

Nutritional Interactions Influencing Diseases of Potato

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ABSTRACT

Nutrient management can decrease the severity of a number of important potato diseases, and certain practices, such as maintaining a low pH for scab control, have been followed for that single objective. More commonly, growers have incorporated fertility modifications into their particular disease and farming situations. Unfortunately, disease minimization may or may not be consistent with optimal fertilization for yield, quality, and profitability. Optimization for one disease may not match that for another, and the exact mechanisms involved are often complex and poorly understood. Potato growers will continue to experience conflicting production constraints. These constraints include price-driven needs for yield improvement and expense reduction; customer-driven demands for quality improvement; varietal shifts driven by the above considerations rather than by disease reduction; increasing pressure to justify, shift and reduce pesticide use; continuing concerns about nitrogen and phosphorus movement in groundwater and runoff; and increased attention to management of rotation crops.

On the positive side, nutrient management strategies for highly specific situations continue to improve and practices addressing nutrient and disease variability within fields are becoming more sophisticated. In this context, there are opportunities for cultural management practices that reduce disease pressure and reliance on chemical controls. To be effectively integrated into such specialized management systems, the

mechanisms of these control measures and the conditions under which they are practical will need to be better understood. Likewise, disease responses to these tactics need to be better quantified to allow an adequate cost-benefit analysis. With mounting concerns about the effects of agricultural pesticides on food safety, farm workers, and the environment, management of plant-available nutrients may become practical approaches for disease suppression in the future.

RESUMEN

El manejo de nutrientes puede disminuir la severidad de muchas enfermedades importantes de papa y ciertas prácticas, tal como el mantener un pH bajo para el control de la sarna, se ha seguido con este simple objetivo. Con frecuencia, los productores de papa han incorporado modificaciones de la fertilidad con respecto a ciertas enfermedades en particular y condiciones de cultivo. Desgraciadamente, la reducción de la enfermedad puede ser consistente con una fertilización óptima para rendimiento, calidad y rentabilidad. Lo que puede controlar una enfermedad puede no ser bueno para otra enfermedad y los mecanismos involucrados son a menudo complejos e insuficientemente comprendidos. Los productores de papa continuarán experimentando limitaciones conflictivas en la producción. Estas limitaciones incluyen la influencia del precio de los artículos para mejorar el rendimiento y la reducción de los gastos; influencia de las demandas del consumidor para el mejoramiento de la calidad; cambios de variedad debido a las consideraciones anteriores más que a la reducción por enfermedades; incremento en la presión para la justificación; cambios y reducción en el uso de pesticidas; preocupación continua acerca del movi-

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miento del nitrógeno y fósforo en el agua del suelo y su pérdida y un aumento de atención en la rotación de cultivos. En el lado positivo, las estrategias en el manejo de nutrientes para situaciones altamente específicas continúan mejorando y las prácticas referentes a los nutrientes y la variabilidad de las enfermedades dentro del campo se están volviendo más sofisticadas. En este contexto, existen oportunidades para el manejo de prácticas culturales que reducen la presión de la enfermedad y la confianza en el control químico. Para estar efectivamente integrado a tales sistemas especializados de manejo, el mecanismo de estas medidas de control y las condiciones bajo las cuales son practica, necesitarán ser mejor comprendidas. Asimismo, las respuestas de estas tácticas necesitan ser mejor cuantificadas para permitir un adecuado análisis costo-beneficio. Con referencia a los efectos de los pesticidas agrícolas en la seguridad alimentaria, los trabajadores y el medio ambiente, el manejo de los nutrientes disponibles para la planta pueden convertirse en una manera de enfocar la práctica para la supresión de enfermedades en el futuro.

INTRODUCTION

In making decisions on the amount, source, and timing of fertilizer and lime, potato growers attempt to optimize a financial return for yield and tuber quality while minimizing harvest, storage, environmental, and marketing risks. These decisions are made in the context of fertilizer costs, varietal differences, soil characteristics, water considerations, and the shifting management requirements of the maturing crop. The final plan also should provide as much hedge as is feasible against seasonal variability in nutrient demand and loss. Within this fertility decision matrix there is an optimum solution. Embedded within this matrix is the consideration of disease control. Growers might want to reduce disease risk by modifying fertility, or they might want to modify their fertility practices without substantially increasing the disease risk.

