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Phytophthora erythroseptica (Pink Rot) Development in Russet Norkotah Potato Grown in Buffered Hydroponic Solutions I. Calcium Nutrition Effects

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Abstract *Phytophthora erythroseptica* Pethyb. causes a disease known as pink rot in potatoes, which is responsible for substantial pre and post harvest tuber loss. Disease outbreaks are associated with excessive soil moisture, moderate temperature, late season development, and a lack of potato cultivar resistance. Because disease resistance is becoming less effective, understanding other potential solutions is critical. Mineral nutrition of plants is known to be associated with disease development and severity of many diseases, but is not generally considered in relation to outbreaks of pink rot. Calcium (Ca) is essential and considered one of the most important nutrients associated with plant defense, but it has not been studied or consequently linked to the severity of pink rot in potato. A hydroponic growth system was established to study the effects of calcium on *P. erythroseptica* infection and colonization in Russet Norkotah potato roots. Russet Norkotah potatoes were grown with 3, 86, 172, and 343 mg L^{-1} Ca in association with the pathogen. The degree of disease severity was assessed by means of quantitative real time polymerase chain reaction (RT PCR). The suppression of infection and disease severity by increased available Ca was statistically significant, decreasing with each increment of Ca between 3 and 343 mg L^{-1}. These data provide strong evidence that Ca nutrition is important in disease suppression and that the amount of available soil Ca can affect plant health and the ability of *P. erythroseptica* to infect the host.

Resumen *Phytophthora erythroseptica* Pethyb causa una enfermedad conocida como pudrición rosa en papa, que es responsable de pérdidas substanciales de tubérculo en pre y post cosecha. Los establecimientos de la enfermedad están asociados con excesiva humedad del suelo, temperatura moderada, desarrollo tardío durante el ciclo y falta de resistencia varietal. Considerando que la resistencia a la enfermedad se ha vuelto menos efectiva, es crítico el entendimiento de otras soluciones potenciales. Se sabe que la nutrición mineral en plantas está asociada con el desarrollo y severidad de muchas enfermedades, pero generalmente no se le considera en relación a los establecimientos de pudrición rosa. El calcio (Ca) es esencial y es considerado como uno de los nutrientes más importantes asociado con la defensa de la planta, pero no ha sido estudiado o ligado consecuentemente a la severidad de la pudrición rosa en papa. Se estableció un sistema de crecimiento hidropónico para estudiar los efectos del calcio en la infección y colonización por *P. erythroseptica* en raíces de papa Russet Norkotah. Las papas Russet Norkotah se cultivaron con 3, 86, 172, y 343 mg L^{-1} Ca en asociación con el patógeno. El grado de severidad de la enfermedad se evaluó mediante la reacción en cadena de la polimerasa cuantitativa de tiempo real (RT PCR). La supresión de la infección y de la severidad de la enfermedad mediante el aumento del Ca disponible fue estadísticamente significativa, disminuyendo con cada incremento del Ca entre 3 y 343 mg L^{-1}. Estos datos aportan una sólida evidencia de que la nutrición con Ca es importante en la supresión de la enfermedad y que la cantidad de Ca disponible en el suelo

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puede afectar la salud de la planta y la habilidad de *P. erythroseptica* para infectar al hospedante.

Keywords *Solanum tuberosum* · Pink rot · Potato disease · Quantitative RT PCR

Introduction

It is estimated that up to nine percent of total potato (*Solanum tuberosum* L.) production in the United States is lost to tuber rot during storage (Attallah and Stevenson 2007). Pink rot, caused by the fungal pathogen *Phytophthora erythroseptica* Pethyb. is one of the major post harvest rot diseases (Taylor et al. 2004). The potato storage environment of high humidity, cool temperatures, poor air circulation, close proximity of tubers, and wounding during harvest creates optimal conditions for infection and disease development (Attallah and Stevenson 2007; Salas et al. 2000). However, it is likely that the majority of infection occurs in the field before harvest (Blodgett 1945; Cairns and Muskett 1939). Pink rot is a soil-borne disease and once present *P. erythroseptica* can maintain high populations within a field for several years especially when potatoes are grown in short rotations. Soil borne pathogen populations build in the soil somewhat proportional to length of years between potato crops and it is specifically known that *P. erythroseptica* infection increases with short rotations (Myers et al. 2008; Peters et al. 2005).

