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Methodology and Assessment of the Susceptibility of Potato Genotypes to Phytophthora Erythrosetpica Causal Organism of Pink Rot

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METHODOLOGY AND ASSESSMENT OF THE SUSCEPTIBILITY OF POTATO GENOTYPES TO *PHYTOPHTHORA ERYTHROSETPICA* CAUSAL ORGANISM OF PINK ROT

By

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By Erica Fitzpatrick-Peabody

Thesis Advisor: Dr. David H. Lambert

An Abstract of the Thesis Presented
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Phytophthora erythroseptica Pethyb., causal organism of potato (*Solanum tuberosum* L.) pink rot is a soil-borne ubiquitous oomycete pathogen that can cause severe losses in both the field prior to harvest and during storage. The efficacy of the most effective fungicide, mefenoxam for control of *P. erythroseptica* is in jeopardy due to the widespread development of resistance in the US. Cultivar resistance may provide the best option for management of *P. erythroseptica* in the future. Recently published reports of cultivars susceptible to *P. erythroseptica* are based on evaluation techniques involving detached tubers and nontuber germplasm rather than field evaluations. Screening detached tubers excludes the stem stolon infection pathway by which a majority of *P. erythroseptica* infections occur.

In tuber inoculations and field evaluations from 2004 to 2006, 24 cultivars were evaluated for their response to *P. erythroseptica* infection. In 2007 field trials, 15 additional cultivars were evaluated, based upon their shared lineage with those cultivars demonstrating resistance in the three previous field years. Six standard cultivars were evaluated in all four field trial years (2004-07), three resistant and three susceptible. Cultivar response was evaluated in terms of incidence of *P. erythroseptica* rot. The objective of this study was to conduct the first *P. erythroseptica* cultivar susceptibility evaluation under field conditions. This research included the development of protocol for evaluating potato genotypes in field settings as well as baseline data for comparing results obtained utilizing different evaluation techniques.

Overall, in the field trials the red skinned cultivars were classified as the most susceptible or highly susceptible in comparison to other cultivars evaluated. For the 17 cultivars evaluated in all three field year trials (2004-06) Red LaSoda (21.4%) and Russet Norkotah (19.9%) were the most susceptible. Red cultivars that were evaluated for three years included Red Gold (16.8%), Red Pontiac (12%), and Dark Red Norland (10.4%). Russet type cultivars included the susceptible cultivar, Goldrush (16.9%) and those moderately resistant Ranger Russet (9.6%) and Russet Burbank (6.9%) as well as one demonstrating resistance Gem Russet (1.1%). For white type cultivars Shepody (16.3%) was susceptible, while Kennebec (4.8%) and FL-1867 (4.4%) had reasonable resistance. The white type cultivars, though variable showed the most resistance, particularly Snowden (1.5%), Atlantic (0.8%), and Pike

(0.3%). The 4 cultivars demonstrating the most resistance were all 1st to 3rd generation progeny of Lenape (B5141-6).

Tuber inoculations based on an *in-vitro* assay using zoospore suspensions did not always correspond closely to field conditions and failed to identify some cultivars having high levels of resistance under normal growing conditions.

The *P. erythroseptica* cultivar susceptibility of most commercial cultivars is variable with few demonstrating substantial resistance. To date there has not been any single cultivar that has been shown to be immune to *P. erythroseptica*. With limited cultural and chemical management options for *P. erythroseptica* future management of the disease largely depends upon the release of new cultivars with improved resistance.

DEDICATION

This thesis is dedicated to my sister Aimee Kathryn Fitzpatrick. Aimee passed away shortly before I started Graduate School and working on pink rot. During her long illness Aimee was always very interested and involved in what was happening in our lives. My work with pink rot started shortly after she left us, though I believe that Aimee would have been involved in the research. Aimee, I am sure that if you were still here I would have found multiple pink rot related tasks that you could have assisted with!

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I would like to thank Dr. David Lambert for his guidance and never ending dedication on this project. Without hesitation Dave has always been exceptionally supportive, especially during the recent writing process. Dave has been an excellent source of plant pathology knowledge on various subjects, always willing to take the extra time to explain many subjects. I would also like to acknowledge Elbridge Giggie for his help and support with maintaining much of the research trial aspects of this project. Without the resources of the Aroostook Farm including field trial plots, greenhouse, laboratory space and equipment, and research storage lockers this research would not have been possible. I thank my thesis committee for their professional and technical guidance. I would like to thank McCain Foods USA Inc., for realizing the importance of this work and supporting the continuation of these trials to see the work through to the end. In addition, many thanks to Lacey Snyder for her help with field trials. Lastly, I would like to thank my family for their help and patience while I have spent many evenings and weekends working on this project during the past five years. My husband, Barrett has spent many hours with me at the Aroostook Farm sorting through smelly fruit fly infested boxes of pink rot, collecting seed for trials, inoculating tubers, blending vermiculite inoculum, among many other tasks.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

PHYTOPHTHORA ERYTHROSPETICA LITERATURE REVIEW

Chapter Abstract

Phytophthora erythroseptica Pethyb., causal organism of potato (*Solanum tuberosum* L.) pink rot is a soil-borne ubiquitous oomycete pathogen that can cause severe losses in both the field prior to harvest and during storage. The disease is found in all potato production areas of the United States and is endemic to most potato growing regions around the world. The name pink rot describes the diagnostic pink or salmon color that the internal tissues of infected tubers turn when exposed to air for 20-30 minutes. *P. erythroseptica* is most serious under conditions of high soil moisture, especially later in the growing season often associated with fields with poor drainage or late season irrigation. *P. erythroseptica* infections are initiated by dormant inoculum in the form of oospores that germinate when conditions are favorable. Tubers may become infected with *P. erythroseptica* in the field via the stolons or under moist field conditions by germinating zoospores entering through tuber eyes and lenticels. *P. erythroseptica* is pathogenic on plants other than potatoes, including some that are common rotation crops in potato production. Historically, the phenylamide fungicide, metalaxyl, or its more recent enantiomer, mefenoxam, has been very effective in controlling *P. erythroseptica*. The efficacy of the only fungicide to control *P. erythroseptica* is in jeopardy with widespread mefenoxam resistance in the US. *P. erythroseptica* isolates insensitive to mefenoxam

have been shown to have a selective advantage. Random amplified polymorphic (RAPD) DNA analysis of a collection of *P. erythroseptica* isolates both mefenoxam sensitive and resistant identified a low level of genetic variation in those populations. Limited information is available on the susceptibility of various cultivars to *P. erythroseptica* and most that is available is outdated. Recently published lists of *P. erythroseptica* cultivar susceptibility have been based on evaluation techniques involving detached tubers and nontuber germplasm rather than field evaluations. Screening detached tubers excludes the stem stolon infection pathway by which a majority of *P. erythroseptica* infections occur. A brief review of the literature pertaining to *P. erythroseptica* cultivar susceptibility research by evaluation technique, including tuber inoculations, tuber disc assay inoculations, microplantlet inoculations, field inoculations, and development of transgenic cultivars with resistance is included.

Introduction

Dr. George H. Pethybridge first observed *Phytophthora erythroseptica* Pethyb. causal organism of potato (*Solanum tuberosum* L.) pink rot, in 1909 in potato research plots at an experiment station in Clifden, County Galway, in Western Ireland. In 1913 Pethybridge described this new *Phytophthora* species as *P. erythroseptica*. Pethybridge observed rotting tubers that turned a characteristic pink color when cut and exposed to air, which was different than the tuber rotting caused by *Phytophthora infestans*, causal agent of potato late blight (Pethybridge, 1913). Pethybridge isolated this new pathogen on nutrient jelly, describing and naming it *P.*

erythroseptica (Large, 1940). *P. erythroseptica* is a soil-borne, ubiquitous oomycete endemic to most potato growing regions around the world (Vargas and Nielsen, 1972). Severe losses can occur in both the field prior to harvest and during storage. The storage phase of the disease is the most economically important to potato growers. *P. erythroseptica* is most serious under conditions of high soil moisture, especially later in the growing season, and is often associated with fields with poor drainage or late season irrigation (Bonde, 1938; Goss, 1949). Cultural management options for the disease are limited and mostly inadequate to manage the disease under current potato production practices. *P. erythroseptica* is considered an emerging and serious disease problem of potatoes. *P. erythroseptica* has become increasingly problematic in the United States and Canada since the 1990's.

