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Management of soilborne diseases of potato

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Abstract. A large number of soilborne diseases that affect potato are important in the United States. In the Midwestern USA, early dying, involving *Verticillium dahliae* and *Colletotrichum coccodes* and the storage rots, pink rot and leak tuber rot, caused by *Phytophthora erythroseptica* and *Pythium ultimum* are among the most serious. Various aspects of the biology and aetiology of these pathogens have been investigated to improve our understanding of the factors involved in disease development. These studies have addressed knowledge gaps and have assisted in the development of management strategies and tactics for each disease. Disease management integrates cultural practices, use of agrochemicals and to some degree, host resistance. Unfortunately, cultural management practices alone are currently inadequate to control these diseases, causing the potato industry to become over-reliant on the use of agrochemicals for effective management. Current research efforts are directed at the identification and incorporation of genetic resistance into cultivars with acceptable horticultural characteristics to provide more effective disease management.

Introduction

Several very important potato pathogens in the USA originate from soilborne inoculum. The most important of these soilborne diseases can be separated into two primary groups; diseases that affect crop development and diseases that affect tuber quality. Soilborne diseases that affect crop development include Rhizoctonia canker, black dot, potato early dying (Verticillium wilt) and numerous nematodes. Soilborne diseases that affect tuber quality include common scab, powdery scab, pink rot, leak, black dot, black scurf, root knot nematode, and Fusarium dry rot. Among these, black dot, Verticillium wilt, pink rot and leak tuber rot are the most important in the Midwestern states of North Dakota and Minnesota. Disease management includes the integration of crop rotation, cultural practices, host resistance and agrochemicals.

Potato early dying is arguably the most economically damaging disease complex of potato in the USA when considering direct losses of yield and quality and the cost of control (Rowe and Powelson 2002). In the Midwestern USA, the disease complex is most important in the French fry processing sector, which relies on long season potato cultivars such as Russet Burbank. *Verticillium dahliae* is generally regarded as the primary pathogen involved in this disease complex (Rowe and Powelson 2002). This fungus survives as microsclerotia in the soil for extended periods of time (Davis and Huisman 2001). *V. dahliae* is a variable fungus, separated into groups based on vegetative compatibility (Rowe and Powelson 2002). Vegetative compatibility group (VCG) 4 is the most aggressive on potato, with subgroup 4A the most important (Joaquim and Rowe 1991; Strausbaugh 1993). Soil inoculum levels are known to influence disease severity (Ben-Yephet and Szmulewich 1985). Previous research in the Midwestern USA has demonstrated that an economic threshold of ≥8 *V. dahliae* propagules/g (vppg) of soil triggers the use of the soil fumigant metam sodium (Nicot and Rouse 1987), although more recent work has cast doubt on the relationship of *V. dahliae* soil populations and yield of potato (Davis *et al*. 2001). This more recent work suggests edaphic factors, such as organic matter and sodium concentration in the soil, influence disease severity, potato yield and perhaps inoculum efficacy.

Although *V. dahliae* is the most important pathogen in this complex, the root lesion nematode *Pratylenchus penetrans* and the black dot pathogen *Colletotrichum coccodes* are also involved (Otazu *et al*. 1978; Davis and Huisman 2001). Coinfection of *V. dahliae* and *C. coccodes* in the same plant hastens plant maturity and reduces plant development more so than either pathogen alone (Otazu *et al*. 1978; Tsror (Lahkim) *et al*. 1999). Most potato cultivars are very susceptible to *V. dahliae* and *C. coccodes*. However, two cultivars, Alturas and Ranger Russet (Novy *et al*. 2003), developed within the last decade, have resistance or tolerance to Verticillium wilt. They now account for nearly 10% of potato production for French fry processing. Unfortunately, the rest of this market sector relies on the use of metam sodium as a soil fumigant for the management of potato early dying. There have been numerous examples of control failure with metam sodium that required investigation, especially since this agrochemical is expensive and can potentially have significant negative impacts on the environment.

Pink rot and leak tuber rot, collectively referred to as 'water rots', are caused primarily by the soilborne fungi *Phytophthora erythroseptica* and *Pythium ultimum*, respectively. These two fungi cause problems with tuber quality and integrity of the stored potato crop. One could argue that in the USA, tuber rots caused by *P. erythroseptica* and *P. ultimum* are economically more important on a yearly basis than any other disease affecting

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tuber quality. Late blight tuber rot infections tend to be acute and spectacularly devastating when they occur. However, in most production years, few growers experience economic loss from this phase of the disease. Pink rot and leak tuber rot are chronic and endemic diseases, present every year in nearly every potato production region. Storage rot surveys conducted in each of the past nine years in North Dakota and Minnesota indicate that pink rot and leak tuber rot are of almost equal importance with one or the other being more important in any one year (R. J. Taylor and N. C. Gudmestad, unpubl. data).

Differences in the aetiology of pink rot and leak tuber rot are significant, which ultimately affects disease management (Taylor *et al*. 2004). Infection of pink rot usually occurs in the field, before harvest, when zoospores of *P. erythroseptica* infect stolons, tuber eyes or lenticels (Lambert and Salas 2001). Infection by *P. ultimum* is strictly through wounds made at harvest (Salas and Secor 2001). Cultural practices alone are frequently inadequate to manage pink rot and leak tuber rot, which has caused the potato industry to become overly reliant on the use of mefenoxam (metalaxyl)-based fungicides for disease control. Unfortunately, mefenoxam resistance has been reported in *P. ultimum* and is widespread in *P. erythroseptica* (Taylor *et al*. 2002). Understanding the impact of mefenoxam resistance on disease management in addition to the development of alternative and effective management strategies is of utmost importance for the control of water rots.

