Characterization of Resistance to Early Blight in Three Potato Cultivars: Incubation Period, Lesion Expansion Rate, and Spore Production

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ABSTRACT

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Early blight incubation periods (degree-hours from inoculation until the lesion radius reaches 0.35 mm) and lesion expansion rates (micrometers of lesion radius per degree-hour during leaf wetness) were measured on intact plants of field-grown potato cultivars Kennebec, Norchip, and Rosa at about 18, 30, and 45 days after emergence. Incubation periods were shorter and lesion expansion rates were greater on lower leaves and on older plants. During leaf wetness, lesion expansion increased in a linear manner over a range of 6 to 24 hr and in response to temperatures ranging from 9 to 27 C. Incubation periods and lesion expansion rates were described by a linear function of leaf position, plant physiological age (Pdays after emergence), and interaction of leaf position and plant age. Incubation periods on 18-day-old Norchip were shorter than on Kennebec and Rosa; 45-day-old plants were no longer markedly different. Lesion expansion rates were lowest on Rosa. Cultivar differences became less apparent as the plants grew older. Spore production per square millimeter of lesion was measured from individual lesions on leaves harvested from field-grown plants at 74 and 92 days after planting. Spore production increased as a linear function of lesion area. Plant age (Pdays after emergence) and leaf position did not have a significant effect on spore production. Spore production was lowest on Kennebec; Norchip and Rosa were not significantly different. Spore production was not correlated with the maturity class of the cultivar.

Additional keywords: *Alternaria solani*, heat summation, resistance components, *Solanum tuberosum*.

Early blight, caused by *Alternaria solani* (Ell. & Mart.) Jones & Grout, is one of the major causes of defoliation of potatoes in the northeastern United States. It has been repeatedly observed that early-maturing cultivars are more susceptible than later-maturing cultivars (1,4,11). Furthermore, older leaves are more susceptible to early blight, and susceptibility increases as the plants grow older (9,11–13,16). We observed that the infection efficiency (number of lesions per number of conidia applied) was greater on older leaves and increased markedly as the plants grew older (8). However, differences in infection efficiency of *A. solani* among cultivars did not fully explain the early blight resistance ranking of three potato cultivars. Thus, other components of resistance, such as the incubation period (IP), the lesion expansion rate (LER), and spore production (SP), may contribute to field-observed differences in cultivar resistance (4,9,11,12,16). For example, Harrison et al observed large lesions on the lower leaves, while the upper leaves were asymptomatic even though they harbored the pathogen (4). Most studies, however, do not mention whether larger lesions result from a shorter IP, a greater LER, or a combination of both. Likewise, cultivar differences in SP have been documented for *A. solani* on tomato (7). However, in order to construct an early blight simulation model which is useful in pest management, there remains the need to determine whether leaf position and plant age affect SP in potato.

In this report, plant-age-related changes in IP, LER, and SP in three potato cultivars with different degrees of resistance are described. These detailed data are essential in the construction of a simulation model for the management of potato early blight.

MATERIALS AND METHODS

Cultural conditions. Certified seed tubers of Kennebec, Norchip, and Rosa potatoes were planted on 25 May 1984 and 24 May 1985 at the Homer C. Thompson Research Farm at Freeville, NY. Norchip (early-maturing) is reported as highly susceptible, Kennebec (mid-season) as having an intermediate level of resistance, and Rosa (late-maturing) as being highly resistant to early blight (1). Potato seed consisted of small whole tubers or seed pieces (Kennebec, 1984) weighing about 50 g each. Seed pieces were treated with mancozeb dust (Manzate 8D, E. I. duPont de Nemours and Co., Wilmington, DE). Four-row plots (16 plants/row), 3.7 m long, with 0.9 m between rows, were planted with a 23-cm spacing between plants. The plots were planted in areas that were not planted with potatoes for the two previous years. Four plots of each cultivar were planted in a completely randomized design. Fertilizer (167 kg each of N, P, and K per hectare) and the insecticide carbofuran (Furadan 15G, 3.4 kg a.i./ha, FMC Corp., Middleport, NY) were applied at planting. The herbicide linuron (Lorox 50 WP, 1.7 kg a.i./ha, E. I. du Pont de Nemours and Co., Wilmington, DE) was applied after planting but prior to plant emergence. During the growing season, the insecticide azinphos-methyl (Guthion 25EC, 0.88 kg a.i./ha, Chemagro Corp., Kansas City, MO) or endosulfan (Thiodan 50WP, 1.1 kg a.i./ha, FMC Corp., Middleport, NY) was applied when necessary. Metalaxyl (Ridomil 2EC, 0.189 kg a.i./ha, Ciba-Geigy Corp., Greensboro, NC) was applied to prevent late blight, caused by *Phytophthora infestans* (Mont.) de Bary, on a 2-wk schedule from 12 July to 9 August 1984 and from 1 August to 15 August 1985. Percent plant emergence was determined for 256 plants per cultivar on 13 June, 15 June, 19 June, and 22 June 1984 and for 384 plants per cultivar on 15 June, 17 June, 19 June, 22 June, and 26 June 1985. Plants were hilled on 3 July 1984 and 1 July 1985.

