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Andrew Jensen, Editor. ajensen@potatoes.com; 509-760-4859

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Pathogen Dynamics and Management of Verticillium Wilt of Potato

Dennis A. Johnson and David Wheeler
Department of Plant Pathology, Washington State University, Pullman, WA

Introduction

Verticillium wilt is a potentially devastating disease of potato, causing infected plants to die prematurely. The disease is caused principally by *Verticillium dahliae,* but *V. albo-atrum* and other species of *Verticillium* also infect potato. Initial inoculum of *V. dahliae* is primarily soil borne microsclerotia that survive in soil, while that of *V. albo-atrum* consists of melanized hyphae. Because *V. albo-atrum* does not form microsclerotia this species survives for relatively shorter durations in soil. *Verticillium dahliae* has an extensive host range of over 200 dicotyledonous species and widespread distribution in temperate climates; whereas, *V. albo-atrum* has a more limited host range. *Verticillium dahliae* is favored by warmer temperatures than *V. albo-atrum*. *Verticillium dahliae* predominates in production areas where the average daily summer temperatures commonly exceed 27ºC (80.6ºF) 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 29ºC (64.4 to 84.2ºF). *Verticillium albo-atrum* is commonly found where the average daily temperatures normally do not exceed 21ºC 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. *Verticillium nigrescens* (now classified as *Gibellulopsis nigrescens*) and *V. tricorpus* also infect potato and other plants, but they are generally considered weakly aggressive or nonpathogenic (Skotland 1971, Slattery and Eide 1980). A strain of *V. albo-atrum,* which is not aggressive on potato, infects and is aggressive on alfalfa in the Pacific Northwest.

Infection and Disease Development

Microsclerotia in soil are an initial source of inoculum required for infection. Microsclerotia germinate in response to plant root exudates after which hyphae colonize the root surface and cortex. Disease symptoms occur after 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 (Vallad and Subbarao 2008). Root surfaces of resistant 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 (Atallah et al. 2007). Verticillium wilt-resistant plants have less vascular colonization than susceptible ones (Slattery 1981).

Some plants, depending on the strain of *V. dahliae*, support cryptic systematic infections (no symptom expression) and are termed asymptomatic hosts. Several mustards, sudangrass, Austrian winter peas, and sweet corn are asymptomatic hosts. However, the level of vascular colonization and microsclerotia development varies according to fungus strain and host species (Wheeler and Johnson 2016).

Microsclerotia form in colonized host tissue during senescence and continue to develop until stems dry to a low moisture content (Slattery 1981). They contribute to future inoculum levels when incorporated into the soil and can persist in field soils for up to 10 or more years. Microsclerotia embedded in stem residue retain viability longer than those existing free in soil and are capable of repeated germination over time. 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 2 or 3 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 (Joaquim et al. 1988). More than 90,000 microsclerotia can be introduced into soil by a single infected stem (Slattery 1981). More microsclerotia are produced and turned into the soil from susceptible than moderately resistant cultivars. Microsclerotia are then distributed throughout a field with the movement of colonized host debris by soil cultivation. In addition, infested soil carried on the surface of potato seed tubers can be another source of inoculum in potato (Dung et al. 2013a).

Symptom Development

Symptom expression and yield reductions in potato are influenced by soil and environmental conditions and become pronounced during times of heat stress and high rates of evapotranspiration. Initial infections may occur early in the growing season during rapid vegetative growth, but wilt symptoms usually do not develop until the later during tuber bulking and maturation. Initial symptoms appear as interveinal chlorosis on leaves of individual or groups of plants scattered among healthy-appearing plants. Wilting and necrosis follow and progress from the stem base to the top of plants. Foliar symptoms are often unilateral, affecting one side of a stem or a limited number of stems on one side of a plant. 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. Vascular browning may develop in tubers of some cultivars. The effects of Verticillium wilt on potato yield are variable, commonly ranging from 10 to 15% reduction in yield, but may reach 30 to 50% (Rowe and Powelson 2002).

Verticillium Strains

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 sometimes cultivar within a species. Isolates can be separated into vegetative compatibility groups (VCGs) based on their ability to undergo hyphal anastomosis or fusion with other isolates. Distinct sub-specific groups are recognized which contain host-adapted pathotypes that are prevalent and aggressive on particular hosts. The potato pathotype belongs to VCG 4A and is prevalent and aggressive on potato. Isolates of *V. dahliae* from potato are distinctly different than those from mint. Isolates of the mint pathotype belong to VCG 2B, will infect potato, but will not cause severe wilt symptoms in potato (Dung et al. 2013b).