Infection in a field occurs through the eyes, lenticels, wounds, roots, and stolons (Lonsdale et al. 1980). Symptoms are purplish or black eyes, enlargement of lenticels, spongy/granular texture, and discoloration at the attachment of the stolon (Drechsler 1929; Goss 1949; Lonsdale et al. 1980; White 1946). *Phytophthora* inoculum and subsequent infection can occur through mycelium, sporangia, cysts, and zoospores (Lonsdale et al. 1980). Zoospores create a unique approach to infection because they are the only self-mobile fungal structures. Either excessive or standing water provide the optimal conditions for zoospores to find and infect hosts (Bonde 1938; Rowe and Schimitthenner 1977). Zoospores locate their hosts by means of chemotaxis, a chemical attraction that acts through amino acids such as glutamic and aspartic acid (Khew and Zentmyer 1973).

Above-ground plant structures are not infected by zoospores or mycelium, although heavy infection of the stem can cause wilting of the plant (Cairns and Muskett 1939). Severity of *Phytophthora erythroseptica* infection is associated with several environmental factors besides water. The optimum temperature range for infection and growth is between 15 and 30°C (Cairns and Muskett 1939; Salas et al. 2000). Infection is most severe at 25°C and is rare below 5°C or above 35°C (Jones 1954). Large tubers, early lifting, and thin skinned or early maturing varieties are also associated with high levels of pink rot (Boyd 1960; Goss 1949; Peters and Sturz 2001; Peters et al. 2004; Salas et al. 2003).

All potato cultivars grown in North America have some level of susceptibility to pink rot, none are completely resistant (Peters and Sturz 2001). The degree of resistance varies between incidence and severity for cultivars. Very susceptible cultivars include the thin and red skinned cultivars, namely: Warba, Snowden, Norland, and Russet Norkotah (Goss 1949; Salas et al. 2003). Moderately resistant cultivars include late season maturity types, Russet Burbank, Irish cobbler, Kasota, and Butte (Goss 1949; Peters and Sturz 2001; Peters et al. 2004).

Few fungicides are effective in controlling pink rot because the infections occur below the soil surface, and control is dependent upon systemic delivery (Porter et al. 2007). Also, isolates of *P. erythroseptica* have developed resistance to the few available fungicides (Taylor et al. 2002). Mefenoxam is the active ingredient for the primary fungicides used to control pink rot; which acts systemically by disrupting the ribosomal RNA Polymerase of the pathogen (Salas et al. 2003). The ability for a pathogen to develop resistance to a pesticide is quickened when the mode of action is specific as in mefenoxam. New schemes to manage infection need to be identified to prevent pink rot infection from increasing field and storage losses. Post-harvest applications of sodium hypochlorite and various salts and phosphorous acid have been found to prevent spread of infection in storage, but optimal control should occur before harvest to ensure maximum yield and minimum storage loss (Miller et al. 2006; Mills et al. 2005). The recent discovery of *P. erythroseptica* races resistant to Mefenoxam and cultivar susceptibility suggest that cultural management is needed in order to prevent and manage pink rot (Osusky et al. 2004).

Although best management practices have been summarized for minimizing pathogen infections (Miller and Hopkins 2007), these authors observed that many growers have severe infections of *P. erythroseptica* despite optimal management scenarios. The percent of plants infected within problematic fields of south-eastern Idaho has ranged from 15% to 70% resulting in some fields unharvested (Personal comm. Jeff Miller). Potatoes are a common component in cropping systems in southeastern Idaho, where soils are predominately alkaline. However, a unique area exists to the west of Rexburg, Idaho, where many soils are now acidic due to relatively high rates of nitrogen fertilizer and low carbonate irrigation water applied to potatoes grown on very sandy soils with low cation exchange capacity (CEC) (Personal comm. Hopkins; Horneck et al. 2007). The apparent correlation of relatively greater severity of *P. erythroseptica* infection of potatoes grown in these soils has led to the hypothesis that pH may be a causal factor to increased pink rot severity (Benson et al. 2009). However,

acidic low CEC soils simultaneously have low base saturation, possibly leading to calcium (Ca) and/or magnesium (Mg) deficiencies, especially in Idaho where growers are not accustomed to applying these nutrients due to high concentrations in most soil and water resources (Stark et al. 2004). Adjustments in mineral nutrition could reduce disease severity (Datnoff et al. 2007; Marschner 1995). In particular, calcium (Ca) may reduce pink rot severity because it has been found to reduce related diseases in other plants (Rahman and Punja 2007).

