Comments on the Feature “Potato Early Dying: Management Challenges in a Changing Production Environment”

In the November 2002 issue of Plant Disease, a review article was published entitled “Potato Early Dying: Management Challenges in a Changing Production Environment” by Randy Rowe and Mary Powelson (21). *Verticillium* wilt (potato early dying) is a major factor in potato culture in most production areas. Management practices for minimizing economic losses due to this disease are and will continue to be important in potato production. The review article covers many of the management issues. However, a number of important management practices were either not covered or covered inadequately. We would like to address some of these.

The role of plant nutrition. Proper management of plant nutrition has a major impact on *Verticillium* wilt severity. Depending on the variety, plant nutrition is a key factor for the expression of *Verticillium* wilt tolerance. Because this is a significant management tool (3), it needs to be addressed in an article focusing on *Verticillium* wilt. Davis et al. (12) showed that, in addition to suppressing *Verticillium* wilt by as much as 95%, N-P treatments also reduced the rate of increase of soil-borne inoculum of *Verticillium dahliae* following a potato crop. Generally, as N and P are increased and kept in balance, both wilt incidence and *V. dahliae* colonization values are reduced, which, in turn, can result in significant reductions of *V. dahliae* soil populations (12,13). With many cultivars possessing only a degree of resistance or tolerance to *Verticillium* spp., proper attention to nutrition can minimize the economic impact of wilt infections. Nutrition is a major management tool utilized by growers and crop management consultants in the Pacific Northwest.

Development and availability of *Verticillium* wilt-resistant cultivars. Rowe and Powelson (21) point out that, although considerable effort has gone toward developing resistant potato cultivars, only one successful cultivar (Russet Nugget) with resistance to *Verticillium* spp. has been released in the past 20 years. This statement ignores the fact that, since 1984, a series of successful potato cultivars possessing varying levels of either resistance or tolerance to *Verticillium* wilt have been released. For the most part, these cultivars have been utilized successfully in niche markets (e.g., Frontier Russet, Gemchip,

Chipeta, Gem Russet, Ida Rose, and Ban-nock Russet, to name a few); however, two of them (Ranger Russet released in 1991 and Umatilla Russet released in 1998) are emerging as cultivars with widespread appeal. When compared with cultivars used in the top eight potato-producing states by the National Agricultural Statistics Service in 2002 (19), Ranger Russet was third from the top when percent acreage was considered among the sum of acreage in all eight states. To date, the Russet Burbank cultivar still remains in first place, while the “successful” Russet Nugget cultivar mentioned by Rowe and Powelson remains in thirteenth place. In the Pacific Northwest, Ranger Russet is the second most popular cultivar, whereas Russet Nugget isn’t considered to be a significant commercial cultivar.

Immunity to *Verticillium* spp. is not required, because some degree of resistance or tolerance coupled with appropriate cultural practices can prevent any economic damage by the pathogen and allow high yields and quality. The successful Ranger Russet cultivar is not resistant to *V. dahliae* (stem colonization is not suppressed), but it is highly tolerant, as described by Mohan et al. (17; Ranger Russet described in publication as clone A7411-2). When managed with the proper nutritional balance, symptoms of *Verticillium* wilt are rarely seen in Ranger Russet. The success of Ranger Russet has been due to its out-performance of Russet Burbank in terms of yield, earlier maturity, and higher product recovery in processing because of its better shape and higher specific gravity.

The lack of success of *Verticillium* spp.-resistant cultivars has less to do with breeding success than with other factors—success being defined as grower adoption rather than availability of a quality resistant cultivar. Entrenched cultivars are difficult to replace. The potato industry in the Pacific Northwest was standardized with Russet Burbank and, without a compelling reason for change, acceptance of new cultivars is not rapid. Russet Burbank remains the most commonly grown potato in the top eight potato-producing states. *Verticillium* wilt can be largely managed in the Russet Burbank potato when proper management is practiced (e.g., nutrition and use of green manures; 3). If Russet Burbank were highly susceptible to *Verti-*

cillium wilt and major losses could not be avoided through management, this cultivar rapidly would have been replaced by new releases.

Progress in the availability of resistant cultivars continues with the newly released Alturas cultivar. This cultivar, with reported resistance to *Verticillium* spp. (20), is receiving wide acceptance by the industry because of its high yields and outstanding quality. In 32 trials in Idaho, Oregon, and Washington, Alturas has yielded 37% more than Russet Burbank while simultaneously producing a higher percentage of premium U.S. #1 tubers (24). In 2003, Alturas was among the top five cultivars being produced by the Idaho Certified Potato Seed program (16), making seed adequately available.

