

## Quantification of General Resistance of Potato Cultivars and Fungicide Effects for Integrated Control of Potato Late Blight

W. E. Fry

Department of Plant Pathology, Cornell University, Ithaca, NY 14853.

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### ABSTRACT

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Areas under the disease progress curves were more reliable than the apparent infection rates or final disease ratings for the quantification of effects of fungicide and general resistance on infection by *Phytophthora infestans* in potatoes. General resistance and fungicide application each reduced disease increase and the effects of each were additive. This relationship between general resistance and fungicide was similar whether fungicide dosage was adjusted by altering the concentration of weekly applications or by

varying the intervals between applications. Among eleven commercial cultivars and one breeding line, the difference in general resistance between the most resistant and most susceptible clones was estimated to be equivalent to weekly applications of about 0.7 kg mancozeb (a.i.)/ha. Growers should be able to complement general resistance in potato cultivars by adjusting fungicide either by altering the dose per scheduled application or by altering the interval between applications.

*Additional key words:* disease management, epidemiology.

Potato late blight [caused by *Phytophthora infestans* (Mont.) d By.] is one of the most destructive diseases of potatoes. Because of the variability of this pathogen, race-specific oligogenic resistance has not been useful for control (10). Potato cultivars now grown commercially in the USA do not have high levels of general resistance to late blight (2, 3, 10). Consequently, growers have relied heavily on periodic application of protectant fungicides and have used large amounts of fungicide for potato late blight control. For example, in the northeastern USA, potatoes received 35% of all the fungicide applied by farmers in that region in 1971 (1).

Generally, there are two methods whereby fungicide efficiency can be enhanced (4). The first is to apply fungicide only when needed—according to a forecasting scheme. Several effective schemes for forecasting potato late blight have been developed (5, 6, 8, 12). The second is the adjustment of application rates to complement the general resistance of a cultivar. For most plants, general resistance has not been quantified, and reliable guidelines are not available. Nevertheless, growers on Prince Edward Island, Canada, have taken advantage of the moderate general resistance of the potato cultivar Sebago, by applying less fungicide to plantings of it than to those of other cultivars (7).

The quantification of general resistance of potato cultivars to *Phytophthora infestans* has been initiated (3). A mancozeb fungicide was applied weekly and the effects of different amounts of fungicide on cultivars with moderate or slight general resistance (Sebago and Russet Rural, respectively) were measured. Because general resistance and periodic application of a fungicide each

may reduce the rate of disease increase, the effect on disease of a given level of general resistance is comparable to that provided by periodic application of a given level of fungicide. Reduction in the apparent infection rate ( $r$ ) (11) in plots of Sebago was equated to the amount of fungicide required to reduce  $r$  to that same level in plots of Russet Rural. The difference in resistance between Russet Rural and Sebago was estimated to be equivalent to weekly applications of 0.42-0.67 kg mancozeb (a.i.)/ha (3). Unfortunately, the relative susceptibilities of most potato cultivars to late blight are not known precisely enough to allow reliable adjustment of fungicide dosage.

The research reported here had three goals: (i) to determine whether parameters other than the apparent infection rate might be useful for assessing the combination of fungicide and general resistance; (ii) to determine whether fungicide dosage can be adjusted as effectively by alteration of timing as by alteration of amount per application, and (iii) to quantify the levels of general resistance of several potato clones to late blight.

### MATERIALS AND METHODS

**Field plot design.**—Treatments consisted of small plots of potatoes with or without fungicide and inoculated with *P. infestans*. Treatments were randomized in complete blocks and there were either three or four complete blocks, depending on the experiment. In 1975 and 1976, plots were five rows wide (0.9 m between rows) and 4.6 m long. In 1977, plots were four rows wide and 4.6 m long. Plots were separated from each other by fallowed areas 3.7 to 4.6 m wide.

**Cultural procedures.**—Foundation or certified potato seed-pieces were planted at approximately 23 cm spacing on 26 May 1975, 3 and 4 June 1976, and 1-3 June 1977.

