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Potato Early Dying: Management Challenges in a Changing Production Environment

The potato (*Solanum tuberosum* L.) had its start in the Andean highlands of South America, where archeological evidence indicates it has been cultivated for at least 8,000 years (72). Today it is grown on all continents except Antarctica. Serving as a primary food source to indigenous people when the Spanish explorers arrived in Peru in the mid-1500s, the potato traveled the globe as a valuable staple, fueling armies, improving diets, and changing economies (Fig. 1). The importance of the potato goes beyond the feeding of nations, however. Today potato starch is used in the production of paper, adhesive, and textile goods, and in edible binding agents and low-fat food additives. The potato yields up a highly absorbent biodegradable material for use in disposable diapers. It provides starch products to keep oil well drilling bits smooth and to hold together the ingredients in lipsticks and cosmetic creams, and it provides a substance that works as a flocculation agent in water purification systems, replacing petroleum-based chemicals (33).

China is the world's largest producer of potatoes, followed by the Russian Federation (33). It is the most important vegetable crop in North America, where in 2000, nearly 690,000 ha were grown, with an average yield of 32.6 metric tons/ha and a farm gate value of over $2.7 billion.

The potato is subject to several diseases caused by root-infecting pathogens. Two of particular significance are the soilborne fungi *Verticillium dahliae* and *V. albo-atrum*. The potato root is also a host to the root-lesion nematode *Pratylenchus penetrans.* The two fungal pathogens alone, or in conjunction with *P. penetrans*, cause a disease called potato early dying (PED), also known as early die, early maturity wilt, and Verticillium wilt (64). This disease is endemic in many potato production areas of the United States, particularly in the Midwest and Pacific Northwest. In fields with a long history of potato production, it is a consistent yield constraint that requires intensive management. On land new to potato production, it may be absent in the first few years the crop is grown, but it almost invariably develops over time, requiring implementation of control measures to maintain high yields.

In the last decade, the North American potato industry has undergone considerable changes. Production is increasingly being

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Publication no. D-2002-0829-01F

Fig. 1. Early engraving of *Papas peruanorum* from 1613. From Hughes (33) courtesy of The Granger Collection, New York.

shifted into areas of irrigated sandy soils, mostly in the Pacific Northwest and north-central states. Land area under management by individual producers is increasing, and profit margins are decreasing. Production is shifting away from primary dependence on the cultivar Russet Burbank toward a broader cultivar base. Environmental concerns regarding pesticide applications have continually increased, particularly with regard to groundwater contamination and off-target drift. This is especially significant as it relates to the continued use of soil fumigants. This shifting production environment has not yet substantially impacted the management of PED, but as these changes continue to pervade the potato industry, mounting economic and environmental pressures will likely require changes in management strategies for this disease.

Symptoms. The PED syndrome is characterized by a general decline of plants 4 to 6 weeks earlier than normal maturity. Although specific, diagnostic symptoms are not associated with the disease, foliage shows various degrees of chlorosis and necrosis (Fig. 2), sometimes associated with wilting or dying of individual leaflets or stems. In the early stages, individual vines may die and remain conspicuously erect in contrast to healthy plants (Fig. 3). A light brown vascular discoloration in basal stem tissues is usually present in symptomatic plants. This symptom, however, is not diagnostic since vascular discoloration can result from stress factors unrelated to PED. As the disease develops within a field, widely scattered individual plants or groups of plants often show early symptoms, resulting in a nonuniform decline of the stand (Fig. 4). In severe cases, plants across an entire field will die over a several-week period.

Fig. 2. Foliar symptoms of potato early dying showing various degrees of chlorosis and necrosis.

Economic importance. When disease develops throughout a field midway through the growing season and then becomes severe during the period of maximum tuber bulking, a significant reduction in tuber size and total marketable yield can result. In North America, yield reduction in moderately diseased fields can easily be 10 to 15%, and in severely diseased fields it can be as high as 30 to 50% (64). The economic impact of PED across the potato industry is significant because of the direct losses resulting from low yields and because expensive, preplant soil fumigation has become a routine disease management practice, particularly in irrigated production areas (70).

Understanding the PED Syndrome

***Verticillium dahliae*: the primary causal agent.** PED is caused primarily by the soilborne fungus *Verticillium dahliae.* The fungus is favored by moderate-to-high soil temperatures, but is inhibited at temperatures above 30°C, so it is generally restricted to temperate climates (49). While PED is caused primarily by *V. dahliae* in most areas of the United States, *V. albo-atrum* may be the dominant pathogen in cooler production areas of the most northern U.S. states and southern Canada, where average soil temperatures during the growing season rarely exceed 25°C (63,64,70). Verticillium wilt is a monocyclic disease, i.e., it has only one cycle of disease and inoculum production per season (Fig. 5). *V. dahliae* survives from season to season as microsclerotia (Fig. 6) in the soil, either free or embedded in plant debris, or as mycelium in the vascular ring of the tuber. Microsclerotia are stimulated to germinate in response to root exudates (49,54). The

Fig. 3. Erect stems characteristic of potato early dying.

Fig. 4. Field symptoms of potato early dying. Note nonuniform decline of the stand.

