Correlation of Growing Season Environmental Variables and the Effect of Early Dying on Potato Yield

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ABSTRACT

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Regression models for potato yield (Y) and yield relative to controls (RY) in relation to soil population densities of *Verticillium dahliae* and *Pratylenchus penetrans* at planting were developed based on 8 yr of data from Ohio microplot studies. The effect of environmental variables on variability in Y and RY left unexplained by models (i.e., residuals) then was investigated. Residuals for controls and treatments with *P. penetrans*, *V. dahliae*, and *P. penetrans* + *V. dahliae* were separately correlated with environmental variables calculated for various starting points and interval lengths of the growing season. Correlations of residuals with environmental variables for 12- to 18-day intervals were the most informative. Residuals of Y for all treatments were negatively correlated ($P < 0.05$) with several temperature variables over a 12- to 18-day period beginning 47–53 days after planting, suggesting a general depression of potato yield due to high temperature. Residuals of RY for treatments with *V. dahliae* and *P. penetrans* + *V. dahliae* were negatively correlated with several 18-day temperature variables beginning at 17–26 days after

planting and again with some 18-day temperature variables at 68–71 days, suggesting a sensitivity of infected plants to high temperatures during these times. Total precipitation over an 18-day interval was negatively correlated with residuals of Y for the treatment with *P. penetrans* + *V. dahliae* beginning at 44 days after planting and again at 53–59 days. Residuals of RY for the treatment with *V. dahliae* were negatively correlated with precipitation accumulated over 12–18 days beginning at 38 days after planting and again at 62–65 days after planting. Six years of data from microplot experiments in a different Ohio location were analyzed similarly to assess the reliability of correlation results. There were sufficient similarities in correlation patterns for the two locations to suggest that periods of high temperature having a negative effect on yield of infected plants were correctly identified. If these relationships hold, it will be possible to forecast environmental impact on yield reduction due to potato early dying well in advance of symptom appearance.

Additional keywords: agrometeorology, *Solanum tuberosum*, yield loss models.

Potato early dying is a serious disease problem in many areas where potatoes (*Solanum tuberosum* L.) are grown intensively (12). Research in Ohio has implicated the root-lesion nematode, *Pratylenchus penetrans* (Cobb) Filipjev & Schuur. Stekh., as an interactive pathogen with the soilborne fungus, *Verticillium dahliae* Kleb., in development of this syndrome (13). Linear regression was used in an earlier analysis of Ohio microplot data to predict the amount of yield reduction relative to controls caused by *V. dahliae* and *P. penetrans*, based on their preplant population densities (6). High variability in yield reduction relative to controls, partly due to year-to-year variation, resulted in a relatively low level of predictability, however. Discriminant analysis was determined to be a viable alternative to regression models (6). High

and low yield losses were predicted with a successful classification rate of about 90% based on preplant population densities of the two pathogens.

Understanding the effects of environment on the severity of potato early dying and associated yield reduction is hampered by the long time span of disease progression. Discrete symptoms on aerial structures arising shortly after a determinative environmental event are more easily quantified than the general systemic symptoms characterizing the early dying syndrome. Root infection and colonization by *V. dahliae*, which begins soon after root initiation, do not produce foliar symptoms until much later in the season (12). More severe disease levels and greater yield reduction were noted in Ohio experiments in seasons that had relatively high late-season temperatures than in milder seasons (13).

Coakley et al (3) described a technique to correlate environmental variables with disease intensity by summarizing variables within discrete time periods of various lengths (e.g., 30-day period) and then advancing the calendar onset of the periods by a

selectable number of days (e.g., starting on day of year 170, then day 175, etc.). Later, Coakley et al (2) were able to correlate several weather variables to disease severity of wheat stripe rust (caused by *Puccinia striiformis* West.). Significant variables identified by this process were reexamined in 1-day steps to refine the relationships. With this method, severity of wheat stripe rust over 18 yr was found to be most highly related to precipitation frequency from April 5 to June 2, mean maximum temperature from January 4–24, and total precipitation from March 14 to April 5 (2). The logic of this procedure seemed applicable to an epidemiological study of potato early dying.

The goal of our studies, therefore, was to further understand the epidemiology of potato early dying by determining the influence of environmental variables on the early dying/yield loss system. Specific objectives were to revise previously derived regression models based on preplant pathogen densities for yield relative to controls (6) by incorporating data from two additional years; derive similar regression models for tuber yield in grams per plant based on the same pathogen densities; and, identify environmental variables that might account for variability in yield and yield relative to controls left unexplained by the regression models.

MATERIALS AND METHODS

Available for analysis was an 8-yr (1980–1987) data set from factorial microplot experiments conducted at Wooster, OH (6,12), nearby (< 0.5 km) weather station data (1980–1984), and hourly meteorological data recorded by a CR-21 datalogger (Campbell Scientific, Logan, UT) at the experimental site (1985–1987). The last 2 yr of data were not used in developing previously reported models (6). Included as treatments each year were Wooster silt loam soil infested with *V. dahliae* alone at two or three population densities, *P. penetrans* alone at two or three population densities, *V. dahliae* + *P. penetrans* at each of the individual pathogen densities, and an uninfested control. Details of experimental methods by which these data were obtained may be found elsewhere (6,13). An additional 6 yr of data from microplot experiments with an identical factorial design conducted in a Rifle peat soil (1980–1983, 1985–1986) at Celeryville, OH, and on-site, daily weather data were reserved for validation studies. The potato cultivar Superior was used in all years at both locations.

The first step in the analysis was to separately regress tuber yield and yield relative to the control on preplant population densities of *V. dahliae* and *P. penetrans*. Means for each treatment combination were used in the analysis. Mean tuber yields of all treatments within a year also were divided by the yield for the control in the same year to form relative yields. Stepwise regression methods (10) were applied to determine significant pathogen effects. Once the best-fitting model was determined, based on significant coefficients and largest coefficient of determination (r^2), residuals and standardized residuals were calculated and carried forward to the next step in the analysis. A residual is the observed minus predicted value (e); a standardized residual (e^*) is a residual divided by its standard deviation and has a variance equal to one. We selected residuals for the control and for the treatments with highest preplant densities of *P. penetrans* alone, *V. dahliae* alone, and *P. penetrans* + *V. dahliae* for further analysis. There were four residual values for the yield model and three residuals for the relative yield model each year. The residuals of relative yield for controls did not vary, because, by definition, these relative yields were equal to 1.0. Standardized residuals were plotted by year to assess year-to-year trends.