Seed-pieces consisted of small whole tubers or pieces of tubers, each weighing about 50 g. Pieces of tubers were treated with a mancozeb dust prior to planting, but small whole tubers were planted without treatment. Herbicide [linuron 50 WP, 1.7 kg (AI)/ha] was applied after planting but prior to plant emergence. Fertilizer (168 kg N, 336 kg P, 168 kg K/ha) was applied at planting time. Plants were hilled in 1975 and 1977 when 25-50 cm tall. Plants were not hilled in 1976. Insecticide [0.9-1.1 kg carbaryl (AI)/ha, 1 kg oxydemeton (AI)/ha, or 0.77-1.1 kg methamidophos (AI)/ha] was applied as needed in 1975 and 1976. Aldicarb [3.3 kg (AI)/ha] was applied at planting in 1977. Fungicides were chlorothalonil (Bravo 6F) in 1975 and mancozeb (Manzate 200, 80 W) in 1976 and 1977. Fungicides were applied hydraulically in spray volumes equivalent to 935 liter/ha by a hand-held nozzle at a pressure of 14 kg/cm<sup>2</sup> in 1975 and 1976 and with a tractor-mounted boom at 9 kg/cm<sup>2</sup> in 1977. Herbicide, used as a vine killer, (dinoseb, 3.5 liters in 47.5 liter diesel fuel/ha) was applied during the second week of September in 1975 and 1976. Vine killer was not applied in 1977.

Conditions conducive to disease increase were maintained in several experiments by sprinkler irrigation (0.17 cm water/hr) for 30 min between 0730 and 0830 hr and for 30 min between 1930 and 2030 hr daily from the third or fourth week in July until the second week in September each year. The conduciveness of the environment to potato late blight was assessed in 1977 by calculating Blitecast severity values during the season (8). Relative humidity and temperature were recorded with a hygrothermograph located in a standard weather shelter within the plant canopy. Rainfall was recorded with a standard rain gauge.

Inoculations were made during the third or fourth week in July of each year by spraying a portion of a plant in the center of each plot with a suspension (5-15 ml) of *P. infestans* [race 1, 2, 3, 4] sporangia and zoospores (2.4 × 10<sup>3</sup> sporangia/plot in 1976 and 2.5-5 × 10<sup>4</sup> sporangia/plot in 1975 and 1977). In some cases, when inoculation was unsuccessful, a potato plant with about ten late blight lesions caused by *P. infestans* race (1, 2, 3, 4) was transplanted into the center of each plot. Lesions resulting from spray inoculations usually appeared within 5 days after inoculation, and lesions resulting from transplanting an infected plant into a plot usually appeared within 7 to 12 days.

**Disease estimates.**—The proportion of tissue affected

(percent defoliation plus percent infected) was estimated as described previously (4). Assessments were made every 2-7 days from the time first symptoms appeared until application of vine killer in 1975 and 1976 and until 9 September 1977. Estimates were made more frequently early in the season than late. For some analyses, apparent infection rates (*r*) were obtained by calculating the regression of log<sub>e</sub> *x*/(1-*x*) on time where *x* = proportion of tissue affected (11). Regressions were calculated for the intervals in which disease (*x*) progressed from 0.02-0.08 to 0.92-0.98 in 1975 and 1976 and from 0.05 to 0.90 in 1977. The arcsin transformation was used in the analyses of final percent disease. For other analyses the area under the disease progress curve (ADPC) was calculated as described by Shaner and Finney (9).

$$ADPC = \sum_{i=1}^n [(x_{i+1} + x_i)/2] [t_{i+1} - t_i]$$

where *x<sub>i</sub>* = proportion tissue affected at the *i*th observation and *t* = time (days) after inoculation at the *i*th observation, and *n* = total number of observations. Values for ADPC were normalized by dividing the ADPC by the total area of the graph (= the number of days from inoculation to the end of the observation period × 1.0). The normalized ADPC is referred to as relative ADPC. Units for ADPC are days-proportion, and the relative ADPC has no units.

## RESULTS

**Choice of parameter to estimate the effects of treatment on epidemics.**—Apparent infection rates (*r*) were not always reliable indicators of fungicide or general resistance effects. Because *r* is influenced by weather as well as by fungicide and general resistance, *r* calculated for epidemics progressing under differing environmental conditions might not reflect accurately the effects of fungicide or general resistance. For example, in 1977, disease in plots of cultivar Hudson treated weekly with 0.22 kg mancozeb/ha increased from *x* = 0.05 to *x* = 0.9 primarily during the middle 15 days of the 44-day epidemic when conditions, judged from Blitecast severity values, were relatively unfavorable for late blight. Disease in plots treated weekly with 0.89 kg mancozeb/ha never attained *x* = 0.9; however, progression of these epidemics from *x* = 0.05 to their maxima occurred mainly within the last 14 days, when the environment was relatively favorable for late blight. Apparent infection rates during