Green manures. The use of green manures in a crop rotation program can be an effective management tool for minimizing the economic damage from *Verticillium* wilt. Rowe and Powelson cite the work of Davis et al. (8) describing the suppressive effects of green manures, where the response to certain green manure treatments was found to be equivalent to that of soil fumigation, with an 81% decrease in disease severity and a 35% increase in tuber yield. The statement is further made, however, that “The problem with this tactic is that two to three consecutive years of a green manure are needed to suppress disease and increase tuber yield.” This assumption of Rowe and Powelson is not accurate. Although the initial experiment utilized 2- to 3-year trials, it did not establish that this was essential, and it was never stated by Davis et al. (8) that 2 to 3 years were required. To the contrary, more recent data (4,7) shows this not to be true. Subsequent work, directed at making this approach commercially practical, indicates that, once a suppressive effect has been established in a soil, a single green manure can be sufficient to maintain or re-establish the effect (4,7).

One still might argue that even growing a green manure for a single season is not economically feasible. However, this need not be a major problem. First, sudangrass, one of our best green manure treatments, is a good forage crop. When grown, a cash green forage cutting can be harvested in midsummer, and the regrowth then can be put down in late fall as a green manure.

Second, a green manure can be part of a double-cropping system. Finally, although a more difficult and long-term approach, U.S. agricultural policy could be adjusted to encourage grower utilization of cover crops. Such a policy would solve our overproduction problems and help nurture the soil for long-term sustainability.

The final consideration is whether growers actually utilize this green manure management practice. Although this information is not available in scientific journals, it is evident both in trade journals and with personal observations. For example, an article in *American Vegetable Grower* describes successful grower usage of green manure treatments for *Verticillium* spp. control with sudangrass (14). During the 2003 American potato meetings in Spokane, WA, a tour was taken of farms of the area to demonstrate common practices used by successful Washington growers. Among these practices, the use of green manures of both sudangrass and sweet corn, as we have previously described (4), were being used successfully for the control of *Verticillium* wilt of potato without the use of sodium metam (Vapam). As more growers learn about and get experience with this approach, usage should increase over time.

Finally, it should be pointed out that green manures and cover crops have many benefits besides *Verticillium* wilt suppression. As a result of the use of sudangrass as a green manure, substantial yield benefits beyond the effects of *Verticillium* spp. control have been documented (6). In several trials where *Verticillium* wilt incidence was negligible, sudangrass treatments still led to significant increases in yield and U.S. #1 tubers. The use of green manures for improving and maintaining soil tilth, fertility, nutrient and water retention, and as slow release fertilizers is well appreciated in circles of organic and sustainable agriculture; however, possibly the addition of organic matter to soil as a consequence of green manures is most significant. Our most recent survey of potato fields (5) suggests this to be true. When 3 years of data from more than 100 potato fields were compiled to provide a descriptive model of wilt incidence, potato yields, quality, and tuber size, it was observed that, as organic matter of field soils increased, *V. dahliae* root infections were less frequent, and yields, size, and grade increased in Russet Burbank potato. Many growers, including those involved with conventional agriculture, are beginning to appreciate this and are adopting practices that rebuild the soil organic matter and the associated micro-bial community.

The relationship of *Fusarium* spp. to green manure treatments. When referring to the article by Davis et al. (8), Rowe and Powelson erroneously state that "Populations of nonpathogenic *Fusarium oxysporum* are particularly implicated in

suppression of *Verticillium* wilt." Davis et al. (8) did not mention *F. oxysporum* in their article or implicate it as the factor explaining the effect of green manures on *Verticillium* control. Instead, several lines of evidence were provided to suggest biological control with green manures. Among these lines of evidence, disease reduction was highly correlated with both nonspecific microbial activities and major changes in microbial populations, as evidenced by increases of nonpathogenic *Fusarium* spp. (e.g. *F. equiseti*). *Fusarium* was provided as an example of a fungal genus that was increasing, thereby exemplifying increased microbial activity. In no way was it indicated as a causal factor. The working hypothesis was that the observed wilt suppression results from a complex interaction of soil organic matter, the associated microbial community, and, finally, their combined effect on the root colonization dynamics by pathogens and competitors. This relationship between a number of soil factors and disease severity for *Verticillium* wilt has been published (5).