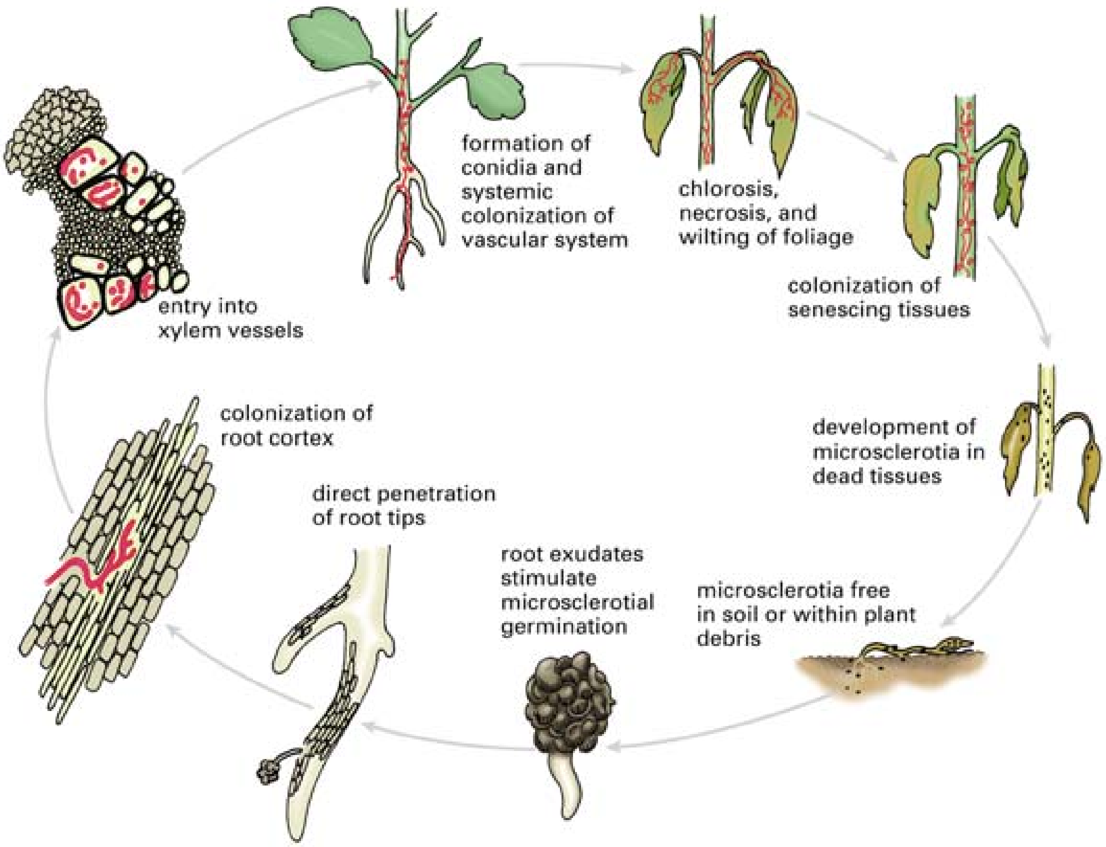

Fig. 5. Verticillium wilt is a monocyclic disease with only one cycle of disease and inoculum production per season. From Berlanger and Powelson (6). Drawing courtesy Vickie Brewster and Jesse Ewing.

Fig. 6. Microsclerotia of *Verticillium dahliae*.

effective rhizosphere influence of roots on microsclerotia averages about 100 µm (34). The likelihood of plant infection is directly related to the population of microsclerotia in soil (13,55,59,60). Hyphae originating from germinating microsclerotia infect at or just behind root tips (Fig. 7), from the zone of elongation to a few millimeters beyond (10,30,62). After penetration, hyphae grow through cortical tissues toward developing vascular tissue and along the endodermis surrounding the stele (10). Gerik and Huisman (30) detected numerous, superficial cortical infections in cotton 1 cm and more beyond the root tip, well behind the region of undifferentiated tissue. They estimated that in cotton there are several thousand cortical invasions by *V. dahliae* for every successful vascular infection. The same may be true for potato. For systemic disease to occur, the xylem vessels must be invaded. Once penetrated, hyphae grow and sporulate. Conidia are dispersed within xylem elements and move through cell walls readily via pit apertures (62). Rapid, systemic infection of the plant soon follows, and foliar symptoms of wilting, chlorosis, and necrosis become apparent. As the foliage begins to senesce, the fungus leaves the xylem elements and colonizes the surrounding nonvascular tissues. Microsclerotia are soon formed in the dying leaves and stems (Fig. 8) (49,54,56). Following incorporation of dead tissues into soil during subsequent cultivations, the microsclerotia are slowly released as the tissues decay. On average, the largest contribution to the soil inoculum density is reached during the second growing season after incorporation of crop refuse (40,57). In the soil, microsclerotia can remain viable for more than a decade (49). They survive well over a range of soil moisture and temperature conditions, but lose viability most rapidly in wet, warm soil, where they are colonized and degraded by various bacteria and fungi (79).

