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Symposium contribution/Contribution au symposium

Verticillium wilt of potato – the pathogen, disease and management[†]

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Abstract: Verticillium wilt is a major disease of potato caused by either *Verticillium dahliae* or *Verticillium albo-atrum*. Both species are soilborne fungi that invade xylem elements, disrupt water transport in plants and cause vascular wilt in a variety of hosts. Despite the broad host range of *V. dahliae*, a degree of host adaptation occurs with some isolates exhibiting different levels of aggressiveness depending on the host species and even cultivar within a species. In addition, isolates can be separated into vegetative compatibility groups (VCGs) based on the ability to undergo hyphal anastomosis with other isolates. Distinct sub-specific groups have been recognized which contain host-adapted pathotypes that are aggressive and prevalent on particular hosts. Isolates of *V. dahliae* collected from potato stems, tubers and potato fields in the USA mostly belong to VCG 4A and VCG 4B, with the VCG 4A isolates being highly aggressive on potato compared with isolates of VCG 4B and other VCGs. In contrast, isolates collected from potatoes grown in Israel were predominantly VCG 2A and VCG 4B. Initial inoculum of *V. dahliae* is primarily soilborne microsclerotia. *Verticillium dahliae* can be transmitted in certified seed tubers, but tuber-borne inoculum appears to have little effect on verticillium wilt symptoms and potato yields. Vascular infection by *V. dahliae* of seed tubers of the moderately susceptible potato cultivar 'Russet Burbank' resulted in negligible effects on the development of verticillium wilt symptom, did not significantly contribute to aboveground stem infection or the formation of microsclerotia in debris, and did not significantly contribute to progeny tuber infection. An importance of tuber-borne inoculum is the potential to introduce inoculum to soils not previously used to grow potato or where a management practice such as fumigation has been applied to reduce soilborne inoculum. Management strategies should focus on reducing initial inoculum in soil and restricting vascular infection and pathogen development within the host. Tactics that may reduce initial inoculum include crop rotation, soil fumigation, green manures, soil solarization, and bio-fumigants. Cultivar resistance restricts pathogen infection and colonization of plants. Integration of several management tactics and a better understanding of soil health will be needed for lasting and economic management of the disease.

Keywords: potato early dying, soilborne pathogens, *Verticillium albo-atrum*, *Verticillium dahliae*

Résumé: La verticilliose, causée par *Verticillium dahliae* ou *V. albo-atrum*, est une grave maladie de la pomme de terre. Les deux champignons terricoles envahissent le procambium, perturbent le transport de l'eau dans les plantes et provoquent la flétrissure vasculaire chez de nombreuses plantes hôtes. Malgré le large éventail des hôtes de *V. dahliae*, on remarque un certain degré d'adaptation des hôtes à certains isolats affichant divers degrés d'agressivité, selon les espèces d'hôtes ou même les cultivars au sein d'une même espèce. De plus, les isolats peuvent être divisés en groupes de compatibilité végétative (GCV), basés sur la capacité d'anastomose des hyphes avec d'autres isolats. Des groupes subspécifiques distincts qui contiennent des pathotypes agressifs adaptés à l'hôte, répandus chez certains hôtes, ont été identifiés. Des isolats de *V. dahliae*, collectés sur des tiges de pommes de terre, sur des tubercules et dans des champs aux États-Unis, appartiennent principalement au GCV 4A et au GCV 4B, les isolats du GCV 4A étant les plus agressifs à l'égard de la pomme de terre, comparativement au GCV 4B et aux autres GCV. Par contre, les isolats collectés sur des pommes de terre cultivées en Israël appartenaient majoritairement au GCV 2A et au GCV 4B. L'inoculum initial de *V. dahliae* consiste principalement de microscléroties terricoles. *Verticillium dahliae* peut être

