight and receptivity (9). These inconsistencies might be explained by our use of leaves harvested from field plot-grown plants as opposed to the use of intact leaves on potted plants of a single cultivar in the previous study (9). From studies carried out on greenhouse-grown plants, we observed that the incubation period (time from inoculation to symptom expression) was markedly longer on intact plants than on detached leaves. It is therefore possible that the receptivity data from other studies (9,10) may have been confounded with the incubation period. Our findings that receptivity and tuberization were poorly correlated do not imply that tuberization may not be correlated with other components of resistance, such as the incubation period or the lesion expansion rate (9,10).

A segmented linear model was used to describe mathematically the changes in the receptivity of each stratum as the plants grow older during different growing seasons. In this model, receptivity is described entirely as a function of temperature (plant physiological age being temperature driven) and precipitation. It therefore can be used for rapid predictions or simulations of receptivities. This is a distinct advantage over models relating receptivity to tuberization, which would require destructive sampling, or a model that would accurately partition plant dry matter into different plant organs in different cultivars.

The greater receptivity in 1985, which was drier than 1984, confirms previous observations that water-deficient plants are more susceptible to early blight (8). This, however, is contradictory to Rotem's observations that receptivity was higher in well-watered plants (9). Again, this discrepancy might be explained by Rotem's use of potted plants. Although in our study cumulative precipitation was the only measured difference between the two growing seasons and its inclusion in the segmented regression model improved model performance, it is not necessarily the only factor influencing receptivity.

The receptivity of the early-maturing Norchip was significantly different from that of the mid-season cultivars Kennebec and Rosa. The latter two cultivars were not significantly different from each other. Different interactions between strata and plant age were observed in the three cultivars. In the case of Kennebec and Rosa, the receptivity of strata converged as the plants grew older. For Norchip, on the other hand, differences between strata did not change significantly as the plants grew older. Kennebec and Rosa shared a common difference from Norchip that could explain the stratum effect: Both were later-maturing cultivars. Therefore, shoot growth continued for a longer period, with the consequence that the physiological age of different portions of the canopy may have been less uniform than in Norchip. Both were 30 to 45 cm taller than Norchip by the final receptivity assessment. Because of the denser canopies, shading of the leaves

TABLE 2. Regression results for the effect of Pday* on whole-plant receptivity for Kennebec, Norchip, and Rosa

Cultivar	Source	df[a]	SS[b]	R^2_{adj}[c]	
Kennebec	Model	2	0.5067	0.784	
	Error	55	0.06120		
	Variable	Coefficient	ASE[d]		Significance
	Intercept	−0.1699	0.01759		$P < 0.001$
	Pday*	0.00005451	0.000003857		$P < 0.001$
Cultivar	Source	df	SS	R^2_{adj}	
Norchip	Model	2	0.7400	0.683	
	Error	58	0.1182		
	Variable	Coefficient	ASE		Significance
	Intercept	−0.09911	0.01787		$P < 0.001$
	Pday*	0.00004543	0.000004061		$P < 0.001$
Cultivar	Source	df	SS	R^2_{adj}	
Rosa	Model	2	0.3609	0.712	
	Error	54	0.0604		
	Variable	Coefficient	ASE		Significance
	Intercept	−0.0943	0.01423		$P < 0.001$
	Pday*	0.00003921	0.000003399		$P < 0.001$

[a] Degrees of freedom

[b] Sum of squares.

[c] Coefficient of determination (adjusted for degrees of freedom).

[d] Asymptotic standard error.