Production of inoculum. Conidia of a field isolate of *A. solani* were used for the IP and LER experiments. Inoculum was prepared by a modified technique for conidium production of *Cochliobolus heterostrophus* (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 the mesh on inoculated V-8 agar petri dishes for 7 days at

21 C in a dark incubator. The mesh was then 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 (Sylvania, F40WW) with a 12-hr photoperiod. The conidium-covered mesh was then stored in a desiccator at 4 C until use 2 to 8 wk later.

Quantification of effects of cultivar, plant age, and leaf position on IP and LER. Because of the difficulty in maintaining vigorous detached leaves for periods greater than 7 days, these studies were carried out in field plots on intact potato plants of the cultivars Kennebec, Norchip, and Rosa. The IP and LER experiments were carried out as follows: In 1985, four stems from two plants of each cultivar were inoculated on 28 June, 10 July, and 25 July with a single field isolate of *A. solani*. The plants were sprayed with a conidial suspension at 9:00 P.M. and covered with plastic bags until 9:00 the following morning. The position of leaves present at the time of inoculation was noted as the node number from the soil line. Leaves were photographed at 4- to 12-day intervals until abscission occurred. The photographs were enlarged and lesions darkened with a fine-tipped felt pen. The prints were placed on a light table, and the area of individual lesions was determined with a video image analysis system (Delta-T Devices Ltd., 128 Low Road, Burwell, Cambridge, England).

The IPs and LERs were corrected for variable environmental conditions in the field, using temperature data and the duration of periods of leaf wetness recorded during the experiments. Leaf wetness duration was measured with a leaf wetness sensor (3) fastened to the adaxial surface of an intact potato leaflet. The sensor was placed in a plot of Norchip at 30 cm from the soil and tilted at 30° from the horizontal. Both sensor and leaf were secured with wooden stakes to prevent movement and damage to the leaflet's surface by the sensor. The sensor was connected to an AC channel of a CR21 data logger (Campbell Scientific, Inc., Logan, UT), and leaf wetness readings were recorded every 20 min. The response of the sensor ranged from 0 mV (dry leaf surface) to a maximum of 150 mV (continuous water film). From observations of leaves in a mist chamber, readings of 10 mV and over were considered to be from wet leaves. Because the canopy densities of the three cultivars were similar for the duration of the experiment (Table 1), the leaf wetness data from the Norchip canopies were used for Kennebec and Rosa. A preliminary study in 1984 revealed that when the plants were still small (with a leaf area of about 0.6 m^2 per plant), leaf wetness duration was not markedly different for sensors placed at heights of 15, 30, and 45 cm in the canopy. Later in the growing season, leaf wetness durations at 15 cm were markedly shorter than those at 30 or 45 cm. However, most of the leaves at 15 cm had died by mid-season and no longer were a factor. Temperature was recorded with a hygrothermograph in a louvered weather shelter placed between the plots at 20 cm above the soil surface.

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 of 30 C (14). The Pdays for each day were determined by calculating the physiological time accumulated during each hour and summing for each 24-hr period. Physiological time was calculated as follows:

$$\begin{aligned} P_i &= 0 && T_i < T_a \\ P_i &= 0.417[1 - ((T_i - T_b)^2 / (T_b - T_a)^2)] && T_a \leqslant T_i < T_b \\ P_i &= 0.417\,[1 - ((T_i - T_b)^2 / (T_c - T_b)^2)] && T_b \leqslant T_i < T_c \\ P_i &= 0 && T_c \leqslant T_i \end{aligned} \quad (1)$$

where P_i is the physiological time accumulated during the ith hour of the day, T_i is the mean temperature (C) during the ith hour, T_a is 7 C, T_b is 21 C, and T_c is 30 C (14).

Effects of duration of leaf wetness and temperature on lesion expansion. Because of space limitations, effects of temperature and leaf wetness duration on the radial growth of lesions were determined in separate greenhouse and incubator experiments. Norchip plants were grown in the greenhouse in clay pots, 12.7 cm in diameter, containing a peat-vermiculite mixture (1:1, v/v) amended with 2.3 kg of 14-14-14 (N-P-K) per cubic yard of the mixture. The plants were inoculated 50 days after emergence with an aqueous conidial suspension (3,000 conidia per milliliter) of the field isolate of *A. solani*. The plants were placed in a mist chamber at 20 C for 24 hr with a 12-hr photoperiod. They were returned to the greenhouse bench until the appearance of necrotic spots on the leaves (about 7 days after inoculation). The plants were then returned to the mist chamber (20 C) and exposed to a 12-hr light-dry and 12-hr dark-mist regime for 7 days. Under these conditions, lesions expanded and assumed the characteristic "target board" appearance of lesions in the field.

The effect of temperature during leaf wetness on lesion expansion was quantified with early-blighted leaves, which were detached, tagged, and photographed. The leaves were then misted with distilled water, placed in sealed plastic bags, and placed for 12 hr in dark incubators set at 9, 15, 18, 21, 24, or 27 C. After the exposure to the different temperatures, the leaves were photographed again. The areas of the lesions before and after the treatments were measured with the Delta-T image analysis system. The lesion radius was estimated by the formula for a circle. The experiment was performed three times, and the areas of 141 lesions were measured.

The effect of the duration of leaf wetness on lesion expansion was determined in a similar manner. Leaves with lesions were treated as above and placed in an incubator at 21 C for 6, 9, 12, 15, 21, or 24 hr. Leaf surfaces were kept wet while in the incubator, and the leaves were photographed immediately after the leaf wetness exposure. The experiment was done twice, and the areas of 101 lesions were measured. The radial growth of lesions was determined as for the temperature experiments.

