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Potato Early Dying: Causal Agents and Managemen

Where potatoes (*Solanum tuberosum* L.) have been in production for a number of years, premature vine death and declining yields are often a problem. This syndrome, called "early maturity wilt" or "potato early dying" (PED), is a factor limiting production in many areas (3,16,18,23,27).

In long-established potato production areas in the United States, especially in the north central states (Ohio, Michigan, and Wisconsin), the Red River Valley (Minnesota and North Dakota), and Idaho, the early dying syndrome has developed slowly over many years. In some cases, growers do not realize that their yield expectations are low and have come to consider early maturity a normal situation on their land.

A factor further complicating grower recognition of this disease in long-established production areas has been the trend in the last 10–20 years toward increased yields owing to changes in production practices, including improved cultivars, increased use of fertilizers and irrigation, and improved pest control. In many cases, the disease may not have caused actual yield reductions but may have limited yield increases that could have been realized from investments made in cultural improvements and pest control.

In contrast to its gradual development in older production areas, this syndrome has come to the forefront very quickly in newly irrigated desert production areas of Washington and Oregon (23,27). After high initial yields on these "virgin" soils, the early dying pattern often has developed quickly with subsequent croppings. Growers with large investments in land and irrigation systems have become quite alarmed and have often recognized the problem more quickly than those who have dealt with it on a chronic basis for many years.

Symptoms of PED are difficult to distinguish from normal senescence and may initially involve only reduced growth. Early foliar symptoms may appear as uneven chlorosis of lower leaves on a few plants. Later, some wilting of leaflets may occur, but more typical is uneven death of lower leaflets. Leaf yellowing and death then proceed up the stems, which often remain erect (Fig. 1). A light brown vascular discoloration is often visible at the stem base when sliced. Vascular discoloration at the stem end of tubers is also typical of PED but may result from other causes. Advanced symptoms usually do not occur until after flowering and may consist of decline of isolated plants or, in severe cases, early maturity of an entire crop (Fig. 2) (3,16,17,27). Confusion may occur in diagnosis of PED because the symptoms are highly variable and also may be associated with other diseases or physiological problems. In addition, early stages of PED may be confused with normal senescence of the lower leaves of healthy plants.

The effect of PED on yield is highly variable. Losses up to 30% (6–12 t/ha) have been documented in Idaho (3), New York (30), and Ohio (28). In an Oregon study (23), two comparable fields under center-pivot irrigation were compared—one new to potato production and one with three previous potato crops. Yield in the latter field, where PED was severe, was approximately 50% that of the former. In spite of these observations, yield decline is not always associated with foliar symptom development (29). This probably results from environmental effects on the amount of vascular infection and from the compounding effects of variable temperature, moisture, and/or nutritional stresses that may occur during crop growth.

Causes of Potato Early Dying

The primary cause of PED is the soil fungus *Verticillium* (16,17,20,24). Two species, *V. albo-atrum* (Reinke & Berthold) and *V. dahliae* (Kleb.), are involved. Prior to the early 1970s, both species were considered forms of *V. albo-atrum*, but they are now generally recognized as separate species (16,17). They differ in that *V. dahliae* forms true microsclerotia as survival structures, whereas *V. albo-atrum* forms melanized

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Fig. 1. Symptoms of potato early dying in cv. Superior infected with *Verticillium dahliae.*

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Fig. 2. Symptoms of severe potato early dying in an Ohio field of cv. Norchip in early August.

hyphae within infected tissues. They also differ in temperature sensitivity. *V. albo-atrum* grows optimally at about 21 C, whereas optimal growth of some *V. dahliae* isolates occurs as high as 27 C. *V. dahliae* is the more widespread species and predominates in the north central states and the Pacific Northwest where average summer temperatures frequently exceed 25 C. *V. albo-atrum*, alone or with *V. dahliae*, is involved in PED in cooler production areas such as Maine, the Red River Valley, and the winter production areas of Florida where average temperatures do not normally exceed 21–24 C during the growing season.