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transmis par les pommes de terre de semence certifiées, mais les inoculum portés par les tubercules semblent engendrer peu des symptômes relatifs à la verticilliose ou influencer les rendements. L'infection vasculaire des pommes de terre de semence par *V. dahliae* du cultivar moyennement susceptible 'Russet Burbank' n'a pas vraiment favorisé l'apparition des symptômes de la verticilliose, n'a pas provoqué de façon significative l'infection des tiges aériennes ou la formation de microsclérotes dans les débris, ni n'a contribué de façon notable à l'infection des tubercles provenant du tubercule mère. Un des dangers découlant des inoculum transmis par les pommes de terre de semence est la possibilité d'introduire ceux-ci dans des sols qui n'ont pas servi préalablement à la culture de la pomme de terre ou qui ont été traités par fumigation afin de réduire les inoculum terricoles. Les stratégies de gestion devraient se concentrer sur la réduction de l'inoculum initial du sol et sur la restriction de l'infection vasculaire ainsi que de la croissance de l'agent pathogène chez l'hôte. Les stratégies qui peuvent contribuer à réduire l'inoculum initial incluent la rotation des cultures, la fumigation des sols, l'utilisation d'engrais verts, la solarisation du sol et l'emploi de biofumigants. La résistance des cultivars réduit également l'infection et la colonisation des plantes par l'agent pathogène. L'intégration de plusieurs stratégies de gestion et une meilleure compréhension de la santé des sols seront requises en vue d'assurer une gestion à long terme et économiquement viable de la maladie.

Mots clés: agents pathogènes terricoles, mort prématuée de la pomme de terre, *Verticillium albo-atrum*, *Verticillium dahliae*

Introduction

Verticillium wilt is a major economic disease of potato (*Solanum tuberosum* L.) wherever the crop is commercially grown. The disease is caused by either *Verticillium dahliae* Kleb. or *Verticillium albo-atrum* Reinke & Berthold. Both species are soilborne fungi that invade xylem elements, disrupt water transport in plants and cause vascular wilt in a variety of hosts. They were considered forms of *V. albo-atrum* prior to the mid 1970s but are now recognized as separate species (Krikun & Orion, 1979). Molecular evidence supports the classification of *V. dahliae* and *V. albo-atrum* as two distinct but closely related species. Carder & Barbara (1991) distinguished the two pathogens using random probes of Southern blots of EcoRI-digested DNA. Sequence analyses of intergenic spacer regions of ribosomal DNA (rDNA) and the β -tubulin gene (Qin *et al.*, 2006), as well as sequences from the internal transcribed spacer regions and several mitochondrial DNA genes (Fahleson *et al.*, 2004; Zare *et al.*, 2004; Pantou *et al.*, 2005), also support the separation of the two species. Pathogen ecology of *V. albo-atrum* and *V. dahliae*, and disease epidemiology and management of Verticillium wilt of potato are discussed in this paper.

The pathogen

Verticillium dahliae has an extensive host range and widespread distribution in temperate climates (Schnathorst, 1981; Rowe *et al.*, 1987; Chen, 1994). Hosts include over 200 dicotyledonous species, including herbaceous annuals and both herbaceous and woody perennials. The fungus survives for relatively long time periods in soil as microsclerotia (Green, 1980). *Verticillium albo-atrum* has a more limited host range. This species does not form microsclerotia and survives for relatively shorter durations

than soil as melanized hyphae. *Verticillium dahliae* is favoured by warmer temperatures than *V. albo-atrum*. *Verticillium dahliae* predominates in production areas where average daily summer temperatures commonly exceed 27 °C such as the Columbia Basin of central Washington and north central Oregon, southern Idaho, and the mid western USA. Disease severity tends to increase as the mean air temperature increases from 18 to 29 °C. Differences in aggressiveness among isolates of *V. dahliae* may be partially due to variation in growth capabilities at different temperatures, with the more aggressive isolates exhibiting more growth over a wider range of temperatures than less aggressive isolates (Daayf *et al.*, 1998). *Verticillium albo-atrum* is more commonly found where the average daily temperatures normally do not exceed 21 °C during the growing season such as in Maine, the Red River Valley of Minnesota and North Dakota, southern Canada, and winter production areas in Florida (Powelson & Rowe, 2008). *Verticillium nigrescens* Pethybr. and *Verticillium tricorpus* I. Isaac may also infect potato and other plants, but they are generally considered weakly aggressive or nonpathogenic (Isaac, 1949; Skotland, 1971; Slattery & Eide, 1980).