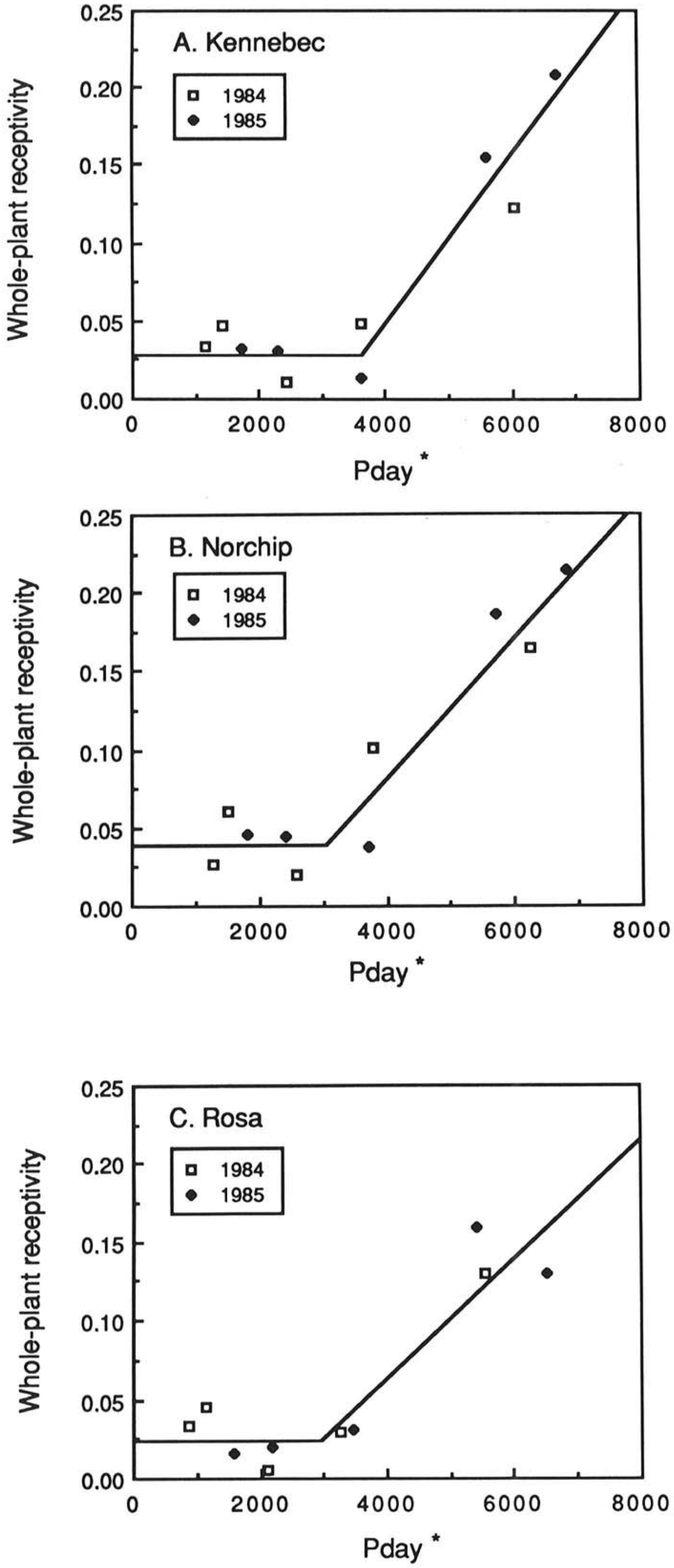

Fig. 8. Whole-plant receptivity (lesions per germinated conidium) to *Alternaria solani* plotted against Pday* in 1984 and 1985 for the potato cultivar **A,** Kennebec, **B,** Norchip, and **C,** Rosa.

in the lower strata may have contributed to the stratum effect. Shading of potato plants was observed to increase susceptibility to early blight in greenhouse experiments (11).