A number of potato diseases are affected to some degree by mineral nutrients. These nutrient effects could include alterations in the physiological or structural components of the plant's defense system, increased antagonistic microbial activity, or direct toxicity to the pathogen. The reverse situation, in which nutritional needs (or their measurement) are altered as a result of disease, is less important. Typically, dis-

ease-nutrient relationships have been investigated by initially imposing a wide range in rates of one or more minerals on the crop to screen for significant effects. In some instances, future studies are conducted at fertilizer rates that are more realistic or, alternately, disease levels are monitored in fertility trials as the opportunity arises. Finely tuned nutrient recommendations for disease suppression with accompanying yield, quality and cost analyses for specific varieties are generally the exception. Because so many factors are involved, growers are usually informed of possible nutrient effects and advised to consider modifications if their conditions allow. The challenge is to adapt disease-management strategies to what are economically and environmentally acceptable nutrient-management practices.

POTATO SCAB

Scab is caused by certain streptomycetes, primarily *Streptomyces scabiei*, the "common scab" pathogen. Virulent species of these otherwise saprophytic filamentous bacteria produce a toxin, thaxtomin, which kills patches of periderm cells and elicits production of newly suberized layers, which leave raised or pitted scabs on the tuber surface (Loria et al. 1997). Common scab is associated with drier (Lewis 1970), lighter and looser (Fitch 1935) soils. Severity is most affected by soil pH (Giles 1918), increasing in a sigmoidal pattern over the range of 5 to 7 with a midpoint in the vicinity of 5.7 (Dippenaar 1933) to 6.2 (Blodgett and Cohen 1935). Scab is managed by maintaining or creating soil conditions that minimize severity, selecting less-affected fields for planting susceptible varieties, practicing crop rotation, and by minimizing seed transmission.

Maintaining or lowering soil pH to less than 5.2 to 5.5 can usually suppress common scab; this threshold varies in practice with variety, inoculum potential, soil type, and moisture. Growers often discern that the relationship of scab severity to pH is imperfect. This discrepancy might arise from pH variability on a small scale, from variability in the other controlling factors, or from mineral or microbial interactions which have yet to be explained. Acidity directly affects *S. scabiei*; the pathogen is unable to grow much below a pH of 5 (Dippenaar 1933; Lambert and Loria 1989a; Waksman 1922). In contrast, the "acid scab"-inciting species *S. acidiscabies* tolerates *in vitro* pHs to 3.8 and is not limited by soil acidity (Bonde and McIntyre 1968; Lambert and Loria 1989b). The acid tolerance

of *S. turgidiscabies* appears to be intermediate (Miyajima et al. 1998).

Liming or other practices that raise pH within the 5 to 7 range increase common scab severity. Although Horsfall et al. (1954) suggested that the lime effect results from increased Ca rather than decreased H, no credible evidence supports this interpretation. In acid soils, gypsum amendments, which substantially increase available calcium without affecting pH, do not increase scab, whereas equivalent calcium additions in the form of lime increase both pH and scab (Lambert and Manzer 1991; Terman et al. 1948). For example, in a soil with an initial pH of 4.2, scab incidence in control, gypsum, or lime treatments (both at 1 MT ha^{-1} Ca) were 21%, 18%, and 53% in the year of infestation with *S. scabiei* and 0%, 0%, and 32% in the year following infestation. Final soil pH values were 4.4, 4.5, and 5.5, respectively (Lambert and Manzer 1991).

A positive relationship between higher periderm Ca content and scab has been suggested (Davis et al. 1974, 1976a, 1976b), despite the general benefits of increasing calcium availability in alkaline soils. Such associations need to be interpreted cautiously, as calcium concentrations in scabby periderm are several-fold higher than those in adjacent healthy skin (Houghland and Cash 1956; Lambert and Manzer 1991). Likewise, concentrations of various other elements are also higher in lesion tissue, the elevated levels being an effect rather than a cause of scab (Lambert and Manzer 1991). Associations of periderm calcium with increased disease, independent of this effect, have not been reported.