Despite the broad host range of *V. dahliae*, a degree of host adaptation occurs with some isolates exhibiting different levels of aggressiveness depending on the host species and even cultivar within a species. In addition, isolates can be separated into vegetative compatibility groups (VCGs) based on their ability to undergo hyphal anastomosis with other isolates. Distinct sub-specific groups have been recognized which contain host-adapted pathotypes that are aggressive and prevalent on particular hosts (Chang & Eastburn, 1994; Daayf *et al.*, 1995; Bhat & Subbarao, 1999; Douhan & Johnson, 2001). Studies of *V. dahliae* isolates collected from potatoes and potato fields in the USA found the majority of isolates to belong to VCG 4A and VCG 4B, with VCG 4A being highly

aggressive on potatoes compared with isolates of VCG 4B and other VCGs (Joaquim & Rowe, 1991; Omer *et al.*, 2000, 2008). In contrast, a study by Ebihara *et al.* (1999) paired Japanese isolates with standardized tester strains and the lone isolate from potato included in the study was weakly compatible with the VCG 2A tester strain. Interestingly, isolates collected from potatoes grown in Israel were predominantly VCG 2A and VCG 4B. The presence of VCG 4B but lack of VCG 4A in Israel was hypothesized to be the result of the importation of seed potatoes from Europe (Korolev *et al.*, 2000). The presence of different VCGs occurring on potatoes grown in different areas of the world may be a result of the transportation of infected seed tubers or infested soil carried on the surface of tubers; however, the geographic origin of these potato-adapted pathotypes remains unknown.

The use of molecular markers to differentiate *Verticillium* populations occurring on potato has produced mixed conclusions. Comparison of random amplified polymorphic DNA (RAPD) markers from 15 *V. albo-atrum* isolates from potato and 20 isolates from alfalfa produced a clear distinction between the two pathotypes (Barasubiye *et al.*, 1995). In Japan, Komatsu *et al.* (2001) used RAPD and repetitive extragenic palindromic polymerase chain reaction (REP-PCR) analyses and observed that 15 out of 16 *V. dahliae* isolates from potato shared a similar genetic background, regardless of geographic origin or sample date. However, a study conducted on 12 *V. dahliae* isolates collected in California, Oregon and Idaho (including one isolate from potato) found that they all shared the same RAPD profile regardless of VCG or host, and correlations among pathogenicity, VCG and RAPD banding patterns were not observed (Bhat & Subbarao, 1999). It should be noted that RAPD analysis is very sensitive to experimental conditions and other molecular marker techniques, such as restriction fragment length polymorphisms (RFLP), amplified fragment length polymorphism (AFLP), and sequence-based analysis are considered more robust and reproducible (Weising *et al.*, 2005).

The development of sequence-based analyses provides the ability to identify polymorphisms at the single nucleotide level. Analyses of sequences from the intergenic spacer regions of ribosomal DNA and the β -tubulin gene grouped five potato isolates from Oregon and Idaho in the same clade (Qin *et al.*, 2006). A combined analysis of AFLP fingerprints and six DNA sequences concluded that VCG 2A and VCG 4B isolates from Israel and Spain belonged to the same lineage and subclade (Collado-Romero *et al.*, 2008). The same study found both VCGs possessed the same sequence at a *V. dahliae*-specific polymorphic DNA locus, but the single North American

VCG 4A isolate from potato included in the study contained a novel sequence. These studies demonstrate the potential of sequence-based analysis, used in combination with VCG identification, to determine phylogenetic and epidemiological relationships among *V. dahliae* isolates collected from different potato-growing regions.

The disease

Verticillium wilt is the major component of potato early-dying complex. Potato early dying refers to the early senescence and death of a potato crop and can be caused by several factors besides *V. dahliae* and *V. albo-atrum* including *Colletotrichum coccodes* (Wallr.) Hughes, soft rot bacteria, combined infections by *Pratylenchus penetrans* (Cobb) Chitwood & Oteifa and *V. dahliae*, and nutrient deficiencies (Rowe *et al.*, 1987; Mohan *et al.*, 1992; Davis & Huisman, 2004).