***P. erythroseptica*: A review**

The Irish Department of Agriculture and Technical Instruction established a temporary field station in Clifden in 1909 in response to continuing reports that potatoes in Western Ireland were infected with several diseases other than the infamous potato late blight (Large, 1940). Dr. George H. Pethybridge who was head of the Irish Department of Seeds and Plant Disease Division traveled from Dublin each year to the Clifden field station in May and stayed there until October. The scientist reported his investigations annually in the journal published by the department. Reports of Pethybridge's research, "Were some of the most varied and interesting ever made on potato diseases." Pethybridge was stationed at the field station in Clifden from 1909 until 1916. Pethybridge's work focus was then shifted

from potatoes to flax in response to the demand of the aircraft industry for additional linen.

After first describing the pathogen in Ireland in 1913 Pethybridge again reported the disease in Holland in 1915. *P. erythroseptica* was not reported again until 1919 by Cotton in Scotland. Several locations in England and Wales reported the disease in 1921 (Cairns and Muskett, 1933b). *P. erythroseptica* was first reported in the United States in Maine by Bonde in 1938 (Bonde, 1938). The first report of the disease in the western United States was in Idaho in 1945 (Goss, 1949). Similar reports followed from throughout the United States. The disease has been reported in countries in North and South America, Europe, the Middle East, the Far East, as well as Australia (Lambert and Salas, 2001).

The name pink rot describes the diagnostic pink or salmon color that the internal tissues of infected tubers turn when exposed to air for 20-30 minutes (Pethybridge, 1913). The pink-salmon coloration occurs when tyrosinase oxidizes phenolic compounds produced as a stress response by infected tubers (White, 1945). Later (approximately 60 minutes) the pink color will change to a purplish-brown to black color (Pethybridge, 1913). *P. erythroseptica* lesions have been found to contain large endogenous bacterial populations. Some bacteria isolated from *P. erythroseptica* lesions are capable of producing extracellular cell wall degrading enzymes that are able to degrade tuber tissues (Sturdy and Cole, 1974). Other *Phytophthora* species including *Phytophthora megasperma* may cause pink rot of potato (Cairns and Muskett, 1933a). *P. erythroseptica* is not unique in producing the pink coloration in tuber tissues. Other *Phytophthora* species including *Phytophthora*

megasperma and *Phytophthora cryptogea* can infect potato with similar symptoms of *P. erythroseptica* (Vargas and Nielsen, 1972; Rowe and Schmitthenner, 1977). Physiological disorders to a lesser extent can cause infected potato tissue to turn pinkish in color (Lambert and Salas, 2001). Often *P. erythroseptica* infections are associated with a strong ammonia odor, especially in commercial potato storage situations where infected tubers are present. Infected tubers are rubbery in texture, but remain intact retaining their structure and firmness (Pethybridge, 1913). *P. erythroseptica* tuber infections increase cell permeability and allows the leakage of electrolytes into the external medium (Lucas, 1998). This loss of cell semipermeability explains why *P. erythroseptica* infected tuber tissue becomes wetter compared to healthy tissue. Infected lenticels and eyes will often become swollen due to excessive water and black where oxygen has access to infected tissue (Pethybridge, 1913). Infections typically spread from infected stolons and subsequent growth of the pathogen will be mostly uniform throughout the tuber. Once soil has been removed, *P. erythroseptica* lesions are often clearly bordered by an obvious black line. Below ground *P. erythroseptica* infection symptoms include darkened roots. Typically the disease is found on mature plants near the end of the season.

P. erythroseptica infections are initiated by dormant inoculum in the form of oospores that germinate when conditions are favorable. *P. erythroseptica* mycelium is not capable of growing very far from a food source in soil, suggesting it was not an important source of inoculum in the soil (Vujičić and Park, 1964). Oospores have the ability to survive for several years in plant debris or soil outside the living host. Oospores have been found just beneath the tuber periderm in tubers that appeared

healthy (Lonsdale *et al*., 1980). Tubers may become infected with *P. erythroseptica* in the field via the stolons or under moist field conditions by germinating zoospores entering through tuber eyes and lenticels (Cairns and Muskett, 1939; Goss, 1949). Sporangia and zoospore germination occur under warm moist conditions (Goss, 1949). Boyd reported that larger tubers were most frequently infected with *P. erythroseptica* when compared to smaller sized tubers (Boyd, 1960).

Surface abrasions due to mechanical harvesting and storing activities also provide a route of entry for the *P. erythroseptica* pathogen (Pethybridge, 1913). Inoculum is able to survive on the surface of healthy tubers (Cunliffe, 1978). Soil infested with oospores may adhere to other surfaces, such as equipment or seed pieces, and serve in the long-range dispersal of *P. erythroseptica*. Infection can occur in the field through stolons or directly through the eyes (Cairns and Muskett, 1939). While the roots, stems, and stolons are all susceptible, tuber infections usually occur through diseased stolons (Pethybridge, 1913). Infection mostly occurs in the field, though transmission can occur during storage through eyes under high humidity conditions (Lonsdale *et al*., 1980).

Oospores are the propagules by which dissemination of the pathogen occurs. The introduction of *P. erythroseptica* into a production area via infected seed may occur (Cunliffe *et al*., 1977). Seed tubers can become infected with *P. erythroseptica* by contact with diseased tubers in storage. Seed that has been superficially infected by diseased tubers can produce *P. erythroseptica* infected daughter tubers. Planting *P. erythroseptica* infected seed may serve as the source of inoculum in uninfested soil. Transportation by means of seed may also account for the introduction of *P.*

erythroseptica into new regions or the introduction of new and different *P. erythroseptica* strains (Cunliffe *et al*., 1977; Johnson and Duniway, 1997). It is likely that potato infecting isolates of *P. erythroseptica* have been distributed globally through the movement of infected seed tubers.

Often it is difficult to identify *P. erythroseptica* based on foliar symptoms unless the infection is extreme, which was noted early by Pethybridge (1914). Common above-ground symptoms seen in a field infected with *P. erythroseptica* infection are limp plants with late season leaf chlorosis, stunting, wilting and at times leaf abscission (Goss, 1949). Stems of infected plants become gray to black in color and are easily pulled up due to the rotting of the infected roots. In severe infections when tubers completely rot, the plants will collapse and die. Occasionally, damage to the underground stem will cause the production of aerial tubers, usually near the base of the stem (Jones, 1945).

The sexual organ of the *P. erythroseptica* oomycete, the oospore, is the structure that typically persists in the soil serving as an inoculum source. Oospores readily form in plant tissues, including stems, stolons, roots, and tuber periderm, as well as on agar plates. Oospores either germinate directly or release zoospores (Pethybridge, 1913). Oospores are thick-walled (2.5 µm) and serve as the resting structure for the pathogen. The non-pigmented oogonia are large, averaging 30 x 35 µm in diameter with unicellular amphigynous antheridia, which are 13 x 14-16 µm (Stamps, 1978). Oospores are thick walled and thus capable of resisting environmental conditions to a certain extent. Oospores are able to survive for several years in the absence of a host (Pethybridge, 1913; Cairns and Muskett, 1933b).

Oospores fed to snails have been documented to germinate following digestion by the snails (Gregg, 1957).

The asexual structure of *P. erythroseptica* is the nonpapillate sporangium, which is variable in shape with a tapered base and average dimensions of 26 x 44 µm (Stamps, 1978). Sporangia are produced *in-vitro* by oospores or mycelium in soil extract, bog water (Pethybridge, 1913) or Petri's solution (Vujičić and Calhoun, 1966). The sporangia are borne terminally on sympodial sporangiophores, branching immediately below the sporangium only in water. Sporangia germinate indirectly by producing motile zoospores or directly by producing germ tubes with continued mycelial growth (Pethybridge, 1913). Older sporangia only germinate by the production of a germ tube (Chapman and Vujičić, 1965). Young sporangia contain an obvious central vacuole and other storage vacuoles (Vujičić *et al*., 1965). Sporangial formation of zoospores involves differentiation and cleavage of the cytoplasm to form and release the zoospores. A chilling period of the aqueous medium is required to stimulate *in-vitro* zoospore formation and release (Pethybridge, 1913; Vujičić and Colhoun, 1966). Discharge of the sporangial contents occurs upon rupture of the non-protruding papilla (Chapman and Vujičić, 1965).