Correlation with environmental variables. The objective in this portion of the analysis was to try to explain under- and overpredictions from the two regression models by use of environmental data accumulated during the growing season. The technique used was similar to that of Coakley et al (3), except that we analyzed regression residuals, interval onset advance remained constant rather than having a variable range definable down to 1-day steps, and statistical analysis was done separately rather than being internal to the program. The following summary environmental variables were calculated: cumulative number of days having an average temperature >24 C, cumulative number of days with average temperatures <19 C, cumulative degree days (base = 7 C), mean high temperature, mean low temperature, cumulative precipitation, and ratio of cumulative precipitation to cumulative degree days. Precipitation was used in place of soil moisture, and the ratio of precipitation to degree days can be interpreted as a crude measure of soil moisture supply and demand (8). The choice of the 7 C temperature was based on the physiological threshold for growth (1). The 19 C and 24 C temperatures were selected based on their ability to discriminate annual trends in the number of relatively warm and cool days. A FORTRAN program was written to output summary environmental values for 6X-day periods, where $X = 1, 2, 3,...14$. Each 6X-day period provided a 'window' on a portion of the growing season (2). Starting dates began at 2 days after planting, and interval onset was incremented at 3-day intervals until the end of the growing season was reached 88 days after planting. For example, the first 12-day window (i.e., $X = 2$) began on day 2 and extended to day 13 (inclusive). The second window began on day 5 and continued until day 16, and so on, until the last of 26 windows began on day 77 and ended on day 88. This procedure resulted in a total of 210 values for each environmental variable. Summary environmental variables from the windows were separately correlated with residuals from yield and relative yield models.

Data from microplot experiments conducted at Celeryville, OH, 80 km NW of Wooster, were used to test results from Wooster. Experimental design each year was identical to that at Wooster. Results from 1980–1983 and 1985 were reported previously (6,13); an additional year of data from 1986 was newly available. Environmental variables were formed and correlations with residuals from a best-fitting regression model were done as before, with one exception. At Celeryville, the on-site weather station reported only high and low daily temperatures, so we based our calculations of degree days and mean daily temperatures on equations that simulated diurnal temperature variation rather than simply taking the mean of high and low temperatures (9).

RESULTS

Preplant models. Mean tuber yields at Wooster over 8 yr were best explained by the equation:

$$Y = 777 - 293(\text{canopy}) - 45.1(\ln[V \times P + 1]) \\ + 41.5(\text{canopy} \times [\ln[V \times P + 1]]) - 36.1(\ln[V + 1]), \quad (1)$$

where Y = tuber yield (g/plant), ln is the natural logarithm, V = *V. dahliae* (cfu/cm³ of soil), and P = *P. penetrans* (vermiforms/100 cm³). Canopy was a qualitative factor that equaled 1 if a crop canopy (i.e., potatoes growing between those in microplots) was present (1980–1984) and 0 if the canopy was absent (1985–1987). This equation explained 48% of the variation in yield for 96 observations over 8 yr when adjusted for the number of predictors in the model (i.e., adjusted $r^2 = 0.48$, $n = 96$). A positive coefficient for (canopy × ln[$V \times P$ + 1]) indicated that the pathogen interaction caused greater yield loss without a canopy than with one.

Mean yields relative to controls at Wooster were best explained by:

$$RY = 0.95 - 0.033(\ln[V \times P + 1]) - 0.043(\ln[V + 1]) \\ + 0.138(\text{canopy}), \quad (2)$$

where RY = relative yield, and other terms are as before. The adjusted r^2 was 28%.

Similarly, data from Celeryville microplots were regressed on preplant pathogen densities and crop canopy effect. Mean yields from 6 yr of experimental data were described by:

$$Y = 3,085 - 2,476(\text{canopy}) - 281(\ln[V \times P + 1]) \\ + 264(\text{canopy} \times [\ln[V \times P + 1]]). \quad (3)$$

The adjusted r^2 for this regression was 94% ($n = 63$), much higher than the result from Wooster data. Equation 3 differed from equation 1 in that the preplant density of *V. dahliae* alone was not a significant factor of yield loss.
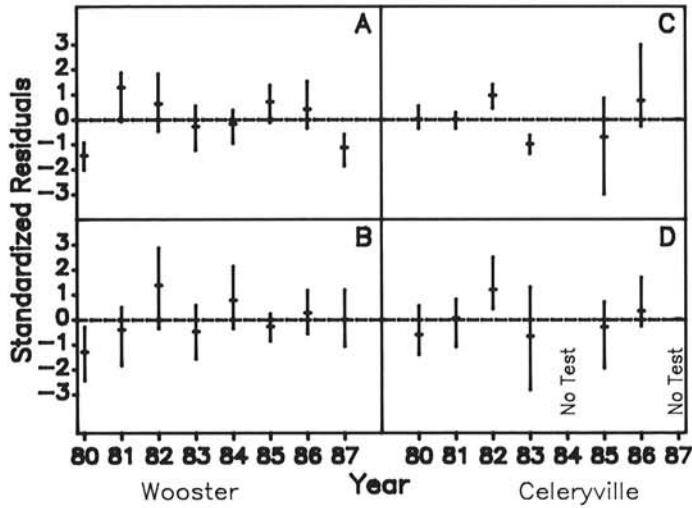
Relative yields from Celeryville data were described by the following model:

$$RY = 0.93 - 0.084(\ln[V \times P + 1]) + 0.053(\text{canopy} \times [\ln[V \times P + 1]]). \quad (4)$$
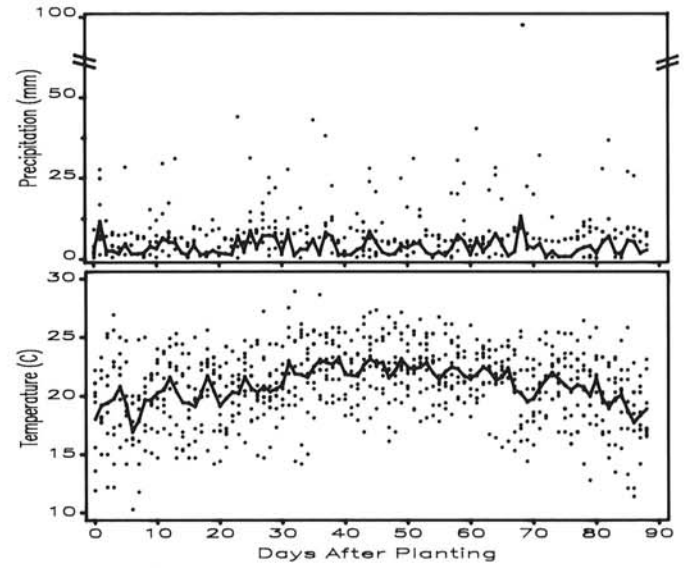

Fig. 1. Range (vertical line) and mean (cross hatch) of standardized residuals taken from four multiyear regression models (equations 1–4 in text) of potato tuber yield (A,C) or tuber yield relative to controls (B,D). Data from microplot experiments on potato early dying conducted at Wooster, OH (A,B), and Celeryville, OH (C,D), sorted by year of experiment.

Fig. 2. Mean daily air temperatures and precipitation amounts at Wooster, OH, beginning on the day after planting potatoes in microplots, 1980–1987. Means of variables over 8 yr are connected with a solid line and zero precipitation events are not shown.
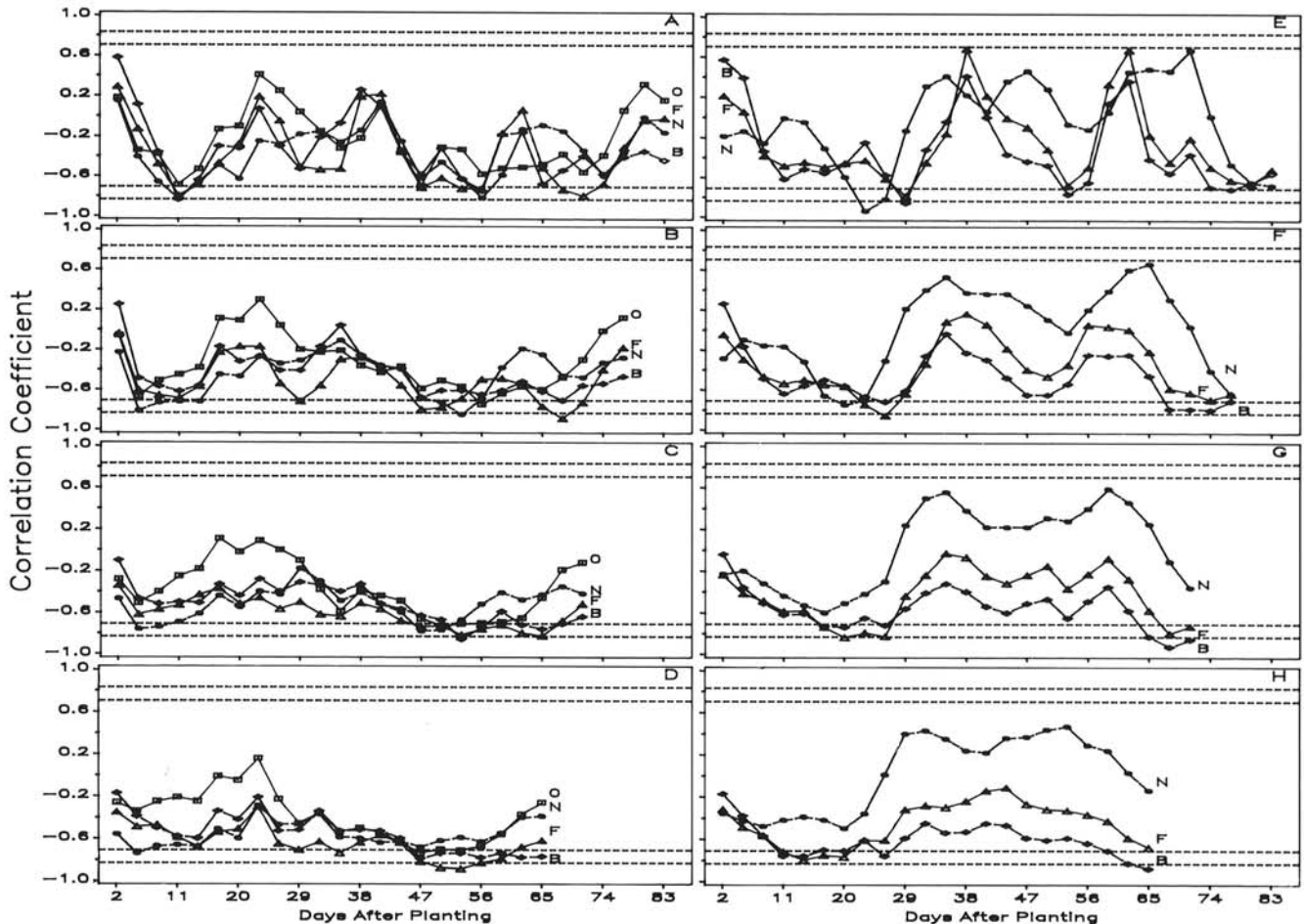

Fig. 3. Residuals of potato tuber yield (A–D) and relative yield (E–H) of four treatments from regression models (eqs. 1 and 2 in text) correlated with degree days accumulated over 6 (A,E), 12 (B,F), 18 (C,G), and 24 (D,H) days at Wooster, OH. Correlation coefficients are plotted at the beginning of the respective time interval. Inner set of horizontal lines represent the 0.05 level of significance and the outer set the 0.01 level. Symbols: 0 (□) = control, N (○) = *Pratylenchus penetrans* alone, F (△) = *Verticillium dahliae* alone, B (◇) = both *P. penetrans* and *V. dahliae*.