Role of root-lesion nematodes. Root-lesion nematodes (*Pratylenchus* spp.) are migratory endoparasites that can enter root tissues and feed upon them (Fig. 9) and also can move freely through soil from root to root. Four species are commonly associated with potato roots in North America: *P. crenatus, P. neglectus, P. penetrans,* and *P. scribneri* (50). All have a wide host range that includes many crop and weed species. Some hosts facilitate large increases in nematode populations, whereas others support only limited populations due to poor reproduction. If soil populations of root-lesion nematodes are quite high, growth and development of potato may be affected, particularly with *P. penetrans*. However, the primary importance of these nematodes in potato production is their synergistic interaction with *V. dahliae*. Coinfection of potatoes with both *V. dahliae* and *P. penetrans* can result in earlier onset of disease symptoms and thus lower yields. This occurs at populations of both pathogens that would have much less effect if acting individually (9,10,51,70,84). This pattern holds true regardless of the geographic origin of *P. penetrans* from production areas in the north-central or Pacific Northwest United States (R. C. Rowe and A. E. MacGuidwin, *unpublished*). Nematode populations as low as one vermiform per cm^3 of soil can trigger the interaction, but higher populations have no additional effect (71). Among the other three species, *P. crenatus* does not interact with *V. dahliae,* and *P. scribneri* and *P. neglectus* seem to be only mildly interactive; however, the latter two have not been studied extensively (31,83,84).

The mechanism of the synergism with root-lesion nematodes is unknown, but it is

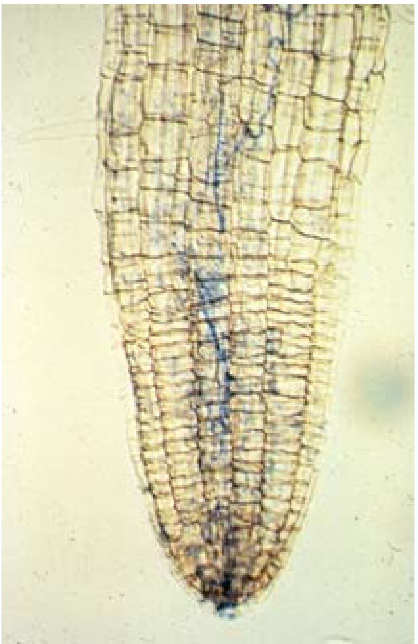

Fig. 7. Hyphae of *Verticillium dahliae* (stained blue) originating from germinating microsclerotia and infecting at or just behind potato root tip. From Bowers et al. (10).

Fig. 8. Microsclerotia of *Verticillium dahliae* formed on the surface of dying potato stems.

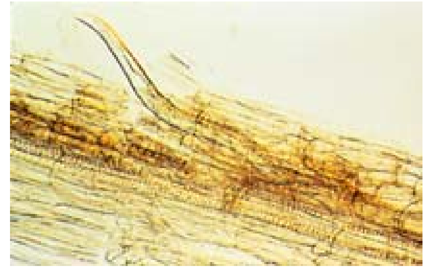

Fig. 9. Root-lesion nematode (*Pratylenchus penetrans*) feeding within a potato root resulting in a characteristic necrotic lesion. From Bowers et al. (10).

not due to nematode feeding sites providing entry for *Verticillium.* Based on controlled infection studies, nematode feeding sites on potato roots were not spatially related to entry sites of *V. dahliae* on the same roots (10). Compared to treatments without nematodes, higher rates of root tip infection occurred in the presence of several species of *Pratylenchus*. Feeding by root-lesion nematodes may increase root exudation and hence the size of the rhizosphere zone, which may then stimulate germination of additional microsclerotia. Alternatively, nematode activity may stimulate root branching, leading to increased contact with microsclerotia. Plants co-infected with *V. dahliae* and *P. penetrans* had increased vascular colonization of both roots and stems by *V. dahliae* compared with plants infected by *V. dahliae* alone (10), suggesting that the nematode affects host physiology in some way that promotes vascular colonization.

Host-adapted pathotypes of *V. dahliae*. In contrast to other vascular wilt fungi, particularly *Fusarium oxysporum*, *V. dahliae* had been regarded as being more genetically homogeneous (32,37). This perception arose because *Verticillium* species have a wide host range with little host specificity, host resistance to *Verticillium* has not been widely available in crop plants, and few physiologic races of *Verticillium* have been identified. In recent years, this perception of genetic homogeneity in *V. dahliae* has changed. Genetically diverse groups have been shown to exist within the species by using vegetative compatibility analysis (65). Vegetative compatibility is the ability of hyphae from two isolates of the same species to anastomose and form a stable heterokaryon. This trait is genetically controlled. Populations of compatible isolates are referred to as vegetative compatibility groups (VCGs) (41,46) and are identified using specific mutant tester isolates (38,39,41). In *Verticillium*, hyphal anastomosis followed by formation of a heterokaryon is the only known means of genetic exchange among individuals. Thus, vegetatively incompatible isolates are thought to be genetically separated from each other. Isolates in different VCGs may vary in many characteristics, including those related to pathogenicity and aggressiveness.

In the last decade, subspecific groups within *Verticillium* spp. have been identified using vegetative compatibility analysis (41,69). Isolates of *V. dahliae* recovered from infected host plants and from soil belong to three to five distinct VCGs (3,7,18,38,39,41,75,81). Nearly all isolates infecting potato belong to VCG 4 (39,41,61,75). These are subdivided into two distinct subgroups, VCG 4A and VCG 4B, which are identified by specific tester isolates (39). In pathogenicity tests with isolates from both groups, all are pathogenic to potato, but those in VCG 4A are collectively more aggressive and may compose a host-adapted pathotype (9,39,61). Thus far, VCG 4A has been found only in North America. VCG 4B isolates commonly infect potato, but are less aggressive on that host. Isolates in VCG 4B also attack several other hosts, including cotton and tomato (41), and appear to be geographically more widespread. In addition to being commonly found across North America, VCG 4B isolates have been found in Spain (42), Israel (3), and elsewhere (41). Isolates of VCG 4A interact synergistically with the root-lesion nematode *P. penetrans*, resulting in earlier symptom development and lower tuber yields, whereas isolates of VCG 4B are much less synergistic (9).