Zoospores of *P. erythroseptica* have two flagella characteristic of those found in the orders Peronosporales and Saprolegniales. The two flagella differ in their distal endings (Vujičić *et al*., 1968). The tinsel type flagellum is of uniform thickness, while the whiplash flagellum has a thin prolongated end. A sheath covers the end of each flagellum and both flagella have lateral hairs. The tinsel type contains lateral hairs 2 µm in length up to the end of the flagellum. The lateral hairs of the whiplash

type flagellum are not present on the end and are shorter being 0.6 μm in length. As the motility of the zoospore slows the shape of the zoospore changes from oval to spherical and at the ends of each flagellum knob-like structures appear. Prior to the zoospore becoming completely immobile, the flagella detach and float away. The production and role of zoospores under field conditions has not been described.

Shortly after describing *P. erythroseptica*, Pethybridge first observed in this newly identified species an inverted form of sexual reproduction (Pethybridge, 1913). Until that time sexual reproduction in oomycetes was thought to only occur when the fertilization tube from the male antheridia penetrated the female oogonium. Pethybridge stayed up the entire night looking through a microscope in order to watch and document through drawing this newly observed form of (amphigenous) sexual reproduction (Large, 1940). Throughout the night hours, Pethybridge observed a female oogonium, push its tip into the antheridium. The tip of the oogonium incept began to swell within the antheridium and burst from the top of the antheridium. In only 30 minutes the developing oogonium had increased considerably in size. The oogonium contained cytoplasm that was beginning to gather together to form the oosphere or unfertilized female gamete. At this same stage the funnel-shaped stalk or base passing through the antheridium was easily seen through the microscope. Approximately 15 hours after the oogonium penetrated the antheridium, the oogonium had attained full size (Pethybridge, 1913). Later, a former student of Pethybridge, Paul Murphy, demonstrated that the actual fusion of the two sexual nuclei occurred when the thick wall of the oospore was mature, though the male nucleus had reached the unfertilized egg at an earlier stage (Murphy, 1918).

Pethybridge was the first to describe this novel form of sexual reproduction, but it has since been identified in several other species of the genus *Phytophthora* (Large, 1940).

Isolates classified as *P. erythroseptica* exhibit pathogenicity to a wide range of plants, including many solanaceous as well as non-solanaceous species. Historically, members of the *Solanaceae* family are the most susceptible to damage associated with *P. erythroseptica*. Other hosts that have been identified include yellow calla (*Zantedeschia elliottiana* Engl.) and pink calla (*Zantedeschia rehamanii* Engl.) (Tompkins and Tucker, 1947) and lupin (*Lupinus* spp.) (Trapero-Casas *et al*., 2000). *P. erythroseptica* was reported as causing stem and root rot on tomato (*Lycopersicon esculentum* Mill.) in New South Wales (Gillings and Letham, 1988). The *P. erythroseptica* isolates from tomato did not cause pink rot on wound inoculated potato tubers. In pot tests through the artificial inoculations of 90 different non-solanaceous species, *P. erythroseptica* was found to be pathogenic on 17 of those 90 species (Whelan and Loughane, 1969). Included in that list were barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), and wheat (*Triticum vulgare*), all of which are common rotation crops in potato production.

In 2005, Idaho commercial agricultural fields were surveyed and plants were collected from various potato rotation crops to assay for the presence of *P. erythroseptica*. Using semi-selective medium *P. erythroseptica* was isolated from the roots of barley and wheat from growers' fields. The same species collected from the commercial fields were grown in the greenhouse and artificially inoculated with *P. erythroseptica*. In the greenhouse inoculations, hairy nightshade (*Solanum*

sarrachoides), cutleaf nightshade (*Solanum triflorum*), kochia (*Kochia scoparia* (L.) Schrad.), tomato, and bell pepper (*Capiscum annuum* L.) were noted as *P. erythroseptica* hosts (Porter *et al*., 2006).

P. erythroseptica was first reported in South America from Peru in 1972 infecting potatoes (Vargas and Nielsen, 1972). The Peruvian isolates were classified as *Phytophthora erythroseptica* var. *erythroseptica*. A new variety, *Phytophthora erythroseptica* var. *pisi* was described in England in 1959 infecting peas (*Pisum sativum* L.) in the greenhouse (Bywater and Hickman, 1959).

Previously, *P. erythroseptica* or strains of the species have been reported causing disease on other hosts, but were later rejected as such when subjected to closer scrutiny (Ho and Jong, 1989). These crops include cultivated wild rice (*Zizania palustris* L.) (Gunnell and Webster, 1988), arrowleaf clover (*Trifolium vesiculosum* L.), vetch (*Vivia angustifolia* L.), and sugar cane (*Saccharum officinarum* L.). *P. erythroseptica* was originally described on red raspberry (*Rubus idaeus* L.) as the cause of root rot of red raspberry (Converse and Schwartze, 1968), but this name was later rejected and the pathogen was described as *Phytophthora fragariae* var. *rubi* (Wilcox *et al*., 1993).

P. erythroseptica is a diploid homothallic organism, thus the populations are largely inbred due to the self-fertilization. One of the most descriptive features of *P. erythroseptica* identification is the presence of only amphigynous antheridia. Isolates producing both amphigynous and paragynous antheridia should not be classified as *P. erythroseptica* (Ho and Jong, 1989).

P. erythroseptica cultural control recommendations include: planting only certified, disease-free seed, careful monitoring and scheduling of late season irrigation (Merkens *et al*., 1995), establishing good skin set prior to harvest and avoiding mechanical injury (Salas *et al*., 2000). Optimum temperatures for the pathogen are in the range of 24 to 28º C (Vargas and Nielson, 1972). The pathogen is more active at warm temperatures; delaying harvest until pulp temperatures are between 7 and 10º C will help avoid wound infection if disease is in the field (Salas *et al*., 2000). The two most critical factors in *P. erythroseptica* control are moisture and temperature.

The incorporation of 3- to 4-year crop rotations, if possible, should help reduce *P. erythroseptica* incidence. Rotations with at least one alternate crop between potato crops significantly reduced *P. erythroseptica* disease incidence (Lambert, unpublished). Longer rotations than the traditional 1:1 potato rotation typically employed in Northeast North America conferred additional tuber resistance to *P. erythroseptica* infection. In inoculations of tubers from field trials with a 3-year rotation there was significantly less *P. erythroseptica* development than in tubers inoculated from 2-year rotation soils. The effect of tillage management was not significant. Longer crop rotations appear to enable the soils to have more disease suppressive properties (Peters *et al*., 2005a). Alternative options for *P. erythroseptica* control are limited to longer and possibly unique crop rotations.

P. infestans, casual organism of potato late blight, can potentially be a very devastating disease in potato production, but can be managed with timely fungicide applications based upon validated late blight forecasting programs. In the United

States, losses associated with *P. erythroseptica* can be far more severe and devastating to growers on a yearly basis. Growers facing *P. erythroseptica* problems do not have an arsenal of fungicides available to effectively treat the pathogen. The heterothallic nature of the *P. infestans* pathogen and dominance of one mating type in the US has made the production of oospores rare. This makes the elimination of potential inoculum sources from infected seed lots or cull piles much more practical. *P. erythroseptica* inoculum in the soil can survive for several years as oospores.

***P. erythroseptica* and mefenoxam resistance**

Historically, the highly systemic phenylamide fungicide, metalaxyl, or its more recent enantiomer, mefenoxam, have been most effective in controlling *P. erythroseptica* (Wicks *et al*., 2000; Johnson and Duniway, 1997; Torres *et al*., 1995; Zink, 1995). The biochemical single site mode of action for mefenoxam involves the inhibition of the biosynthesis of ribosomal RNA polymerase I (Davidse *et al*., 1983). There are other fungicides registered for control of *P. erythroseptica* in potato although their effectiveness is variable and consistently poorer than mefenoxam. Management practices for *P. erythroseptica* control often include applications of mefenoxam, especially to highly susceptible cultivars. When applying fungicides for *P. erythroseptica,* the best control has been achieved by applying products in-furrow at planting or to the foliage during early tuberization (Wicks *et al*., 2000; Platt *et al*., 2001). In Maine, the most effective means and most widely practiced application of mefenoxam has been applying the compound in-furrow at planting.