Calculation of IP and LER. To incorporate the effects of time and temperature on fungal growth, IPs and LERs were expressed in degree-hours. The degree-hours for the development of *A. solani* were calculated from the relationships between the relative growth rate of lesions and the temperature and the duration of leaf wetness (see Results). Firstly, equation 5 (see Results) was simplified by subtracting the minimum temperature, to give

$$\text{RLRG} = 0.0426 \times (\text{TEMP} - 3.52) \quad (2)$$

where RLRG is lesion radial growth relative to that at 27 C, and TEMP is temperature (C). Equation 2 was then multiplied by 0.041, from equation 5. An intercept of 0 was used for the effect of leaf wetness duration on relative lesion radial growth, because lesions on greenhouse-grown plants did not expand in the absence of leaf wetness, and the y intercept of equation 5 was not significantly different from 0. Degree-hours were then calculated from mean hourly temperatures for each hour after inoculation:

TABLE 1. Leaf area per plant at the three inoculation times for potato cultivars Kennebec, Norchip, and Rosa

	Day of the year		
Cultivar	179 (18)[a]	191 (30)	206 (45)
Kennebec	0.20[b] (0.02)	0.61 (0.06)	1.16 (0.06)
Norchip	0.17 (0.03)	0.68 (0.14)	0.97 (0.15)
Rosa	0.20 (0.05)	0.59 (0.09)	1.09 (0.10)

[a] Days after median emergence.
[b] Leaf area (m^2) per plant. Numbers in parentheses are standard errors.

$$\text{degree-hours} = \sum_{i=1}^{n} 0.00175 \times (T_i - 3.52) \quad (3)$$

where T_i is the average temperature during the ith hour.

Because preliminary analysis revealed that lesion radius increased in a linear manner with cumulative degree-hours, a simple linear equation of lesion radius as a function of cumulative degree-hours was calculated for each leaf on each stem. From these equations, the IP for each leaf was calculated as the degree-hours from inoculation to the occurrence of a mean lesion radius of 0.35 mm. This end point was selected because of the limits of resolution of the image analysis system and because lesions with smaller diameters are still turgid from internal leaf moisture. Fungal growth in lesions with a radius of 0.35 mm or less appeared to be independent of leaf surface moisture. Microscopic examination of 150 lesions on Kennebec, Norchip, and Rosa revealed that *A. solani* did not sporulate in lesions less than 0.35 mm in radius. The LER for each leaf was estimated by the slope of the curve plotting lesion radius as a function of cumulative degree-hours.

Measurement of SP. Experiments were done in 1984 on leaves harvested from field-grown Kennebec, Norchip, and Rosa potato

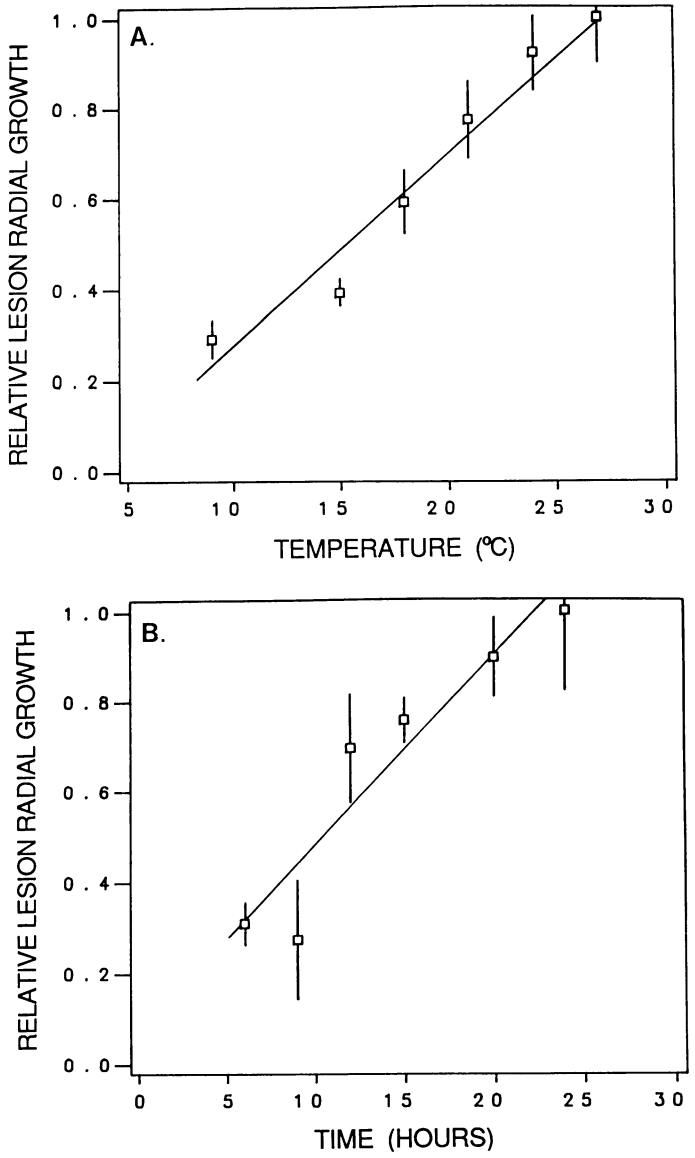

Fig. 1. A, Effect of temperature during a 12-hr period of leaf wetness on lesion radial growth, relative to the mean radial growth at 27 C. **B,** Effect of the duration of leaf wetness at 21 C on lesion radial growth, relative to the mean radial growth for 24 hr.