TABLE 1. Effect of different amounts of mancozeb on late blight caused by *Phytophthora infestans*

Mancozeb <sup>a</sup> (kg/ha)	Final disease rating (proportion)	Apparent infection rate <sup>b</sup> (per unit/day)	Relative area under the disease progress curve <sup>b</sup>
0.00	0.98 A <sup>c</sup>	0.28 A	0.54 A
0.22	0.86 B	0.19 BC	0.28 B
0.44	0.87 B	0.22 BC	0.25 B
0.89	0.69 C	0.21 BC	0.15 C
1.79	0.35 D	0.18 C	0.04 D

<sup>a</sup>Mancozeb was applied weekly to small plots of Hudson potatoes.

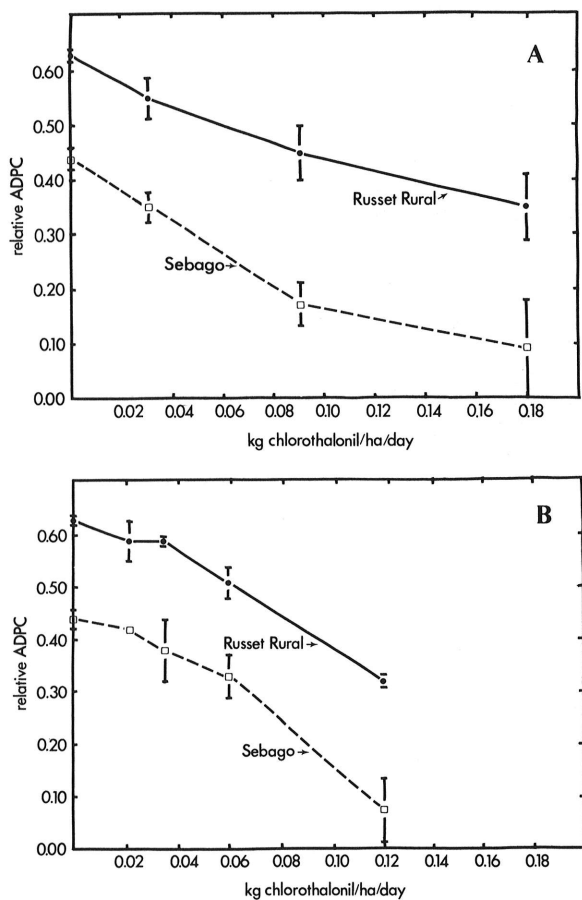
<sup>b</sup>Calculation of the apparent infection rate and area under the disease progress curve are described in text.

<sup>c</sup>Numbers followed by the same letter within a column are not significantly different (*P* = 0.05) according to Duncan's new multiple range test.

the intervals of  $x = 0.05$  to  $x = 0.9$  for the two treatments were essentially the same (Table 1).

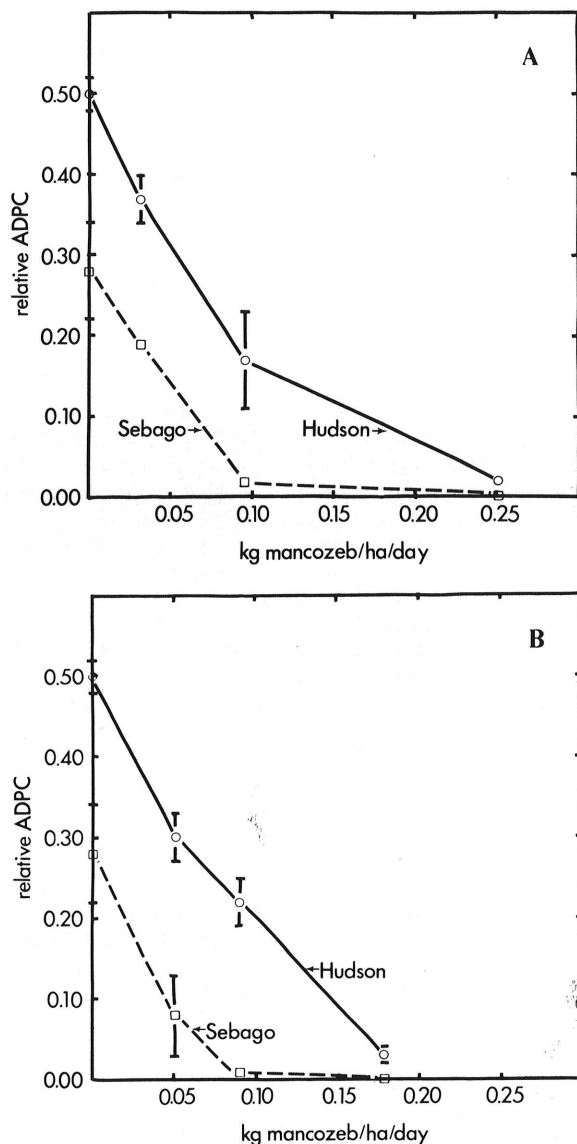
The final disease rating, apparent infection rate ( $r$ ), and area under the disease progress curve (ADPC) were compared to determine how each reflected differences due to different fungicide dosages (Table 1). Final disease rating seemed as accurate as ADPC and more so than  $r$  in this case. However, final disease rating would be inadequate to distinguish between treatments in which 100% disease ( $x = 1$ ) was attained at different times. Consequently, the ADPC was used to equate effects of fungicide doses to effects of levels of general resistance.