P. erythroseptica isolates collected from different states were tested for metalaxyl sensitivity in the late 1980's and early 1990's with no evidence of metalaxyl resistance detected (Stack *et al*., 1993). However, in 1993 the first case of *P. erythroseptica* insensitivity to metalaxyl was reported in Maine. Three isolates had ED_{50} values > 320 μg/ml (Lambert and Salas, 1994). The following year *P. erythroseptica* insensitivity to metalaxyl was also reported in New York (Goodwin and McGrath, 1995). Metalaxyl resistance was subsequently reported in New Brunswick, Canada (Salas *et al*., 1998). North Dakota State University conducted an international survey screening for *P. erythroseptica* mefenoxam (metalaxyl) resistance from 1997 to 2000 (Taylor *et al*., 2002). This survey documented the first case of resistance occurring in Idaho in 1998. Mefenoxam insensitivity was first documented in Minnesota during the 2000 survey. Subsequently, in 2003-04 resistant populations have been confirmed in Colorado, Nebraska, Michigan, and Wisconsin (Secor *et al*., unpublished). Several *P. erythroseptica* isolates were tested for mefenoxam sensitivity on Prince Edward Island (PEI), Canada from 1999 to 2001 and all isolates were found to be highly sensitive to mefenoxam. The lack of evidence of mefenoxam resistant *P. erythroseptica* on PEI is interesting, because growers have regularly used mefenoxam prophylactically for the control of aerial and soil borne *Phytophthora* pathogens (Peters *et al*., 2003). To date, mefenoxam resistance has not been reported from outside North America. The continued mefenoxam sensitivity in areas like Australia is partly contributed to the lack of substantial selection pressure from mefenoxam applications (Wicks *et al*., 2000). The disease pressure associated with *P. infestans* is typically not as widespread or severe

in Australia, requiring less frequent application of fungicides with activity against *Phytophthora*.

Some production areas have documented the extent of *P. erythroseptica* mefenoxam resistance occurrence in commercial fields. A recent survey in Idaho documented the mefenoxam sensitivity of *P. erythroseptica* infected tubers collected from six different counties. The survey found that over 70% of the *P. erythroseptica* isolates collected were classified as highly resistant to mefenoxam (Porter *et al*., 2007). A similar survey of over 50 grower storages in Aroostook County, Maine in 2005 found similar results (Fitzpatrick and Lambert, 2006). Overall, 70% of the 162 isolates recovered were mefenoxam resistant using an *in-vitro* assay. For the 44% of growers with a recent history of mefenoxam use, 86% of *P. erythroseptica* isolates were resistant. Samples collected from growers without a recent history of mefenoxam averaged 49% resistant.

P. erythroseptica isolates insensitive to mefenoxam have been shown to have a selective advantage (Fitzpatrick and Lambert, 2006; Taylor *et al*., 2006; Porter *et al*., 2007). Even in the absence of selection pressure from mefenoxam applications, some *P. erythroseptica* resistant isolates appear to be more aggressive than sensitive isolates. *P. erythroseptica* disease was more severe in tubers treated with mefenoxam and inoculated with mefenoxam resistant *P. erythroseptica* than tubers not treated with mefenoxam (Taylor *et al*., 2006). Thus, the potential for increased disease incidence exists when mefenoxam is applied to a field with populations of mefenoxam resistant *P. erythroseptica*. Research in Maine has found related results. A trial established in 2003 was inoculated with 20% mefenoxam resistant strains to

track any yearly increase in resistant isolates. In the absence of mefenoxam applications from 2003 to 2005 the number of resistant isolates recovered using an *in-vitro* assay increased significantly. The increasing proportions of resistant isolates in untreated field trials over a 3-year period indicate fitness equal to or greater than that of sensitive isolates (Fitzpatrick and Lambert, 2006). The mefenoxam resistant *P. erythroseptica* isolates appear to have a distinct selective advantage that will likely allow the resistant isolates to persist in the soil environment.

The genetics of mefenoxam resistance in *P. erythroseptica* populations is not well understood. It is unclear if it is a single gene or if multiple genes are involved in mefenoxam resistance. Successive selfed generations of single oospore *P. erythroseptica* isolates of different mefenoxam sensitivity phenotypes were evaluated (Abu-El Samen *et al*., 2005). From resistant and sensitive parents there was a lack of segregation for mefenoxam sensitivity among S1 and S2 progeny isolates. The majority of S1 and S2 progeny isolates from parents with intermediate resistance also had intermediate resistance, but with considerable quantitative shifts toward increased insensitivity. Progeny isolates from S1 and S2 generations indicated that a single gene exhibiting incomplete dominance did not control *P. erythroseptica* mefenoxam resistance. *P. erythroseptica* mefenoxam resistance may be under the control of more than one major gene and perhaps some minor genes of additive effect. Variation in sensitivity might also reflect differences in active site mutations, if this is the basis for mefenoxam resistance.

The widespread development of mefenoxam resistant *P. erythroseptica* populations is of importance, because mefenoxam is the only fungicide truly effective

against the pathogen. The emergence of *P. erythroseptica* as a pathogen of increasing incidence and economic losses is somewhat due to the partial loss of mefenoxam efficacy in some growing regions. The competitive nature of these resistant isolates and growth of resistant isolates in a population despite the absence of selection pressure from mefenoxam applications is troubling. The longevity of the effectiveness of mefenoxam in the future is certainly questionable and will partly depend on measures taken to prevent the development and spread of mefenoxam resistant *P. erythroseptica*.

***P. erythroseptica* isolate virulence diversity**

The homothallic nature of *P. erythroseptica* does not require the presence of mating types for sexual reproduction to occur (Ho and Jong, 1989). Therefore, *P. erythroseptica* populations are largely inbred and homozygous due to the repeated selfing and consequently are of limited genetic diversity (Peters *et al*., 2005b). Sexual reproduction involving different mating types as in *P. infestans* represents a means by which the organism can increase its genetic diversity and its aggressiveness (Fry and Goodwin, 1997). The variability in *P. erythroseptica* isolate virulence has been investigated, including the associated disease incidence among different isolates used for inoculations. In addition, several isolates have been assessed using allozyme banding patterns and RAPD analysis.

Various researchers have made observations on differences in *P. erythroseptica* isolate virulence based upon disease incidence or the rate of disease spread in tuber tissue associated with different isolates used for inoculations.

Significant differences were not detected among 47 *P. erythroseptica* isolates including those mefenoxam sensitive and resistant from California, Idaho, Maine, Minnesota, and New York (Johnson, 1998). The isolates were evaluated on Russet Burbank and Russet Norkotah using tuber disk assay inoculations. In tuber inoculations of 34 cultivars comparing two *P. erythroseptica* isolates from Minnesota and North Dakota, the cultivar by isolate interaction was not significant (Salas *et al*., 2003). In greenhouse microplantlet inoculations of 20 cultivars using five *P. erythroseptica* isolates, 4 sensitive and 1 resistant to mefenoxam, differences in virulence among isolates was not found (Peters and Sturz, 2001). Despite the lack of differences in isolate virulence observed in the inoculation studies *P. erythroseptica* isolates insensitive to mefenoxam have been shown to have a selective advantage (Fitzpatrick and Lambert, 2006; Taylor *et al*., 2006; Porter *et al*., 2007). Resistant *P. erythroseptica* isolates grew faster in culture producing 7 to 21 times as many oospores as sensitive strains (Porter *et al*., 2007). Taylor *et al*., (2006) determined that the pathogenicity (% incidence on tubers not treated with mefenoxam) of two highly mefenoxam resistant isolates (47%) significantly exceeded those of pairs of sensitive (36%) or moderately resistant *P. erythroseptica* isolates. Even in the absence of mefenoxam applications it appears that isolates mefenoxam resistant differ in terms of virulence causing disease incidence.

Using cellulose-acetate electrophoresis allozyme assays (Goodwin *et al*., 1995), the enzyme glucose-6-phosphate isomerase (G*pi*) locus has been identified for both mefenoxam sensitive and resistant *P. erythroseptica* isolates originating from Maine, New York, and PEI (Peters *et al*., 2001). The allozyme-banding pattern

genotypes in all isolates tested were homozygous at the G*pi* locus 91/91. These results indicate that *P. erythroseptica* has a distinct G*pi* genotype, but not the diversity at this locus among isolates from different regions or varying levels of mefenoxam sensitivity as was found in the population of *P. infestans*. The homozygous pattern observed in *P. erythroseptica* isolates is consistent with the homothallic nature of the oomycete. Different genotypes of *P. infestans* have differing banding patterns, which is consistent with the sexual recombination occurring between different mating types in the species (Goodwin *et al*., 1998).