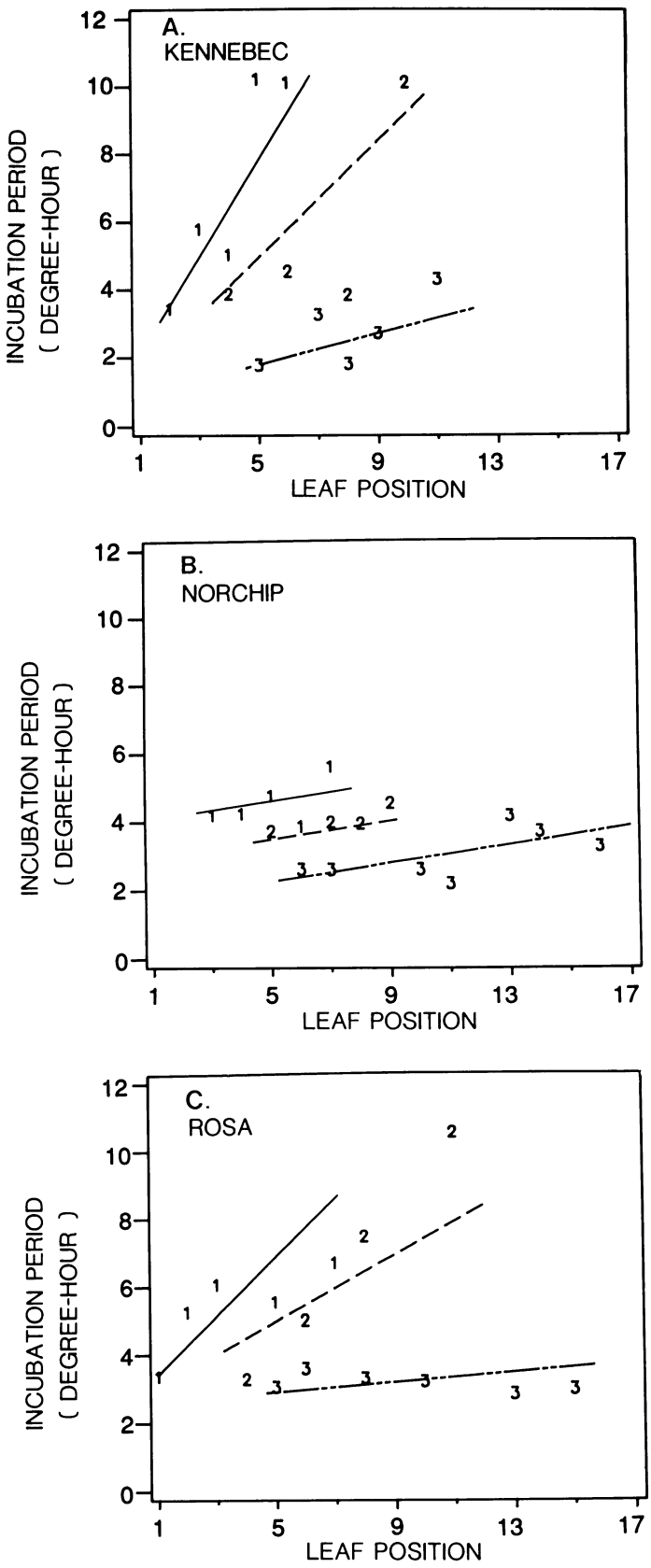

Fig. 2. Effect of plant age (Pdays) and leaf position on the incubation period of Kennebec (A), Norchip (B), and Rosa (C). The smallest numbers on the x axis designate leaves occupying the lowest postions in the canopy. The numerals 1, 2, and 3 are the means (n = 4) of observed incubation periods for plants inoculated at the first, second, and third inoculation times (35, 47, and 62 days after planting, respectively). The lines are the model predictions.

plants to determine the influence of plant physiological age and leaf position on SP. Leaves were harvested at 3:00 p.m. at 74 and 92 days after planting. Plant physiological age in Pdays was calculated at each harvest. Leaf position in the canopy was noted as the number of nodes from the soil line. Conidia that had formed in the field prior to the SP experiments were blown off both sides of the lesions with a compressed air jet. The leaves were then placed upright in trays of distilled water. Selected leaflets were misted with distilled water and enclosed in a moisture chamber to induce sporulation. A moisture chamber consisted of a plastic 9-cm petri dish lined with moistened filter paper, with a notch cut in the side of the dish to admit the petiolule. The leaves were placed in a dark incubator at 18 C for 12 hr. Conidia were then collected from both sides of each lesion with a vacuum collector (ERI Machine Shop, Iowa State University, 124 ERI Bldg., Ames) into a vial containing 1 ml of 1% $CuSO_4$ (w/w) and two drops of Tween 20 per 450 ml. The $CuSO_4$ was added to prevent spore germination.