The discussion that follows is intended to demonstrate the approach our research group has undertaken to more fully understand the biology and aetiology of the pathogens involved in the early dying complex and the water rot storage disease syndrome. The overall goal has been to fill the knowledge gaps for each disease-causing pathogen so as to improve disease management options for the potato industry. Whenever possible, our data will be discussed within the context of the information generated by other research groups where these diseases are also important.

Early dying

Although the biology and ecology of *V. dahliae* is relatively well understood, there are aspects of the pathogen that required further definition to improve disease management. Soil pathogens can be affected by several soil physical properties (Rothrock 1992), and tillage is known to affect several of these properties and exert an influence on disease development (Peters *et al*. 2003, 2004). With *Verticillium* spp., soil inoculum levels are known to vary spatially and temporally, but much of that work was interpolated and quite old. Wilhelm (1950) demonstrated that the vertical distribution of *Verticillium albo-atrum* varied considerably, with the greatest proportion residing in the upper 30 cm of soil, nearest the surface. More recently, *V. dahliae* was found to be concentrated primarily in the upper 20 cm soil strata (Ben-Yephet and Szmulewich 1985; Hamm *et al*. 2003). Results of our research in the Midwestern USA has determined that the inocula of *V. dahliae* is concentrated in the upper 10 cm (Taylor *et al*. 2005). We believe that changes in tillage practices, specifically those directed at soil conservation, are directly responsible for the concentration of inoculum in the upper 10 cm soil strata. Research by our potato pathology group has demonstrated that tillage practices influence survival of both pathogens as well as the efficacy of metam sodium (Taylor *et al*. 2005).

Conservation tillage is a commonly used practice in crops planted in rotation with potato. Conservation tillage, known variously as reduced tillage, no tillage or minimum tillage, are practices intended to preserve crop residue near the soil surface to enhance soil organic matter content, protect soil from erosion and several other benefits. Chisel ploughing, as opposed to the traditional tillage practice of mouldboard ploughing, is the most frequently used method of conservation tillage. Mechanical harvesting of potatoes leaves the crop residue at the soil surface where *V. dahliae* resides. The equipment currently utilised for reduced tillage practices do little to incorporate or mix the soil layers (Taylor *et al*. 2005), resulting in >70% of the *V. dahliae* inoculum residing in the upper 10 cm of soil. In contrast, mouldboard ploughing inverts the soil strata thereby causing a significant amount of the *V. dahliae* inocula to reside in soil at depths of 20 cm. We feel that older studies, and those studies conducted in potato production areas where mouldboard ploughing is still common, explain the contrasting results between our work and that found in the literature. Since metam sodium is applied as a liquid but must volatilise into a gas to permeate through the soil profile to act on the microsclerotia of *V. dahliae*, the concentration of soil inoculum at the surface provides a significant challenge in successful soil fumigation. Our studies concluded that much of the metam sodium gas is lost to the atmosphere in the upper 10 cm resulting in very poor mortality of the *V. dahliae* microsclerotia and the concomitant loss of disease control (Taylor *et al*. 2005). Simple inversion of the soil strata using mouldboard ploughing significantly improved disease control of early dying. Not only does mouldboard ploughing improve the efficacy of metam sodium fumigation (Taylor *et al*. 2005) but this tillage practice increases the mortality of *V. dahliae* propagules in the soil (Fig. 1*a*) and also significantly reduces black dot (Fig. 1*b*), an observation that supports previous studies (Denner *et al*. 2000). These results are in direct contrast with an earlier study on *Rhizoctonia solani*, in which case disease severity was reduced with conventional tillage practices compared to mouldboard ploughing (Gudmestad *et al*. 1978).

The length of rotation also affects the management of early dying, primarily by affecting the soil populations of *V. dahliae* (Fig. 2). Soil populations of *V. dahliae* can be 2- to 4-fold higher in soils with a 2 year potato rotation (Fig. 2*a*) compared to a 3-year potato rotation (one potato crop in three years) (Fig. 2*b*). Higher soil populations make effective control via soil fumigation with metam sodium much more difficult. For example, if we accept an economic threshold of 8 vppg (Nicot and Rouse 1987) and an efficacy of metam sodium of no more than 70% (Taylor *et al*. 2005), then it is easy to understand that soil populations of *V. dahliae* of >25 vppg before fumigation will likely leave a resident population above threshold. For this reason, our recommendations are that potato rotation durations should not exceed one potato crop in three years. Additionally, seasonal variations of *V. dahliae* populations clearly indicate that it takes one and a half to two years before the decomposition of potato crop debris will be sufficient enough to obtain effective fumigation (Joaquim *et al*. 1988; Taylor *et al*. 2005). When