Molecular-based techniques, including restriction fragment length polymorphism (RFLP) and polymerase chain reaction (PCR), are beginning to enhance our understanding of the genetic diversity within *Verticillium* (24,27,47,69). Thus far, however, molecular diagnostics have been effective primarily at differentiating among *Verticillium* species, with only limited success in differentiating subspecific genetic groups (24).

Transmission of *V. dahliae* in seed potatoes. Transmission of *V. dahliae* in infected seed tubers is an obvious mechanism for long-distance spread of host-adapted pathotypes and infestation of clean land. In the early 1970s, Easton et al. (26) found that up to 50% of commercial seed lots imported into the Columbia Basin of Washington were infected with both the "dark mycelial" and "sclerotial" types of *V. albo-atrum*, the latter actually being *V. dahliae*. In Israel in the early 1980s, seed potatoes imported from Europe were found to be free of *V. dahliae*, but seed lots produced in Israel had incidences of tuber infection as high as 22% (58). In a recent survey (80) of seedborne pathogens in Israeli potato seed stocks, *V. dahliae* was detected in about a third of the seed lots, with about 10% of the seed lots having greater than 5% of the tubers infected.

In recognition of the importance of VCG 4A strains of *V. dahliae* to North American potato production, in the late 1990s, a systematic survey was conducted of tubers from seed lots grown in diverse seed producing areas (61). Tuber samples were collected from 224 certified seed lots grown in 14 U.S. states and four Canadian provinces (Table 1). *V. dahliae* was detected in 65 (30%) of the seed lots tested. A total of 162 isolates were assessed by vegetative compatibility analysis, and all belonged to VCG 4, with two-thirds belonging to VCG 4A and the rest in VCG 4B. In a greenhouse pathogenicity test, plants inoculated with VCG 4A isolates developed earlier and more severe symptoms, and plants died earlier than plants inoculated with VCB 4B isolates.

Extensive infection of certified seed lots certainly explains the widespread distribution of VCG 4A strains across North American potato production regions. It also raises questions concerning the relative importance of seedborne compared with soilborne inoculum of *V. dahliae* in initiating PED within a given crop. Further research is needed to determine the economic importance of introducing inoculum of *V. dahliae* in seed tubers and whether seed potato certification standards need to be changed to include tolerances for tuber infection by this pathogen.

Management Strategies for PED

Host resistance. In 2000, approximately 75% of the potato acreage in North America was cropped to seven cultivars. All but Ranger Russet are moderately to highly susceptible to PED (Fig. 10). Although potato-breeding programs have devoted considerable effort toward developing resistant cultivars, only one successful cultivar (Russet Nugget) with resistance to *Verticillium* has been released in the past 20 years. Therefore, a major long-term strategy for reducing losses from PED must be the development of resistant cultivars.

Resistance to *Verticillium* in diploid and tetraploid *Solanum* species is polygenic and complex (15–17,36). Incorporation of resistance from species other than *S. tuberosum* into new cultivars has been a challenge. Two genotypes in *Solanum chacoense*, a diploid wild species, were recently identified as resistant (48). In inheritance studies, a single dominant gene, V_c, controlled the resistance in one of these genotypes. This was the first report of a single dominant gene conferring resistance toward Verticillium wilt in potato. Transfer of this gene to tetraploid germ plasm and the development of resistant cultivars may provide effective, economical control of PED for the short term.

The development of plant transformation techniques has opened new avenues for creating disease-resistant potatoes. One highly successful approach to engineering has involved generating plants that synthesize antifungal proteins. The alfalfa antifungal peptide defensin, isolated from seeds of *Medicago sativa*, was cloned into Russet Burbank. Expression of the *alf*AFP peptide in transgenic Russet Burbank provided robust resistance to PED in the greenhouse and in field studies at two diverse field locations, the Columbia Basin of Washington and the central sands of Wisconsin (29). This single transgene imparted a disease resistance phenotype that provided disease control equivalent to that achieved through soil fumigation. Strategies for management of resistance genes, once they have been successfully transferred to *S. tuberosum*, will probably hinge on practical consideration of the new market realities that are rapidly emerging throughout the potato industry in North America.

Soil fumigation. Effective control of PED has often required the use of soil fumigants that possess broad-spectrum biological activity. Metam sodium, the fumigant of choice for management of this disease, has been used for several decades. Its activity depends on its conversion in the soil to methyl isothiocyanate (MITC). In North America, the estimated annual use of metam sodium on potatoes exceeds 10.2 million kg of active ingredient (2). Over 59,000 ha are treated at an average cost of $250 to $300 or more per hectare, with typical application rates ranging from 140 to 180 kg a.i./ha. Metam sodium is often applied as a liquid and then incorporated

Table 1. Detection and vegetative compatibility characterization of *Verticillium dahliae* isolates recovered from tuber samples of certified seed lots grown in North America, adapted from Omer et al. (61)