Contamination of noninfested fields with *Verticillium* can occur by wind or mechanical movement of soil particles containing viable propagules, but a primary means is introduction on the surface or within tissues of infected seed tubers (3,16,17). Additionally, *Verticillium* may occur naturally in some areas in association with roots of native vegetation (17). In these cases, serious outbreaks of PED may result from intensive cultivation of potatoes or other highly susceptible host crops, leading to large increases in *Verticillium* population levels from propagules already present in the soil. Once established in a field, *Verticillium* can survive in soil for many years in a dormant state as microsclerotia or melanized hyphae, either free or embedded in organic debris (17). Because of its wide host range, the fungus can also maintain itself at low levels on roots of many symptomless crop and weed species (17).

Although *Verticillium* is the primary pathogen in potato early dying, other organisms also have been associated with this syndrome. Interestingly, the importance of associated pathogens may differ in various potato production areas. Nematodes have been commonly implicated (3,11). Studies in Ohio (29), Wisconsin (14), and Israel (15) have confirmed the involvement of root-lesion nematodes (*Pratylenchus* spp.) in PED. In Oregon (13) and Wisconsin (25), a connection with soft rot bacteria (*Erwinia carotovora*) has been established. Other fungi have also been considered as components, primarily *Fusarium* spp. and *Colletotrichum atramentarium* (21,32). Recent studies in Wisconsin (14) and Idaho (4), however, have discounted the latter as playing a significant role in PED.

The Role of Nematodes

The involvement of nematodes in PED has long been suspected as a result of field experiments demonstrating some control of the disease with fumigant and nonfumigant nematicides (28,30). Studies with other crops that have implicated nematodes, particularly root-lesion nematodes, in predisposing plants to vascular wilt fungi have also suggested that infection by *Verticillium* spp. is not the sole cause of this disease.

Root-lesion nematodes are commonly found in most soils regularly cropped to potato in the eastern United States and Canada. *Pratylenchus penetrans* (Cobb) Filipjev & Schuur.-Stekh. is the most prevalent species, but *P. crenatus* Loof and *P. scribneri* Steiner are also commonly found. Others, including *P.*

neglectus (Rensch) Filipjev & Schuur.-Stekh., *P. alleni* Ferris, and *P. vulnus* Allen & Jensen, are less common (1,8,12).

Since 1980, detailed microplot studies on PED have been conducted in Ohio. These studies have used fumigated soil and the *Verticillium*-susceptible cultivar Superior to critically evaluate the interaction of *V. dahliae* and *P. penetrans* and their effects on potato yield under field conditions, while maintaining control over many variables (18,29). These studies, and similar Wisconsin tests with cv. Russet Burbank (14), have conclusively demonstrated the ability of these two microorganisms to interact and produce PED symptoms under field conditions. In 1985 and 1986, the interaction was also demonstrated with cv. Superior in three major Ohio soils as well as in parallel studies in nonfumigated silt loam (R. C. Rowe, *unpublished*). Data from these microplot studies over a 7-year period have followed consistent trends in which little or no effect has been observed with *P. penetrans* alone, a slight to moderate effect with *V. dahliae* alone, and a synergistic response in the presence of both pathogens (Table 1A). In some years, symptom severity has been associated with up to 50% reduction in tuber yields (Table 1B), similar to responses shown in field fumigation studies (28,30). In other years, yield response has been much less, indicating that the effects of PED on yield are influenced by environmental variables as well as by initial pathogen population levels. Work is under way now to better define these effects.

Parallel microplot studies in Ohio with other species of *Pratylenchus* have also shown that not all species are equal in ability to interact with *Verticillium* in potato (26). Although *P. penetrans*, at field populations commonly occurring in Ohio, has consistently interacted with *V. dahliae* to produce PED symptoms and tuber yield decreases, no interaction with *P. crenatus* has been observed in the same studies (Table 1C,D). Surveys in 1985 and 1986 of commercial potato fields on Long Island in New York showed a similar relationship. Although mixed populations of these two nematode species occurred in all fields studied, *P. penetrans* predominated in portions of