Random amplified polymorphic (RAPD) DNA analysis of a collection of *P. erythroseptica* isolates both sensitive and resistant to mefenoxam from Maine, Idaho, New Brunswick, and PEI identified a low level of genetic variation in those populations (Peters *et al*., 2005b). A very limited number of polymorphic RAPD markers were identified. Researchers were not able to find a RAPD marker that correlated with mefenoxam sensitivity. Only very minor genetic variation was discovered by RAPD screening. The minor variation revealed was not correlated with isolate source or mefenoxam sensitivity. Despite the homothallic nature of *P. erythroseptica* more polymorphic RAPD markers were expected to be detected. The authors attributed the limited genetic diversity revealed among the various isolates of *P. erythroseptica* to be due to the relatively recent introduction of a small founding population in North America.

Based upon allozyme-banding and RAPD analysis, the genetic diversity among *P. erythroseptica* isolates in North America is limited. Significant differences in virulence among isolates have not been detected in cultivar susceptibility

evaluations, but it is the virulence by variety interaction that is important rather than the differences in virulence. In terms of pathogenicity, mefenoxam insensitive *P. erythroseptica* isolates have a higher incidence of infection than those that are sensitive to mefenoxam. In the absence of mefenoxam applications it appears that resistant isolates also have a higher degree of virulence.

P. erythroseptica **cultivar susceptibility: A review**

Limited information is available on the susceptibility of various cultivars to *P. erythroseptica* and most of what is available is outdated. Past evaluations included potato cultivars no longer commercially produced. Pethybridge mentioned 9 cultivars, all of which proved to be more or less susceptible (Pethybridge, 1913). The most extensive of evaluations included a 1933 evaluation of 42 cultivars in which varying degrees of susceptibility was noted, but no cultivar was found to be particularly resistant (Cairns and Muskett, 1933b). A 1945 evaluation in British Columbia, Canada concluded that of 9 cultivars tested, all appeared equally susceptible (Jones, 1945). Goss (1949), in Nebraska, evaluated 9 cultivars in soil inoculation tests. The trial concluded that the Irish Cobbler was the least susceptible with 6% rot, while Warba (46%) and Pawnee (42%) were the most susceptible. Lennard (1980) evaluated cultivar susceptibility in 17 cultivars both in *P. erythroseptica* infested soil and by using tuber inoculations in Scotland from 1973-74. They reported some differences in susceptibility between cultivars as being evident, although some results were inconsistent when tests were repeated or different test methods were used.

More recently, information has been published on cultivar susceptibility to *P. erythroseptica* using tuber inoculations in the lab, tuber disc lab assays, greenhouse microplantlet inoculations, and field screening. Those studies found that cultivars vary greatly in their susceptibility to *P. erythroseptica*. The published susceptibility evaluations using different plant parts and methodologies have not been compared to data obtained in field trials. The limited field trials evaluating *P. erythroseptica* cultivar susceptibility prior to the research conducted in this thesis work included only a 1997 field trial in Maine and 2002 field screening trial in Idaho. A majority of recent research on cultivar susceptibility to *P. erythroseptica* has been based on evaluation techniques involving detached tubers or nontuber germplasm rather than field evaluations.

Tuber inoculation assessments

Fourteen commercial cultivars and experimental breeding lines were evaluated in 1992 using plugs of *P. erythroseptica* mycelium and oospores for tuber inoculations. Minimal differences were found in the measurement of disease severity, which was depth of rot (Stack *et al*., 1994).

Recently, a large-scale tuber inoculation study was conducted that evaluated the susceptibility of 34 different commercially common cultivars to *P. erythroseptica* infection (Salas *et al*., 2003). Tuber inoculations were accomplished using zoospore suspensions, in which one apical and two lateral eyes were inoculated using two different isolates of *P. erythroseptica*. The data for the assessed cultivars were analyzed based on three different tuber skin color categories (reds, whites, and russets) for comparative purposes, and most were evaluated for three years. Those

cultivars found to be the most and least susceptible to infection were Russet Norkotah (88.1%) and Atlantic (31.6%), respectively. Of the white cultivars, Snowden (85%) was found to be the have the highest incidence of infection. The white cultivars that showed the lowest degree of susceptibility were, in order FL-1900 (23.4%), Atlantic (31.6%), FL-1833 (45.9%), Norchip (47.0%), and Pike (47.8%). Of the russet cultivars evaluated, Ranger Russet (43.3%) was the least susceptible cultivar followed by Russet Burbank (50.1%). The red cultivar Viking (78%) was the most susceptible. The least susceptible of the red cultivars were nearly identical in terms of *P. erythroseptica* incidence, which were NorDonna (51.6%) and Norland (52.2%).

Peters *et al*. (2004) screened 6 different cultivars for susceptibility to *P. erythroseptica* using tuber inoculations in which Norland (72.1%) and Shepody (59%) were significantly more susceptible than the other cultivars. Goldrush (40.2%) and Russet Burbank (42.2%) were similar in terms of susceptibility, while Butte (36.3%) and Yukon Gold (35.8%) had lower incidences of disease, although the differences were minimal

Recently, a breeding program in the United States quantified the level of susceptibility to *P. erythroseptica* of selected germplasm (Thompson *et al*., 2007). Three clones were identified as highly resistant to *P. erythroseptica* using tuber inoculations. Three clones with wild species in their recent genetic background, Etb 6-5-2, J101K6A22, and ND6956b-13, demonstrated resistance to *P. erythroseptica* in tuber inoculation assessments. The background of Ebt 6-5-2 included *Solanum etuberosum* and *Solanum berthaultii.* J101K6A22, from *Solanum bulbocastanum,* is

a parent of ND6956b-13, which likely also derived its *P. erythroseptica* resistance from *S. bulbocastanum*.

Trials at the University of Wisconsin from 1999 to 2005 evaluated several hundred different common commercial cultivars and breeding lines by inoculating tubers (James *et al*., 2001; 2002; 2003; 2004; 2005; 2006; 2007). Overall, most entries were highly susceptible to *P. erythroseptica*. In some cultivars there were large differences between the incidence of infection and the mean area of symptomatic tissue. No tuber symptoms were observed on the tubers of LB2-96 in 1999, on W 1980-4 in 2001, or ARS 00-1069-5 in 2002, or the breeding line J138 in 2004. In all years, several breeding lines had a percentage of affected surface area lower than the susceptible standard commercial cultivars.

Tuber disc assay inoculations

The response of tuber discs of both Russet Burbank and Russet Norkotah inoculated with *P. erythroseptica* were evaluated (Johnson, 1998). Following incubation, the cultivar response was determined by measuring the lesion diameter, which was converted using a monomolecular transformation. The average lesion diameter was 0.66 for Russet Burbank and 0.31 for Russet Norkotah. The author did note that lesion development may be a defense response and that Russet Burbank may actually be less susceptible than Russet Norkotah. The support for this hypothesis was based on the disease lesions and differences in the surrounding tissues observed between the two cultivars. Russet Burbank expressed round, dark, well-defined lesions with margins while the lesions on Russet Norkotah were lighter and irregular without distinct margins. The tissue beyond the lesion margin remained firm in

Russet Burbank, while the same tissue area in Russet Norkotah became soft and degraded.

Microplantlet inoculation assessments

A rapid greenhouse screening method was developed to evaluate the susceptibility to *P. erythroseptica* of nontuber potato germplasm using tissue cultured microplantlets screening only root, stolon, and stem tissues (Peters and Sturz, 2001). Twenty cultivars were included, which were categorized for evaluation and correlation purposes based upon four crop maturity groupings of early, midseason, late, and very late. A disease severity index (DSI) scale rating was used to assess the susceptibility of each inoculated microplantet. Microplantlets of the cultivars Goldrush, Yukon Gold, AC Novachip, and Shepody, which were all classified as mid to early season maturing, showed the highest disease severity. The cultivars Ranger Russet, Snowden, Russet Burbank, and Butte, which were all late to very late season cultivars, had the lowest disease severity in that order. A majority (60%) of the cultivars were classified as moderately susceptible based on the mean DSI. Ranger Russet and Butte, which both demonstrated moderate resistance, are genetically related in that Butte is one of the parents of Ranger Russet. In this study, late season field maturity cultivars were significantly more resistant to disease development than those with early or midseason maturity.