**Effects of fungicide and general resistance.**—The difference in resistance between two cultivars was estimated in terms of relative ADPC at varying levels of fungicide applied per unit of time (Fig. 1). Fungicide



**Fig. 1-(A, B).** Effect of different amounts of chlorothaloniol on the relative area under the disease progress curve (ADPC) for epidemics of late blight in plots of Russet Rural and Sebago potatoes in 1975. The ADPC has been normalized as indicated in the text. The actual ADPC's at zero fungicide (chlorothaloniol) for Russet Rural and Sebago were 34.88 and 24.11 days-proportion respectively, and epidemics occurred during a 55-day period. Standard errors (vertical lines) less than  $\pm 0.01$  relative ADPC are not indicated. **A)** Fungicide amount was 0, 0.21, 0.63, or 1.26 kg chlorothaloniol (AI)/ha applied weekly. **B)** Fungicide amount was altered by applying 0.42 kg/ha at 19-, 12-, 7-, or 3.5-day intervals.

levels were varied by applying different amounts at constant intervals (Fig. 1-A) or by applying constant amounts at different intervals (Fig. 1-B). In 1975, chlorothaloniol was applied to Russet Rural and Sebago. The amount was varied (i) by applying 0.42 kg/ha every 3.5, 12, or 19 days; or (ii) by applying 0.21, 0.63, or 1.26 kg/ha every seven days. Disease was measured for 55 days so that the total area of the graph was 55.0 days-proportion.



**Fig. 2-(A, B).** Effect of different amounts of mancozeb on the area under the disease progress curve (ADPC) for epidemics of late blight in plots of Hudson and Sebago potatoes in 1976. The ADPC has been normalized as indicated in the text. The actual ADPC's for zero fungicide on Hudson and Sebago were 24.91 and 14.12 days-proportion, respectively, and the epidemic occurred during a 50-day period. Standard errors (vertical lines) less than  $\pm 0.01$  relative ADPC are not indicated. **A)** Fungicide amount was 0.00, 0.224, 0.672, or 1.792 kg (AI)/ha applied weekly. **B)** The amount of mancozeb was 0.36 kg/ha applied at 7-, 4-, and 2-day intervals.

The effect of chlorothalonil on reducing the ADPC was about the same whether the dosage was adjusted by altering chlorothalonil concentrations or intervals between applications. The ADPC's for zero chlorothalonil for Russet Rural and Sebago were 34.88 and 24.11 days-proportion, respectively. The normalized ADPC's were 0.63 and 0.44, respectively. The effect of chlorothalonil on ADPC was about the same for each cultivar. Application of 0.42 kg chlorothalonil/ha every 3.5 days (approximately 0.12 kg/ha/day) reduced the ADPC by 0.31 and 0.36 for Russet Rural and Sebago, respectively. Application of 1.26 kg/ha every 7 days (0.18 kg/ha/day) reduced the ADPC by 0.28 and 0.35 for Russet Rural and Sebago, respectively. The difference in resistance between these two cultivars was equivalent to the effect of about 0.06-0.08 kg chlorothalonil/ha/day estimated by alteration of frequency of application and 0.09-0.15 kg chlorothalonil/ha/day estimated by alteration of fungicide concentration per application (Fig. 1).