The adjusted r^2 was 55% for this model.

Differences in tuber productivity per plant between the sites can be inferred from the intercepts of equations 1 and 3. With a crop canopy, the cultivar Superior yielded about 500 g per plant at Wooster and about 600 g per plant at Celeryville. Without a canopy, yields at Wooster were nearly 800 g per plant, whereas at Celeryville yields were more 3,000 g per plant. The intercept terms in equations 2 and 4 were the predicted RY when all other terms, including canopy, were equal to 0. With one exception, these intercepts were not significantly different from 1.0 ($P >$ 0.05). When a canopy was present at Wooster, the intercept was 1.09, which was different from 1.0 ($P < 0.05$).

Standardized residuals from the four models (equations 1–4) were separated by year and their ranges and means plotted (Fig. 1). Residuals were affected by the year from which the observation came, suggesting that environmental variables might explain additional variation in yield. Standardized residuals of yield from Wooster in 1980 and 1987, for example, were entirely negative, indicating overprediction (Fig. 1A). Although the expected sum of residuals over the 8 yr is 0 (10), the range of residuals in these 2 yr did not even include 0. In 1981 and 1985, residuals of yield from the Wooster model were mostly positive, indicating underprediction.

Placement of annual ranges relative to 0 seemed to be less consistently separated by year for residuals of relative yields than tuber yields. For example, there were 11 of 12 underpredicted yields (i.e., positive e) (Fig. 1A) but only 7 of 12 underpredicted relative yields for Wooster in 1981 (Fig. 1B). Of course, one reason for choosing to model yield loss as a proportion of control yield was to reduce the effect of year-to-year variation, since control plants will respond to nonpathogenic environmental effects potentially in the same manner as plant in infested soil.

Standardized residuals of yield from Celeryville had a relatively narrow range when plants were grown in a canopy and a very large range when the canopy was absent in 1985 and 1986 (Fig. 1C and D). In 1985, the preplant model greatly overpredicted the yield of plants exposed to a high inoculum of *V. dahliae* alone. In 1986, the model underpredicted by about 750 g per plant the yield of a high nematode plus low fungus treatment. Even if these outliers are neglected, the range of residuals in these years (2.4 and 2.3 standardized units) still would be greater than residuals from earlier years. It would appear, therefore, that the effect of canopy had a large influence on the parameters of the regression model.

Correlation with environmental variables at Wooster. Daily mean air temperatures and cumulative precipitation between plantings and harvests were plotted, and an average over the 8-yr study period was calculated (Fig. 2). Daily temperature data were well spread out over the 8 yr. As expected, precipitation on any given day generally was low or 0 and relatively few days had >10 mm of rain.

There were numerous significant correlations between environmental variables and residuals. The correlations of the five different temperature variables with residuals were closely related; therefore, in the interest of brevity, only those for degree days are shown (Fig. 3) and comparisons among temperature variables are noted in the text. Increase in interval length had a stabilizing effect on correlation coefficients as the relationship was examined over the growing season in 3-day steps. Information content for analytical purposes seemed to peak at intervals of 12–18 days in length. Thereafter, new significantly correlated periods were not found. A significant negative correlation of an environmental variable with residuals in this analysis indicated that yields or relative yields were less than predicted as the quantity of the
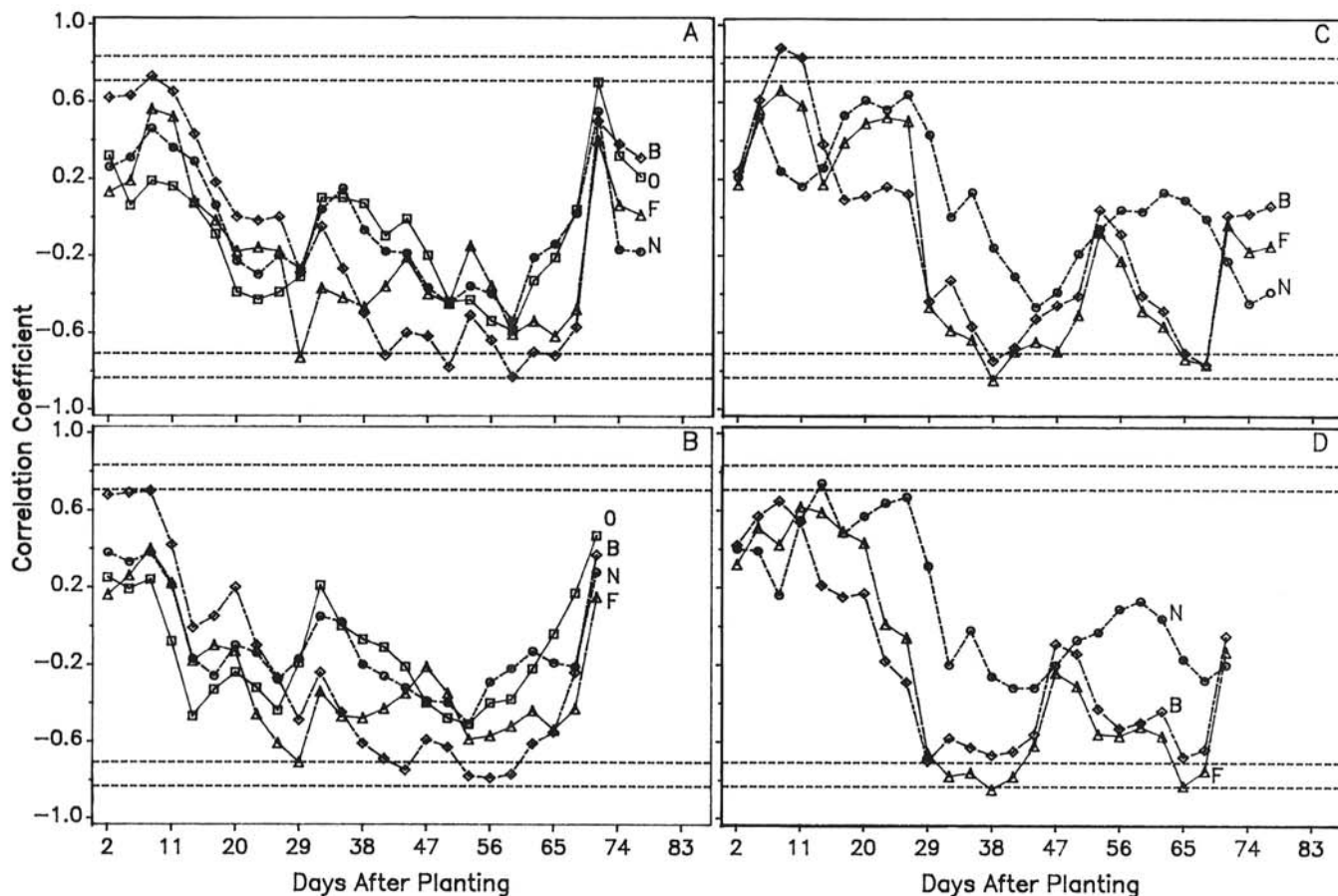