The scab situation in the alkaline soils typical of western North America is distinct from that in acidic soils. As pH is increased above 8 with calcium hydroxide, scab incidence declines (Blodgett and Cohen 1935). Menzies (1950) likewise reported that scab decreased above pH 8 and incidence in alkaline soils could be reduced with sources of soluble calcium, gypsum and calcium oxide, but not with lime. In a series of experiments in heavily infested soils with pH values ranging from 7.5 to 8.0, scab severity was reduced with sulfur sources. Both gypsum and elemental sulfur (ES) at 673 kg ha^{-1} S decreased scab without a substantial reduction in pH (Davis et al. 1974, 1976a). Growing potatoes without any fertilizer P substantially increased scab compared to the other four P treatments, which ranged from 84 to 336 kg ha^{-1} P_2O_5 (Davis et al. 1976a). Scab could not be reduced by increasing or by decreasing the standard rate of phosphorus. In another study, various rates of ES decreased scab when irrigation thresholds were

100 kPa or above. Elemental S increased yield by an average of 20% and sulfur treatment also increased petiole P (Davis et al. 1976b).

Treatment of calcareous soils with ES has diverse effects, including conversion of calcium carbonate to gypsum, improvement of water penetration, and increased Mn availability (Tisdale and Nelson 1975). The additional salutary effects of ES on plant growth and phosphorus uptake under these conditions suggest a broad range of possible reasons for scab reduction. Progress in this area will require a better understanding of the mechanisms involved and of the sets of circumstances required for soil modification to be economical.

Attempts to reduce scab by lowering soil pH with ES or ammonium sulfate have had mixed results for reasons which were not always determined (Keinath and Loria 1989). Sulfur is oxidized to sulfuric acid by *Thiobacillus* spp. and other bacteria. Oxidation is most rapid in warm ($> 25^\circ\text{C}$), moderately wet, acidic soils in which the appropriate bacteria are present in sufficient numbers (Tisdale and Nelson 1975). The ES should be finely ground and thoroughly mixed to allow sufficient reaction by the time of tuber set, when potatoes are most susceptible to the disease. All of these expectations might not be met when ES is applied at planting, and this may explain the poor results obtained in some trials (Dippenaar 1933).

One long-term study (Terman et al. 1948) illustrates various aspects of acidification for scab control. In a gravelly loam soil with a pH of 5.0, ES at 1.12 MT ha^{-1} was severely toxic to potatoes and permanently reduced the potential yield of the treated plots. After 9 years, pH was reduced by 0.6 units and soil calcium decreased by half. In equivalent plots where lime was applied at 2.24 and 3.37 MT ha^{-1} , the pH increased to 5.9 and 5.8, respectively, and a substantial scab problem developed over the 9-year period. Subsequently, all plots were treated with various rates of ES or ammonium sulfate. In the heavily scabbed plots, 672 and 1008 kg ha^{-1} ES reduced the scab index by 30% and 58%, respectively. After single treatments with 94, 187 or 281 kg ha^{-1} N as ammonium sulfate, scab was decreased by 16%, 41%, and 65%. After a second year of treatment, reductions averaged 29%, 86%, and 90%, respectively. In general, a given amount of ammonium sulfate produced a greater reduction in scab at a lower initial pH than at a higher one.

Barnes (1972) applied 0.5 MT ha^{-1} ES and reduced scab 27% with a pH change of 6.1 to 5.4. In a subsequent trial, 0.5 or 1 MT ha^{-1} ES reduced common scab by 50% with pH reduc-

tions from 5.2 to 4.6 and 4.2. The authors of both papers cautioned against over-application of ES. Reduction of ES to hydrogen sulfide, which is toxic to *S. scabiei* *in vitro* (Vlitos and Hooker 1951), has been considered as a possible mechanism of S-induced scab reduction. This conversion requires anaerobic conditions, such as might result from waterlogging, and its practical significance under typical field conditions is unknown.

While growers in areas with acidic soils still express interest in the use of ES to reduce scab problems, the general trend has been to manage such soils at somewhat higher pH levels and cation availabilities to improve tuber quality, fertilizer efficiency, and rotation crop performance.

Other elements have been investigated for control of common scab (see Keinath and Loria 1989), particularly manganese. Its availability in soil increases with acidity and soil moisture, supporting the hypothesis that Mn toxicity to *Streptomyces* is a major mechanism in pH and irrigation effects and that Mn applications would further reduce scab. In many cases, no benefits have been obtained (Keinath and Loria 1989) and phytotoxicity may result (Barnes 1972).