The reliability of current methods for estimating soil populations. In their discussion of strategies for *Verticillium* spp. control, Rowe and Powelson (21) further indicate that future exploitation of host resistance should provide strategies to increase the longevity of resistance genes. However, if these approaches are to be appropriately and successfully implemented, a reliable, sensitive method for quantifying *V. dahliae* in soil and tubers is needed. The authors then continue with the following statement: "Plating soil on semi-selective media has been shown to be inconsistent and unreliable for estimating soil populations." Termorshuizen et al. (23) then is cited to have demonstrated this. However, as co-authors of this article, we cannot agree with this statement. The article by Termorshuizen et al. (23) described the comparison of soil assay results from a number of different labs utilizing a number of different assay methods for identical soil samples. There were, indeed, inconsistent results because all assay methods did not work equally well. However, the article also identified the assay method (dry plating with an Anderson sampler) as giving the most consistent results. Labs using this method (with one notable exception) reported very similar inoculum densities for most soils—including a consistent 40% recovery of spiked soils. Thus, soil assays performed with a reliable method and trained workers gave consistent and reproducible results. The inability of one lab to duplicate the results of many others, for whatever technical reason, does not make the assay inconsistent. Only inconsistent results within the same lab would raise serious concerns about reliability. In our own experience, we have found the assay procedure to give consistent, reproducible results from plot subsampling during a

growing season, from year to year, and from lab to lab. A recent example of this involved a study involving labs at both Aberdeen, ID, and Berkeley, CA, for several years in more than 100 fields (5). This study involved split soil samples from each plot site and independent analyses from each lab. From year to year, results were essentially identical. Using this assay procedure to analyze soil for *V. dahliae* from replicated plots with different treatments, we repeatedly have been able to compare the effect of treatments with high degrees of precision and consistency in multiyear experiments with low standard deviations and error. This cannot be accomplished with a technique that is not reliable.

Furthermore, we also have successfully used this same technique for evaluating the stability of resistance of *Verticillium* spp.-resistant potato clones (10)—a technique for which Rowe and Powelson indicate a need. Our experiments have shown no evidence for the loss of *Verticillium* spp.-resistance due to the natural selection of more aggressive *V. dahliae* strains. Our studies demonstrated that *V. dahliae* populations in stems were positively correlated with populations in the soil. With resistance, populations in the stem were lower which, in turn, caused soil populations of *V. dahliae* to become lower over time.

The role of seed potato in the spread of *V. dahliae*. At the conclusion of their article, Rowe and Powelson (21) made a point of stating that one of the five key areas needing attention to advance the management of *Verticillium* wilt is the development of clean planting stock. Presumably, this means seed free of *V. dahliae* and *V. albo-atrum* rather than the many other seedborne pathogens. We do not believe that the case has been made for making this a high-priority item. It would be fine if it were achievable; however, given the current state of the art of the potato seed programs, it probably is not practical. Given the wide global distribution of the pathogen and its presence in all major production areas, it is too late to prevent its introduction. Neither is it feasible to prevent its spread within a growing region. Conceivably, regions that have never had potato production might be spared infestation if clean planting is used to initiate a production schedule. This assumes that contaminated seed is the primary method of spread. Most of the available evidence, however, points at another mechanism for spread. *Verticillium* spp. are saprophytic colonizers of the root cortex of almost all plants. They can be maintained in soil by nonsystemic host plants in an endemic form, although at very low densities. Dispersal of dry soil by wind or moist soil by human or animal traffic easily can account for dispersal in any given region. In infested fields and regions, *Verticillium* inoculum coming from infected

seed pieces would be dwarfed by that already present in the soil profile.

Much of the available evidence supports the cosmopolitan nature of *Verticillium* spp. infestation. Two Idaho field studies involving virgin desert lands previously have suggested that the introduction of *V. dahliae* with potato seed is not a significant causal factor in field infestation by the pathogen (11). This study, which involved two separate locations on virgin ground and 10 *Verticillium*-free seed lots, showed an increase of *V. dahliae* in soil regardless of the seed source. Although *V. dahliae* could not be detected in soil prior to the planting of potato, potato stems resulting from the *Verticillium*-free seed still were infected with *V. dahliae* at season end. This presence of *V. dahliae* was not associated with any of the seed sources per se. At season end, the occurrence of *V. dahliae* in potato stems occurred randomly in "pockets" of the virgin fields. The most logical hypothesis for this is for the pathogen to have been present at low, nondetectable levels. Systemic infection of susceptible plants, such as potato, then will lead to a rapid increase in pathogen populations. In the west, winds commonly blow the soil from field to field with widespread inoculum dispersal and, because naturally occurring desert plants (e.g., saltbush and sagebrush) also may serve as hosts for the pathogen (22), the spread of *V. dahliae* seems imminent, regardless of seed contamination. Similarly, in the state of Washington, Hoyman (15) asked a question regarding the importance of intratuber infection of Norgold Russet potato seed and concluded that it was of no consequence in eastern Washington. Although there still are a number of scientific questions that merit attention, we do not see that use of *Verticillium*-free planting stock is going to be a significant management tool in the major areas of potato production.