The addition of Ca has been found effective in reducing incidence and severity of diseases such as: clubroot (*Plasmodiophora brassicae* Wor.) of crucifers (Brassicaceae) , *Cephalosporium* stripe (*Cephalosporium gramineum* Nis. & Ika.) of wheat (*Triticum aestivium* L.) , root rot (*Phytophthora nicotianae* Das.) of citrus (Rutaceae) , and soft rot (*Pectobacterium carotovorum* Jon.) of potato (*Solanum tuberosum* L.) (Campanella et al. 2002; McGuire and Kelman 1984; Myers and Campbell 1985; Murray et al. 1992). Calcium is an essential nutrient and considered one of the most important nutrients associated with plant defense (Datnoff et al. 2007). The mode of action for calcium is not always clear, but several explanations are possible. Within the plant, Ca is involved in eliciting signal transduction pathways and in membrane and cell wall integrity (Busse and Palta 2006; Datnoff et al. 2007; McGuire and Kelman 1984; Rossignol et al. 1977). In soil, Ca is a key cation integral with cation exchange capacity (CEC) and structural composition of soil. There is potential for increased resistance to pink rot by preventing infection through better physical barriers such as the condition of the tuber skin or improved soil drainage (Messenger et al. 2003; Tzeng et al. 1986). The ability of Ca to act through multiple pathways to prevent infection implies a possible role for Ca in preventing pink rot. Therefore, the objective of this research is to determine the influence of Ca on the level of infection of *P. erythroseptica* in potato roots.

Materials and Methods

Russet Norkotah potatoes were grown in an enclosed hydroponic system within an environmentally controlled growth chamber (Mallory Engineering Inc. Salt Lake City, UT). Uniform potato plantlets were obtained from the University of Idaho (Department of Plant, Soil and Entomological Sciences) potato tissue culture laboratory (Moscow, ID). Potato plants were grown with a 14 h light period with a temperature of 23±1°C, and a 10-hr dark period with a temperature of 17±1°C. The trial was repeated three times with a 4×4 Latin Square design. The 14 L buckets containing nutrient solutions were placed in a wooden box and completely covered with an opaque polyethylene lid to prevent light contamination of the roots. Air was supplied at a constant flow (10 psi) to each nutrient solution.

Roots of four to six cm length plantlets (20 total plants per 14 L^{-1} tank) were placed into a modified Steinberg pretreatment solution containing a minimal level (5.5 mg L^{-1}) of Ca to avoid luxury consumption of this nutrient by plantlets (Camp et al. 1987). The pretreatment mg L^{-1} mineral concentrations were 10.94 N, 11.96 P, 14.0 K, 6.1 S, 5.5 Ca, 2.8 Mg, 0.46 Fe, 4.08 Cl, 0.074 Mn, 0.041 B, 0.006 Mo, 0.023 Zn, 0.006 Cu, 0.003 Na (Camp et al. 1987). After 14 days in the pretreatment solution, 16 uniform sized plants per bucket were randomly transferred into a modified Hoagland solution containing mg L^{-1} concentrations were 47.0, 105.1, 165.1, 285.2 N for respective increasing Ca treatments, 7.74 P, 135.44 K, 11.52 S, 8.68 Mg, 1.50 Fe, 3.34 Cl, 0.371 Mn, 0.204 B, 0.029 Mo, 0.114 Zn, 0.029 Cu, 0.014 Na (Camp et al. 1987). Calcium treatment concentrations were varied using Ca $(NO_3)_2$ at 2.9, 85.9, 171.8, 343.6 mg L^{-1}. Nitrogen was balanced by adding 45 mg/L^{-1} as KNO_3 to N levels listed above. Solution pH was held constant at 5.0 through 390 mg L^{-1} 2-Morpholinoethanesulfonic acid (MES) (Sigma-Aldrich, Inc. St. Louis, MO), with minor adjustments made daily as needed with KOH.

Phytophthora erythroseptica isolate 01–21 was provided by the University of Idaho Aberdeen Research Station, Aberdeen, Idaho. Isolate 01–21 was used due to its frequent presence in the growing regions of South-Eastern Idaho and is aggressive in causing pink rot in laboratory experiments (Porter et al. 2007). The isolate was maintained on P_5ARPH *Phytophthora* selective medium (17 g corn meal agar, 100 mg pentachloronitrobenzed (PCNB), 10 mg Rifampicin, 5 mg Primaricin, 250 mg Ampicilin) (Jeffers and Martin 1986). Zoospore inoculum was created according to the protocol of Salas et al. (2003). Inoculum was added to each hydroponic bucket immediately after transfer of plants into treatment solutions. Twenty ml of suspended zoospores at 50,000 spores ml^{-1}(quantified using a hemocytometer) were added to each group of plants.