In other cases, responses have been positive. Mortvedt et al. (1961) found that sand culture solutions with 2 to 20 $\mu\text{g mL}^{-1}$ Mn significantly reduced and completely prevented scab development, respectively. The solution pH in this study, however, ranged from 4.5 to 5.5 (inhibitory or marginal for *S. scabiei*) and control plants not receiving supplemental Mn accumulated 281 $\mu\text{g g}^{-1}$ foliar Mn, more than 10-fold higher than "sufficient" status (Westermann 1993). These data suggest that the baseline Mn availability and acidity in this experiment exceeded those in field soils where Mn supplements might be considered. In a subsequent study (Mortvedt et al. 1963), no differences in scab severity were found in solution culture trials over Mn concentration range of 0.1 to 32 $\mu\text{g mL}^{-1}$. In agar culture, 100 $\mu\text{g mL}^{-1}$ Mn was required to reduce growth of *S. scabiei* by 50%. The availability of Mn in the agar was doubtless much lower, but this figure is nevertheless at least four orders of magnitude higher than concentrations of water soluble Mn in acidic soil.

Under field conditions where Mn concentrations were high in the untreated control, additional manganese sulfate did not significantly reduce scab or increase yield (Mortvedt et al. 1961). However, in a later report with soils of pH 4.9 and 5.5 and low in extractable Mn, 168 kg ha^{-1} manganese sulfate significantly reduced scab without a significant change in yield

(Mortvedt et al. 1963). McGregor and Wilson (1966) applied 31 to 62 kg ha^{-1} manganese sulfate to four Mn-deficient Scottish soils (pH 6.2 to 6.9) and substantially reduced scab in all treatments, increasing the average weight of individual potatoes by 4% to 64%. Davis et al. (1976a) reported that foliar application of chelated Mn at 0.2 kg ha^{-1} slightly but significantly reduced scab on potatoes grown in an alkaline field soil in plots fertilized with ammonium nitrate but not those fertilized with ammonium sulfate (which, presumably, improved Mn availability from soil). Effects on yield were not mentioned and petiole Mn concentrations were within the sufficient range (Westermann 1993).

In all of these field studies where added Mn reduced scab severity, the element appears to have been no more than moderately available to the plants, and hence inconsistent with a toxicity mechanism. An alternate possibility is that abundant Mn improves host resistance to tuber pathogens, possibly in its role as a cofactor with enzymes involved in oxidation/reduction or with direct oxidation of phenolics. In this case, plant manganese concentrations adequate for yield may be suboptimal for disease resistance.

RHIZOCTONIA

Rhizoctonia solani, a fungus present in soil or as "black scurf" on seed, kills and attacks stems, stolons and tuber surfaces, reducing yield and tuber appearance. Although the disease may cause important losses, little work has been done on nutritional effects. Manganese at 62 kg ha^{-1} reduced the incidence of *Rhizoctonia solani* black scurf on tubers from 25% to 11% (McGregor and Wilson 1966). No differences in number of stem lesions were obtained over a range of 0 to 250 kg N ha^{-1} (Honeycutt et al. 1996).

POWDERY SCAB

Powdery scab is a tuber disease caused by the soil- and tuber-borne plasmodiophoromycete *Spongopora subteranea*. Long-lived spores release mobile zoospores that infect roots and subsequently tubers when soil moisture is sufficient. The disease is minimized by varietal selection and inoculum reduction, although chemical control shows some potential.

There have been numerous and contradictory reports of the effects of pH-modifying materials on powdery scab incidence (see Harrison et al. [1997] for a thorough review). Con-

trolled *in vitro* experiments, however, indicate no substantial direct effect of pH on zoospore release or subsequent root infection. Secondary effects of liming or acidifying materials, such as alterations in soil flocculation and drainage or Cu and Zn availability, are apparently involved.

BACTERIAL SOFT ROT

Bacterial soft rot is caused by *Erwinia carotovora* sub-species and *E. chrysanthemi* (Kelman et al. 1989). These bacteria produce large amounts of pectin-degrading enzymes which digest intercellular pectins and macerate tuber and stem tissue. When oxygen availability in tubers is restricted by inadequate storage ventilation or by a water film covering the potato surface, physiologically active resistance to *Erwinia* declines, and passive structural resistance becomes more important. Maintaining cool, dry storage conditions with adequate ventilation is important for disease management.