In 1976, mancozeb was applied to Sebago and to Hudson, a cultivar more susceptible than Sebago, but not quite as susceptible as Russet Rural. Treatments were 0.36 kg/ha applied at different intervals (Fig. 2-B), or application of different amounts at 7-day intervals (Fig. 2-A). Again, the effects of fungicide (mancozeb) on ADPC were similar whether the dosage was adjusted by alteration of application frequency or mancozeb concentration (Fig. 2). Disease was measured for 50 days so that the total area of the graph was 50.0 days-proportion. The ADPC's at zero fungicide for Hudson and Sebago were 24.91 and 14.12 days-proportion, respectively. The normalized ADPC's were 0.50 and 0.28 for Hudson and Sebago, respectively.

When 0.36 kg mancozeb/ha was applied every seven days (0.051 kg/ha/day), the normalized ADPC was reduced by 0.2 for both Hudson and Sebago. When applied every 4 days (0.09 kg/ha/day) it reduced the ADPC by 0.28 for Hudson and 0.27 for Sebago. The effect on ADPC of the greater degree of general resistance in Sebago than in Hudson appeared to be equivalent to the effect on ADPC of about 0.06-0.10 kg mancozeb/ha/day over the range of application intervals tested (Fig. 2-B).

When mancozeb concentration was varied, and application made every 7 days, the ADPC's for each cultivar

were reduced similarly. When 0.22 kg (AI)/ha was applied (0.032 kg/ha/day), the ADPC was decreased by 0.13 for both Sebago and Hudson. At 0.67 kg/ha (0.096 kg/ha/day), ADPC was decreased by 0.33 for Hudson and 0.26 for Sebago. The effect on ADPC of the greater amount of general resistance in Sebago than in Hudson was estimated from the linear portion of Fig. 2-A to be equivalent to the effect on ADPC of 0.060-0.065 kg mancozeb/ha/day.

**Prediction of amounts of fungicide equivalent to various levels of general resistance.**—The relative amounts of general resistance within 11 cultivars and one clone were quantified by relating ADPC's to the effects of small amounts of fungicide (mancozeb) applied to Hudson. One experiment in 1976 and two in 1977 were conducted (Table 2 and 3). By extrapolation from data in Fig. 2 for Superior and in Fig. 3 for Abnaki, Monona, and Norchip, the amounts of mancozeb needed weekly to reduce their ADPC's to that of Hudson would have been 0.11, 0.14, 0.12, and 0.11 kg/ha, respectively. The method of extrapolation is illustrated by using the cultivar Superior as an example. The relative (normalized) ADPC for Superior in 1976 was 0.55 (Table 2). The relative ADPC for Hudson at zero fungicide in 1976 was 0.50, and the difference in relative ADPC between the two cultivars is 0.05. The amount of mancozeb required to reduce the relative ADPC of Hudson by 0.05 was 0.015 kg/ha/day (= 0.11 kg/ha/wk) (Fig. 2-A). Therefore it is estimated that the relative ADPC of Superior sprayed weekly with 0.11 kg mancozeb/ha would be equivalent to the ADPC of unsprayed Hudson. Similarly, by interpolation in Fig. 3, using ADPC's given in Table 3, the differences in general resistance between Hudson and the more resistant cultivars would have been equivalent to the following amounts of mancozeb (kg/ha) applied weekly: Wauseon, 0.03; Russet Burbank, 0.07; Green Mountain, 0.09; Katahdin, 0.14; Kennebec, 0.21; Sebago, 0.27; L-521-7, 0.56.

The combined effect of fungicide dosage and general resistance in the Cornell breeding line (L-521-7) was examined directly in 1977. Plots of this cultivar were sprayed weekly with 0.89 kg mancozeb/ha. This treatment reduced the normalized ADPC from 0.21 to 0.009 ( $\pm 0.004$ ). This was less than the ADPC for Hudson treated with twice as much fungicide (0.05) (Table 1, Fig. 3).