Symptom expression and yield reductions in potato from verticillium wilt are influenced by soil and environmental conditions (Powelson & Rowe, 1993) and are generally more pronounced during times of heat stress and high rates of evapotranspiration (Nnodu & Harrison, 1979; Ewing, 1981; Rowe *et al.*, 1985; Franci *et al.*, 1990). Although infection may occur early in the growing season, wilt symptoms generally do not develop until the later part of the growing season when rapid tuber bulking occurs (Johnson & Miliczky, 1993; Pavek & Corsini, 1994). The disease first appears as interveinal chlorosis on leaves of individuals or groups of plants scattered among healthy appearing plants. Wilting and necrosis then follow and progress acropetally from the stem base. Foliar symptoms are often unilateral. Entire stems eventually become necrotic and senesce prematurely and may remain upright. A tan, vascular discoloration may occur near the stem base but may also result from physiological factors or other pathogens and, thus, is not diagnostic (Baribeau, 1952; Isaac & Harrison, 1968; Thanassoulopoulos & Hooker, 1968). Vascular browning may develop in tubers of some cultivars (El Hadrami *et al.*, 2007; Powelson & Rowe, 2008). The effects of verticillium wilt on potato yield are variable, commonly ranging from 10–15% reduction in yield, but may reach 30–50% (Johnson *et al.*, 1986; Powelson & Rowe, 1993; Rowe & Powelson, 2002). Yield reductions may not be correlated with aboveground symptoms (Nachmias & Krikun, 1984; Rowe *et al.*, 1985).

Synergistic interactions of *V. dahliae* with *P. penetrans*, the root lesion nematode, have been shown to occur in potatoes with VCG 4A of *V. dahliae*, but not with other VCGs (Botseas & Rowe, 1994). When both *V. dahliae* VCG 4A and *P. penetrans* infect a potato, severe

symptoms and significant yield losses often result at population densities of each pathogen which individually would have little or no effect on the crop. Likewise, the VCG 2B pathotype of *V. dahliae* from mint interacted with *P. penetrans* on peppermint and Scotch spearmint, causing increased disease severity, whereas the VCG 4A pathotype from potato did not (Johnson & Santo, 2001). Thus, a three-way interaction among the host, *V. dahliae* pathotype and *P. penetrans* can occur. Severe verticillium wilt symptoms will occur on potato without the presence of *P. penetrans* when inoculum levels are sufficiently high.

Initial inoculum of *V. albo-atrum* consists primarily of melanized hyphae, while that of *V. dahliae* is primarily soilborne microsclerotia. Reported disease thresholds for verticillium wilt in potatoes range between 5–30 cfu cm⁻³ of soil for *V. dahliae* alone and 2–13 cfu cm⁻³ soil when *P. penetrans* is present (Powelson & Rowe, 1993). Microsclerotia germinate in response to plant root exudates (Emmaty & Green, 1969; Mol, 1995) after which hyphae colonize the root surface and cortex. Disease symptoms occur when the pathogen penetrates the stele and invades the xylem, where the fungus produces abundant conidia which are systemically translocated through the vascular system of the host (Fradin & Thomma, 2006; Vallad & Subbarao, 2008). Root surfaces of resistant and non-hosts are colonized to various extents; however, the fungus appears to be restricted from extensively colonizing the cortex and is unable to fully infiltrate the xylem of more resistant cultivars (Fradin & Thomma, 2006; Atallah *et al.*, 2007; Bae *et al.*, 2007; Vallad & Subbarao, 2008). Verticillium wilt-resistant plants have less vascular colonization than susceptible ones (Slattery, 1981; Davis *et al.*, 1983; Hoyos *et al.*, 1991; Atallah *et al.*, 2007; Bae *et al.*, 2007).

Microsclerotia form in colonized host tissue during senescence and continue to develop until stems have dried to a low moisture content (Slattery, 1981). They contribute to future inoculum levels if incorporated into the soil and can persist in field soils for up to 10 years or more (Menzie & Griebel, 1967; Green, 1969; Schnathorst, 1981). Microsclerotia embedded in stem residue retain viability longer than those existing free in soil and are capable of repeated germination over time (Evans *et al.*, 1966; Farley *et al.*, 1971). Infested host debris must be incorporated in the soil and decompose for microsclerotia to be separated and function independently to cause infections. As a result, inoculum potential in soil may be greater two or three years following cultivation of a susceptible crop than the year immediately following the crop, depending on the rate at which colonized host debris is decomposed (Huisman & Ashworth, 1976; Joaquim *et*

al., 1988). More than 90 000 microsclerotia can be introduced into soil by a single infected stem (Slattery, 1981). Microsclerotia are then distributed throughout a field with the movement of colonized host debris by soil cultivation or other mechanical means. In addition, infested soil carried on the surface of potato seed tubers can be another source of inoculum in potato (Robinson & Ayers, 1961; Thanassoulopoulos & Hooker, 1968).