Fig. 4. Residuals of potato tuber yield (A,B) and relative yield (C,D) of four treatments from regression models (eqs. 1 and 2 in text) correlated with precipitation accumulated over 12 (A,C) and 18 (B,D) days at Wooster, OH. Correlation coefficients are plotted at the beginning of the respective time interval. Inner set of horizontal lines represent the 0.05 level of significance and the outer set the 0.01 level. Symbols: 0 (□) = control, N (○) = *Pratylenchus penetrans* alone, F (△) = *Verticillium dahliae* alone, B (◇) = both *P. penetrans* and *V. dahliae.*

measured environmental variable increased. Conversely, a significant positive correlation indicated that yields were greater than predicted.

Residuals of yield for all four treatments were negatively correlated ($P < 0.05$) with degree days starting at 47–56 days after planting (Fig. 3A–D). Negative correlation coefficients were more highly significant with the variable "number of days with a mean temperature >24 C" than with cumulative degree days during this midseason period, indicating a closer linear correspondence for the former. Also, a significant, positive correlation was found for number of days with a mean <19 C. However, correlation coefficients for mean high temperatures over 18-day intervals during this same period were not significant (data not shown). The similarity of the quantitative relationship between cumulative degree days or number of days having a mean temperature >24 C and residuals of yield for all four treatments was examined further by an among-group regression analysis. For both environmental variables accumulated over 18 days, there was no evidence ($P > 0.05$) to reject the hypothesis that there was a single regression line with a common slope and intercept.

The residuals of yield for the treatment with *P. penetrans* and, to a lesser extent, for the other three treatments also were related to hot weather early in the season. Residuals of yield for all treatments were negatively correlated ($P < 0.05$) with number of days >24 C when accumulated over 12–18 days beginning 8–14 days after planting. However, only the correlation of cumulative degree days with residuals of yield for treatment with *P. penetrans* alone was significant during this time over 12- to 24-day intervals (Fig. 3B–D). When correlated with degree days summed over a 6-day period, other treatments showed a significant or nearly significant negative trend (Fig. 3A). Mean high temper-

atures over a 6-day interval also were negatively correlated with residuals of yield for all treatments, beginning around 11 days after planting. Warm weather during a late season period, beginning about 65–68 days after planting, was associated exclusively with negative effects on tuber yield of treatments with *V. dahliae* and *V. dahliae* + *P. penetrans* (Fig. 3A–D).

Cumulative degree days were significantly and negatively correlated with residuals of relative yield of treatments with *V. dahliae* and *V. dahliae* + *P. penetrans* (Fig. 3E–H). The first period began about 17–26 days after planting and another occurred around 65–71 days after planting. Treatment with *P. penetrans* alone was negatively correlated ($P < 0.05$) with degree days accumulated over 6- and 12-day intervals starting at 20 days after planting (Fig. 3E and F). Also, there were no significant correlations between cumulative degree days around 50 days after planting and residuals of yield relative to the control, in contrast to the case of residuals for yield (Fig. 3E–H). The number of days with mean temperatures >24 C accumulated over 12–18 days showed the same negative trend but was not significantly correlated with residuals of relative yield. Mean high temperatures over 18 days also were similar to cumulative degree days but differed in that the treatment with *V. dahliae* + *P. penetrans*, but not *V. dahliae* alone, was significantly correlated with residuals of relative yield during the late season. The number of days with mean temperature <19 C was positively correlated with residuals of relative yield from both of these treatments.