Soft rot can be suppressed with calcium fertilization, as cell walls with higher Ca content are more resistant to enzymatic degradation by pectate lyase and polygalacturonase than those with less Ca (McGuire and Kelman 1984). Electrolyte leakage from treated tissue also is reduced, which has been attributed to improved plasma membrane stability (Kelman et al. 1989). In plant tissue, calcium has regulatory functions and is therefore maintained in the cytoplasm at very low concentrations. Most plant calcium is associated with the cell wall, cross-linking non-esterified polygalacturonic acid residues in pectin. Calcium content in tubers may vary considerably, depending on placement and availability of calcium sources, soil moisture, tuber growth rate, and other factors. Much of the tuber calcium uptake is directly through the tuber roots or periderm, so that placement of supplemental calcium must be in the tuber zone (Kratzke and Palta 1986). Calcium concentrations are highest in the outer periderm, consistent with the higher proportion of cell wall to cell contents there. Potatoes deficient in calcium are more prone to heat stress (Tawfik et al. 1996), internal browning (Collier et al. 1978), and other defects (Dyson and Digby 1975; Kleinhenz et al. 1995). Avoidance of these physiological problems is one objective of grower's improvements in calcium fertility.

In tubers vacuum-infiltrated with calcium (McGuire and Kelman 1986), soft rot varied inversely with increasing Ca concentration, and was nearly prevented at the highest levels (500 $\mu\text{g mL}^{-1}$). However, there are economic and agronomic limita-

tions to achieving such concentrations under field conditions. Use of calcium nitrate, the most available form, is limited to the nitrogen requirement of the crop. Calcium is least available from lime, which must be used in conformation with pH objectives. Gypsum provides intermediate calcium availability, does not substantially alter pH, may be applied in large amounts, but may also be more expensive than lime.

In field studies, large calcium supplements have reduced the rate of soft rot development. For example, 1 MT ha^{-1} Ca from gypsum decreased the volume of soft rot by 28%, whereas an equivalent amount from lime reduced soft rot by only 8% (Lambert and Manzer 1991). In other instances, responses were variable (Bartz et al. 1992) or occurred only in lighter soils with low cation-exchange capacity and low Ca content (McGuire and Kelman 1984). Large quantities of Ca (14 - 27 MT $\text{ha}^{-1} \text{yr}^{-1}$) applied as gypsum delayed aerial blackleg infection and seed piece soft rot (*Erwinia carotovora* subsp. *atroseptica*) (Bain et al. 1996). The effect of these additions on soft rot in the daughter tubers was inconsistent.

Magnesium solutions infiltrated into tubers also reduced soft rot, but to a lesser degree than equivalent amounts of Ca (McGuire and Kelman 1986). In soil, however, Mg and Ca compete for uptake, and Mg supplements may increase rot by excluding Ca (McGuire and Kelman 1984). Increasing potassium fertilization also may affect Ca uptake, reducing it in foliage (Locascio et al. 1992) and either reducing (Locascio et al. 1992) or increasing (Porter et al., 2004) it in tubers.

VERTICILLIUM WILT

Verticillium wilt, caused by *V. dahliae* and *V. albo-atrum*, is the primary component of the potato early dying syndrome (Powelson and Rowe 1993). Plants affected by these soil-borne fungi may exhibit uneven foliar chlorosis, wilting, and early senescence. The disease is managed by a combination of practices, including rotation, fumigation, and judicious use of irrigation. Nitrogen rates may have a modest effect on Verticillium wilt in some potato varieties, and higher rates may suppress vine senescence. In the very susceptible, mid-season 'Kennebec', O'Sullivan and Reyes (1989) found no consistent effect on stem disease severity or on frequency of pathogen isolation from plants grown in plots with nitrogen rates over the range of 0 to 245 kg ha^{-1} . In one of two years under the heaviest disease pressure, suboptimal N increased disease severity and *Verticillium* colonization in comparison to some

but not all of the higher N rates used. Excessive rates of N delayed senescence, but did not improve yield.