Source of seed lots	Seed lots from which *V. dahliae* was isolated (%)	Isolates tested and found to be VCG 4A (%)
Alberta	33 (15)[a]	0 (7)[b]
British Columbia	12.5 (8)	31 (13)
Idaho	33 (6)	73 (11)
Maine	19 (32)	45 (11)
Michigan	30 (10)	67 (3)
Minnesota	50 (2)	100 (1)
Montana	40 (42)	87 (31)
Nebraska	50 (4)	100 (1)
New Brunswick	6 (18)	100 (1)
New York	23 (26)	14 (7)
North Dakota	36 (11)	100 (8)
Oregon	12.5 (8)	13 (15)
Pennsylvania	67 (3)	75 (4)
Prince Edward Island	0 (1)	0
South Dakota	100 (1)	100 (12)
Washington	40 (20)	83 (18)
Wisconsin	25 (16)	75 (4)
Wyoming	100 (1)	100 (11)
Total tested	(224)	(65)

[a] Number of seed lots tested in parentheses.
[b] Number of isolates typed for vegetative compatibility group (VCG) in parentheses.

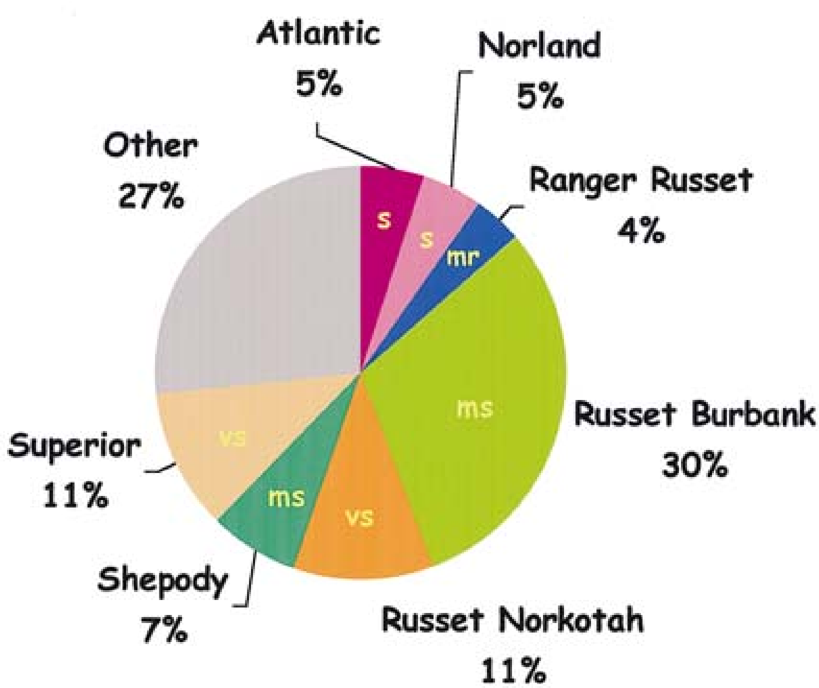

Fig. 10. Percent seed production acreage and reaction to *Verticillium* species of the seven most commonly grown potato cultivars in North America. vs = very susceptible; s = susceptible; ms = moderately susceptible; mr = moderately resistant.

into the soil through tillage followed by irrigation. Today in the Pacific Northwest, metam sodium is frequently used in combination with 1,3-dichloropropene to control Columbia root knot nematode (*Meloidogyne chitwoodii*) and stubby root nematode (*Paratrichodorus* spp.). The latter vectors the *Tobacco rattle virus,* the cause of corky ring spot disease. However, 1,3-dichloropropene is not efficacious in reducing soil populations of *Verticillium* when used at nematicidal rates. Metam sodium at 140 kg a.i./ha and 1,3-dichloropropene at 160 kg a.i./ha reduce soil populations of both *Verticillium* and the two parasitic nematodes (35). Fields are usually fumigated in the fall prior to spring planting of potatoes. Yield increases have been reported of 5 to 10 tons/ha in the Pacific Northwest (22,23) and 16 to 32% in Israel (4).

Some sites in the United States, Europe, and Australia have recently experienced inconsistent performance of metam sodium. Poor performance of the fumigant in the Netherlands may be due to enhanced biodegradation in the soil (74). Enhanced biodegradation is an accelerated decay of pesticides through biological activity. Populations of soil microbes that break down MITC increased dramatically when metam sodium was applied annually for several years (66). In Australia, metam sodium applied to soils that had not previously been fumigated was converted (93%) into MITC, which persisted for 17 days (82). In marked contrast, when metam sodium was applied to a previously fumigated soil, less than half (42%) was converted into MITC, which then declined to zero in 7 h (Fig. 11). Because most potato soils in North America are not fumigated more than every 3 to 4 years, biodegradation of metam sodium is probably not a major consideration. However, growers and crop consultants are advised to be aware of the potential for reduced efficacy associated with frequent fumigation.