Total precipitation over 12- and 18-day intervals was not significantly correlated with residuals from the control or treatment with *P. penetrans* alone, and was negatively correlated only once, beginning at 29 days after planting, with the treatment with *V. dahliae* alone (Fig. 4A and B). Total precipitation over 12-day
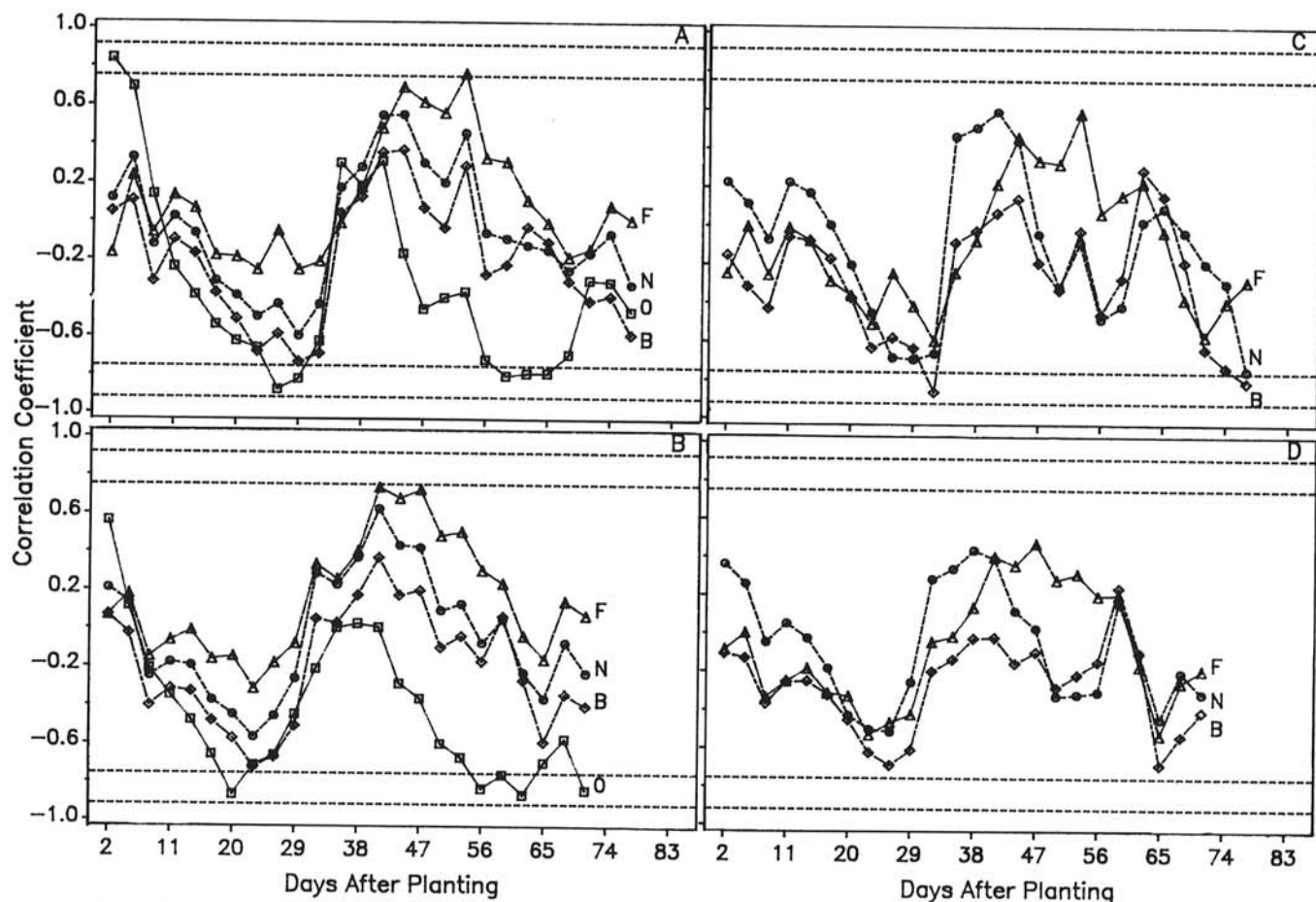

Fig. 5. Residuals of potato tuber yield (A,B) and relative yield (C,D) of four treatments from regression models (see eqs. 3 and 4 in text) correlated with degree days accumulated over 12 (A,C) and 18 (B,D) days at Celeryville, OH. Correlation coefficients are plotted at the beginning of the respective time interval. Inner set of horizontal lines represents the 0.05 level of significance and the outer set the 0.01 level. Symbols: 0 (□) = control, N (○) = *Pratylenchus penetrans* alone, F (△) = *Verticillium dahliae* alone, B (◇) = both *P. penetrans* and *V. dahliae*.

intervals, beginning at 41, 50, and again at 59–65 days after planting, was negatively correlated with residuals of yield for the treatment with *V. dahliae* + *P. penetrans*. Similarly, cumulative precipitation over 18-day intervals was negatively correlated with the treatment with *V. dahliae* + *P. penetrans* at 44 and from 53 to 59 days after planting.

Residuals of relative yield of the treatment with *V. dahliae* were negatively correlated at two different times with precipitation accumulated over 12–18 days (Fig. 4C and D). The first period reached a minimum starting at 38 days after planting, and the second occurred at 65–68 days after planting. Correlation of precipitation with residuals of relative yield for the treatment with *V. dahliae* + *P. penetrans* followed the same pattern as treatment with *V. dahliae* alone but had fewer significantly negatively correlated time periods and was positively correlated with residuals of relative yield 8–19 days after planting ($P < 0.01$). Residuals of relative yield for the treatment with *P. penetrans* were positively correlated ($P < 0.05$) with cumulative precipitation over an 18-day time span beginning at 14 days after planting (Fig. 4D).

The correlation pattern for the ratio of total precipitation to cumulative degree days was similar to that of precipitation alone (results not shown). There were, however, more significant positive correlations during the early season period than was previously noted for precipitation.

Correlation with environmental variables at Celeryville. Because so little variation in yield was left unexplained by the preplant model for Celeryville data (equation 3), correlations between cumulative degree days and residuals of yield from all treatments may, for all practical purposes, be difficult to interpret (Fig. 5A and B). For residuals of relative yield, only the treatment with *V. dahliae* + *P. penetrans* was significantly correlated with

degree days (Fig. 5C and D); however, the general pattern appeared quite similar to that at Wooster (Fig. 3F and G).

Residuals of relative yield from treatments with *P. penetrans* for 18-day intervals and *V. dahliae* + *P. penetrans* for 12- and 18-day intervals were positively correlated with precipitation, beginning about 26–32 days after planting (Fig. 6C and D). At roughly 53–59 days after planting, there began a period in which precipitation was negatively correlated with treatments with *P. penetrans* (12- and 18-day intervals) and *V. dahliae* + *P. penetrans* (12-day interval). Residuals of treatment with *V. dahliae* followed the same pattern but were not significant. The pattern of correlations for the ratio of precipitation to degree days with residuals of yield and relative yield was very similar to that of precipitation alone at Celeryville (results not shown).