Field inoculation assessments

Prior to the field inoculation trials done in the following thesis work, the only known field inoculated cultivar susceptibility trials for *P. erythroseptica* were done in Presque Isle, Maine in 1997 (Lambert, unpublished). Eleven cultivars were screened

and the cultivars Red Gold and Russet Norkotah were both highly susceptible, with greater than 30% *P. erythroseptica* tuber rot. Katahdin, Norwis, Allegany, Mainestay, and Superior had moderate levels of *P. erythroseptica* infection. Russet Burbank and FL-1533 had less than 10% rot, while both Snowden and Atlantic had less than 5% rot.

In Idaho in a 2002 national powdery scab susceptibility field trial that included various cultivars from other breeding programs in the US, significant levels of *P. erythroseptica* were present at harvest (Miller *et al*., 2003). The presence of *P. erythroseptica* allowed for an additional evaluation of *P. erythroseptica* cultivar susceptibility under natural field conditions. Russet Norkotah, Shepody, and AF 1758-7 all were highly susceptible, with greater than 10% *P. erythroseptica* tuber rot. Cultivars that were the least susceptible included Atlantic and Russet Burbank. Gem Russet indicated some level of resistance with no *P. erythroseptica* rot found. It must be remembered that there is a relationship between powdery scab lesions and the occurrence of *P. erythroseptica*. Powdery scab lesions on tubers provide a means of entry for *P. erythroseptica* zoospores under moist field conditions. In the Idaho study significant powdery scab pressure coupled with ideal conditions for *P. erythroseptica* zoospore release may have contributed to the high levels of disease seen in the trial. Despite the powdery scab disease pressure, the trial provided a valid look at the field *P. erythroseptica* susceptibility of several cultivars and breeding lines under natural infection conditions.

Transgenic cultivars and susceptibility

Transgenic potato lines that express antimicrobial peptides have demonstrated substantial *P. erythroseptica* resistance (Osusky *et al*., 2004; Osusky *et al*., 2005). The researchers used small, cationic antimicrobial peptides (CAPs) isolated from the skin secretions of the European red frog (*Rana temporaria*) (Osusky *et al*., 2004). Temporin A was N-terminally modified (MsrA3) and expressed in potato plants. The MsrA3 conferred substantial resistance against *P. erythroseptica* and a close relative, *P. infestans*. Temporin A CAPs provide both antibacterial and antifungal activities. In this study, the researchers modified the N terminus to increase the affinity of temporin A for negatively charged lipids. The new gene, msrA3, encoded a modified temporin A, MsrA3, in the potato cultivar Desiree in which it was expressed. Both plants expressing MsrA3 and non-transformed potato plants were inoculated with *P. erythroseptica*. The internal tissues of the inoculated control tubers turned the diagnostic pink color while the sectioned tubers from plants expressing MsrA3 did not turn pink in color. A small area of infection was evident, but the infection did not move beyond the small point of inoculation. The *P. erythroseptica* infected area of internal tuber tissues was 9 – 29%, while the infected area of non-transformed tubers was 100%. Resistance was stable through one generation of vegetative seed propagation, as tubers from a second generation of transformed plants were tested and the results were similar. A synthetic derivative of the cationic antimicrobial dermaseptin B1 found in the skin secretions of the arboreal frog (*Phyllomedusa bicolor*), MsrA2, was expressed in a different transgenic potato line (Osusky *et al*., 2005). Expression of MsrA2 in potato plants also significantly reduced the *P.*

erythroseptica affected area when tubers were inoculated, which was similar to the expression of MsrA3. MsrA2 exhibited more broad-spectrum resistance to several oomycete and fungal pathogens as well as *Erwinia* than the expression of MsrA3. Currently, consumers have not accepted genetically modified potatoes or potato products in the marketplace. The two new genes identified, MsrA2 and MsrA3 with anitmicrobial peptides if expressed at low levels in transgenic potato plants could potentially effectively improve the *P. erythroseptica* resistance of cultivars currently in production (Osusky *et al*., 2004; Osusky *et al*., 2005).

Conclusions

To date there has not been any single potato cultivar that has demonstrated immunity to *P. erythroseptica*. Most all trials have shown varying levels of susceptibility relative to other cultivars evaluated. Tuber inoculation evaluations have recently found Russet Norkotah, Snowden and Shepody to be highly susceptible to *P. erythroseptica*, while Atlantic and Pike have demonstrated reasonable levels of resistance (Salas *et al*., 2003). Microplantlet evaluations are somewhat correlated with tuber inoculation data and suggested that there could be a genetic basis for the relationship between time of crop maturity and *P. erythroseptica* genotype susceptibility (Peters and Sturz, 2001). A recent evaluation of several clones from a breeding program, including the germplasm of wild species has indicated that *P. erythroseptica* resistance may be found in wild species and is highly heritable (Thompson *et al*., 2007). A non-traditional approach involving the development of

transgenic potato lines expressing a cationic peptide conveying resistance to the *P. erythroseptica* has been identified (Osusky *et al*., 2004; Osusky *et al*., 2005).

Resistance to *P. erythroseptica* is not found in many commercial cultivars. The efforts of traditional breeding programs in the past have not been directed towards developing clones with *P. erythroseptica* resistance. It is crucial for breeding programs to screen breeding lines to identify those demonstrating resistance to *P. erythroseptica*. Accurate screening methods need to be available for evaluating parental material and advanced clones. The commercial lack of acceptance of transgenic potatoes strengthens the need for the development of cultivars with *P. erythroseptica* resistance by means of traditional breeding. It is unlikely that cultivars will be immune to the pathogen, but it is pertinent to develop cultivars with improved *P. erythroseptica* resistance.

Until recent years, the published trials relating to *P. erythroseptica* susceptibility were based on cultivars no longer commercially produced. Work that has been recently done evaluating many common cultivars for susceptibility to *P. erythroseptica* has been based primarily on tuber inoculation data. Screening detached tubers excludes the stem stolon infection pathway, by which a majority of *P. erythroseptica* infections occur. Screening done in the greenhouse using nontuber germplasm does not quantify the level of *P. erythroseptica* resistance under field growing conditions. Research relating cultivar susceptibility to *P. erythroseptica* to field evaluations is scarce. The validation of *P. erythroseptica* resistance in field trials is needed to compare the other evaluation methods published to date. Cultivar

resistance may provide the best option for management of *P. erythroseptica* in the future.

Chapter 2

RESPONSE OF POTATO CULTIVARS TO *PHYTOPHTHORA ERYTHROSEPTICA* INFECTION

Chapter Abstract

Phytophthora erythroseptica Pethyb., causal organism of potato (*Solanum tuberosum* L.) pink rot is a soil-borne ubiquitous oomycete pathogen that can cause severe losses in both the field prior to harvest and during storage. The efficacy of the most effective fungicide, mefenoxam for control of *P. erythroseptica* is in jeopardy due to the widespread development of resistance in the US. Cultivar resistance may provide the best option for management of *P. erythroseptica* in the future. Recently published reports of cultivar susceptible to *P. erythroseptica* were based on evaluation techniques involving detached tubers and nontuber germplasm rather than field evaluations. Screening detached tubers excludes the stem stolon infection pathway by which a majority of *P. erythroseptica* infections occur.

In tuber inoculations and field evaluations from 2004 to 2006, 24 cultivars were evaluated for their response to *P. erythroseptica* infection. In 2007 field trials 15 additional cultivars were evaluated, based upon their shared lineage with those cultivars demonstrating resistance in the three previous field years. Six standard cultivars were evaluated in all four field trial years (2004-07), three resistant and three susceptible. Cultivar response was evaluated in terms of incidence of *P. erythroseptica* rot. The objective of this study was to conduct the first *P. erythroseptica* cultivar susceptibility evaluation under field conditions. This research

included the development of a protocol for evaluating potato genotypes in field settings as well as baseline data for comparing the results of other evaluation techniques employed.