Table 1. Effects of combined population levels of *Verticillium dahliae* and two *Pratylenchus* species on symptom expression and tuber yield of potato cv. Superior grown in fumigated soil in Ohio field microplots in Rifle peat soils in 1983[a]

	Symptom expression[b,c]					Tuber yield[b,d]				
		V. dahliae[e]					*V. dahliae*			
	A	0	1	2	P[f]	**B**	0	1	2	P
P. penetrans[g]	0	0.7	1.2	1.0	0.65	0	413	345	350	0.67
	1	0.9	1.5	2.2	0.00	1	365	275	238	0.03
	2	1.0	2.3	2.5	0.00	2	453	240	269	0.01
	3	1.1	2.9	2.8	0.00	3	334	164	252	0.14
	P[f]	0.25	0.00	0.00		P	0.52	0.00	0.10	
	C	0	1	2	P	**D**	0	1	2	P
P. crenatus[g]	0	1.3	0.9	0.8	0.15	0	326	467	385	0.31
	1	0.7	0.9	1.0	0.50	1	426	382	438	0.88
	2	0.7	0.9	0.9	0.72	2	330	447	476	0.04
	3	1.1	1.1	1.4	0.55	3	297	478	393	0.15
	P	0.64	0.74	0.18		P	0.60	0.60	0.77	

[a] Adapted from Riedel et al (26).
[b] Each matrix reports results of increasing *V. dahliae* populations from left to right and increasing *Pratylenchus* populations from top to bottom.
[c] Each value represents the average of 15 microplot plants evaluated visually 90 days after planting on a scale of 0 = no visible symptoms; 1 = some chlorosis, especially in older leaves; 2 = general chlorosis coupled with some necrosis and wilting; 3 = extensive necrosis and wilting or death.
[d] Each value represents the average yield in grams per plant of 15 microplot plants harvested 90 days after planting.
[e] Population levels of *V. dahliae* added to soil at planting: 0 = none, 1 = about 1 cfu/g of soil, 2 = about 10 cfu/g of soil.
[f] P denotes linear trend significance level, based on contrasts of the data means, for the change in a variable with increasing population levels of one pathogen at a constant population level of the other.
[g] Population levels of *Pratylenchus* species added to soil at planting: 0 = none, 1 = about 20 vermiforms/100 cm^3 of soil, 2 = about 50 vermiforms/100 cm^3 of soil, 3 = about 150 vermiforms/100 cm^3 of soil.

fields where PED was severe and *P. crenatus* predominated in areas where PED was less severe or absent (R. Loria, *unpublished*). Potato is a good host for both *Pratylenchus* species, and each is commonly found within potato roots as a migratory endoparasite. Species-specific reactions in PED suggest, then, that the interaction of root-lesion nematodes with *V. dahliae* involves mechanisms more complex than root wounding. Alterations in host physiology may occur that affect response to infection and/or colonization by *Verticillium*.

The Blackleg Connection

The involvement of *E. carotovora* in PED has received much attention recently. *E. carotovora* causes potato blackleg, as well as an aerial soft rot in which portions of stems distant from the base of the plant decay, often with no associated blackening of the lower stem. Premature vine death may follow both blackleg and aerial soft rot, but this usually is readily distinguished from vine death due to PED by the completely hollowed pith of the dead vines (22).

In some areas, *E. carotovora* has also been associated with systemic vascular infections that result in symptoms very much like those of PED (Fig. 3). In an Oregon field study, *V. dahliae, E. c.* subsp. *atroseptica* (Van Hall) Dye, and *E. c.* subsp. *carotovora* (Jones) Dye each were associated with PED-like symptoms, but their relative involvement varied from field to field (13). *V. dahliae* was most strongly associated with symptoms in fields that had been cropped to potatoes for several years. Conversely, the soft rot erwinias were most strongly associated with symptom expression in fields previously cropped to potatoes for 1 year or less. The ability of soft rot erwinias to cause symptoms similar to those of PED was confirmed in greenhouse studies. Inoculation of cv. Russet Burbank by root dipping with *E. c.* subspp. *carotovora* and *atroseptica* and *V. dahliae* showed that all three organisms could induce typical PED symptoms (13). Symptoms produced by *V. dahliae*, however, were more severe than those caused by the bacterial pathogens.