Verticillium dahliae exhibits little or no saprophytic activity in soil and changes in soil populations of the fungus have been attributed to production of conidia by germinating microsclerotia, microbial decay of plant residues with subsequent release of microsclerotia, and production of secondary microsclerotia (Evans *et al.*, 1967; Emmaty & Green, 1969; Farley *et al.*, 1971; Green, 1980; Slattery, 1981; Joaquim *et al.*, 1988). Conidia can also be produced during plant senescence but are not thought to be significant in the disease cycle of annual crops (Green, 1969; Vallad & Subbarao, 2008); however, conidia are capable of surviving up to two weeks in soil (Green, 1969) and may be a factor for increase in the incidence of wilt in perennial crops such as mint (Johnson *et al.*, 2006). Microsclerotia and conidia can be moved within and between fields by surface irrigation water (Easton *et al.*, 1969).

Verticillium dahliae can persist on roots of some cereal crops and other non-hosts without causing disease symptoms. Microsclerotia produced on roots of resistant and non-host plants have been thought to be a means of pathogen replenishment and prolonged persistence in soil (Lacy & Horner, 1966; Fradin & Thomma, 2006; Eynck *et al.*, 2007; Vallad & Subbarao, 2008). However, Benson & Ashworth (1976) concluded that parasitic colonization of non-host crop roots by *V. dahliae* (referred to as *V. albo-atrum* – microsclerotial type in that study) was not a significant survival mechanism under field conditions. Now that techniques are available to differentiate among strains of *V. dahliae*, the populations should be thoroughly characterized when quantifying populations from soil and evaluating associations with various host and non-host plants.

Verticillium spp. can be transported long distances in infected certified seed tubers used for planting. A 1968–1969 survey detected *V. albo-atrum* and *V. dahliae* in 39% of 244 certified seed lots, with incidences in seed lots typically between 1–2% and rarely greater than 5% (Easton *et al.*, 1972). A more recent study of seed lots imported from northern Europe to Israel between 1995 and 1998 detected *V. dahliae* in 20–30% of seed lots at incidences less than 5% and found up to 16% of seed lots with *V. dahliae* infection in > 5% of seed tubers (Tsror *et al.*, 1999). Surveys of 224 seed lots intended for North

American production fields in 1995 and 1996 detected *V. dahliae* in 29% of the lots and 3.6% of the seed tubers, from which 64% of the isolates examined were VCG 4A, 33% were VCG 4B and 3% were VCG 4AB (Omer *et al.*, 2000). The detection of *V. dahliae* in certified potato seed lots and prevalence of the more aggressive VCG 4A isolates in both seed tubers and Pacific Northwest fields (Omer *et al.*, 2008) may have important implications in both seed and production crops as well as the epidemiology and distribution of the disease.

Despite the presence of *Verticillium* spp. in certified seed lots, tuber-borne inoculum has little effect on verticillium wilt symptoms and potato yields in various potato cultivars (Robinson & Ayers, 1961; Easton *et al.*, 1972; Hoyman, 1974; Tsror *et al.*, 1999); however, severity of wilt resulting from tuber-borne infection can vary among cultivars (Robinson & Ayers, 1961). In a recent study (Dung, 2009), vascular infection of seed tubers by *V. dahliae* in the moderately susceptible potato 'Russet Burbank' exhibited a negligible effect on the development of verticillium wilt symptoms, did not significantly contribute to aboveground stem infection or the formation of microsclerotia in debris, and did not significantly contribute to progeny tuber infection. The importance of tuber-borne inoculum is that the pathogen, or a particular strain of the pathogen, can potentially be introduced into soils not previously used to grow potatoes or where a management practice such as fumigation has been applied to reduce soilborne inoculum.

Management

Disease intensity is a function of interacting factors among the host, pathogen and environment over time (Fry, 1982). *Verticillium dahliae* and *V. albo-atrum* are monocyclic pathogens on potato, and disease intensity is directly related to quantity of initial inoculum, efficacy of initial inoculum, and length of time that the host and pathogen interact (Van der Plank, 1963). The efficacy of initial inoculum indicates the rate of disease increase and summarizes the effects of environment, host resistance, cultural practices and aggressiveness of the pathogen (Van der Plank, 1963; Fry, 1982). The size of the initial pathogen population does not increase during the growth of an annual crop, unless additional inoculum is carried into a field from an external source such as irrigation water. However, intensity (severity and incidence) of verticillium wilt has been significantly related to initial inoculum levels in some field studies but not in others (Nnodu & Harrison, 1979; Smith & Rowe, 1984; Davis & Everson, 1986; Nicot & Rouse, 1987; Xiao & Subbarao, 1998). A lack of correlation between initial inoculum

levels and disease intensity may be associated in part, with studies inadequately quantifying the spatial pattern and efficacy of initial inoculum in the soil and the presence or absence of highly aggressive, host-adapted strains.