Two plants from each group were destructively sampled beginning two days after inoculation and repeated every three days for a total of five samples, with the last sample collected 14 days after inoculation. Only root and stolon tissues were used to determine pathogen levels. The tissues were cut and removed at the root/stem interface. Root and stolon tissues of the two plants from each group were pooled to represent a single sampling. The tissues were washed with a 10% bleach solution then rinsed with deionized water, then stored at −80°C before lyophilizing. Deoxyribonucleic acid DNA was extracted from 275 mg of ground lyophilized tissue through a modification of the

Table 1 Primers for target genes of *Phytophthora erythroseptica* and *Solanum tuberosum*

Organism	Gene	Primer sequence (5′→ 3′)
P.erythroseptica	*rpb* 1	GAT GAA ACT AAG CGC CTT CTC
		CGA CAA TAG TCT TCA AGG TGG AT
S. tuberosum	*act*	TGA ACA CGG AAT TGT CAG CA
		GGG GTT AAG AGG GGC TTC AG

[a] Primers designed by Attallah and Stevenson (2007)

method described by Kidwell and Osborn (1992). Reagents used in DNA extraction were 10% of suggested values because of minimal root mass. Samples were quantified and adjusted to 25 ng ul^{-1} with a Nanodrop 1,000 spectrometer (Applied Biosystems, Foster City, CA).

Pathogen levels were assessed from the root and stolon tissues according to the methodology described by Attallah and Stevenson (2007) and Valsesia et al. (2005). Samples were analyzed by quantitative real time polymerase chain reaction (RT PCR), and assigned a cycle threshold value when a minimum level of fluorescent DNA was detected. These ct values correspond to initial DNA quantities and were used to create a ratio between the amount of host DNA and colonizing pathogen DNA. The ratio is termed the infection coefficient (IC) and compared to other IC values (Valsesia et al. 2005). The ribosomal polymerase B1 gene (*rpb1*) in *P. erythroseptica* and actin gene (*act*) in potato serve as the constitutively expressed target sequences (Table 1).

Absolute quantification was conducted on a ABio 7300 RT-PCR (Applied Biosystems Foster City, CA) with DNA 1 ng μl^{-1}, 200 nm each primer, and SYBR green mastermix (Applied Biosystems, Foster City, CA) in a 25 µl reaction. Each sample was run in duplicate and averaged. Positive and negative controls were fungal culture DNA and water, respectively. Calcium was quantified as described in Johnson and Ulrich (1959); both shoot and root tissue was treated with a nitric–perchorlic acid digestion and then analyzed on an IRIS Intrepid II XSP (Thermo Scientific Electron, Waltham, MA).

Infection coefficients from each sample time and treatment were analyzed using PROC MIXED with Tukey-Kramer adjustments in SAS (SAS Institute, Cary, NC). The general effects model had Ca nested within trials. Due to multiple samples collected over time for each treatment, a repeated measure step was included in the analysis. There was no significant interaction between time and Ca, therefore infection coefficients were combined across sampling dates and analyzed with Ca as the only variable.

Table 2 Effects of four levels of solution Ca on *Pythophthora erythroseptica* colonization in Russet Norkotah roots

Mean		P value		
Ca	IC value[a]	86	172	344
3	0.9338	0.0286	0.0019	0.0005
86	0.8646		0.1204	0.0257
172	0.8191			0.3655
344	0.7938			

[a] IC value, is a ratio based upon constitutively expressed genes in the host and pathogen range for normal Ca levels

Results

Russet Norkotah potatoes grown hydroponically with various levels of Ca differed significantly (F = 0.0025) among the Ca treatments in the amount of root colonization of *P. erythroseptica*. A significant increase in infection coefficients was observed at the 3 mg L^{-1} solution Ca when compared to any of the other three Ca levels (Table 2). Calcium at 86 mg L^{-1} did not produce significantly different infection coefficient rates than 172 mg L^{-1} but did produce a significantly higher infection coefficient than 344 mg L^{-1}. Calcium levels of 172 and 344 mg L^{-1} were not significantly different from each other. The lowest infection coefficient was associated with 343 mg L^{-1} Ca. Pathogen infection coefficients increased as Ca levels decreased (Table 2).

Increasing Ca levels in the hydroponic solution resulted in more Ca within the entire plant. Calcium in plant root and foliage tissue increased as Ca treatment levels increased

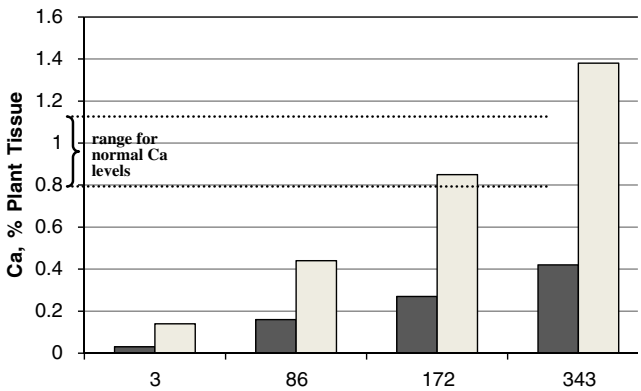

Fig. 1 Calcium concentration of root and shoot tissue of Russet Norkotah potatoes when grown in 3, 86, 172, and 344 mg Ca L^{-1} in a hydroponic solution

from 3 to 344 mg L^{-1} Ca (Fig. 1). Percent Ca concentrations of hydroponic potatoes were within the 0.6–1.0% range that is considered normal for potatoes at the pre-tuber growth stage (Mills and Jones 1996).