The spores from each lesion were then transferred to a grid for counting by filtering the spore suspension through a piece of graph paper with a 2.5-mm grid. The conidia on the filter paper were counted under a dissecting microscope.

Immediately after harvest, the leaves were photographed, prints were made, and the area of the necrotic tissue in each lesion was measured from photographs with a Delta-T image analysis system. For the remainder of this paper, the term *lesion* refers only to the necrotic portion of lesions.

Statistical analysis. Median emergence dates were calculated by probit analysis of emergence as a function of days after planting, by means of PROC PROBIT of the Statistical Analysis System (15).

To determine the effect of temperature on LER, the radial

TABLE 2. Regression results for the effect of leaf position and plant age on incubation periods for potato cultivars Kennebec, Norchip, and Rosa

Cultivar	Source[a]	df[b]	SS[c]	R^2_{adj}[d]	Variable	Coefficient	SS II[e]	*P*
Kennebec	Model	2	362.639	0.594				
	Error	53	233.141					
	Total	55	595.780					
					Intercept	0.686	2.714	0.4357
					Leaf[f]	2.204	310.237	0.0001
					Age[g] × leaf	−0.006	362.124	0.0001
Norchip	Model	2	37.069	0.333				
	Error	61	67.477					
	Total	63	104.546					
					Intercept	5.638	224.372	0.0001
					Leaf	0.136	7.347	0.0124
					Age	−0.011	32.832	0.0001
Rosa	Model	2	203.864	0.646				
	Error	57	105.784					
	Total	59	309.648					
					Intercept	2.348	57.913	0.0001
					Leaf	1.375	183.779	0.0001
					Age × leaf	−0.004	203.804	0.0001

[a] Only significant variables are listed.
[b] Degrees of freedom.
[c] Sequential sums of squares.
[d] Coefficient of determination (adjusted for degrees of freedom).
[e] Partial sums of squares.
[f] Leaf position from soil line.
[g] Plant age in Pdays accumulated from emergence.

TABLE 3. Regression results for the effect of leaf position and plant age on lesion expansion rate for potato cultivars Kennebec, Norchip, and Rosa

Cultivar	Source[a]	df[b]	SS[c]	R^2_{adj}[d]	Variable	Coefficient	SS II[e]	*P*
Kennebec	Model	2	0.439	0.506				
	Error	53	0.400					
	Total	55	0.839					
					Intercept	0.667	2.814	0.0001
					Leaf[f]	−0.043	0.400	0.0001
					Age[g] × leaf	5.168×10^{-4}	0.069	0.0039
Norchip	Model	3	2.618	0.539				
	Error	60	2.047					
	Total	63	4.665					
					Intercept	1.390	2.370	0.0001
					Leaf	−0.197	1.398	0.0001
					Age	−0.002	0.177	0.0262
					Age × leaf	4.448×10^{-4}	0.775	0.0001
Rosa	Model	2	1.005	0.710				
	Error	57	0.392					
	Total	59	1.397					
					Intercept	0.607	3.865	0.0001
					Leaf	−0.093	0.843	0.0001
					Age × leaf	1.968×10^{-4}	0.538	0.0001

[a] Only significant variables are listed.
[b] Degrees of freedom.
[c] Sequential sums of squares.
[d] Coefficient of determination (adjusted for degrees of freedom).
[e] Partial sums of squares.
[f] Leaf position from soil line.
[g] Plant age in Pdays accumulated from emergence.

growth of lesions for each temperature was expressed as a proportion of the mean radial growth at 27 C (at which lesion expansion was most rapid) and regressed as a function of temperature. To determine the effect of the duration of leaf wetness on lesion growth, the radial growth of lesions was expressed as a proportion of the mean radial growth for 24 hr and regressed as a function of the duration of the wetness period.

Linear regressions of lesion radius as a function of cumulative degree-hours since inoculations were done with PROC GLM of the Statistical Analysis System (15).

Preliminary analyses suggested linear effects of plant physiological age (Pdays) and leaf position on IP, LER, and SP. Therefore, only linear variables were included in the models. The effects of leaf position, plant physiological age, and the product of leaf position and plant age on IP, LER, and SP per square millimeter were identified for each cultivar by stepwise regression by means of PROC STEPWISE of the Statistical Analysis System (15). Variables were added to the models if the F statistic was significant at the 0.15 level. After a variable was added, variables already in the model were removed if they did not produce an F statistic that was significant at the 0.15 level.

RESULTS

Plant emergence. Probit analysis revealed that in 1984, Norchip emerged first, at 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. Therefore, for the IP and LER experiments in 1985, Norchip was inoculated at 18.7, 30.7, and 45.7 days after emergence (137.9, 238.6, and 348.8 Pdays, respectively); Kennebec was inoculated at 17.8, 29.8, and 44.8 days after emergence (131.6, 232.3, and 343.3 Pdays, respectively); and Rosa was inoculated at 17.4, 29.4, and 44.4 days after emergence (128.7, 229.4, and 339.6 Pdays, respectively). For the SP experiments in 1984, Norchip was inoculated at 51.3 and 69.3 days after emergence (413.7 and 551.2 Pdays, respectively); Kennebec was inoculated at 49.5 and 67.5 days after emergence (400.2 and 537.7 Pdays, respectively); and Rosa was inoculated at 47.0 and 65.0 days after emergence (381.9 and 519.4 Pdays, respectively).