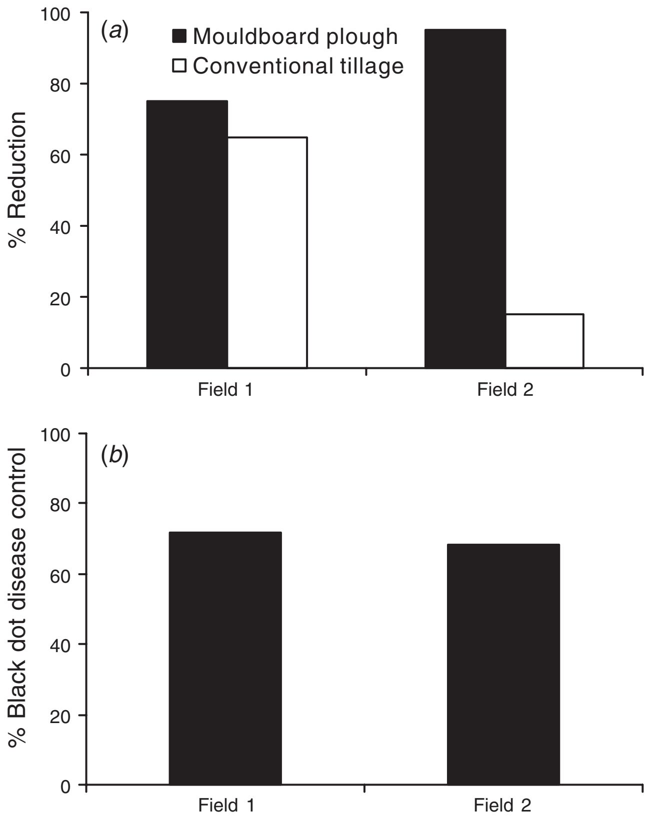

Fig. 1. Effect of mouldboard ploughing relative to conventional tillage on reduction of *Verticillium dahliae* microsclerotia in the upper 20 cm of soil (*a*) and on the control of black dot (*b*) in two fields in Minnesota. Data taken on a georeferenced basis in two fields split by tillage practice over a 3-year period, 2003–2005.

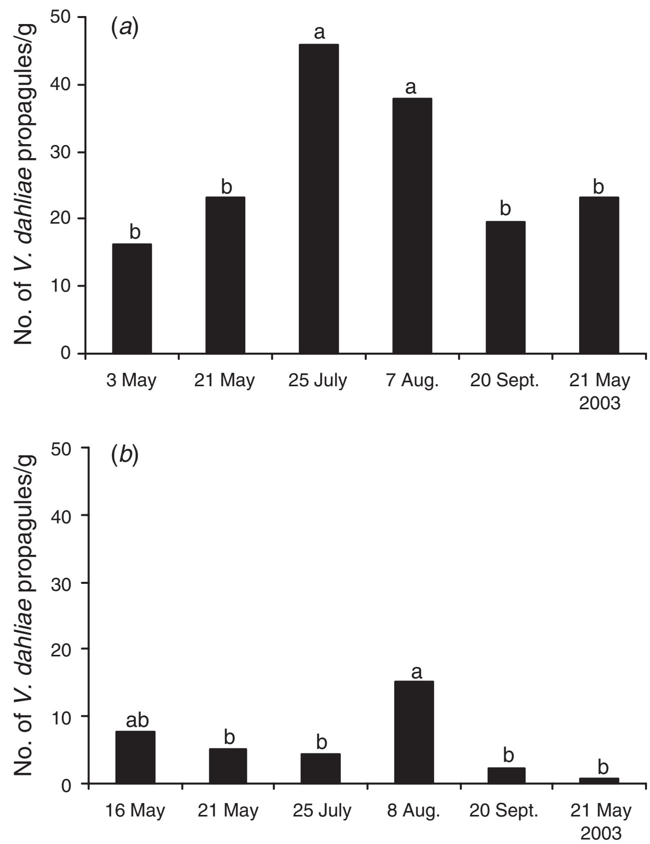

Fig. 2. Propagules of *Vertillium dahliae* recovered over the course of a growing season from field soils planted to potato in a 2-year (*a*) and 3-year (*b*) rotation. Soils were sampled in 2002, which was the year before each field was cropped to potato. (Data taken from Taylor *et al*. 2005)

V. dahliae soil inoculum is protected by crop debris it cannot be killed by metam sodium, resulting in poor efficacy (Taylor *et al*. 2005). The data generated by our research group have been important in reducing soil populations through cultural practices such as mouldboard ploughing and by improving efficacy of metam sodium applications.

The early dying complex in the USA is exacerbated by the presence of *C. coccodes* – the black dot pathogen. *C. coccodes* can cause reductions in yield and quality by itself (Johnson 1994; Tsror (Lahkim) *et al*. 1999), but appears to be particularly important with coinfections of *V. dahliae* (Otazu *et al*. 1978; Tsror (Lahkim) and Hazanovsky 2001). A great deal of attention has been given to tuber infections of *C. coccodes*, which causes a tuber blemish and much of what we know about the disease black dot is from this very important phase of the disease (Read and Hide 1995; Lees and Hilton 2003). However, foliar infections of *C. coccodes* are known to occur and to be an important component of the disease (Johnson and Miliczky 1993; Johnson 1994). It also appears that the fungus preferentially grows towards the roots and stolons rather than towards the apex (Nitzan *et al*. 2006*b*). Whether or not this is the mechanism by which the fungus reaches the vascular tissue is not known at this time. We also do not know the importance of seedborne (Johnson *et al*. 1997) compared with soilborne inoculum (Cullen *et al*. 2002), but there is information suggesting the importance of either source may be cultivar specific (Nitzan *et al*. 2005). Unfortunately, metam sodium is ineffective in the management of black dot, presumably because the microsclerotia of *C. coccodes* are significantly larger than those of *V. dahliae* making them resistant to this biocide.