Crop rotation. Although populations of microsclerotia in soil will decline following rotation to a nonhost crop (40), crop rotation generally has not been regarded as a practical tactic for management of *V. dahliae*. The fungus colonizes the roots of a wide range of plant species, including both those immune and susceptible to systemic infection (12,43,52). Recently, the host range specificity and virulence spectrum of *Verticillium* strains in different hosts has been determined (7,8). Bell pepper, cabbage, cauliflower, cotton, eggplant, and mint isolates exhibited host specificity and differential pathogenicity on other hosts, whereas isolates from artichoke, lettuce, potato, strawberry, tomato, and watermelon did not. On potato, *V. dahliae* isolates from artichoke, eggplant, lettuce, strawberry, tomato, and watermelon caused severe vascular discoloration and wilting; the bell pepper, cabbage, and cauliflower isolates were less aggressive and caused mild symptoms; and the cotton and mint isolates were nonpathogenic. Isolates from bell pepper, eggplant, and tomato belonged to VCG 4; the cotton isolate to VCG 1; and the remaining isolates to VCG 2. In the Netherlands, potato cultivars were more susceptible to potato isolates than to the faba bean isolates (57). In Washington, potato is sometimes planted in fields removed from mint production, but recent studies have shown that *V. dahliae* isolates infecting mint are usually VCG 2B, rather than the VCG 4 isolates that infect potato (25). Broccoli is immune to root infection by isolates of *V. dahliae* from noncrucifer hosts (8), which makes it an attractive rotation crop for PED management in some cropping systems. Host specificity does exist, and not all isolates from susceptible hosts are pathogenic on potato. Therefore, management of PED through crop rotation is a distinct possibility if the *V. dahliae* isolates from the rotation crop lack specificity to potato.

A complicating factor in disease management through crop rotation is that roots of some nonhosts including cereals (barley, buckwheat, field corn, oats, Sudan grass, and wheat), legumes (alfalfa, Austrian winter pea, clover, and milkvetch), and brassica crops (canola, radish, and turnip) support low populations of *V. dahliae* (20). The vascular tissues of these nonhosts also may be colonized by *V. dahliae* when plants are grown in soil heavily infested with the pathogen (20). The fact that numerous plant species can act as bridging hosts for *V. dahliae* and maintain populations of microsclerotia in soil between susceptible crops reduces the efficacy of this practice for management of PED.

Organic amendments. Organic matter in soil may be important in suppression of PED. A survey of potato fields in Idaho (19) showed an apparent inverse relationship between severity of PED and soil integrity. Factors such as organic matter, organic nitrogen, and increased nutrient availability were most closely related to PED suppression and resultant higher tuber yields. Factors related to loss of soil integrity (sodium and reduced nutrient availability) were related to increased severity of PED and lower tuber yields. Davis and coworkers (19) suggested that organic matter might be a factor that could be manipulated for suppression of PED.

One broad strategy being explored is the use of organic amendments such as green manures, composts, and animal manures. The early works of Millard and Taylor (53) and Sanford (73) demonstrated that green manures suppress diseases caused by certain soilborne pathogens. In addition, beneficial effects of increased organic matter include less surface crusting, increased water infiltration, and increased populations of soil microorganisms, whose activity is essential for the maintenance of highly productive soils (67).

Suppression of PED has been achieved with the plow down of a green manure crop (21). Compared with 3 years of a weed-free fallow, three successive green manure crops of Sudan grass decreased disease severity by 81% and increased marketable tuber yield by 35%. The response was equivalent to that of soil fumigation (Fig. 12). Other crops grown as green manures such as Austrian winter pea, canola, oats, and rye also have suppressed disease and enhanced tuber yields. The problem with this tactic is that two to three consecutive years of a green manure are needed to suppress disease and increase tuber yield. For green manuring to be a viable approach for management of PED, a shorter time frame is required. Members of

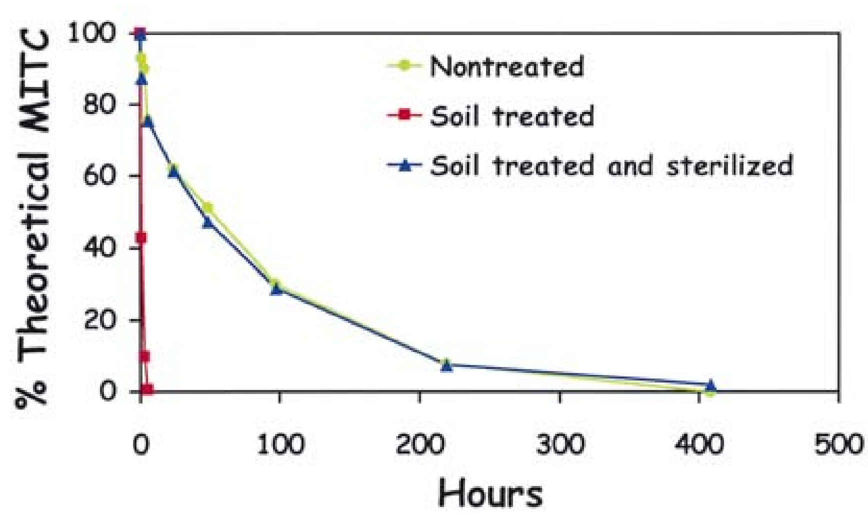

Fig. 11. Methyl isothiocyanate (MITC) change after metam sodium application to soils. Soil A has no known previous exposure to metam sodium, soil B has a previous history of metam sodium use, and soil Bs is soil B after sterilization. Adapted from Warton et al. (82).

the family Brassicaceae have been effective in suppressing Verticillium wilt. Rotation to broccoli and incorporation of fresh residue into the soil immediately following harvest of broccoli heads resulted in a decrease in soil populations of *V. dahliae* and a reduction in severity of Verticillium wilt of cauliflower (76) and potato (5).