A synergistic relationship between *V. dahliae* and *E. c.* subsp. *carotovora* was demonstrated in potato cvs. Norgold Russet and Russet Burbank in Wisconsin (25). Plants inoculated with both *V. dahliae* and *E. carotovora* showed less growth and more foliar chlorosis and wilting than plants inoculated with *V. dahliae* alone. Furthermore, blackleg, a primary symptom of infection by *E. c.* subsp. *carotovora*, developed in more stems of plants inoculated with both pathogens than in stems of plants inoculated with only the bacterium.

Kirkland (13) examined interactions of *E. c.* subsp. *carotovora* or *atroseptica* with *V. dahliae* by monitoring the severity of PED symptoms in root-dip coinoculation tests with cv. Russet Burbank. Symptom expression was more severe in plants coinoculated with *V. dahliae* and either soft rot erwinia than in plants inoculated with any pathogen alone. In contrast to the synergistic interactions observed by Rahimian and Mitchell (25), the effect of concurrent infection with *V. dahliae* and the soft rot erwinias was additive rather than synergistic, and increases in symptom severity were paralleled by increases in colonization of the basal stem region by *V. dahliae*. A similar relationship was observed in the field where *E. c.* subspp. *carotovora* and *atroseptica* each appeared to enhance vascular colonization by *V. dahliae*.

These studies suggest that soft rot erwinias may directly cause PED-like symptoms in some situations or may play an important role in disease epidemics by enhancing *V. dahliae* colonization and, thereby, intensifying symptom expression. Further research in this area is needed to completely define the role of soft rot erwinias in PED (22).

Control Strategies

Selection of control strategies for PED must be based on an understanding of the biology of the pathogens and the effects of various agricultural practices. *Verticillium* is a monocyclic pathogen, i.e., inoculum is present in the soil at planting and additional inoculum produced in roots and stems during disease development becomes available only for infection of subsequent crops. The amount of infection that occurs in a given crop is a function of the population level of propagules of the fungus in the soil, environmental conditions, and predisposing factors such as host cultivar and the presence of other associated pathogens, e.g., *Pratylenchus* spp. After infection, *Verticillium* progressively colonizes the host xylem elements, leading to decline of the crop. The rate of colonization and the host's response to it are also critical in the economic outcome of the disease, i.e., reduced yield. This phase of the disease progresses over a 60- to 120-day period and also depends on environmental and other predisposing factors.

Control of PED may be achieved by reducing either the amount of root infection or the rate of vascular colonization by *V. dahliae*, or both. The most direct way to reduce root infection is to reduce the amount of soilborne inoculum. Burning of potato vines has been of some value in delaying the buildup of inoculum on "new" potato ground and in fields that recently have been fumigated (9). After several successive potato crops, however, the level of soilborne inoculum generally is sufficient to cause PED.

Crop rotation has long been considered an important part of disease management schemes for PED. Unfortunately, *Verticillium* inoculum is relatively persistent in soil. In Idaho, the minimum time to effectively reduce inoculum with grain rotations in moderately infested land is 5–10 years (3,5). A 4-year study of alternate grain and potato cropping in Ohio showed that populations of *V. dahliae* in soil generally increased in years following potatoes but returned to lower levels following subsequent grain crops (T. Joaquim, *unpublished*). Although short 2- to 3-year rotation practices alone do not result in effective control of PED, they are useful in the total management scheme.

Soil fumigation may be used to reduce high levels of soilborne inoculum. A variety of fumigants with fungicidal activity have been widely used to control PED, but cost is usually a limiting factor (9,24). In recent years, application of metam-sodium through center-pivot sprinkler irrigation systems has become common practice in light-textured soils of the Midwest and Pacific Northwest (Fig. 4). This has been effective if the primary pathogen is *Verticillium* but not if *Erwinia* is extensively involved. It is not effective on heavier textured soils because of poor penetration. Use of soil fumigants can increase yields substantially in heavily infested soils, and effects on disease severity and yield sometimes persist into subsequent potato cropping seasons (9).