TABLE 2. Relative susceptibilities of eight potato cultivars to *Phytophthora infestans* in 1976 as estimated by three parameters

Cultivar	Final disease rating (proportion)	Apparent infection rate <sup>b</sup> (per unit per day)	Relative area under the disease progress curve <sup>b</sup>
Green Mountain	0.95 BC <sup>a</sup>	0.20 DE	0.37 D
Hudson	>0.99 A	0.47 B	0.50 AB
Katahdin	>0.99 AB	0.33 C	0.39 CD
Kennebec	0.98 ABC	0.24 D	0.33 DE
Russet Burbank	>0.99 AB	0.35 C	0.45 BC
Sebago	0.93 C	0.21 DE	0.28 E
Superior	>0.99 A	0.68 A	0.55 A
L-521-7	0.64 D	0.12 E	0.19 F

<sup>a</sup>Numbers followed by the same letter within a column are not significantly different ( $P=0.05$ ) according to Duncan's new multiple range test.

<sup>b</sup>Calculation of the apparent infection rate and area under the disease progress curve are described in the text.



## DISCUSSION

Of the three parameters evaluated, the area under the disease progress curve (ADPC) was judged more reliable than the apparent infection rates or final disease ratings for reliably estimating the effects of fungicide and/or general resistance. The final disease rating is useful only if epidemics do not progress to completion or near completion by the end of the season. Because the apparent infection rate ( $r$ ) is influenced by weather as well as by general resistance and fungicide, it is useful to compare treatments only if the environment is equivalently favorable for disease during the intervals of calculation. For example,  $r$  was calculated for Hudson plots treated with 1.79 kg mancozeb/ha/wk when the environment was moderately favorable for late blight, but was calculated for plots treated with 0.22 kg mancozeb/ha/wk during an interval less favorable for late blight. The apparent infection rates for the two treatments were not significantly different, although the ADPC for plots treated with 1.79 kg/ha was about 15% that of plots treated with 0.22 kg/ha (Table 1). The ADPC reflected both the onset as well as the rates of epidemic development.

The ADPC might be a less reliable indicator of differences among treatments if the amounts of initial inoculum are variable. In an experiment where plots received different amounts of initial inoculum, but epidemics were observed during the same time interval, apparent infection rates were a more reliable parameter to assess differences among treatments (4).

Fungicide (mancozeb or chlorothalonil) produced similar reduction of ADPC whether applied to a moderately resistant or susceptible cultivar. Thus the effect of fungicide was considered directly additive to that of general resistance (Fig. 1, 2). The relationship between ADPC and fungicide does not require transformation or other manipulation. Thus, use of the ADPC to estimate effects is more convenient than use of apparent infection rates, which required transformation (3).

Estimations of the relative levels of general resistance in terms of fungicide equivalents were similar whether the

estimate was made by altering fungicide amount per weekly application or by altering the interval between applications of constant amounts of fungicide. In 1976, the effect on ADPC of the greater resistance in Sebago than in Hudson was estimated equivalent to the effect on ADPC of 0.06-0.10 kg mancozeb/ha/day when the interval between applications was altered, and 0.060-0.065 kg mancozeb/ha/day when the amount per weekly application was altered. These estimates agree well with a previous prediction (3). In 1975, the effect on ADPC of

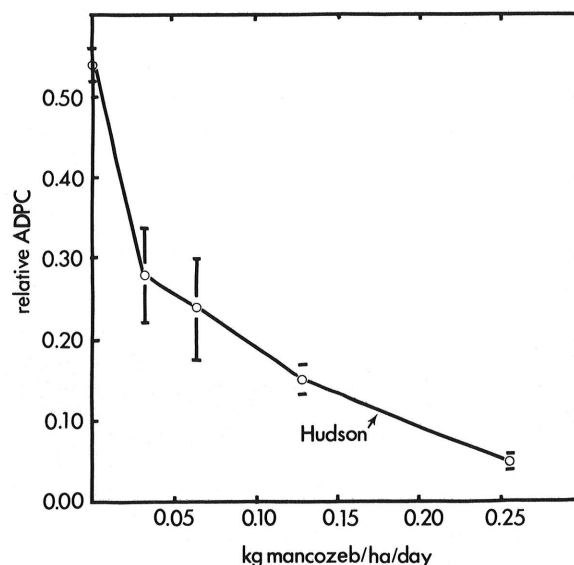


Fig. 3. Effect of different amounts of mancozeb on the area under the disease progress curve (ADPC) for epidemics of late blight in plots of Hudson potatoes in 1977. The ADPC has been normalized as indicated in the text. The ADPC for Hudson without fungicide was 23.70, and the epidemic occurred during a 44-day period. Standard errors (vertical lines) less than  $\pm 0.01$  relative ADPC are not indicated. Fungicide amount was 0.0, 0.224, 0.448, 0.896, or 1.792 kg/ha applied weekly.