Interactions with Other Pathogens

Co-infections of *V. dahliae* and *Colletotrichum coccodes* cause severe wilt symptoms and reduced yields, often more severely than in single-pathogen infections (Mohan et al. 1992, Tsror and Hazanovsky 2001). Synergistic interactions of *V. dahliae* with *Pratylenchus penetrans* also occur in potato with VCG 4A of *V. dahliae*, but not with other VCGs. When both *V. dahliae* VCG 4A and *P. penetrans* infect 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. Disease thresholds for Verticillium wilt in potato range between 5-30 colony-forming units (cfu)/cm^3 of soil for *V. dahliae* alone and 2-13 cfu/cm^3 soil when *P. penetrans* is present (Powelson and Rowe 1993). Likewise, the VCG 2B pathotype of *V. dahliae* from mint interacts with *P. penetrans* on peppermint and Scotch spearmint, causing increased disease severity, whereas the VCG 4A pathotype from potato does not (Johnson and Santo 2001). Thus, three-way interactions among the host, *V. dahliae* pathotype and *P. penetrans* occur on potato and mint.

Pathogen Dynamics

The quantity of *V. dahliae* in soil of potato fields may increase during the growing season (Dung et al. 2013a). *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 (Joaquim et al. 1988, Slattery 1981). Conidia can also be produced during plant senescence but are not thought to be significant in the disease cycle of annual crops (Vallad and Subbarao 2008); however, conidia are capable of surviving up to 2 weeks in soil and may be a factor for increase in the incidence of wilt in perennial crops such as mint. Microsclerotia and conidia are moved within and between fields by surface irrigation water (Easton et al. 1969).

Verticillium dahliae asymptomatically persists on roots of some cereal crops, grasses, mustards, and some weed species. Microsclerotia produced on roots and in stems of asymptomatic hosts are potentially a means of pathogen replenishment and prolonged persistence in soil (Vallad and Subbarao 2008). However, Benson and Ashworth (1976) concluded that parasitic colonization of asymptomatic hosts by *V. dahliae* was not a significant survival mechanism under field conditions.

Verticillium spp. can be transported long distances in infected certified seed tubers used for planting and in infested soil accompanying tuber transport. *Verticillium albo-atrum* and *V. dahliae* were detected in 39% of 244 certified seed lots in the late 1960s, with incidences in seed lots typically between 1 to 2% and rarely greater than 5% (Easton et al. 1972). 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) have important implications in both seed and production crops as well as the distribution of the disease.

Soil associated with seed tubers (tare dirt) was found to be infested with *V. dahliae* in over 82% of seed lots sampled in 2009 to 2011. Samples mostly contained <50 cfu/g soil but some contained > 500 cfu/g. Most isolates (93%) were VCG 4A. Additionally, infested tare dirt was shown to be important for infecting plants in the field, especially when levels of the fungus were originally low in field soil (Dung et al. 2013a).

Despite the presence of *Verticillium* spp. in certified seed lots, tuber-borne inoculum generally has little effect on wilt symptoms and potato yield (Dung et al 2012, Easton et al. 1972); however, severity of wilt resulting from tuber-borne infection varies among cultivars (Robinson and Ayers 1961). 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 (Dung and Johnson 2012). 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 potato or where a management practice such as fumigation has been applied to reduce soilborne inoculum.

Disease Management

Verticillium wilt caused by *V. dahliae* is difficult to manage because microsclerotia are difficult to destroy, the fungus infects and causes symptoms on a wide range of plants, and the fungus asymptomatically infects a number of plants used in rotation with potato and weeds in potato fields. In addition, *V. dahliae* consists of several strains, which interact with asymptomatic rotation and weedy hosts for infection and quantity of microsclerotia production (Frederick et al 2017, Wheeler and Johnson 2016). Furthermore, *V. dahliae* interacts synergistically with the root lesion nematode and with *Colletotrichum coccodes*. Efficacious systemic fungicides nor contact fungicides are not available. Furthermore, technology to place contact fungicides in root zone to protect actively growing roots is not currently available. Lastly, high levels of plant resistance have not been incorporated into commercially acceptable potato cultivars.

Management strategies for Verticillium wilt should focus on reducing initial inoculum levels in soils below threshold populations at which the fungus can develop and restrict vascular infection. Moreover, practices should be implemented to prevent the introduction of the pathogen to areas where the pathogen population is below the action threshold (Rowe and 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, soil solarization, and bio-fumigants. Host resistance restricts pathogen infection and colonization of plants (Atallah et al. 2007; Vallad and 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

Disease resistance is an active process by which the host opposes, completely or to some degree, the effects of the pathogen (Johnson and Gilmore 1980). Resistance is expressed when disease symptoms or pathogen signs are restricted on the host. Resistant and partially resistant cultivars to Verticillium wilt restrict vascular colonization 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 (Davis et al. 1994; Slattery 1981). Expression of resistance is influenced by environmental factors, and resistant cultivars can become infected and show wilt symptoms when planted in soils with high inoculum levels. 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. Resistant cultivars will continue to restrict colonization during this later stage of crop development.