Controlling soilborne populations of other pathogens associated with PED may also be useful in a disease management strategy. Some fumigant and nonfumigant nematicides have suppressed PED to a limited degree in some locations (28,30). This probably results from a reduction in the population of *Pratylenchus* spp. and thus a reduction in PED severity, despite the presence of *Verticillium*.

Management practices that modify the rate of stem colonization by *V. dahliae* or increase the host's tolerance to colonization also may be useful control measures for PED. In Idaho, irrigation and plant nutrition have been found to correlate significantly with the severity of PED and with colonization of potato stem tissues by *V. dahliae* (4). In these studies, disease was more severe with gravity-flow furrow irrigation than with sprinkler irrigation. Although it is not clear how the method of irrigation affects PED, a relationship with nitrogen availability has been suggested (3,4). With furrow irrigation, nitrogen often accumulates within the upper 7.5–15.0 cm of the soil profile. In contrast, nitrogen may be more uniformly distributed throughout the soil with sprinkler irrigation. When nitrogen is less available to the plant's root system because of leaching or poor distribution, disease incidence and

Fig. 3. Potato early dying symptoms in cv. Norgold Russet infected with *Erwinia carotovora* subsp. *carotovora*.

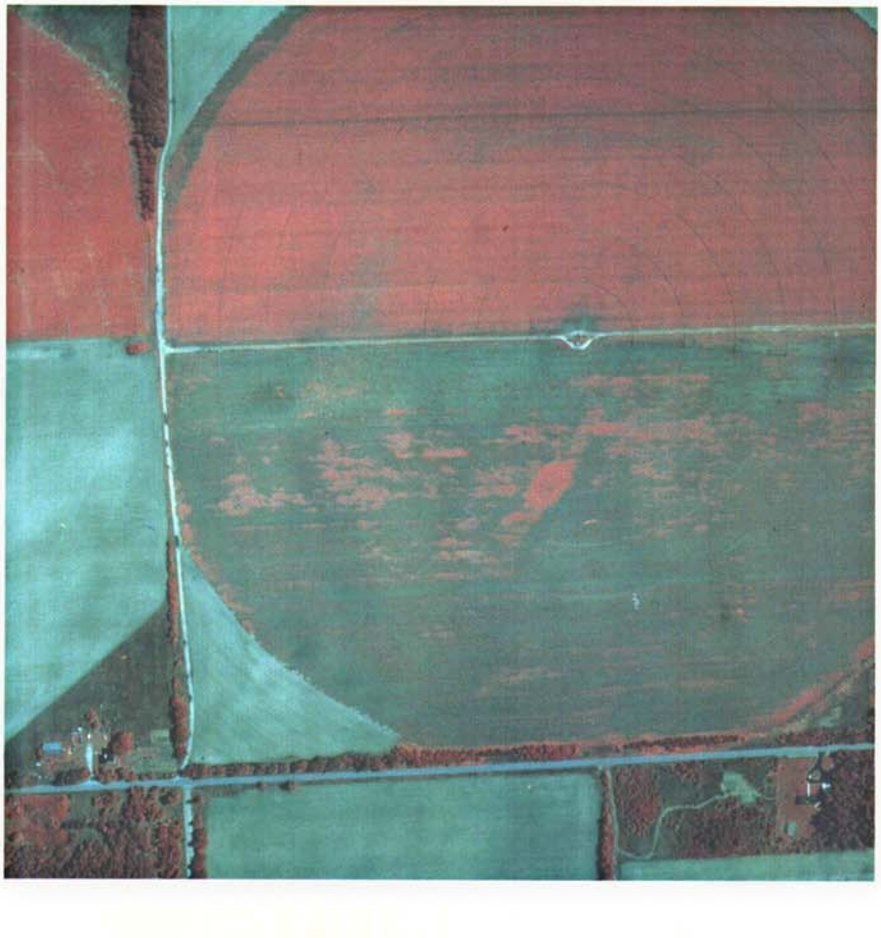

Fig. 4. Aerial infrared photograph of a 60-ha potato field with a history of severe potato early dying (red indicates healthy vegetation). Metam-sodium (470 L/ha) had been applied through a center-pivot irrigation system the previous fall to the upper half of the field.