DISCUSSION

The regression model of Francl et al (6) for relative yield was revised by considering additional years of data. Equations 2 and 4 can be compared with our previous models:

$$RY = 0.98 - 0.036(\ln[V \times P + 1]) \text{ (Wooster)} \qquad (5)$$

$$RY = 0.91 - 0.039(\ln[V \times P + 1]) \text{ (Celeryville)} \qquad (6)$$

The adjusted r^2 for equation 5 was 12% ($n = 72$), whereas that for equation 6 was 44% ($n = 54$). An increase in the adjusted r^2 from 12 to 28% between the old and new Wooster models (equations 5 and 2) indicated that a marked improvement in explanatory power was achieved by having 2 yr of additional data and by adding the preplant population density of *V. dahliae*
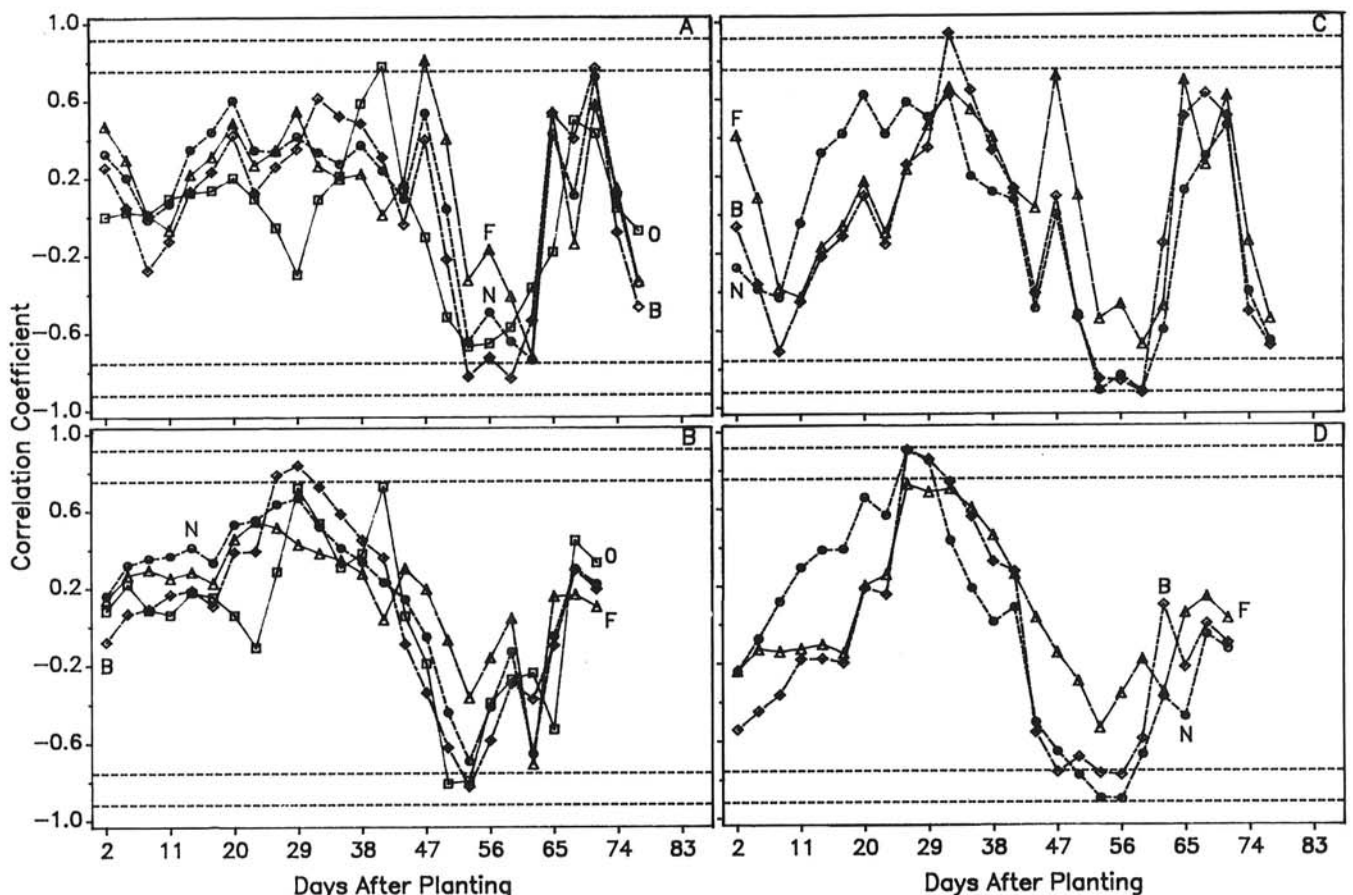

Fig. 6. Residuals of potato tuber yield (A,B) and relative yield (C,D) of four treatments from regression models (see eqs. 3 and 4 in text) correlated with precipitation accumulated over 12 (A,C) and 18 (B,D) days at Celeryville, OH. Correlation coefficients are plotted at the beginning of the respective time interval. Inner set of horizontal lines represent the 0.05 level of significance and the outer set the 0.01 level. Symbols: 0 (□) = control, N (○) = *Pratylenchus penetrans* alone, F (△) = *Verticillium dahliae* alone, B (◇) = both *P. penetrans* and *V. dahliae*.

and the canopy effect as separate terms. Models from Celeryville data were improved similarly. A change in the model was necessitated to account for the interaction of pathogen-related yield loss and crop canopy that became apparent after the experimental protocol was amended in 1985. Competition among plants for light becomes important at canopy closure, which in potato occurs during the period of tuber bulking. Potato cultivar Superior infected with *V. dahliae* + *P. penetrans* began to senesce shortly after canopy closure (7); thus, diseased plants were less able than healthy plants to take advantage of the available light in years when a canopy was absent. It also is conceivable that higher plant tissue temperatures presumably present in the absence of canopy shading would be advantageous to *V. dahliae*, because optimal colony growth takes place at 21–27 C, depending on the isolate (14). The original and revised models presently are being evaluated with data collected in commercial potato fields.