Management strategies for verticillium wilt should focus on reducing initial inoculum levels in soils below threshold populations at which disease can develop and restrict vascular infection and pathogen development within the host. Moreover, practices should be implemented to prevent the introduction of the pathogen to areas where the pathogen population is below the action threshold (Rowe & Powelson, 2008), such as fields where potato has not been previously grown or where sanitation practices have reduced initial inoculum to below thresholds. Tactics that reduce initial inoculum include crop rotation, soil fumigation, green manures, soil solarization and bio-fumigants. Host resistance restricts pathogen infection and colonization of plants (Fradin & Thomma, 2006; Atallah *et al.*, 2007; Bae *et al.*, 2007; Vallad & Subbarao, 2008) and eliminating *Verticillium* spp. in seed tubers restricts introduction of the pathogen into new areas. Integration of several management tactics is needed for lasting and economic management of the disease.

Resistance

Resistant cultivars offer an effective and efficient tactic to reduce the effects of verticillium wilt in potato and should be the core of integrated disease management strategies for verticillium wilt of potato. However, resistance has not been widely used in the past to manage verticillium wilt and other diseases and pests of potato. 'Russet Burbank', a moderately susceptible cultivar to verticillium wilt has dominated potato production in many regions for nearly 100 years. The relatively small number of resistant potato cultivars available for potato production is not due to a lack of genetic resources in potato but rather to past decisions to manage potato diseases with what were then relatively inexpensive pesticides that had broad-spectrum activity (Johnson & Rowe, 2008). However, most fungicides are not effective against verticillium wilt and resistance was recognized early as a potential disease management tactic for the disease. Early evaluations for verticillium wilt resistance were performed by Nielsen (1948) in the arid, irrigated area of southern Idaho. Extensive testing for resistance now occurs in several regions (Susnoschi *et al.* 1976; Corsini *et al.*, 1985, 1988, 1990).

Disease resistance is an active process by which the host opposes, completely or to some degree, the effects of the pathogen (Johnson & Gilmore, 1980). Resistance

is expressed when development of disease symptoms or pathogen signs are restricted on the host. Resistant and partially resistant cultivars to verticillium wilt restrict vascular colonization by *V. dahliae* and *V. albo-atrum* and subsequent microsclerotia formation by *V. dahliae*. Disease severity is reduced in the current crop and the amount of inoculum returned to the soil is reduced for subsequent crops (Slattery, 1981; Davis *et al.*, 1994). Expression of resistance is influenced by environmental factors. Resistant cultivars can become infected and show wilt symptoms when planted in soils with high inoculum levels. Juvenile potato plants in the rapid vegetative growth stage generally do not show wilt symptoms, but symptom development occurs in susceptible cultivars once tuber-bulking occurs (McLean, 1955). Susceptible cultivars that are late in maturity may appear resistant because they remain in the juvenile stage for a relatively long time, but succumb once the plant enters the rapid, tuber-bulking stage (Busch & Edgington, 1967). Resistant cultivars will continue to restrict colonization during this later stage of crop development (Davis *et al.*, 1983). Quantitative real-time PCR assays can be used to measure stem colonization over time in resistant and susceptible cultivars and to identify resistant germplasm (Dan *et al.*, 2001; Atallah *et al.*, 2007; Bae *et al.*, 2007).

Sources of resistance to verticillium wilt in potato have been identified (Davis *et al.*, 1983; Corsini *et al.*, 1985, 1988; Mohan *et al.*, 1990). Several partially resistant cultivars that have been commercially grown include 'Alpha', 'Alturas', 'CalWhite', 'Chipeta', 'Gemchip', 'Goldrush', 'Ranger Russet', 'Russet Nugget' and 'Western Russet'. 'Bannock Russet' is moderately resistant to verticillium wilt, but tubers are very susceptible to *Phytophthora infestans*, hollow heart, and shatter bruise, so the cultivar has not gained acceptance with the potato industry. This illustrates that new resistant cultivars must also have acceptable agronomic traits with no major defects. A challenge to potato improvement programmes is to replace cultivars that are highly susceptible to verticillium wilt, such as 'Russet Norkotah'. The repeated cropping of susceptible cultivars has increased inoculum levels of both *V. dahliae* and *V. albo-atrum* in soil, with subsequent increased incidence of verticillium wilt symptoms in production regions due to extensive colonization of the pathogen in plant tissues (Slattery, 1981).