severity may increase. Among all cultural factors considered, nitrogen availability has been most commonly associated with PED. In southeastern Idaho, field surveys have shown close correlations of *V. dahliae* colonization of potato stems with the electrical conductivity of soil and NO_3-N, potassium, and phosphorus levels in petioles collected before mid-July. These cultural variables have been observed to account for 71% of field variability related to *V. dahliae* colonization in stems of cv. Russet Burbank (4).

Cultural management may also be useful when combined with soil fumigation. Figure 5A shows the effect of various preplant nitrogen application rates on disease expression in cv. Russet Burbank in parallel fumigated and nonfumigated plots in Idaho. Disease suppression caused by both factors appears additive. In contrast, nitrogen availability had no consistent effect on disease expression in cv. Norgold Russet (Fig. 5B), and suppression of PED symptoms resulted only from fumigation.

The use of disease-resistant cultivars ultimately may be the most practical method of PED control. Potato clones with high levels of resistance have been developed in the USDA breeding program at Aberdeen, Idaho. Extensive testing of these clones indicates that true resistance to colonization of stem tissues by *V. dahliae* has been combined with desirable vine and tuber characteristics similar to those of cv. Russet Burbank. Two clones that possess a high degree of resistance are A66107-51 (Fig. 6) and A68113-4. Their maturity class is similar to that of cv. Russet Burbank, and both show high yield potential in the presence of *V. dahliae* (6).

Although PED can be managed by using resistant genotypes, market acceptance of available clones has not been widespread. Additionally, early maturing potato genotypes with high quality are commonly very susceptible to *V. dahliae*. Until acceptable resistant cultivars become available, control of PED must rely on integrated disease management systems involving crop rotation, site and cultivar selection, irrigation and nutritional management, and, in some cases, soil fumigation.

Implementation of Integrated Disease Management Systems

Because useful control strategies for PED are preventive rather than curative, growers must be able to assess potential crop liability before planting to make valid management decisions. Integrated disease management systems can then be implemented to take full advantage of available controls. Estimates of crop liability to damage by PED have historically been based on experience in a given field. Although disease history records can provide a guide to potential PED severity, many growers are not sure from past records alone which organisms were involved. Because control practices recommended for PED are aimed at specific soilborne pathogens, the previous cause of PED must be known for each problem field. Another factor affecting the reliability of crop history data is that environmental conditions during the growing season can have a major influence on PED severity. Thus, a field may have a high PED potential that may not be evident from disease history records because full disease potential was inconsistently expressed in previous years.

Aerial infrared photography may be useful in identifying and assessing PED in commercial potato fields. Because remote sensing technology, as it currently exists, does not distinguish among various plant stresses, ground-based assessment must be conducted to verify that what was observed in the photograph was really PED. In Wisconsin and the Pacific Northwest, many growers contract with private companies to have aerial infrared photographs taken of their fields every 7–14 days throughout the season. These photographs can provide clues as to patterns of disease development in the field. They also can be used to monitor effects of soil fumigation treatments applied before planting (Fig. 4).

Assessment of disease liability by sampling soils for *Verticillium* populations before planting has also been widely tested (2,31). Determination of threshold levels for economic loss is the first step. Estimates of 10 cfu/g of air-dried soil have been postulated for Idaho (7),