Similar results were obtained with 'Russet Burbank', but not with susceptible 'Norgold Russet' (Davis and Everson 1986). Severity of wilt in Russet Burbank was correlated with lower petiole N and P values on the last assay date. Plants receiving insufficient N showed increased wilt symptoms, and recovery of *V. dahliae* from petioles of plants grown with no preplant N was nearly four times that for the optimal N treatment. In Norgold Russet, nitrogen rate had no effect on disease in untreated plots. In a subsequent study with three consecutive plantings, wilt symptoms and colonization in Russet Burbank were much more severe in plots without N fertilization than in those receiving 240 to 300 kg ha⁻¹ N in preplant or split applications (Davis et al. 1994). In the second and third years, stem colonization by *Verticillium* was higher in the no nitrogen check than in the high N treatments. Relative to pre-plant nitrogen applications, splitting the N application improved yield and reduced soil populations of *V. dahliae* in the first and second year (Davis et al. 1990). Phosphorus effects were more complicated. In the first year, wilt severity decreased with P application. In the second year there were N × P interactions. In the third year (no P applied), wilt severity generally increased with previous P application despite the fact that soil populations of and stem colonization by *Verticillium* decreased as P levels increased in that year.

In a three-year trial inoculated with both *V. dahliae* and *V. albo-atrum*, Platt and Arsenault (2001) investigated effects of 70 to 280 kg ha⁻¹ N and P levels in the determinate, susceptible variety 'Yukon Gold.' Their results indicate that NPK fertility that is otherwise optimal for yield and quality is compatible with minimizing the severity of *Verticillium* wilt. Excess N does not improve control, although extreme N or P deficiencies may aggravate the disease in certain varieties, possibly those that are very susceptible or are more determinate.

Ammonium nitrate and diammonium phosphate are the standard nitrogen sources for potato at planting. The form of nitrogen can be a factor in *Verticillium* wilt of various crops, with ammonium decreasing disease severity relative to nitrate (Dutta and Issac 1979; Huber and Watson 1970, 1974; Pennypacker 1989). Of the several possible mechanisms suggested, soil acidification has received the most attention. Ammonium acidifies the rhizosphere when exchanged for H⁺ at the root surface or generates hydrogen ions during its microbial con-

version to nitrate. In vitro, growth of *V. dahliae* is inhibited over the pH range of 4 to 5 (Bell 1989).

In very acidic soils, *Verticillium* is not generally a problem in cotton, but can be if such soils are limed (Shao and Foy 1982; Orellana et al. 1975). These effects are associated with Al (Orellana et al. 1975) and Mn toxicity (Shao and Foy 1982). An aluminum sulfate amendment that concurrently decreased pH from 8.0 to 4.5 decreased *Verticillium* wilt incidence in cotton from 55% to 0% (Baard and Pauer 1981). The response of *Verticillium* in potato over the pH range of 5 to 7 is less well documented. Van der Meer (1925) found infection in Dutch potato fields over the examined pH range of 4.4 to 6.6. Wilhelm (1950) reported infection of California potatoes in fields ranging from 5.3 to 5.9, and stated that the disease was widespread in other crops from soils with pH as low as 4.6. In a more detailed study with eggplant, Elmer and Ferrandino (1994) compared fertilization with ammonium sulfate, which reduced the rhizosphere pH to 4.9, 0.4 units lower than fertilization with calcium nitrate before anthesis. In this case, ammonium reduced disease severity at a low but not a high inoculum density, and the authors suggested that high inoculum densities might have been a factor in Wilhelm's reports.

Verticillium wilt of potato is generally less a problem in northeastern North America, where soil pH soils are typically low. The foregoing results suggest that maintaining a low soil pH for scab control might have the modest secondary benefit of reducing *Verticillium* inoculum buildup, but that acidification would be of lesser value for management of heavily infested fields.

The ammonium ion is somewhat toxic to *V. dahliae* in vitro at concentrations of two to four times normal nitrogen rates for potato (Dutta and Isaac 1979; Duncan and Himelick 1986), and this might be a factor for roots near the fertilizer band prior to nitrification. Additional possibilities are that the ammonium source prolongs the more resistant juvenile potato growth stage (Huber and Watson 1974), decreases levels of root carbohydrates (Pennypacker 1989), stimulates a more antagonistic microflora in the rhizosphere (Dutta and Issac 1979), solubilizes Mn and other trace elements (Elmer and Ferrandino 1994), or that nitrate depresses production of toxic phenolics (Király 1976). Further studies or additional analysis of related studies might indicate whether there are opportunities to reduce *Verticillium* wilt (or common scab) by modifying the form of nitrogen used in fertilizers, whether pH has a prac-

tical effect on *Verticillium* severity in potato, and how mono- and diammonium phosphates compare to ammonium sulfate and nitrate sources in their effects on disease susceptibility.