Our research group has concentrated our efforts on understanding the infection frequency of various plant parts relative to yield (Gudmestad *et al*. 2005). Previous research in Europe has suggested that belowground plant parts, stems, stolons and roots are the most rapidly colonised by *C. coccodes* (Read and Hide 1995; Andrivon *et al*. 1998). Our data demonstrate that aboveground stems are more rapidly colonised by this fungus and that yield loss is associated with the infection frequency of this plant part (Fig. 3) (Gudmestad *et al*. 2005). Data obtained to date also suggest that soilborne inoculum of $\geq$70 *C. coccodes* propagules/g of soil is sufficient to negatively affect tuber yield. We are in the process of developing a duplex real-time PCR technique to quantify soil populations of *V. dahliae* and *C. coccodes* (N. C. Gudmestad and J. S. Pasche, unpubl. data). The *C. coccodes* primers used in the duplex are based on previously published studies (Cullen *et al*. 2002) and the DNA sequences used to develop the *V. dahliae* were derived

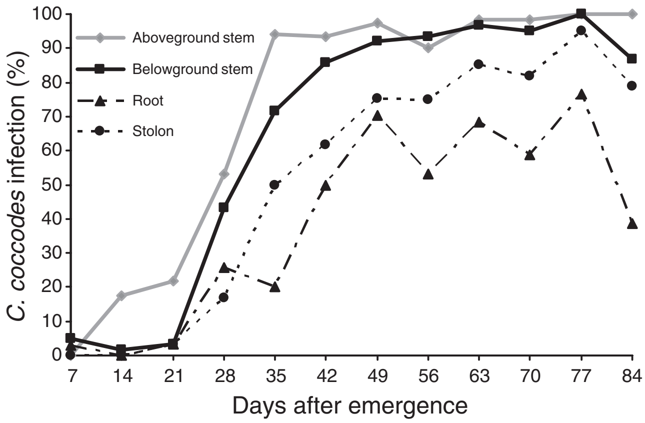

Fig. 3. Frequency of *Colletotrichum coccodes* recovery from aboveground stems, belowground stems, stolons, roots and stolons during the growing season.

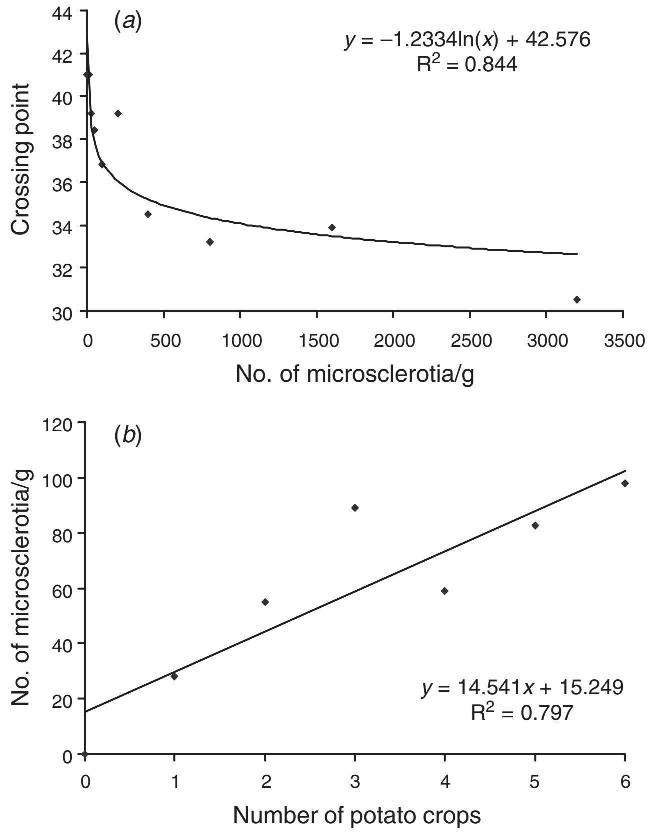

Fig. 4. Relationship of fluorescence (F1/F2) to microsclerotia of *Colletotrichum coccodes* detected from artificially infested field soil (*a*) and the relationship between the number of potato crops and population of *C. coccodes* in fields ($n = 45$) tested using real-time PCR (*b*).

from studies characterising this pathogen (Dobinson *et al*. 2000). We have been able to correlate signal strength with numbers of *C. coccodes* microsclerotia (Fig. 4*a*). Real-time PCR will be a useful tool in developing effective management strategies for *V. dahliae* and *C. coccodes*. Data obtained to date suggest that the number of potato crops planted in a field directly influences the soil population of *C. coccodes* (Fig. 4*b*). As the number of times potato is grown on a field increases, so does the population of the black dot fungus. Fields with excessively high populations can be avoided and planted to a rotational crop. The rate of metam sodium can be adjusted based on the level of *V. dahliae* in the soil optimising its use and minimising the overuse of this agrochemical.