Effects of temperature and duration of leaf wetness on radial growth of lesions. The effect of temperature on radial growth was as follows:

$$RLRG_{(temp)} = -0.1499 + 0.0426 \times TEMP \qquad R^2 = 93.45 \quad (4)$$

in which $RLRG_{(temp)}$ is lesion radial growth relative to that at 27 C, and TEMP is temperature (C) (Fig. 1A). The minimum temperature for lesion expansion (3.52 C) was estimated by calculating the x intercept of equation 4.

The effect of duration of leaf wetness on radial growth was as follows:

$$RLRG_{(time)} = 0.0846 + 0.0410 \times TIME \qquad R^2 = 80.31 \quad (5)$$

in which $RLRG_{(time)}$ is lesion radial growth relative to that for 24 hr, and TIME is leaf wetness duration (hr) (Fig. 1B).

Effect of leaf position, plant age, and cultivar on IP. For each cultivar, IP was regressed as a function of leaf position, plant age, and the product of leaf position and plant age. Pairwise comparisons revealed that the multiple regression lines of the three cultivars were significantly different ($P = 0.001$). Therefore, the model containing only significant independent variables was identified for each cultivar by stepwise regression (15). Stepwise regression revealed that for the three cultivars, IP was shortest on the lower, and therefore the oldest leaves (Fig. 2). This was supported by the positive coefficients for the leaf position effect (Table 2). Leaf position effects were greater for Kennebec and Rosa than for Norchip, based on the coefficients from the stepwise regression (Table 2). The effect of leaf position on IP did not change markedly in Norchip as the plants grew older, as indicated by the lack of interaction of plant age and leaf position, while the effect decreased significantly in Kennebec and Rosa, as seen by the lower slopes of the regression lines on older plants than on younger plants (Fig. 2). This was supported by significant interaction of plant age and leaf position (Table 2). The IP became shorter on older plants, which is indicated by the downward shift in the regression lines for plants of increasing age (Fig. 2). Cultivar

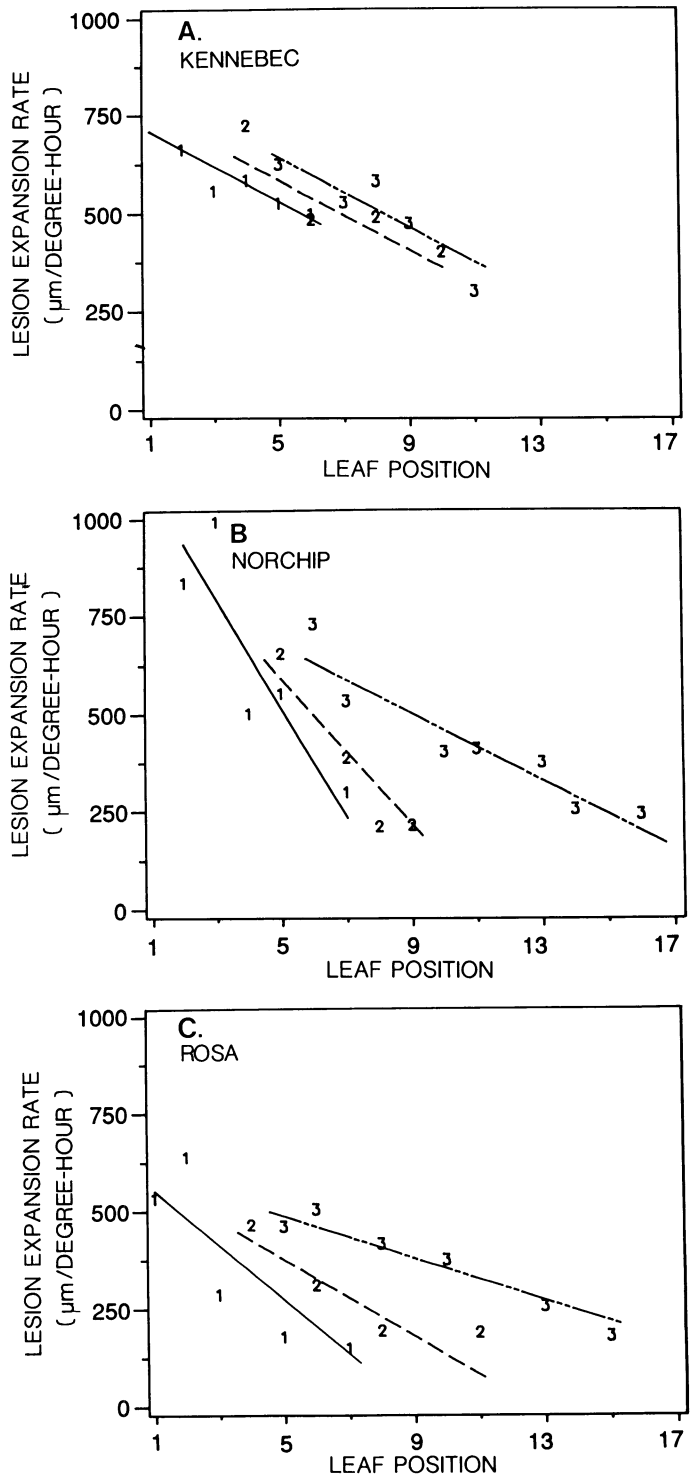

Fig. 3. Effect of plant age (Pdays) and leaf position on the lesion expansion rate of Kennebec (A), Norchip (B), and Rosa (C). The smallest numbers on the x axis designate leaves occupying the lowest positions in the canopy. The numerals 1, 2, and 3 are the means ($n = 4$) of observed lesion expansion rates for plants inoculated at the first, second, and third inoculation times (35, 47, and 62 days after planting, respectively). The lines are the model predictions.