TABLE 3. Relative susceptibility to *Phytophthora infestans* in 1977 of eleven potato cultivars and clones as estimated by three different parameters

Cultivar	Final disease rating (proportion)	Apparent infection rate <sup>b</sup> (per unit per day)	Relative area under the disease progress curve <sup>b</sup>
Abnaki	1.00 A <sup>a</sup>	0.55 A	0.62 A
Green Mountain	0.89 D	0.17 GHI	0.44 EF
Hudson	0.98 BC	0.28 D	0.54 BC
Katahdin	0.91 D	0.17 GHI	0.41 F
Kennebec	0.79 E	0.15 HI	0.29 G
Monona	>0.99 AB	0.46 B	0.59 AB
Norchip	>0.99 AB	0.38 C	0.60 A
Russet Burbank	0.96 C	0.24 EF	0.45 EF
Sebago	0.69 F	0.13 IJ	0.27 G
Wauseon	>0.99 AB	0.29 D	0.50 CD
L-521-7	0.58 G	0.10 J	0.21 H

<sup>a</sup>Numbers followed by the same letter within a column are not significantly different ( $P=0.05$ ) according to Duncan's new multiple range test.

<sup>b</sup>Calculation of the apparent infection rate and area under the disease progress curve are described in the text.

the greater resistance in Sebago than in Russet Rural was equivalent to the effect on ADPC of 0.06-0.08 kg chlorothalonil/ha/day when the interval between application was altered, and 0.09-0.15 kg chlorothalonil/ha/day when the amount per weekly application was altered.

In both years fungicide was used more efficiently by applying low concentrations at frequent intervals rather than by applying high concentrations less frequently. For example, application of 0.36 kg/ha mancozeb every two days (0.179 kg/ha/day) to Hudson in 1976 reduced the ADPC to 0.03 but application at 1.792 kg/ha every 7 days (0.256 kg/ha/day) was required to reduce the ADPC to 0.02 (Fig. 2). The disease control attained in the two cases was equivalent, but frequent application of low concentration required only about 70% as much fungicide as weekly application at high concentration.

Because fungicide is used most efficiently when applied frequently at low concentration, the most efficient means to adjust fungicide dosage to complement general resistance in a cultivar is probably to adjust the concentration of fungicide per frequent application. However, fungicide dosage can also be adjusted to complement general resistance by minor modification of the application interval.

Fungicide is used efficiently if applied only when needed. When the dosage per application was adjusted to complement the general resistance of a cultivar and then applied according to a forecasting technique it was used even more efficiently (4). From information in this study, one can suggest that the forecasting technique itself could be adjusted to complement the general resistance in cultivars. For example, under conditions especially or moderately favorable for late blight, the spray recommendations from Blitecast are a 5-day spray schedule or a 7-day spray schedule (8). A 5-day spray schedule of 1.79 kg mancozeb/ha corresponds to 0.358 kg/ha/day. If this dosage provides adequate late blight control on Hudson then the amount required for Sebago should be  $0.358 - 0.065 = 0.293$ , which corresponds to a 6-day spray schedule at 1.76 kg/ha. Similarly, a 7-day schedule for Hudson corresponds to a spray schedule of about 9 days for Sebago.

The range in general resistance within the commercial cultivars was estimated to be equivalent to the effects on ADPC of 0.41 kg mancozeb/ha applied weekly. Line L-521-7 had the highest level of general resistance, and the effect of this level of resistance was equivalent to the effect of ADPC of 0.56 kg mancozeb applied weekly to Hudson. These estimates are conservative, and the effect of high

levels of general resistance may be even more useful to control disease when combined with fungicide. For example, by analysis of Fig. 2 and 3, one can calculate that application of 0.05-0.06 kg mancozeb/ha/day, or about 0.4 kg/wk, was sufficient to reduce the relative ADPC of Hudson or Sebago by about 0.20, the ADPC of nonsprayed L-521-7. Thus application of 0.4 kg mancozeb/hr/wk might suppress late blight to near zero in L-521-7 and the effect on disease control of the greater resistance in L-521-7 than in Hudson may be as large as the effect of 1.3 kg mancozeb/ha/wk applied to Hudson.

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