VCGs are known to exist for both *V. dahliae* and *C. coccodes* and represent a significant amount of diversity among populations of these two pathogens (Joaquim and Rowe 1991; Strausbaugh 1993; Heilmann *et al*. 2006; Nitzan *et al*. 2006*a*). Similar to *V. dahliae*, differences exist in aggressiveness among VCGs of *C. coccodes*, and we are able to differentiate among these groups using amplified fragment length polymorphism (AFLP) analyses (Heilmann *et al*. 2006; Nitzan *et al*. 2006*a*). We believe AFLP analysis, once specific bands are converted to sequence-characterised amplified regions or SCAR markers, will be a useful tool in further studies involving the biology and management of black dot (Heilmann *et al*. 2006).

Pink rot and leak tuber rots

The incidence and severity of pink rot and leak tuber rot can vary considerably from year to year. This variability necessitates vigilance by growers in the careful implementation of the management options that exist for each disease. For example, tuber pulp temperatures at harvest are known to have a significant impact on the development of leak tuber rot (Salas and Secor 2001). The incidence and severity of leak tuber rot is significantly higher at tuber temperatures above 21°C and is nearly arrested at temperatures below 10°C. Similar studies by our research group have determined that tuber pulp temperatures at harvest also influence pink rot development (Salas *et al*. 2000). Although infection by *P. erythroseptica* was initially believed to occur only in the field, before harvest, our studies have demonstrated that high infection rates in storage are usually due to postharvest infections (Salas *et al*. 2000) and that the degree of wounding and tuber pulp temperatures have a significant influence on the development of this phase of the disease. Tuber pulp temperatures above 18°C increase postharvest infections by the pink rot pathogen (Salas *et al*. 2000). Therefore, an important cultural management practice for the water rot complex is to avoid harvesting potatoes when tuber pulp temperatures exceed 18°C. Recently, a management tactic was developed to reduce post-harvest infections of *P. erythroseptica* with the application of phosphoric acid onto tubers being placed into storage (Miller *et al*. 2006).

Most potato cultivars in production in the USA are susceptible to both pink rot and leak tuber rot (Salas *et al*. 2003), although a few cultivars have moderate levels of resistance to one, but not both, of these diseases. We have recently developed a source of resistance to both pink rot and leak tuber rot, resulting from a somatic hybrid backcross clone derived from *Solanum berthaultii* and *S. etuberosum* (Thompson *et al*. 2007). It will be some time before this source of resistance is reflected in commercially accepted potato cultivars.

Since most potato cultivars are susceptible to pink rot and leak tuber rot, the industry has developed a reliance on the fungicide mefenoxam for disease management. Mefenoxam provides excellent control of pink rot, and fair control of leak tuber rot when applied in furrow (Taylor *et al*. 2004). The advantage of at planting applications of mefenoxam, in furrow, compared with foliar applications for pink rot control, has also been demonstrated in Australia (Wicks *et al*. 2000). The difference in the level of disease control of pink rot relative to leak tuber rot is directly related to differences in aetiology between the two diseases (Taylor *et al*. 2004). After the application of mefenoxam to potato plants, it is known to concentrate in the periderm of tubers (Bruin *et al*. 1982), a phenomenon made possible only with phenylamide fungicides since they are symplastically mobile in plants and capable of movement in the phloem. Wounds made at harvest breech the barrier to infection afforded by mefenoxam, thereby reducing efficacy in leak tuber rot control relative to pink rot (Taylor *et al*. 2004), since *P. ultimum* is a strict wound pathogen. The level of control of leak tuber rot which is provided by mefenoxam is not economic, therefore, we recommend potato growers do not use this fungicide solely for this purpose. In other words, in the absence of disease pressure from pink rot, growers should avoid using mefenoxam for the control of leak tuber rot. It is important to note, however, that wounding of tubers at harvest can also negate the effects of mefenoxam application with the pink rot pathogen (Fig. 5). Therefore, cultural practices that encourage skin set and minimise wounds at harvest are important in preserving the level of control afforded by the application of mefenoxam.

Disease control is further exacerbated by the occurrence of mefenoxam resistance in both the pink rot and the leak tuber rot pathogen (Taylor *et al*. 2002). Mefenoxam resistance in *P. erythroseptica* appears to be widespread in the states of Maine, Idaho, Colorado and Minnesota. We also have detected mefenoxam resistant isolates of the pathogen in North Dakota, Wisconsin and Michigan. Based on data generated by our research group, the inheritance of mefenoxam resistance in *P. erythroseptica*, a homothallic fungus, appears to be inherited quantitatively (Abu El Samen *et al*. 2005). Populations of the pathogen become qualitatively less sensitive to the fungicide in successive generations indicating that once shifts in sensitivity occur, they are not reversible. Most recently, we have demonstrated that mefenoxam resistant populations of *P. erythroseptica* are not only parasitically fit, but in the presence of the fungicide they are likely to cause more disease than in the absence of the fungicide (Taylor *et al*. 2006). These results have a significant impact on disease management strategies and demonstrate the impact that over reliance on a single tactic can have on an industry. As a result, we continually monitor the *P. erythroseptica* populations on individual farms and once mefenoxam resistance is detected, we recommend this fungicide no longer be used. Phosphorous acid based fungicides apparently provide suppression of pink rot, but have no effect on leak tuber rot (Johnson *et al*. 2004). Unfortunately, the multiple applications of phosphorous acid required to achieve this level of control is very expensive, ~2–3 times the cost of mefenoxam based fungicides and may not be economical.