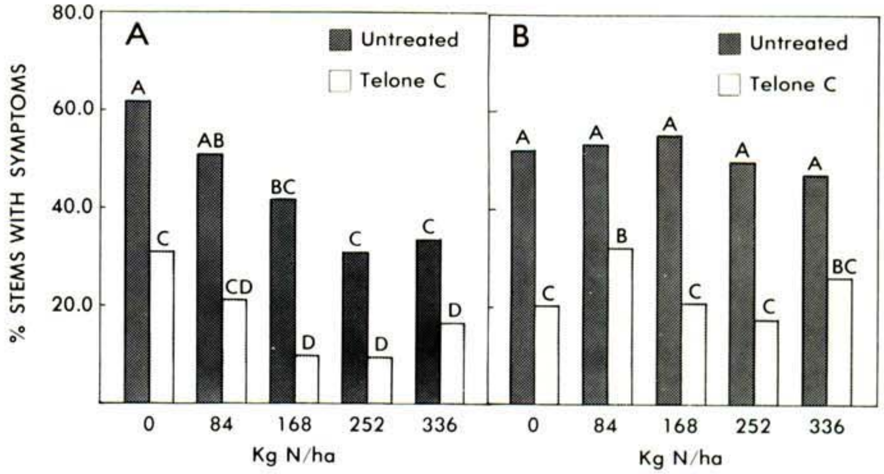

Fig. 5. Differential suppression of potato early dying with Telone C soil fumigation (74% 1,3-dichloropropene plus 17% chloropicrin applied at 296 L/ha) and nitrogen (side-dressed as NH_4NO_3) treatments in potato cultivars (A) Russet Burbank and (B) Norgold Russet. Different letters over bars denote significant differences at $P = 0.05$. (Adapted from Davis and Everson [4])

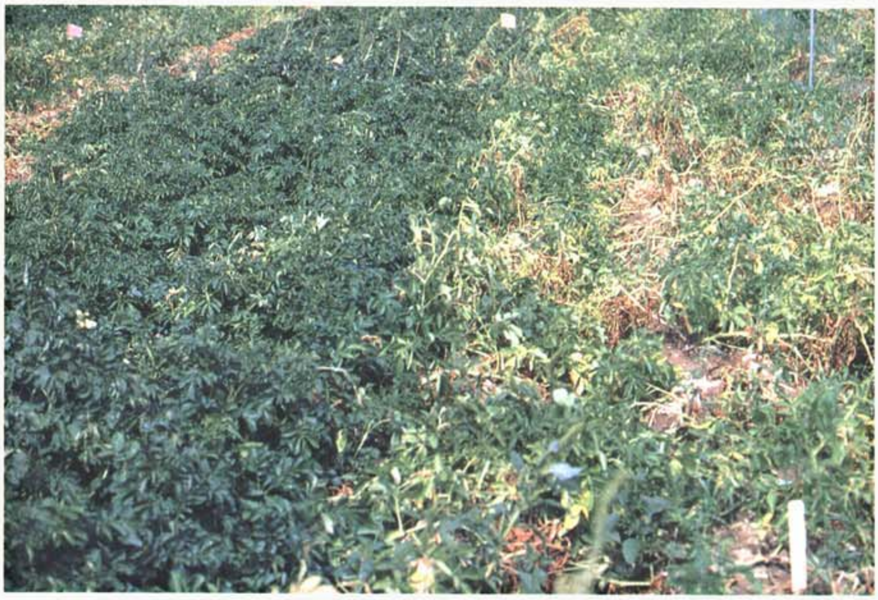

Fig. 6. Comparison of *Verticillium*-resistant potato clone A66107-51 (left) with susceptible cultivar Russet Burbank (right). (Courtesy D. L. Corsini)

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whereas in Colorado the threshold was placed at 18–23 cfu/g (20). In Wisconsin, Nicot and Rouse (19) related incidence of stem infection to soil inoculum density at planting and found 6–10 cfu/g of air-dried soil were necessary to cause 80% stem infection by 100 days after planting (Fig. 7). Subsequent studies showed that measurable yield loss did not occur below this threshold when *V. dahliae* was the only pathogen present. Using Ohio experimental microplot data, Francl et al (10) constructed regression and discriminant models relating preplant soil population levels of both *V. dahliae* and *P. penetrans* to subsequent tuber yield. From these, the minimum population of *V. dahliae* propagules necessary to cause at least a 10% yield reduction in the absence of *P. penetrans* was 11–18 cfu/cm^3 of soil (10).