Resistance should not be confused with tolerance. Tolerance is evident when signs or symptoms on a host genotype are visually similar to those of a susceptible cultivar, but there is less damage to yields caused by the infection (Caldwell *et al.*, 1958; Browning *et al.*, 1977). Visually, tolerant cultivars appear susceptible to the disease, but yields are similar to those of non-infected plants.

Tolerance to verticillium wilt has been indentified in some potato cultivars. For example, 'Kennebec' is susceptible to infection and subsequent colonization of the vascular system, yet yields are generally not reduced by the presence of the pathogen (Mohan *et al.*, 1990). Tolerant cultivars are not as desirable as resistant cultivars for disease management because high numbers of microsclerotia may be produced in colonized plant tissues and returned to soil as initial inoculum for future crops (Slattery, 1981).

Soil fumigation

Fumigation is widely used to reduce soilborne inoculum of *Verticillium* spp. but is both costly and subject to future governmental restrictions (Rowe & Powelson, 2002). The method of application of fumigants must place the active ingredient at the desired depth in the soil profile for the duration required to kill microsclerotia (Hamm *et al.*, 2008). While soil fumigation with an effective fumigant provides adequate control for the current growing season, generally not all of the soilborne inoculum is eliminated. The remaining microsclerotia can infect subsequent crops and begin building up inoculum. The intermediate and long-term effects of soil fumigation on populations of beneficial soil microbes and their effect on disease development have not been fully documented (Kinkel, 2008). After fumigation, precautions must be taken not to re-infest the field with the pathogen.

Soil solarization

Soil solarization by covering the soil surface with a transparent plastic film has been used to reduce the number of *Verticillium* propagules in fields (Katan, 1981). The exact mechanism of action is not understood, but is presumed to be due, in part, either to an elevation of temperature or a stimulation of antagonistic activity (Greenberger *et al.*, 1987). The practice is restricted to hot, dry climates and is a function of soil texture (sandy soils warm faster), soil temperature, soil moisture, and the amount of cloud cover and rainfall. Drawbacks are the need to cover large areas of a field with plastic, disposing of the polyethylene tarpaulins in an environmentally sound manner and leaving the field idle for an extended period during the growing season while it is covered with plastic. Biodegradable traps may be a feasible alternative for one of the objections.

Crop rotation

Crop rotations of three to four years to non-susceptible crops can effectively reduce soil populations of *V. albo-atrum*, but

generally not *V. dahliae* (Busch, 1973; Huisman & Ashworth, 1976; Joaquim *et al.*, 1988; Easton *et al.*, 1992). The reason is the lack vs. presence of microsclerotia for the two respective species. Failure to reduce wilt due to *V. dahliae* following crop rotation has been attributed to a low attrition rate of microsclerotia in soil. In addition, germinating microsclerotia may colonize roots of weeds and non-susceptible crops at low levels thereby maintaining inoculum levels sufficient to infect susceptible hosts (Joaquim *et al.*, 1988). Cross-pathogenicity of certain *V. dahliae* populations on hosts other than potato may also reduce the efficacy of crop rotation (Qin *et al.* 2006; Alkher *et al.*, 2009). However, rotation to non-susceptible hosts can reduce incidence of verticillium wilt and increase crop yields (O'Sullivan, 1978; Subbarao *et al.*, 2007). In a study in Washington, propagules of *V. dahliae* were reduced in potato stems and yields were maintained by alternate cropping or double cropping to non-host crops such as sudangrass, green peas and corn. The effect was more consistent if the non-host crop was planted for two consecutive years (Easton *et al.*, 1992). Green (1969) stated that the choice of rotation crops may be more important than the interval between susceptible crops. Poor management of susceptible weed species such as black nightshade (*Solanum nigrum* L.) can negate the value of rotation (Busch *et al.*, 1978). Susceptible weeds include *Chenopodium album* L., *Capsella bursa-pastoris* (L.) Med., and *Taraxacum* spp. Rotations with susceptible solanaceous crops such as eggplant and susceptible tomato cultivars should be avoided.