When lacking host resistance and chemical control, potato producers are left to manage pink rot and leak tuber rot using cultural methods that limit wounding and encourage tuber maturation. They should also harvest when tuber pulp temperatures are <18°C, and cool the crop in storage as soon as possible. Conservation tillage practices, especially those that appear to promote the development of soils suppressive to pink rot, hold significant promise for the management of this disease in some areas of North America (Peters *et al*. 2003, 2004).

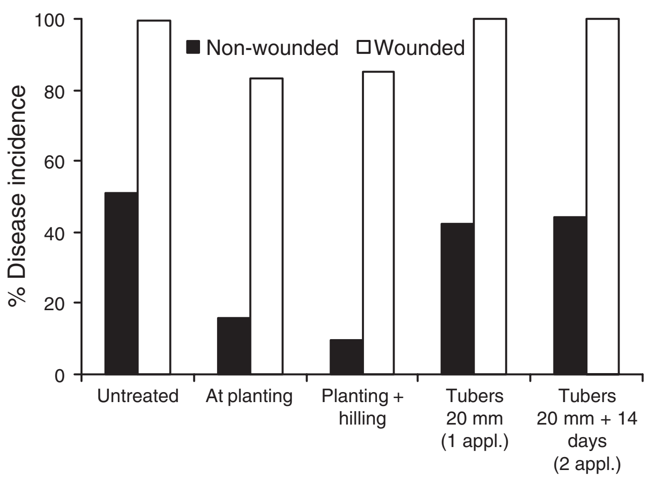

Fig. 5. Pink rot disease incidence in wounded and non-wounded tubers (cv. Russet Burbank) obtained from plants non-treated and treated with mefenoxam in the soil at planting (one application), planting and hilling (two applications), to the foliage when tubers were 20 mm in diameter (one application), and to the foliage when tubers were 20 mm in diameter and 14 days later (two applications). All soil and foliar applications were made at a rate of 200 g a.i./ha.

Summary and future research

Two fungi are involved in the early dying complex throughout most of the USA, *V. dahliae* and *C. coccodes*. Potato plants infected with both pathogens die more rapidly than plants infected with either pathogen alone. Both fungi form microsclerotia that allow them to survive extended periods of time in the absence of a host. Although resistance to *V. dahliae* exists, resistance to *C. coccodes* has not been identified as it relates to early dying, although there are differences in cultivar susceptibility. The introgression of resistance to both diseases will be impeded due to the requirement that commercial cultivars have quality characteristics making them suitable for processing, traits that are complexly inherited.

To date, management of early dying is largely achieved by crop rotation and soil fumigation using metam sodium. The microsclerotia of *C. coccodes*, however, are larger than those of *V. dahliae* rendering them resistant to fumigation by metam sodium. Propagules of *V. dahliae* can be reduced by tillage practices such as mouldboard ploughing, which has also been demonstrated to reduce incidence of black dot. Rapid and accurate determination of soil populations of both fungi using real-time PCR is being developed by several groups. Our focus is in the development of a duplex real-time PCR reaction that will quantify *V. dahliae* and *C. coccodes* simultaneously. This will be a useful tool in future studies on the biology, ecology and interaction of these two pathogens which is important because the true nature of the involvement of *C. coccodes* in the early dying complex is not completely resolved at this time. Quantification of soil inocula of both pathogens can also be an important tool in the management of early dying.

The two most important diseases affecting tuber quality in the USA are pink rot and leak tuber rot, caused by *P. erythroseptica* and *P. ultimum*. These are chronic diseases present each year in nearly every potato growing region. Similar to the treatment of early dying, disease management practices among potato producers are dependent on the use of agrochemicals. Fungicide resistance in the pink rot pathogen is rapidly rendering this disease management tactic useless. Most commercially grown potato cultivars in the USA are susceptible to one or both of these diseases, however, genetic resistance exists and is currently being exploited.

Our research group also is examining the relationship between cultivar resistance and mefenoxam efficacy as it relates to disease development and ultimately, disease management. Cultivars most likely to benefit from mefenoxam applications could be selected as part of a management scheme and mefenoxan might be applied in a targeted manner to supplement the level of disease control afforded by genetic resistance. Preliminary results have demonstrated that judicious applications of mefenoxam, when matched with the level of cultivar susceptibility, may prove to be an efficient and effective approach to reduce infection rates and possibly manage mefenoxam resistance and in turn, help maintain longevity of the compound. Although genetic resistance to pink rot and leak tuber rot remain the most desirable management strategy, the constraints that affect the use of resistance to *V. dahliae* in cultivars that possess acceptable process quality also affects the breeding for resistance to pink rot and leak tuber rot.

Tillage practices have been demonstrated to affect all of the diseases discussed here, although results differ for each type of disease. Mouldboard ploughing has been shown to have positive effects in the management of early dying relative to conventional tillage. However, with pink rot, conservation tillage has been shown to reduce disease incidence. More research is needed on the impacts of tillage practices and the development of Verticillium wilt and black dot as well as for pink rot and leak tuber rot.

Currently, no cultivars are resistant to both Verticillium wilt and black dot. Similarly, there are no commercial cultivars resistant to both pink rot and leak tuber rot. However, resistance to several of these diseases exists and needs to be exploited further. A concerted effort is required to identify resistance to black dot. Furthermore, quality trait loci and DNA-based markers associated with the resistance to all of these diseases are needed to facilitate rapid progress.