An 8-yr data set from the Wooster location met the length criterion suggested by Coakley et al (2). Although less confidence should be placed in the analysis of data from Celeryville because only 6 yr were available, the general similarity of results with those from Wooster was encouraging. In a search for environmental events important to the impact of potato early dying, discrete time intervals of 12–18 days yielded optimal information, presumably because these interval lengths enveloped critical events that occurred at variable times during the different growing seasons. Slightly shorter intervals and time steps less than 3 days were not expected to add much information to what was found in the analysis presented. Obviously, plants integrate the effects of environment throughout their life cycle. In our opinion, true integration of environmental effects would require a deeper understanding of the mechanism of early dying combined with a more sophisticated potato growth model.

High temperatures during midseason and, possibly, shortly after planting appeared to have a negative impact on tuber yield of cultivar Superior in general, but high temperatures were not necessarily related to the effects of potato early dying because control and inoculated plants were affected in the same manner (Fig. 3A and D). The midseason time span comprised a large portion of the tuber-bulking period of cultivar Superior; therefore, it seems likely that all plants underwent a stress-related yield reduction. Other authors have noted the detrimental effect of high temperature on potato yield (1,5,11). Further evidence of this general stress can be found in correlations of degree days with residuals of relative yield (Fig. 3E–H). When healthy control plants were factored into the relationship (i.e., by dividing the treatment yields by those of the control), the midseason and early season environmental effects were removed. Thus, residuals of relative yield were correlated with temperature at distinctly different periods compared with those for yield. Relative yield correlations generally should be related more directly to pathogen effects caused by fungus and/or nematode.

Residuals of relative yield for treatments with *V. dahliae* and *V. dahliae* + *P. penetrans* from the Wooster regression model were negatively correlated ($P < 0.05$) with cumulative degree days twice during the growing season (Fig. 3F and G). Correlation of residuals from these treatments with degree days at Celeryville showed a nonsignificant negative trend during the same periods (Fig. 5C and D). The first period began at about 11–20 days after planting, well in advance of symptom appearance (7), and may represent temperature effects conducive to infection, disease progression, plant dysfunction, and subsequent yield loss (4). The practical value of this environmental event in prediction of potential yield reduction is lessened by the limited control options currently available for potato early dying. The second time period, beginning about 65 days after planting, probably reflects an exacerbation of senescence rate in diseased plants and supports a conclusion drawn earlier on a portion of these same data (13).

For precipitation, the most pronounced correlations appeared to extend over interval lengths of 12–18 days, similar to temperature variables. Although some periods were identified as being significantly correlated with residuals of relative yield at Wooster, these same periods were not confirmed by the analysis of Celery-

ville data (Figs. 4 and 6). The correlation coefficients at Wooster began the season with positive values, dropped to a minima for intervals beginning at about 38 days after planting, increased somewhat, and finally reached another minima at about 65 days after planting (Fig. 4C and D). The correlation coefficients at Celeryville slowly increased from planting until maxima was reached about 26 days after planting, then slowly declined until minima were reached about 53 days after planting (Fig. 6C and D). There are undoubtedly many possible explanations why this discrepancy occurred, including the aforementioned low power of the statistical test due to having fewer years of data from Celeryville. Unique soil-water and soil-nutrient relationships were present at the two sites, one a peat soil with very high water holding capacity and nitrogen reservoir (Celeryville) and the other a silt loam soil with more moderate values (Wooster).

Correlation analysis implicitly tests for the strength of linear correspondence between two variables. At midseason, for example, linearity was greater for the relationship between the number of days with a mean temperature >24 C and residuals of yield than for cumulative degree days and residuals of yield. The ranks of these two environmental variables were reversed later in the season in the correlation with residuals of relative yield. We think it premature, however, to infer that the number of hot, stressful days in a given period was a more important determinant of yield reduction than the cumulative amount of heat units, or vice versa. Further, nonlinear relationships between environment and yield were not specifically examined in this study.

Although it was possible to derive multiple regression models from these data to predict yield or relative yield based on pathogen density at planting and selected significant environmental variables, this analysis was not done for two reasons. First, presentation of a comprehensive list of regression models would be too lengthy and the alternative of presenting a few examples may misdirect attention away from the inexact temporal nature of the relationships. Second, multicollinearity or intercorrelation of predictor variables is a potential problem when determining the relationship between dependent variables (e.g., residuals of relative yield) and predictors (e.g., degree days) (10). The use of residuals rather than secondarily incorporating preplant pathogen population densities into a multiple regression with environmental variables precludes one potential problem of collinearity between the effects of pathogen and environment. However, due caution in development of multiple regression or other multivariate models still would be advisable. For example, at Wooster, both degree days and precipitation were negatively correlated with residuals of relative yield beginning at 65 days after planting (Figs. 3F and 4C). It is impossible to determine from our data the predictor variable that was the cause of this trend, given these results.

The hypothesis that yield reduction caused by potato early dying is affected by environment during the growing season is supported by our results. In an evaluation of results from the two locations, one should be mindful of similarities in regional climate. The weather at Wooster, particularly temperature but, perhaps to a lesser degree, also precipitation, generally is similar to that at Celeryville. One difference between the two data sets is that the Celeryville experiments were routinely planted about 1 wk before those in Wooster (6,13). Therefore, interval onsets calibrated to day of planting in the analysis were not identical to calendar dates at the two locations, and short-term weather effects would not be held in common. A second difference between the two locations was the organic soil at Celeryville and the mineral soil at Wooster. We previously found that potato early dying proceeded similarly and yield reductions were not significantly different in the two soil types when cultivar Superior was grown in microplots; however, an adjustment had to be made for the greater productivity of the organic soil (7).

It must be emphasized that this epidemiological study was correlative or empirical, and that correlation is not proof of cause and effect. Experimental research is needed to arrive at definitive conclusions about the effects of environment on potato early dying. This detailed correlative analysis should help focus those efforts.

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