Overall, in the field trials the red type cultivars were classified as the most susceptible or highly susceptible in comparison to other cultivars evaluated. For the 17 cultivars evaluated in three field year trials (2004-06) Red LaSoda (21.4%) and Russet Norkotah (19.9%) were the most susceptible. Cultivars with red skin that were evaluated for three years included Red Gold (16.8%), Red Pontiac (12%), and Dark Red Norland (10.4%). The russet type cultivars were variable in terms of susceptibility and resistance. Russet type cultivars included the susceptible cultivar, Goldrush (16.9%) and the moderately resistant Ranger Russet (9.6%) and Russet Burbank (6.9%) as well as one demonstrating resistance, Gem Russet (1.1%). For white type cultivars, Shepody (16.3%) was susceptible, while Kennebec (4.8%) and FL-1867 (4.4%) had reasonable resistance. The white type cultivars, though somewhat variable, demonstrated the most resistance, particularly Snowden (1.5%), Atlantic (0.8%), and Pike (0.3%). The 4 cultivars demonstrating the most resistance were all 1st to 3rd generation progeny of Lenape (B5141-6).

Tuber inoculation evaluations using zoospore suspensions did not always correspond closely to field evaluations and did not identify some cultivars having high levels of resistance under normal growing conditions. In tuber inoculations there was no relationship between the lesion size and disease incidence, which would likely not be a useful indicator of cultivar resistance.

The *P. erythroseptica* cultivar susceptibility of most commercial cultivars is variable with few demonstrating substantial resistance. To date there has not been any single cultivar that has been shown to be immune to *P. erythroseptica*. With limited cultural and chemical management options for *P. erythroseptica* future management of the disease largely depends upon the release of new cultivars with improved resistance.

Introduction

Potatoes are the fourth largest crop produced worldwide, following rice, wheat and maize. In Maine, potato production remains the number one agricultural commodity with Maine potato farmers planting 23,100 hectares in 2007 with a total production of 750 metric tons (NASS, 2008).

Pink rot, caused by *P. erythroseptica* is a highly variable disease, which has been increasing in importance and incidence, causing large economic losses annually. The introduction and significant acreage of newer, more susceptible cultivars like Russet Norkotah coupled with the widespread distribution of mefenoxam resistant isolates has made *P. erythroseptica* increasingly problematic in potato production. Currently there is no adequate replacement of mefenoxam replacement for the control of pink rot. The only solution is the development of cultivars with *P. erythroseptica* resistance.

Potato cultivars differ in their susceptibility to *P. erythroseptica*, but most commercially grown cultivars are susceptible to the pathogen. Currently, there is limited information on the susceptibility to *P. erythroseptica* of most of the potato

cultivars commercially produced in the US. Recently published lists of *P. erythroseptica* cultivar susceptibility are based on evaluation techniques involving detached tubers rather than field evaluations. Screening detached tubers excludes the stem stolon infection pathway by which a majority of *P. erythroseptica* infections occur. Tuber inoculation based on an *in-vitro* assay do not correspond closely to field conditions and may not identify some cultivars having high levels of resistance under normal growing conditions.

The objective of this study was to characterize cultivar susceptibility to *P. erythroseptica* cultivar based on field inoculation conditions. The same cultivars used in this field study were also evaluated using a previously described tuber inoculation method (Salas *et al*., 2003). The data from the field evaluations were compared to the tuber inoculations and the results obtained by previous researchers utilizing the same tuber inoculation technique. The development of the field inoculation technique for evaluation of cultivar susceptibility provides a detailed protocol to potentially be used by breeding programs to assess the susceptibility of parental material and advanced breeding clones to *P. erythroseptica*.

Over the four years of field trials, 39 cultivars were evaluated and in three years of tuber inoculations 24 cultivars were assessed. Cultivars evaluated in the fourth year of field trials (2007) were selected based upon their lineage in common with cultivars that demonstrated resistance in the previous three years. The *P. erythroseptica* susceptibility of several cultivars using both field and tuber inoculation evaluations were investigated.

Materials & Methods

Isolates of P. erythroseptica

P. erythroseptica isolates used for the studies were collected from several diseased tubers from fields and storages of commercial growers throughout Aroostook County, Maine. Diseased tubers were cut in half and small (3-4 mm) tuber cross sections were removed with a sterile scalpel from the margins of suspicious lesions. Symptomatic cross sections were plated onto 1.5% water agar (WA, Difco Laboratories Inc., Sparks, MD). WA consisted of 1000 ml deionized distilled water and 1.5% Difco agar. After 4-5 days of growth on WA, small 5 mm diameter plugs characteristic of *P. erythroseptica* were removed and subcultured to potato dextrose agar (PDA, Difco Laboratories Inc., Sparks, MD). All isolates were identified based on morphological characteristics using the key of Stamps (1978). The collection of *P. erythroseptica* isolates was maintained on PDA slants in darkness and used to prepare inoculum for trials. Only mefenoxam sensitive isolates were used as inoculum sources. Five to ten different mefenoxam sensitive *P. erythroseptica* isolates were selected each year to be used as inoculum for trials. The isolates used were all recovered from tubers infected by *P. erythroseptica* from the most recent crop year. This provided a source of isolates that were recently isolated and a representative mix of *P. erythroseptica* collected from commercial growers and trials in the growing region.

Determining mefenoxam sensitivity of P. erythroseptica *isolates*

Each year all five to ten *P. erythroseptica* isolates contained in the isolate collection were tested for mefenoxam sensitivity using an *in-vitro* assay. Clarified

V8 agar containing 750 ml deionized distilled water, 250 ml clarified Campbell's V8 juice (strained through four layers of cheesecloth), 1.5% Difco agar, 2 g calcium carbonate, and 1.5 ml β-sitosterol (30 mg β–sitosterol in saturated ethanol solution) was used. The clarified V8 agar was amended with 5 µg/L mefenoxam (Ridomil Gold 4EC, Syngenta Crop Protection, Inc., Greensboro, NC). Isolates to be tested for mefenoxam sensitivity were subcultured on PDA. Following 4-5 days of growth on PDA, a 5-7 mm diameter plugs were removed from the margins of each actively growing colony and placed on Petri dishes (100 x 15 mm) (Fischer Scientific, Pittsburgh, PA) containing the described mefenoxam amended V8 agar. Inoculated plates were allowed to grow for 3-5 days then examined for growth in the presence of mefenoxam. Isolates were classified as highly resistant, intermediate resistant or sensitive to mefenoxam based upon phenotypic characteristics of the isolates. For isolates classified as highly resistant, prolific mycelial growth and oospore production covered the entire surface of the agar in 3-5 days. Isolates classified as intermediate resistant covered at least half of the surface area of the agar with mycelium and oospores in the same amount of time. For sensitive isolates, only very limited mycelial growth occurred around the agar plugs. This was attributed to the RNA polymerase activity of the mycelial mass on the agar plug that was transferred to the mefenoxam amended agar.

Preparation of *P. erythroseptica* inoculum for field inoculations

For inoculum production, four approximately 5mm plugs were removed from the margins of actively growing colonies on PDA plates and placed on Petri dishes (100 x 15 mm) of clarified V8 agar. Inoculated, clarified V8 agar plates were

allowed to grow for 4-6 weeks in darkness prior to planting. Two to three days prior to planting, inoculum was mixed with fine grade horticultural vermiculite (Whittemore Company, Inc., Lawrence, MA). The entire contents of 50 inoculated Petri dishes, including the clarified V8 agar, mycelium and oospores were mixed with 500 ml of deionized distilled water in a blender on liquefy mode for 2-3 minutes or until the agar was completely liquefied. The blender contents were mixed with 18.9 liters of fine grade horticultural vermiculite. The blender procedure was repeated and the contents of 50 additional plates were again mixed with the same 18.9 liters of vermiculite. In total the equivalent of 100 *P. erythroseptica* inoculated V8 agar plates were hand mixed with each 18.9 liters of vermiculite. The vermiculite was than sifted through 1.3 cm screens to remove any clumps associated with the agar from the vermiculite.