References

Abu-El Samen FM, Oberoi K, Taylor RJ, Secor GA, Gudmestad NC (2005) Inheritance of mefenoxam resistance in two selfed generations of the homothallic *Phytophthora erythroseptica* (Pethybr.). *American Journal of Potato Research* **82**, 105–115.

Andrivon D, Lucas JM, Guerin C, Jouan B (1998) Colonization of roots, stolons, tubers and stems of various potato (*Solanum tuberosum*) cultivars by the black dot fungus *Colletotrichum coccodes. Plant Pathology* **47**, 440–445. doi: 10.1046/j.1365-3059.1998.00267.x

Ben-Yephet Y, Szmulewich Y (1985) Inoculum levels of *Verticillium dahliae* in the soils of the hot semi-arid Negev region of Israel. *Phytoparasitica* **13**, 193–200.

Bruin GCA, Edgington LV, Ripley BD (1982) Bioactivity of the fungicide metalaxyl in potato tubers after foliar sprays. *Canadian Journal of Plant Pathology* **4**, 353–356.

Cullen DW, Lees AK, Toth IK, Duncan JM (2002) Detection of *Colletotrichum coccodes* from soil and potato tubers by conventional and quantitative real-time PCR. *Plant Pathology* **51**, 281–292. doi: 10.1046/j.1365-3059.2002.00690.x

Davis JR, Huisman OC (2001) Verticllium wilt. In 'Compendium of potato diseases'. 2nd edn. (Eds WR Stevenson *et al.*) pp. 45–46. (American Phytopathological Press: St Paul, MN)

Davis JR, Huisman OC, Everson DO, Schneider AT (2001) Verticillium wilt of potato: a model of key factors related to disease severity and tuber yield in southeastern Idaho. *American Journal of Potato Research* **78**, 291–300.

Denner FDN, Millard CP, Wehner FC (2000) Effect of soil solarisation and mouldboard ploughing on black dot of potato, caused by *Colletotrichum coccodes. Potato Research* **43**, 195–201. doi: 10.1007/BF02358079

Dobinson KF, Harrington MA, Omer M, Rowe RC (2000) Molecular characterisation of vegetative compatibility group 4A and 4B isolates of *Verticillium dahliae* associated with potato early dying. *Plant Disease* **84**, 1241–1245.

Gudmestad NC, Huguelet JE, Zink RT (1978) The effect of cultural practices and straw incorporation into the soil on Rhizoctonia disease of potato. *Plant Disease Reporter* **62**, 985–988.

Gudmestad NC, Pasche JS, Taylor RJ (2005) Infection frequency of *Colletotrichum coccodes* during the growing season. In 'Proceedings of the 16th triennial European Association for Potato Research conference'. (Eds E Ritter, A Carrascal) pp. 765–769. (Central Service of Publications of the Basque Government: Vitoria-Gasteiz, Spain)

Hamm PB, Ingham RE, Jaeger JR, Swanson WH, Volker KC (2003) Soil fumigant effects on three genera of potential soilborne pathogenic fungi and their effect on yield in the Columbia Basin of Oregon. *Plant Disease* **87**, 1449–1456.

Heilmann LJ, Nitzan N, Johnson DA, Pasche JS, Doetkett C, Gudmestad NC (2006) Genetic variability in the potato pathogen *Colletotrichum coccodes* as determined by AFLP and vegetative compatibility group analyses. *Phytopathology* **96**, 1097–1107.

Joaquim TR, Rowe RC (1991) Vegetative compatibility and virulence of strains of *Verticillium dahliae* from soil and potato plants. *Phytopathology* **81**, 552–558.

Joaquim TR, Smith VL, Rowe RC (1988) Seasonal variation and the effects of wheat rotation on populations of *Verticillium dahliae* Kleb. in Ohio potato field soils. *American Potato Journal* **65**, 439–447.

Johnson DA (1994) Effect of foliar infection caused by *Colletotrichum coccodes* on yield of Russet Burbank potato. *Plant Disease* **78**, 1075–1078.

Johnson DA, Miliczky ER (1993) Effects of wounding and wetting duration on infection of potato foliage by *Colletotrichum coccodes. Plant Disease* **77**, 13–17.

Johnson DA, Rowe RC, Cummings TF (1997) Incidence of *Colletotrichum coccodes* in certified potato seed tubers planted in Washington State. *Plant Disease* **81**, 1199–1202.

Johnson DA, Inglis DA, Miller JS (2004) Control of potato tuber rots caused by oomycetes with foliar applications of phosphorous acid. *Plant Disease* **88**, 1153–1159.

Lambert D, Salas B (2001) Pink rot. In 'Compendium of potato diseases'. 2nd edn. (Eds WR Stevenson *et al.*) pp. 33–34. (American Phytopathological Press: St Paul, MN)

Lees AK, Hilton AJ (2003) Black dot (*Colletotrichum coccodes*): an increasingly important disease of potato. *Plant Pathology* **52**, 3–12. doi: 10.1046/j.1365-3059.2003.00793.x

Miller JS, Olsen N, Woodell L, Porter LD, Clayson S (2006) Post-harvest applications of zoxamide and phosphite for control of potato tuber rots caused by oomycetes at harvest. *American Journal of Potato Research* **83**, 269–278.