differences were most apparent early in the growing season. Visual comparison of the regression lines for plants inoculated at three different ages revealed that the IPs for Norchip plants for the first inoculation were markedly shorter than the IPs for Kennebec and Rosa. However, the IPs for the three cultivars were not markedly different by the third inoculation. Ultimately, the IPs and the leaf position effects became similar on the three cultivars. These trends were reflected by the negative coefficients for plant age and for the interaction of leaf position and plant age (Table 2).

Effect of leaf position and plant age on LER. For each cultivar, LERs were regressed as a function of leaf position, plant age, and the product of leaf position and plant age. Pairwise comparisons revealed that the multiple regression lines of the three cultivars were significantly different ($P = 0.001$). Therefore, the model containing only significant independent variables was identified for each cultivar by stepwise regression (15). Stepwise regression results revealed that the LERs for the three cultivars were greater on the lower, older leaves than on younger leaves (Fig. 3). This was supported by the negative coefficients for the leaf position effect (Table 3). For Norchip and Rosa, the difference in LER for leaves in different positions was greatest early in the growing season. For Kennebec, the leaf position effect did not change with increasing plant age. This is indicated by the parallel regression lines of LER against leaf position at different plant ages for Kennebec in Figure 3A and the lack of a significant term for the interaction of leaf position and plant age (Table 3).

The LER in the three cultivars increased as the plants grew older, which was reflected by the upward shift in the regression lines (Fig. 3) and the positive coefficients for plant age and for the interaction of leaf position and plant age (Table 3). Early in the season, the LERs for the early-blight-susceptible Norchip were greater than those for Rosa, while the LERs for Kennebec tended to be greater than those for Norchip and Rosa. By the third inoculation, the LERs for the three cultivars were similar.

Effect of cultivar, lesion area, plant age, and leaf position on SP. For each cultivar, stepwise regression revealed that neither plant age nor leaf position had a significant effect on the number of conidia produced per square millimeter of lesion area (Table 4). Spore production was a simple linear function of lesion area (Fig. 4).

Pairwise comparison of the regression lines indicated that SP per square millimeter of lesion area was significantly lower on Kennebec than on Norchip or Rosa. The regression lines for Norchip and Rosa were not significantly different at the 0.05 level. From the y intercept of the regression equations listed in Table 4, the minimum lesion area for SP was estimated to be 3.989 mm^2 for Kennebec, 3.996 mm^2 for Norchip, and 5.978 mm^2 for Rosa.

DISCUSSION

The IP of *A. solani* was shorter and the expansion rate of early blight lesions was greater on the older, lower leaves than on the younger, upper leaves and on older potato plants than on younger ones. These findings for plot-grown potatoes confirm the previous observations on potted potatoes (6,10,12,13,16) and on floating leaf disks (6). The shortest IP observed in the field was about 56 hr (about 0.04 degree-hours per hour), which was consistent with the previously observed values of 40–60 hr (6), 48–72 hr (11), and 48 hr (13). The longest IP we observed was about 12 days on leaves of young Rosa plants.

Differences among the three cultivars were more pronounced for

TABLE 4. Regression results for the effect of potato cultivar and lesion area on spore production

Cultivar	Source	df[a]	SS[b]	P	Coefficient
Kennebec	Intercept	1	324,348	0.1474	−83.331
	Area	1	31,867,833	0.0001	20.888
	Error	66	9,960,664		
Norchip	Intercept	1	890,330	0.0451	−166.937
	Area	1	31,197,544	0.0001	41.772
	Error	56	11,872,223		
Rosa	Intercept	1	2,403,143	0.0001	−280.313
	Area	1	32,303,534	0.0001	46.891
	Error	48	3,706,781		

[a] Degrees of freedom.
[b] Sums of squares.