Cover crops

Incorporation of cover crops, including green manures, and organic amendments into fields before planting potatoes shows potential as a management tactic for verticillium wilt. Cover crops investigated for suppression of verticillium wilt include barley, broccoli, canola, mustards, corn, oat, sudangrass and winter pea. Results have varied (Easton *et al.*, 1992; Davis *et al.*, 1996; Subbarao & Hubbard, 1996; Xiao *et al.*, 1998; La Mondia *et al.*, 1999; Lazarovits *et al.*, 2001; Tenuta & Lazarovits, 2002) and host range of *V. dahliae* strains need to be determined for prospective green manures and specific crop sequences. In addition, long-term replicated field studies from different production areas are needed to confirm and quantify the effectiveness and economic value of green manures and organic soil amendments (Rowe & Powelson, 2004). There is an economic disadvantage to the use of green manures if production of the green manure crop requires a full season out of a cash

crop immediately preceding potato. Green manures are used in some locations in the Columbia Basin of Washington where mustard is double cropped after wheat during the relatively long growing season for that region. However, green manures are currently not widely integrated into most potato production systems.

Irrigation

Verticillium wilt of potato was favoured by moist soils early in the growing season in each of two studies (Cappaert *et al.* 1992, 1994). The possible mechanism for the increase in disease was not known, but excessively wet soils may have promoted shallow root growth with microsclerotia more concentrated in the upper soil profile (Arbogast *et al.*, 1999). Reduced available oxygen in saturated soils would also limit cellular respiration of roots and may deleteriously affect natural defences of the host. Maintaining 70–75% available soil moisture during vegetative growth of the crop and 80% soil moisture during tuber initiation (70% if soil temperatures are < 16 °C, to reduce physiological disorders) may reduce the amount of root infection by *V. dahliae* in irrigated fields (Cappaert *et al.*, 1992, 1994; Gudmestad, 2008; Powelson & Rowe, 2008). Infections by *Spongospora subterranea* (Wallr.) Lagerh., the powdery scab pathogen, and *Colletotrichum coccodes*, the cause of cortical root rot and black dot, may also be reduced by managing soil moisture. However, these soil moisture levels at these levels at tuber initiation can exacerbate common scab. Activity of the common scab pathogen is reduced by moist soils beginning at tuber initiation. With regard to water management, the relative potential importance of all potato diseases must be evaluated and soil moisture managed accordingly (Powelson & Rowe, 2008). Methods of irrigation can also affect severity of verticillium wilt in potato. The disease is generally less severe under overhead sprinkler irrigation than with furrow irrigation (Davis & Everson, 1986).

The strains of *V. dahliae* present in a field should be monitored for assessing the potential effects of management practices on the intensity of verticillium wilt. Dobinson *et al.* (2000) probed a restriction fragment of the putative trypsin gene (*Trp1*), as well as the rDNA repetitive sequences of 20 isolates collected from North American potatoes that were previously identified as VCG 4A and VCG 4B and highly aggressive on potato. Southern blot hybridization differentiated VCG 4A from VCG 4B, demonstrating a potential use in the molecular characterization of *V. dahliae* isolates prevalent on potatoes grown in North America. Sequence-based analysis also offers potential for discriminating potato pathogens

and the different VCGs occurring on potatoes in Europe and North America (Collado-Romero *et al.*, 2008). In addition, reliable field sampling techniques, including sample pattern and size, need to be developed to reliably assess the population of *Verticillium* present in fields. Molecular techniques show promise for such monitoring of the pathogen in fields (Mahuku & Platt, 2002; Kageyama *et al.*, 2003; Atallah *et al.*, 2007; Bae *et al.*, 2007).

Management of verticillium wilt of potato is currently inadequate because of a reliance in many areas of potato production on soil fumigation. More emphasis should be placed on integrating host resistance with tactics that economically and effectively reduce initial inoculum in soil without adversely affecting the environment. These tactics could potentially be cultural, biological, and/or chemical, and may be non-traditional. As an example, suppression of verticillium wilt of eggplant was recently achieved by augmenting soil with earthworms (Elmer & Ferrandino, 2009). The mechanism for reduction was not uncovered, but earthworms are an important component and indicator of soil health. Most certainly, a better understanding is needed of soil health and how soils can be managed to enhance pathogen suppression (Kinkel, 2008).

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