Potato early dying? The "potato early dying" disease, as used by Rowe and Powelson (21), is an ambiguous term that continues the early misconception that the disease is a complex requiring several pathogens to produce the end result. This is not true. *Verticillium* wilt may be caused by either of two soilborne fungi, *Verticillium dahliae* Kleb. or *V. albo-atrum* Reinke & Berthold (3), that may cause the early death of a potato plant. Only one other known primary pathogen can be confused with the cause of *Verticillium* wilt. The black dot disease caused by *Colletotrichum coccodes* (Wallr.) S. J. Hughes also may cause the early death of a potato plant (2,9,18) without the aid of another pathogen. Because the symptoms are similar, it is imperative that quantitative assays be made in the field when working with the so-called "early dying" disease. *Verticillium* wilt and the black dot disease respond differently to varying cultural con-

trols, making it essential that the cause of early dying be defined—particularly in a discussion of management challenges for *Verticillium* wilt, the main focus of the article by Rowe and Powelson (21).

The term "*Verticillium* wilt" more clearly identifies the management challenges presented. All the other components of the early-dying complex are secondary or modulating factors affecting the disease process. Rowe and Powelson (21) point to the importance of *Pratylenchus penetrans* in potato early dying. It is true that this nematode has been shown to be a modulating factor with *Verticillium* wilt and, when present in adequate numbers, it can increase both the incidence and the severity of *Verticillium* wilt. However, so can other factors (2,5,13). *P. penetrans* is not required for a severe problem with *Verticillium* wilt. This has been shown with studies where the root lesion nematode has not been found related to conditions of severe wilt (1). Using various quantitative procedures, Mohan et al. (17) compared the reaction of 40 potato clones and six accessions of *Solanum* spp. with wilt caused by *V. dahliae* both in the field and in the greenhouse under closely controlled conditions. There was a highly significant correlation between the wilt reaction of the clones in the greenhouse, the incidence and progress of wilt and severe wilt in the field, and the degree of colonization of stem apices by *V. dahliae*—in this case, the only causal organism associated with early dying. This again shows that potato early dying may be caused by *V. dahliae* alone, without the aid of another pathogen.

Summary. Rowe and Powelson (21) identify five key areas that need attention for advancing successful management of *Verticillium* wilt in changing times. (i) Suppression of soilborne inoculum: some very effective management practices are already available and practiced by a number of growers; namely, green manures. (ii) Clean planting stock: with the possible exception of a few special situations, we doubt that availability of clean planting stock will be a significant management tool for this disease. (iii) New plant-protection chemicals: although desirable, the current toughening environment restrictions on pesticide use, with little relaxation in sight, make this an unlikely avenue in the future. (iv) Enhanced host resistance: a selection of resistant and highly tolerant, high-quality cultivars are available already. Tolerant cultivars such as Ranger Russet can be grown successfully with current management practices. Pathogens are not static and eventually adapt to most resistant cultivars; therefore, continuous efforts at enhancing host resistance always will be necessary. (v) Improved pathogen monitoring tools: current soil and plant assay methods are both reliable and reproducible in competent hands. Improvements in any or all of these areas are

both desirable and welcome. However, the available current management practices can manage this important disease effectively. A number of growers are using them with success.

In coming years, continued work with green manures and rotations is strongly recommended and should be encouraged wherever possible. Historically, green manures have shown long-term benefits to soil and have been found equal to and even superior to conventional pesticide controls. Investigations into this key area of agriculture offer many potential rewards that can extend all the way from a basic understanding of the interactions of plants and soil microflora to plant nutrition. Although plant nutrition commonly is ignored by plant pathologists, an understanding of nutrition is paramount to an understanding of *Verticillium* spp. control—particularly in potato.

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