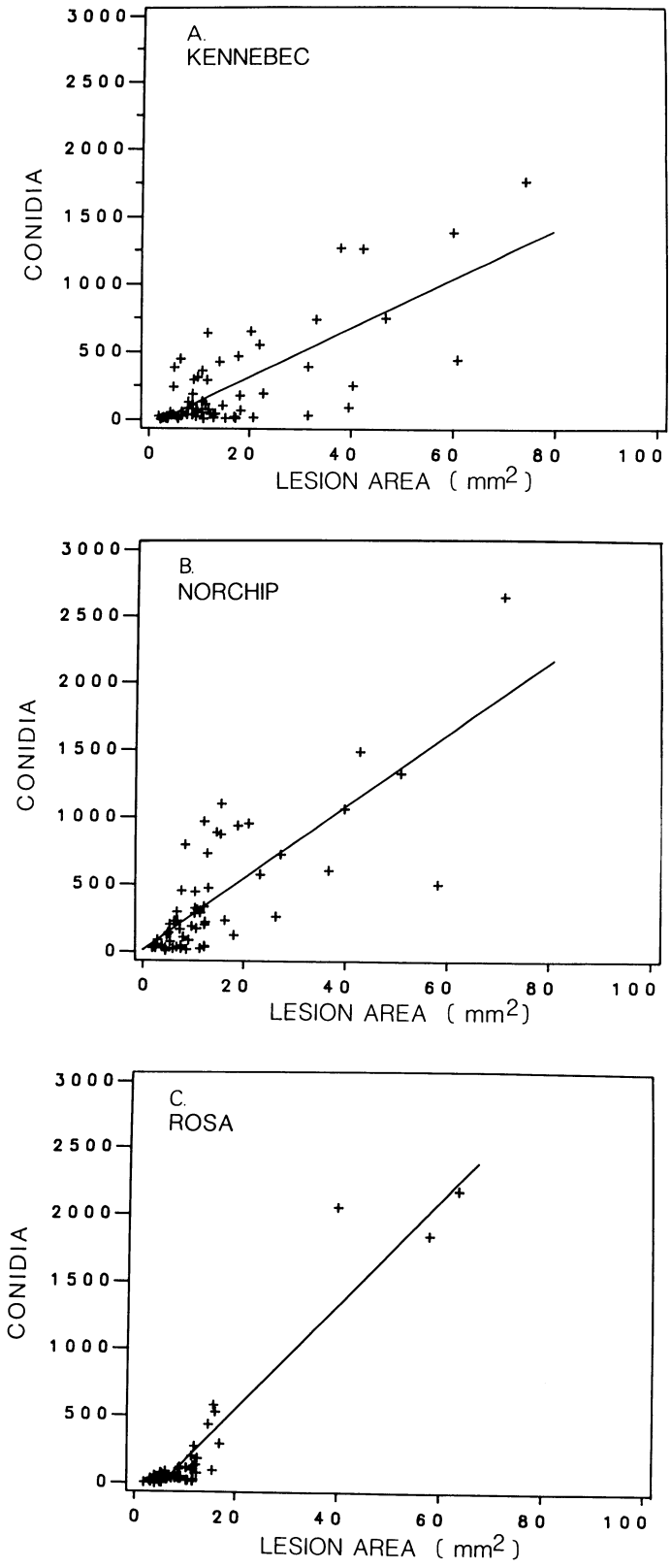

Fig. 4. Number of conidia produced per square millimeter of lesions on Kennebec (A), Norchip (B), and Rosa (C).

the IP than for the LER, the IP being shortest on the early-blight-susceptible and early-maturing Norchip. However, there was no discernible trend between IP for the three cultivars and the tuber dry weight or the ratio of tuber to shoot dry weight. Likewise, no discernible relationship was found between LER and these two growth variables (unpublished results).

We used the same temperature response function for both IP and LER. These two components both reflect the process of host colonization. Because *A. solani* is present only in the necrotic host tissue (11), we assumed that lesion expansion was dependent on leaf surface moisture and temperature. Our findings that the LER increased with temperature are contrary to those of Pound (9) for potted tomato plants. However, since he kept his plants on a greenhouse bench and the leaf surfaces were presumably kept dry, he may have been measuring the effect of temperature on the collapse and desiccation of chlorotic tissue around the necrotic tissue, and not the colonization of leaf tissue per se.

The number of conidia produced per unit of lesion area was found to depend only on the cultivar and not on plant age or leaf position. There was no correlation between the maturity class of the cultivars and SP, although our results were based on only three cultivars. For example, there was no significant difference between the early-maturing Norchip and the later-maturing Rosa. Our results are consistent with those of others because we have found no examples in the literature of plant age and leaf position effects on SP by necrotrophic pathogens. However, the lack of effect in our study may also be due to the advanced age of the plants when the leaves were harvested (about 400 and 530 Pdays). If the effect of leaf position on SP decreased as the plants grew older, such differences may have disappeared by the time we harvested the lesions.

The lower SP per square millimeter of lesion area on Kennebec relative to Norchip and Rosa may be explained by a lower rate of sporulation. Lower rates on resistant cultivars have been observed for *A. solani* on tomato (7) and other necrotrophic pathogens, such as *Helminthosporium turcicum* (5) and *Rhynchosporium secalis* (2). However, although the sporulation rate of *R. secalis* was lower on resistant barley cultivars, there was no marked difference in the total number of spores produced (2). An alternative explanation is that lesion expansion outpaced SP in Kennebec, resulting in a lower number of spores per unit of lesion area.

The minimum lesion areas for SP were smaller than those found by Rands (11), who observed that conidia were rarely found on lesions with areas less than about 12.6 mm^2.

The linear relationship between SP and lesion area was somewhat difficult to understand. A curvilinear function might have been expected, arising from the relationship between the amount of sporulating and nonsporulating tissues on lesions of varying sizes. The linear relationship between SP and lesion area may be explained by the gradual exhaustion of resources in the center of the lesion.

From information produced in this study and in companion studies (unpublished), we believe that we can now explain the relative resistance rankings of the three cultivars. Norchip (susceptible) has a short IP, a rapid LER, and high sporulation, and it supported the highest infection efficiency. Kennebec (moderately resistant) has a moderate IP (long on young leaves or young plants), a moderate LER, and moderately high sporulation, and it supported a high infection efficiency. Rosa (most resistant) has a moderate IP, a low LER, and high sporulation, but it supported the lowest infection efficiency (unpublished results).

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