When the whole-plant receptivity of the three cultivars was compared, Norchip was still different from the later-maturing Kennebec and Rosa. Although whole-plant receptivity was greater early in the growing season and began increasing earlier in the growing season for Norchip than for Kennebec, the whole-plant receptivity of Kennebec surpassed that of Norchip by 7,794 Pday* (about 52 days after emergence). In contrast to the findings for receptivity of individual strata, Kennebec and Rosa were significantly different in terms of whole-plant receptivity. The whole-plant receptivity of Rosa was lower than that of Kennebec early in the growing season, and it increased at a slower rate. This can be explained by the fact that a greater proportion of the canopy is in the more susceptible lower strata in Kennebec than in Rosa. In 1985, 35 days after plant emergence (4,040 Pdays*), the proportion of leaf area in strata 1, 2, 3, 4, and 5 were 0.098, 0.399, 0.275, 0.228, and 0.0 for Kennebec and 0.121, 0.281, 0.322, 0.246, and 0.03 for Rosa. The lower whole-plant receptivity for Rosa helps to explain the field observations that Rosa is more resistant to early blight than Norchip or Kennebec (Pelletier and Fry, *unpublished observations*).

These experiments provide a partial explanation for previous findings that early-maturing cultivars tend to be more susceptible to early blight than later-maturing ones (1,3). The cultivar differences in resistance observed in the field also are due to other components of resistance, such as incubation period, lesion expansion rate, and spore production (6).

The data provided here and elsewhere (6) have provided much of the basis for a computer simulation model of potato early blight. The model describes weather effects, physiological age effects, and cultivar differences in resistance on the dynamics of potato early blight epidemics. The model has been partially validated and describes early blight epidemics well enough to be useful in evaluating disease management strategies (14).

LITERATURE CITED

1. Douglas, D. R., and Pavek, K. K. 1972. Screening potatoes for field resistance to early blight. Am. Potato J. 49:1-6.
2. Harrison, M. D., Livingston, C. H., and Oshima, N. 1965. Epidemiology of potato early blight in Colorado. I. Initial infection, disease development and the influence of environmental factors. Am. Potato J. 42:279-291.
3. Holley, J. D., Hall, R., and Hofstra, G. 1983. Identification of rate-reducing resistance to early blight in potato. Can. J. Plant Pathol. 5:111-114.
4. Neter, J., and Wasserman, W. 1974. Applied Linear Statistical Models. Richard D. Irwin, Inc., Homewood, IL.
5. Nutter, F. W., and MacHardy, W. E. 1981. Timing of additional sprays for control of potato early blight (*Alternaria solani*) when following a late blight forecasting spray schedule in New Hampshire, U.S.A. Prot. Ecol. 3:47-54.
6. Pelletier, J. R., and Fry, W. E. 1989. Characterization of resistance to early blight in three potato cultivars: Incubation period, lesion expansion rate, and spore production. Phytopathology 79:511-517.
7. Pscheidt, J. W. 1985. Epidemiology and control of potato early blight, caused by *Alternaria solani*. Ph.D. thesis. University of Wisconsin, Madison. 242 pp.
8. Rands, R. D. 1917. Early blight of potato and related plants. Wis. Agric. Exp. Stn. Res. Bull. 42.
9. Rotem, J. 1969. The effect of soil moisture level on the incidence of early blight on potato and tomato plants. Isr. J. Agric. Res. 19:139-141.
10. Rotem, J., and Feldman, S. 1965. The relation between the ratio of yield to foliage and the incidence of early blight in potato and tomato. Isr. J. Agric. Res. 15:115-122.
11. Rowell, J. B. 1953. Leaf blight of tomato and potato plants. Factors affecting the degree of injury incited by *Alternaria dauci* f. sp. *solani*. R. I. Agric. Res. Stn. Bull. 320.
12. Sands, P. J., Hackett, C., and Nix, H. A. 1979. A model of the development and bulking of potatoes (*Solanum tuberosum* L.). I. Derivation from well-managed field crops. Field Crops Res. 2:309-331.
13. SAS Institute. 1982. SAS User's Guide: Statistics. SAS Institute, Cary, NC.
14. Shtienberg, D., Doster, M. A., Pelletier, J. R., and Fry, W. E. 1989. Use of simulation models to develop a low-risk strategy to suppress early and late blight in potato foliage. Phytopathology 79:590-595.