Nicot PC, Rouse DI (1987) Precision and bias of three quantitative soil assays for *Verticillium dahliae. Phytopathology* **77**, 875–881.

Nitzan N, Cummings TF, Johnson D (2005) Effect of seed-tuber generation, soilborne inoculum, and azoxystrobin application on development of potato black dot caused by *Colletotrichum coccodes. Plant Disease* **89**, 1181–1185.

Nitzan N, Tsror (Lahkim) L, Johnson D (2006*a*) Vegetative compatibility groups and aggressiveness of North American isolates of *Colletotrichum coccodes*, the causal agent of potato black dot. *Plant Disease* **90**, 1287–1292.

Nitzan N, Evans M, Johnson D (2006*b*) Colonization of potato plants after aerial infection by *Colletotrichum coccodes*, causal agent of potato black dot. *Plant Disease* **90**, 999–1003.

Novy RG, Corsini DL, Love LS, Pavek JJ, Mosley AR *et al* (2003) Alturas: a multi-purpose, russet potato cultivar with high yield and tuber specific gravity. *American Journal of Potato Research* **80**, 295–301.

Otazu V, Gudmestad NC, Zink RT (1978) The role of *Colletotrichum atramentarium* in the potato wilt complex in North Dakota. *Plant Disease Reporter* **62**, 847–851.

Peters RD, Sturz AV, Carter MR, Sanderson JB (2003) Developing disease-suppressive soils through crop rotation and tillage management practices. *Soil and Tillage Research* **72**, 181–192. doi: 10.1016/S0167-1987(03)00087-4

Peters RD, Sturz AV, Carter MR, Sanderson JB (2004) Influence of crop rotation and soil conservation tillage practices on the severity of soil-borne potato diseases in temperate humid agriculture. *Canadian Journal of Soil Science* **84**, 397–402.

Read PJ, Hide GA (1995) Development of black dot disease (*Colletotrichum coccodes* (Wallr.) Hughes) and its effects on the growth and yield of potato plants. *The Annals of Applied Biology* **127**, 57–72.

Rothrock CS (1992) Tillage systems and plant disease. *Soil Science* **154**, 308–315. doi: 10.1097/00010694-199210000-00007

Rowe RC, Powelson ML (2002) Potato early dying: management changes in a changing production environment. *Plant Disease* **86**, 1184–1193.

Salas B, Secor GA (2001) Leak. In 'Compendium of potato diseases'. 2nd edn. (Eds WR Stevenson *et al.*) pp. 30–31. (American Phytopathological Press: St Paul, MN)

Salas B, Stack RW, Secor GA, Gudmestad NC (2000) Effect of wounding, temperature and inoculum on the development of pink rot of potato caused by *Phytophthora erythroseptica. Plant Disease* **84**, 1327–1333.

Salas B, Secor GA, Taylor RJ, Gudmestad NC (2003) Assessment of resistance in tubers of potato cultivars to *Phytophthora erythroseptica* and *Pythium ultimum. Plant Disease* **87**, 91–97.

Strausbaugh CA (1993) Assessment of vegetative compatibility and virulence of *Verticillium dahliae* isolates from Idaho potatoes and tester strains. *Phytopathology* **83**, 1253–1258.

Taylor RJ, Salas B, Secor GA, Rivera V, Gudmestad NC (2002) Sensitivity of North American isolates of *Phytophthora erythroseptica* and *Pythium ultimum* to mefenoxam (metalaxyl). *Plant Disease* **86**, 797–802.

Taylor RJ, Salas B, Gudmestad NC (2004) Differences in etiology affects mefenoxam efficacy and the control of pink rot and leak tuber diseases of potato. *Plant Disease* **88**, 301–307.

Taylor RJ, Pasche JS, Gudmestad NC (2005) Influence of tillage and method of metam sodium application on distribution and survival of *Verticillium dahliae* in the soil and the development of potato early dying disease. *American Journal of Potato Research* **82**, 451–461.

Taylor RJ, Pasche JS, Gudmestad NC (2006) Biological significance of mefenoxam resistance in *Phytophthora erythroseptica* and its implications for the management of pink rot of potato. *Plant Disease* **90**, 927–934.

Thompson AL, Taylor RJ, Pasche JS, Novy RG, Gudmestad NC (2007) Resistance to Phytophthora erythroseptica and Pythium ultimum in a potato clone derived from S. berthaultii and S. etuberosum. *American Journal of Potato Research* in press.

Tsror (Lahkim) L, Erlich O, Hazanovsky M (1999) Effect of *Colletotrichum coccodes* on potato yield, tuber quality, and stem colonization during spring and autumn. *Plant Disease* **83**, 561–565.

Tsror (Lahkim) L, Hazanovsky M (2001) Effect of coinoculation by *Verticillium dahliae* and *Colletotrichum coccodes* on disease symptoms and fungal colonization in four potato cultivars. *Plant Pathology* **50**, 483–488. doi: 10.1046/j.1365-3059.2001.00585.x

Wilhelm S (1950) Vertical distribution of *Verticillium albo-atrum* in soils. *Phytopathology* **40**, 368–376.

Wicks TJ, Davoren CW, Hall BH (2000) Fungicidal control of *Phytophthora erythroseptica*: the cause of pink rot on potato. *American Journal of Potato Research* **77**, 233–240.

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