Although these estimates of economic threshold levels for *V. dahliae* are relatively consistent, attempts to directly relate inoculum density of *V. dahliae* in soil to subsequent PED or yield loss have often met with mixed results. This may be due to variation in sampling techniques, regional climatic or cultural variables, or interacting effects of other pathogens associated with PED. Nevertheless, gaining additional knowledge in this area offers the most promise in implementation of improved management systems. In Ohio, data from field microplot studies showing quantitative relationships between preplant populations of *Verticillium* and root-lesion nematodes and subsequent yield are being used to construct decision models for growers based on the natural logarithms of the preplant populations of *V. dahliae* and *V. dahliae* × *P. penetrans* (10). Yields from 6 years in two locations were correctly classified by discriminant analysis as being above or below a yield loss value of 10% in 71% of the cases. More precise multiple regression models are being developed to forecast yield as a function of cultivar, soil type, and environment, in addition to pathogen populations.

In Wisconsin, a systems approach to achieving additional knowledge useful for interpreting the soil inoculum/disease and yield loss relationships has been initiated using a potato plant growth model. A *Verticillium* submodel, which includes independent functions for both infection and colonization, has been coupled to the growth model. Environmental variables can be incorporated to influence each of these components of the disease cycle separately. Additionally, other pathogens or pests can be coupled to the plant growth model, thus modifying growth and yield in the presence of *Verticillium*. Environmental effects on the plant itself are accounted for by the plant growth model. Additional experimental data are being developed to allow proper empirical relationships to be inserted into this model.

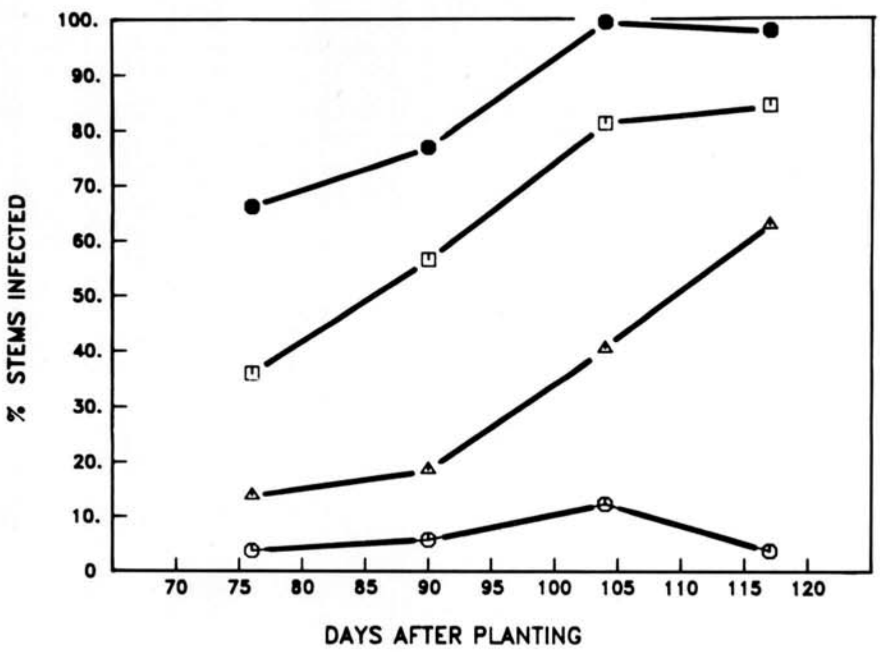

Fig. 7. Relationship between percent Russet Burbank stems naturally infected with *Verticillium dahliae* and days after planting in soil with initial *V. dahliae* populations nondetectable (○) or 1–5 (△), 6–10 (□), or >10 (•) cfu/g of dry soil. (Adapted from Nicot and Rouse [19])

As practical disease forecasting systems for PED are further refined and implemented, growers will be better able to utilize the integrated control systems necessary to manage this disease. Accurate assessment of potential crop liability before planting should diminish present losses caused by potato early dying.

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