Partially resistant cultivars that have been developed and commercially grown include Alpha, Alturas, Bannock Russet, CalWhite, Centennial Russet, Chipeta, Clearwater Russet, Gemchip, Goldrush, Legend, Ranger Russet, Russet Nugget, Umatilla Russet, and Western Russet. Tubers of Bannock Russet are very susceptible to *Phytophthora infestan*s (late blight), hollow heart, and shatter bruise, so the cultivar has not gained acceptance with the potato industry. Western Russet is very susceptible to *Alternaria solani* (early blight). This illustrates that new resistant cultivars must also have acceptable agronomic traits with no major defects. A challenge to potato improvement programs is to replace cultivars that are highly susceptible to Verticillium wilt, such as Russet Norkotah. Gem Russet, Russet Burbank, and Shepody are susceptible to Verticillium wilt. The repeated cropping of susceptible and especially very susceptible potato cultivars has increased inoculum levels of both *V. dahliae* and *V. albo-atrum* in soil with subsequent increased incidence of Verticillium wilt symptoms in commercial fields (Slattery 1981).

Soil fumigation

Soil fumigation with efficacious materials is effective in reducing the viability of the initial level on microsclerotia in soil and result in a delay in wilt development. Soil fumigation is both costly and subject to regulatory restrictions. 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.

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* (Easton et al. 1992; Joaquim et al. 1988). The reason is the lack versus 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 rotation 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 (Alkher et al. 2009; Qin et al. 2006). However, rotation to non-susceptible hosts can reduce incidence of Verticillium wilt and increase crop yields (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 crops such as sudangrass, green peas, and corn. The effect was more consistent if the rotation crop was planted for two consecutive years (Easton et al. 1992). Green (1969) stated that the choice of rotation cops may be more important than the interval between crops of susceptible crops.

Poor management of susceptible weed species that are asymptomatic such as black nightshade (*Solanum nigrum*.) can negate the value of rotation. Susceptible weeds include *Chenopodium album, Capsella bursa-pastoris* and *Taraxacum* spp. Black nightshade and wild oats are particularly susceptible to the potato pathotype of *V. dahliae* (Frederick 2017). 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 (Davis et al. 1996; Easton et al. 1992; La Mondia et al. 1999; Subbarao and Hubbard 1996; Tenuta and Lazarovits 2002).

Several green manure crops have been shown to be asymptomatically infected with *V. dahliae* in the Columbia Basin and microsclerotia production in some asymptomatic hosts has been relatively high in greenhouse tests (Wheeler and Johnson 2016). However, Verticillium wilt may not be severe in subsequent potato crops with such rotations. Explanations are that relatively high numbers of microsclerotia may not develop in green manure crops because of their relatively short fall-growing season with late cool temperatures. The population structure of *V. dahliae* may also change in the soil due to green manures and non-aggressive strains associated with selected rotation crops may provide cross protection against the more aggressive strains. Nevertheless, green manures are successfully used in some locations in the Columbia Basin where mustard is double cropped after wheat during the relatively long growing season of that region.

Irrigation

Verticillium wilt of potato was favored by moist soils early in the growing season in each of two studies (Cappaert et al. 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 defenses of the host. Maintaining 70 to 75% available soil moisture during vegetative growth of the crop and 80% soil moisture during tuber initiation (70% if soil temperatures are <16 ºC (60.8 ºF), to reduce physiological disorders) may reduce the amount of root infection by *V. dahliae* in irrigated fields (Cappaert et al. 1994; Gudmestad 2008). Infections by S*pongospora subterranean*, the powdery scab pathogen, and cortical root rot damage by *C. coccodes* (black dot) are likely to be reduced by avoiding excessive soil moisture. However, relatively dry soil moisture at tuber initiation can exacerbate common scab. With regard to water management, the relative potential importance of all potato diseases must be evaluated and soil moisture managed accordingly (Rowe and Powelson 2008). Methods of irrigation can also affect severity of Verticillium wilt in potato. Verticillium wilt is generally less severe with overhead sprinkler irrigation than with furrow irrigation (Davis and Everson 1986).

Conclusions

Management of Verticillium wilt of potato is inadequate because of a reliance on soil fumigation. Wilt resistance needs to be incorporated into more commercially viable cultivars and integrated 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 and 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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