To the extent that Ca level might affect wilt severity, it is probably beneficial in reducing pectin degradation (Pennypacker 1989; Selvaraj 1974). In crops such as cotton (Hafez et al. 1975) and pistachio (Ashworth et al. 1985), potassium-deficiency increases the severity of *Verticillium* wilt, and *Verticillium* wilt aggravates potassium deficiency symptoms. In potato, this relationship has not been reported.

EARLY BLIGHT

Early blight is a fungal disease caused by *Alternaria solani* and the less virulent *A. alternata*. *Alternaria solani* may incite foliage and stem infections throughout the growing season, but these generally only become visible with the onset of tuber development. Lesion development accelerates as leaves become physiologically mature and senescent (Rotem 1994). *Alternaria alternata* is more commonly a pathogen of damaged tissue, but as a wound-infector, is a major cause of tuber lesions.

Fungicide applications in response to temperature and humidity-based predictive models are the primary strategy for reducing early blight. Nutrient management to prevent stress and premature senescence, however, is also important. Several studies including treatments that exceed commercial practices illustrate fertility effects on early blight. In Barclay et al. (1973), N and P₂O₅ treatments in all combinations of 0, 67 and 134 kg ha⁻¹ (with K₂O at 134 kg) were compared for yield and early blight severity. Versus the standard 134-134-134 treatment, only the N₁₃₄P₀ combination significantly reduced early blight. The authors, however, recommended fertilizing for yield and specific gravity rather than disease control.

In a study combining fertilizer rates of N and P ranging from 0 to 269 kg ha⁻¹ with various numbers of fungicide applications, Soltanpour and Harrison (1974) determined that, over fungicide frequencies, an intermediate N rate improved control vs the non-fertilized check. MacKenzie (1981) investigated early blight response to N over the range of 0 to 200 kg ha⁻¹ with and without fungicide sprays. As N rate increased, the apparent early blight infection rate decreased linearly by eight-fold. The optimum N rate, based on yield curves, was 30 kg ha⁻¹ higher in plots where early blight was not controlled by fungicide treatment.

More recently, early blight reduction has been attempted with post-plant nitrogen supplements. Stevenson and Stewart (1988) applied urea four times or tank-mixed urea with all 10 fungicide applications. None of the urea treatments significantly improved disease control or yield relative to checks receiving the same fungicide treatment. However, in five of the six urea treatments disease severity was lower, and in four of the six, yield was higher than the corresponding fungicide-only control. In two trials reported by Blachinski et al. (1996), neither weekly urea (20 kg ha⁻¹) nor potassium nitrate (12 kg ha⁻¹) supplements reduced early blight or increased foliar N concentrations at a Northern Negev test site. In this growing region, however, *Alternaria* infection is often associated with sand injury (Rotem 1994), and the physiology of resistance to wound-invasion might not be equivalent to the physiology of direct penetration and disease development in mature leaves.

There is a well-known association of *A. solani* severity with increasing tomato yield, and when "yield stress" is relieved by artificially removing young fruit, disease is substantially reduced (Rotem 1994). In this crop, higher fertility may affect *Alternaria* severity by two conflicting mechanisms—positively, by delaying foliar senescence, and negatively, by increasing yield. This is illustrated by a study in which the effects of soil and foliar N on tomato early blight were determined in a factorial arrangement (Zitter and Wolfe 1990). Soil-applied N increased fruit yield substantially (58%) with a corresponding increase in defoliation, whereas foliar urea applications decreased defoliation, despite their contribution to a moderate yield improvement. An association between yield and early blight also has been reported for potato (Rotem and Feldman 1965), although it has not been extensively quantified. If the effect proves substantial and widespread for potato, yield variables should be included in early blight prediction systems and a more sophisticated understanding of nutritional factors needs to be developed.

In other crops, K deficiency increases severity of diseases caused by *Alternaria* (Rotem 1994). A similar response to K deficiency has been reported for potato by Townsend (1935), but was not confirmed by Blachinski et al. (1996).