Soil amendment with spent mushroom compost reduced the severity of PED by 31 and 40% in 2 years of a 4-year study. In all 4 years, yield of marketable tubers was significantly higher in compost-amended plots compared with the nonamended control. Yield increases ranged from 60 to 96% (44). Researchers in Ontario, Canada, are exploring the use of organic by-products as amendments to reduce PED. In field studies in a sandy loam soil, an amendment of meat and bone meal reduced Verticillium wilt severity by 50 to 100% compared with the nonamended control, whereas cattle manure and paper mill biosolids had no effect (45). Not all organic amendments are efficacious in controlling PED. In a Wisconsin study, paper mill sludge was applied at two rates to a silt loam soil. PED symptoms were twice as severe in plots amended with a high rate of composted paper mill residue compared with nonamended soil (68).

Organic matter is thought to suppress *Verticillium* indirectly by either an increase in microbial activity or the release of toxic compounds. Populations of nonpathogenic *F. oxysporum* are particularly implicated in suppression of PED with green manures (21). Green manures also increase accumulations of plant decomposition products that can be deleterious to *Verticillium*. Sudan grass contains a cyanoglucoside compound, called dhurrin, present primarily in the epidermal cells of the leaf tissues (1). The cellular contents of the epidermal and mesophyll cells, which contain the enzyme β-glucosidase, become mixed when the tissue is damaged or begins to decompose. The enzyme catalyzes the hydrolysis of dhurrin to yield *p*-hydroxymandelonitrile, which then dissociates to produce free HCN and *p*-hydroxybenzaldehyde. With *Brassica* spp. amendments, most of the beneficial effects have been attributed to glucosinolates. As the plant tissues break down in soil, glucosinolates, not toxic by themselves, are converted to toxic isothiocyanates, thiocyanates, nitriles, epithionitriles, and oxazolidine-2-thiones (11,28).

The mechanisms by which nitrogenous amendments such as meat and bone meal kill *V. dahliae* were examined in solution bioassays and microcosm studies (77). Both ammonia and nitrous acid, rather than their ionized counterparts ammonium and nitrite, were lethal to microsclerotia. Addition of meat and bone meal (2.5%) to an acidic loam sand resulted in the accumulation of ammonia and death of microsclerotia within 2 weeks. In contrast, when meat and bone meal were added to an alkaline loam soil, neither ammonia nor nitrous acid accumulated and the microsclerotia survived. The concentration of both ammonia and nitrous acid is controlled by pH, organic matter content, soil buffering capacity, and nitrification rate. Accumulation of nitrous acid is the more promising strategy to control plant diseases in acidic soil because it is more toxic than ammonia and is formed at lower concentrations of amendments.

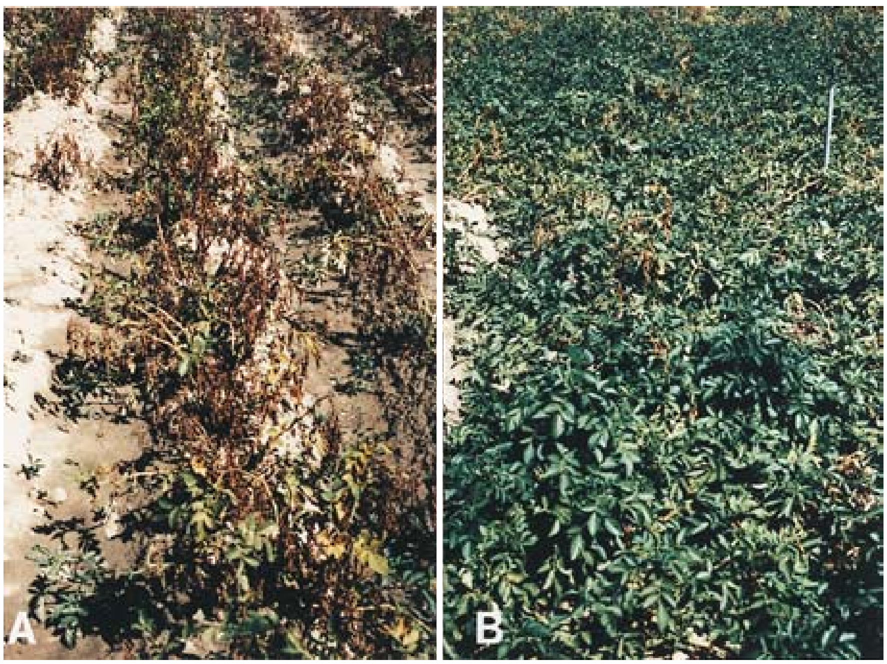

Fig. 12. Effect of a Sudan grass green manure and fallow on potato early dying of cv. Russet Burbank after: A, three successive years of a weed-free fallow, and B, three successive green manure crops of Sudan grass. From Davis et al. (21).

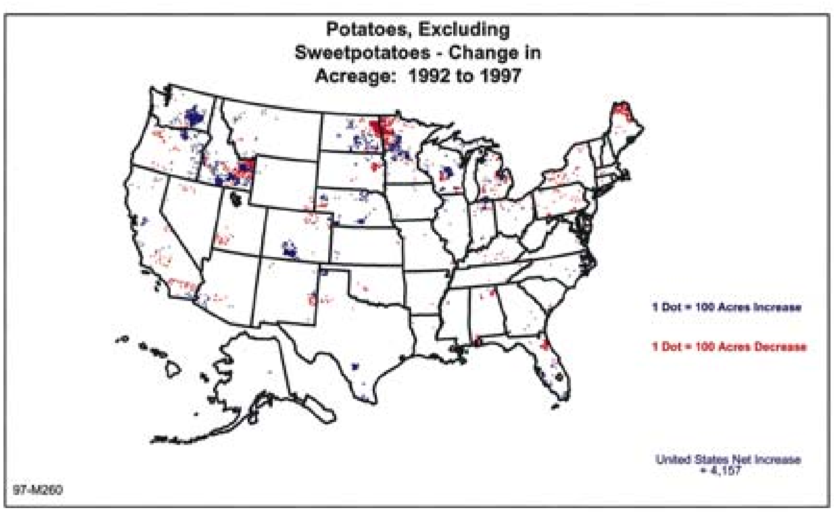

Fig. 13. Change in acreage of potato production in the United States from 1992 to 1997. From 1997 USDA Census of Agriculture, available on-line.