Discussion

Calcium is an essential mineral that has been shown to be important in physiological processes such as plant defense and a deficiency of available Ca can create a more favorable condition for pathogen infection (Rahman and Punja 2007). We found that the addition of Ca reduced the infection coefficient of *P. erythroseptica*, indicating less pathogen DNA with relatively high Ca concentration in hydroponic nutrient solutions. Decreases in infection did not plateau with the Ca rates used in this study, suggesting that further increases in Ca supply to potato roots could further reduce the infection coefficient and subsequent infection by *P. erythroseptica*. These results indicate that pink rot infection may be reduced in commercial potato production when Ca supply to roots and tubers is high.

Calcium has also decreased *Pectobacterium* soft rot when Ca levels in potato tissues were raised (McGuire and Kelman 1984). McGuire and Kelman (1983) found that no surface decay occurred when tubers were vacuum infiltrated in solutions at 12,000 mg L^{-1} Ca. Studies relating to Ca content and *Pectobacterium* soft rot of potato tubers have shown that more susceptible varieties contain low Ca content in the tuber, but that not all resistant cultivars contain high tuber Ca content (McGuire and Kelman 1983). Since there seems to be a lack of disease resistance against pink rot and Ca levels have been implicated in decreasing soft rot severity, the addition of Ca would provide a boost to the natural defense of potato to pink rot and possibly other diseases.

A previous study conducted by Benson, et al. (2009) established that *P. erythroseptica* infections increase as pH decreases. This study was conducted at pH 5.0 to ensure maximum infection and the greatest chance that the effect of Ca could be observed. The effect of Ca on disease infection can be pH dependent because one factor is often inter-related to the other (Myers and Campbell 1985). In this study, a decrease in disease severity was observed as Ca levels were elevated and pH was maintained at 5.0 for all Ca treatments. Acidic soils, especially sandy soils with low cation exchange capacity (CEC) tend to have low Ca concentrations . This occurs because acidity is often developed over time as a function of excess water movement through soils, which leaches Ca. The Ca is replaced by hydrogen ions in the water, which results in a decrease in pH. It was hypothesized that low pH was causing an increase in pink rot incidence in the Idaho fields previously discussed. However, this acidity had developed due to excessive leaching with water low in salts (including Ca and carbonates; Personal comm. Hopkins). Although a previous study showed that pH was indeed a factor in pink rot development (Benson et al. 2009), this study shows that low Ca is also a contributor to the problem.

The mode of action for Ca to promote disease resistance was not the focus of this study and thus still remains unknown, although it is likely that Ca acts through multiple means. Adequate and/or excess Ca has been found to improve soil quality, increase cell wall integrity, thicker skin netting, and ensure proper cell signaling of pathways such as calmodulin, thus reducing the incidence and severity of disease (Rahman and Punja 2007).The effect specifically for *P.erythroseptica* could result from a reduction in zoospore and sporangia pathogenicity and increasing cell wall integrity by resistance to degrading enzymes. Analysis of Ca in the tissue of the plant showed that more Ca was being taken up and used within the plant when grown in higher concentrations of extracellular Ca solutions. Increasing the root mass concentration of Ca particularly suggests the importance of localized effects, which would likely strengthen cell walls and block active sites of polygalactouranase enzymes thus increasing the plants defenses.

Since more severe outbreaks of pink rot are associated with acidic soils, supplemental Ca in the form of calcitic limestone ($CaCO_3$) calcium oxide (CaO), etc., in addition to raising the pH, can substantially increase protection against *P. erythroseptica* infection as these minerals also supply Ca to plants. An upper limit was not established for the effect of Ca in this study, although this study indicates that amending soils that have low soil test Ca with supplemental Ca has the possibility to significantly reduce pink rot outbreaks, which may reduce the amount of yield loss for pre- and post-harvest tubers. Augmenting the soil with soluble Ca provides another tool to the limited control strategies for pink rot management, although field trials need to be performed to develop management strategies.

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