The general consensus is that excess nitrogen applications should not and cannot be expected to replace other types of control for early blight. It is important, however, to monitor and maintain crop nitrogen levels close to the limits imposed by yield, quality and environmental considerations. This will minimize the possibility of a premature descent into senes-

cence, which encourages and is further hastened by early blight infection. Considering the complexity of this issue, further studies on nitrogen optimization to minimize *Alternaria* must incorporate or consider variety-specific N requirements (Huffman-Wohleb and Thornton, 2000), the involvement of other senescence-inducing stresses, fungicide reduction strategies and their effects on the *Alternaria* population, and the potential effects of excess nitrogen on tuber and soil water quality.

LATE BLIGHT

Late blight, caused by *Phytophthora infestans*, is the most explosive of potato diseases, and has the greatest potential to cause yield and quality loss. In temperate areas, the pathogen generally persists from year to year in infected tubers, increases in foliage throughout the growing season, and washes into the soil to infect new tubers. Loss results from premature defoliation, tuber rot, the cost of chemical control, and reduced marketing options for affected crops. Eliminating inoculum sources and chemical control are the most important management strategies.

Plant nutrition might affect late blight in several ways, including direct physiological effects on lesion development. Most nutritional studies have focused on lesion size rather than infection efficiency or sporulation. In general, higher nitrogen rates produce moderate increases in lesion size while higher phosphorus and potassium rates may or may not diminish size (Allen and Orth 1941; Carnegie and Calhoun 1983). Over a 0.1 to 3X normal range of nutrient solutions, increasing the amount of a balanced fertilizer increased susceptibility (Main and Gallegly 1964). Optimal or excessive phosphorus fertilization increases tuber skin thickness, whereas nitrogen and potassium fertilization tend to produce thinner skins (Artschwager 1924). Nitrogen may also delay tuber maturity (Krauss and Marschner 1971). Herlihy (1970) found that higher nitrogen rate increased tuber blight while phosphorus seemed to reduce tuber infection. Thin-skinned tubers are presumably more susceptible to direct penetration and are more likely to sustain easily infectible scuffed surfaces. Excess nitrogen stimulates lush foliage (Beukema and van der Zaag 1990). During the early part of the season, this favors rapid vine growth, which increases the proportion of foliage unprotected by non-systemic fungicides in the latter part of a spray cycle. It is during these growth spurts and wet/warm conditions favoring

blight that the disease may become firmly established in fields. In the latter part of the season, heavy canopy growth retards drying and provides a moist microclimate favorable for infection and spore production (Herlihy 1970; Mills 1938); dense foliage also might be expected to hinder fungicide penetration. Excess nitrogen delays vinekill, which prolongs spore production and may result in persistence of green sporulating tissue into harvest, a major factor in tuber blight infection (Bonde and Schultz 1949). Because fertility management offers little apparent opportunity for late blight management, little attention has been paid to nutrient effects under field conditions. A three-year N fertility trial indicated year-dependent results, associated by the investigators with the growth stage of plants at the time of initial infection (Rubio-Covarrubias and Grunwald, 2000).

VIRUSES

A general assumption is that plants are most susceptible to development of viral diseases when they are well nourished, although subtle nutrient interactions may occur (Bawden and Kassanis 1950). Whether resulting differences in virus titers are translated into corresponding differences in incidence of seed or aphid transmission is not known. There was little effect of substantial nutrient differences on the susceptibility of potato to green peach aphid-vectored PVY infection (Bawden and Kassanis 1950). Plant nutrition may, however, affect vector development and attractiveness (van Emden 1966). In general, organic nitrogen availability has the greatest nutritional effect on aphids. With potato, the maximum growth rate of green peach aphid occurs at optimal nitrogen rates, although the nutritional basis for this is not straightforward (Jansson and Smilowitz 1986). Nitrogen-deficient, lighter colored foliage may be more attractive to aphids (Kennedy et al. 1961). Nitrogen-delayed senescence and vinekill also may be a consideration with viruses, particularly PLRV, which has the greatest potential for spread late in the season. High ($>1000 \mu\text{g g}^{-1}$) concentrations of Mn can markedly enhance the expression of PSTVd (potato spindle tuber viroid) in tomato (Lee and Singh 1972) and other indicator plants.

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