Challenges in a Changing Production Environment

Changes that have impacted the North American potato industry in the last 10 to 15 years are beginning to affect management options for PED. Decreased profit margins and market demands for higher tuber quality are forcing production to be concentrated on irrigated, sandy soils where PED is often most severe (13,14). Potato production is increasing in the central and western U.S. states and decreasing in traditional eastern production areas on rain-fed loam soils (Fig. 13). New potato cultivars that better meet the special needs of food processors and consumers are becoming more profitable than standard cultivars. Gone are the days when potato growers could plant their favorite cultivar, secure in the knowledge that there would be a market for the crop when harvested. A high percentage of potato production now takes place on rented ground under contract, and in the future, more contract production is likely where cultivars and production practices are often specified in advance.

Effective management of PED has always required an integrated approach. However, in this changing production environment, the components of an effective management program may have to change too. In several production areas, primarily irrigated regions, considerable resources are expended annually to fumigate fields. Ever increasing environmental concerns are diminishing the prospects of continued reliance on soil fumigants, particularly where groundwater issues are a concern. The high expense of this option is also becoming a deterrent as profit margins shrink. An alternative approach to managing the soilborne inoculum is to manipulate soils to make them suppressive. Organic soil amendments, which are becoming commercially available, and incorporation of green manure crops may be feasible and durable ways to enhance soil suppressiveness. Soil and plant processes and functions, including soil nutrient status, plant health, and overall crop productivity are greatly impacted by the soil microbiology. Factors driving changes in the soil microbial community are the types of organic amendments, the particular plant species used as a green manure crop, and the physical characteristics of specific soils. To fully exploit the manipulation of soil suppressiveness and incorporate this as an aspect of an effective PED management strategy, a better understanding is needed of the mechanisms by which organic amendments and green manures reduce disease.

Considering the widespread economic impact of vascular wilt fungi in many crops and ornamental plants, it seems that a commercial incentive should exist to develop a soil-applied, systemic fungicide specifically targeted against *Verticillium* in the vascular system. The goal of such a fungicide would be to reduce the extent of vascular colonization to the point where any effect on yield would be minimized. In potato production, this product ideally could be applied as part of the seed-piece dressing at the time of planting, where it would then be absorbed into the growing tissues early in the life of the plant. This type of fungicide could play a key role in an integrated disease management program. Appropriate resistance management strategies would need to be implemented to extend the longevity of such a product.

Most commercial potato cultivars currently grown in North America are susceptible to PED. Seed tuber-to-plant transmission of *V. dahliae* most likely occurs, but its impact on tuber yield of the subsequent crop is unknown. Studies are warranted to determine the significance of seedborne inoculum of *Verticillium* in current-season disease expression and tuber yield reduction. If found to be commercially significant, modification of seed tuber certification standards might be justified to address this phase of the disease.

Since the North American potato industry is now more receptive to utilizing new cultivars that better meet the special needs of food processors and consumers, the time may be ripe for increased incorporation of resistant germ plasm into potato breeding programs. Improved transformation techniques and newly identified genes whose transcripts or protein products have antimicrobial activity have greatly improved the feasibility of engineering resistance to *Verticillium* into potato. Future exploitation of host resistance should provide an environmentally friendly alternative to soil fumigation. Long-term success of this approach will require that strategies to increase the longevity of these resistance genes be developed.

If these approaches are to be appropriately and successfully implemented, a reliable, sensitive method for quantifying *V. dahliae* in soil and tubers is needed. Plating soil on semiselective media has been shown to be inconsistent and unreliable for estimating soil populations (78). DNA-based technologies hold promise for providing a more accurate and repeatable diagnostic tool for measuring soil populations (24,27,47,69). Further precision will be required, however, to identify and quantify specific strains of the pathogen. The development of improved DNA-based techniques for monitoring populations of *V. dahliae* should be a high priority. The availability of this technology, particularly in the form of a commercially available test kit, would be a significant tool for disease managers. Decisions regarding field selection, cultivar and seed lot selection, and application of soil treatments could then be made from a more informed status.

Times change, as do the challenges faced and the strategies required to manage PED both effectively and economically. Successful management will involve five key areas: suppression of soilborne inoculum, new plant protection chemicals, clean planting stock, enhanced host resistance, and improved pathogen monitoring tools. Confidence in the future is implicit in the fact that plant pathologists in collaboration with soil scientists, horticulturists, molecular biologists, and agricultural chemists are exploring new ways to manage this important disease. With the tremendous innovations in technology that are becoming available, new opportunities surfacing in molecular biology, and fine-tuning of management strategies from the past, the future looks bright for improved management of potato early dying.

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