General field trial details and cultural practices

Field plots were established at the Maine Agricultural and Forest Experiment Station, Aroostook Research Farm in Presque Isle, Maine on Caribou gravely loam. The same trial site was used each year (2004-07). All seed was sourced from local seed growers or an extensive variety collection maintained at the experiment station. All cultural practices, including disease and insect control were those recommended for Maine potato production. Each year, in each plot rows were 3 m in length with 92 cm inter-row spacing and 30 cm intra-row seed spacing. Details of field trials are shown in Table 2.1. Whenever possible whole seed pieces were planted, but if planting cut seed was necessary it was pre-cut for 2-3 weeks to allow for adequate suberization. The fertilization was 1120 kg/ha of 14-14-14 (N-P-K) banded at

planting. Admire (imidacloprid, Bayer CropScience, Inc., Research Triangle Park, NC) was applied at planting at a rate of 0.37 µl m^{-1}/ha. Sencor (metribuzin, Bayer CropScience, Inc., Research Triangle Park, NC) was applied pre-emergence at a rate of 0.12 kg/ha for general weed control. Bravo WeatherStik (chlorothalonil, Syngenta Crop Protection, Inc., Greensboro, NC) at a rate of 290 ml/ha was applied weekly for *P. infestans* control. Each year the trials were mechanically hilled once approximately 34 days after planting. Reglone (diquat, Syngenta Crop Protection, Inc., Greensboro, NC) vine desiccant was applied at a rate of 240 ml/ha each year approximately 106 days after planting (Table 2.1). Tubers were mechanically lifted at harvest at which time *P. erythroseptica* diseased tubers were separated and weighed in the field.

Drip irrigation was applied to the plots and was installed after mechanical hilling approximately 34 days after planting. Irrigation was not applied in 2004, but was applied in trial years 2005-07. Irrigation applications were made based upon soil moisture sensors located in the trial. Irrigation was applied late season when soil moisture levels at 20 cm reached approximately >55 kPa. Data from soil moisture sensors was recorded using WatchDog Data Loggers (Spectrum Technologies Inc., Plainfield, IL), which generated soil moisture graphs (Appendix A).

Table 2.1. *P. erythroseptica* field inoculation trials 2004-07 details

Year	No. Cvs.[a]	Planting Date[b]	Hilling Date[c]	Stand Counts[d]	Irrigation Date[e]	Senescence Rating[f]	Desiccant Date[g]	Harvest Date[h]
2004	18	9-Jun	12-Jul	…[i]	…[i]	…[i]	22-Sep	5-Oct
2005	22	6-Jun	12-Jul	6-Jul	16-Aug	5-Sep	3-Oct	25-Oct
2006	24	6-Jun	5-Jul	18-Jul	11-Aug	7-Sep	13-Sep	11-Oct
2007	21	8-Jun	16-Jul	17-Jul	23-Aug	10-Sep	16-Sep	9-Oct

[a] Number of cultivars evaluated each year varied from 18 to 24.
[b] Date of planting and initial inoculation.
[c] Date of second inoculation and mechanical hilling.
[d] Date emergence counts were collected.
[e] Date of first irrigation application.
[f] Date senescence rating scores were recorded.
[g] Date first vine desiccant application was applied.
[h] Date trials were harvested.
[i] … Indicates application not available in that trial year.

Plant emergence data

In trial years 2005-07 stand counts were done for all cultivars in each replicate. The stand count was determined for each cultivar as the (total number of seed pieces emerged divided by the total number of seed pieces planted x 100. Means separation was differentiated for cultivars evaluated in both 2005 and 2006 as combined data and on 2007 trial year data individually using Fisher's least significant difference test (LSD) at P = 0.05 (SAS Institute, version 9.1, Cary, NC).

Plant senescence ratings data

A senescence rating system was developed and implemented to assess the foliar health of all cultivars prior to vine desiccation (Table 2.2). The senescence rating system ranged from 1 to 7, in which a rating of 1 represented a plant in excellent health with no foliar disease symptoms visible. A rating of 6 indicated a

plant with approximately 10% of green stems and foliage remaining, while 7 represented a plant without any green material (dead).

Table 2.2. Senescence rating system for *P. erythroseptica* field trials

Senescence Rating Score	Plant health indicator
1	Overall excellent plant health, no disease symptoms visible.
2	Some browning and yellowing of leaves, overall healthy plant.
3	~75% of green material remaining, some die back, yellowing of leaves.
4	~50% of green material remaining, large amount of die back, open gaps in rows.
5	~25% of green material remaining, extensive die back, significant gaps in rows.
6	~10% of green material remaining, most all of row exposed.
7	Dead plant (no green material including stems or foliage).

In trial years 2005-07, an overall senescence rating was assigned to each replicate approximately 90 days after planting for all cultivars. The senescence score for each of the five replicates was averaged to determine the average senescence score for each cultivar in 2005-07. The senescence rating was established to determine if there was a correlation between the late season foliar health observed in the field and total *P. erythroseptica* rot incidence associated with each cultivar. Means separation was differentiated for cultivars evaluated in both 2005 and 2006 as combined data and on 2007 trial year data individually using Fisher's least significant difference test (LSD) at P = 0.05 (SAS Institute, version 9.1, Cary, NC).

Preparation of *P. erythroseptica* inoculum for tuber inoculations

To produce *P. erythroseptica* zoospores, a modified protocol reported by Vujičić and Colhoun (1966) was used. Lima bean broth was produced by autoclaving 250 g of lima beans in 1000 ml distilled deionized water and then filtering through four layers of cheesecloth. To produce the lima bean agar deionized distilled water was added to the lima bean broth to reach 1000 ml and 1.5% Difco agar was added. Initially, *P. erythroseptica* stock isolates were grown on lima bean agar. After 5-7 days of growth on lima bean agar, three 5-7 mm diameter plugs were removed from the leading edge of colonies. The plugs were placed in shallow levels of lima bean broth in Petri dishes (100 x 15 mm). Cultures in broth were held in the dark at 18º C for 3-4 days to allow for mycelial growth. After 3-4 days lima bean broth was decanted and mycelial mats were rinsed twice with 10 ml sterile distilled water. Following the final rinsing, the mycelial mat plugs were placed in 10 ml of an autoclaved 1:1 solution of Haynesville bog water (local source) and deionized distilled water in the same size Petri dishes. Cultures were kept under continuous fluorescent lighting (Sylvania F20T12CW) at 21-22º C for 3-4 days to induce sporangia production, and the 1:1 bog water solution was replaced 2-3 times daily. The day prior to chilling, the 1:1 bog water solution was replaced with 10 ml of sterile distilled water. To induce zoospore release, cultures were chilled at 7º C for at least two hours. Cultures were warmed at room temperature in the darkness and zoospore release occurred in 15 to 25 minutes. A hemacytometer was used to obtain a standardized inoculum concentration of 3×10^4 zoospores/ml. Throughout inoculations cultures were agitated to avoid accumulation of zoospores near the top of

the water. Zoospore suspensions were kept chilled until 30 minutes prior to inoculations.

Field and tuber inoculations cultivars assessed

A total of 39 cultivars were evaluated in the field over the four year period, though all 39 cultivars were not included each year. In the field from 2004-07, 6 standard cultivars were evaluated during four years, 11 for three years, 7 for two years, and 17 for one year. The 6 standard cultivars included Atlantic, Pike, Red LaSoda, Russet Norkotah, Shepody, and Snowden. The cultivars evaluated in the field from 2004-06 and subsequent tuber inoculations were selected based upon the acreage in commercial production, importance of the cultivar in different market sectors in the US, or inclusion in previous *P. erythroseptica* cultivar evaluations (Peters and Sturz, 2001; Salas *et al*., 2003; Peters *et al*., 2004). Cultivars that were evaluated in 2004-06 field trials (Table 2.3) that had demonstrated resistance were partially the basis for the selection of cultivars evaluated in 2007 field trials (Table 2.4). In 2007 field trials 15 cultivars were evaluated, those cultivars were selected mostly based upon their shared lineage with those cultivars demonstrating resistance in the three previous field years. In three years of tuber inoculations (2004-06), 18 cultivars were evaluated for three years, 4 were for two years, and 2 cultivars were assessed for one year only.

Table 2.3. Potato cultivars evaluated for their response to *P. erythroseptica* in field and tuber inoculation trials from 2004-06[a]

Cultivar	Parentage	Release Date	Maturity Class[c]	Type	Field Years Tested (no.)	Tuber Inoc. Years Tested (no.)
A9304-3	A83043-12 x Western Russet[b]	n/a	ML	russet	1	1
Atlantic	Wauseon x B5141-6 (Lenape)	1976	M	white	4	3
Butte	A 492-2 x Norgold Russet	1977	ML	russet	2	2
Dark Red Norland	clone from Red Norland	1989	E	red	3	3
FL-1533	Norwis x Atlantic	…[d]	EM	white	2	2
FL-1833	…	…	M	white	2	1
FL-1867	FL-162 x Atlantic	1999	M	white	3	2
Gem Russet	A 77182-1 x Russet Norkotah	2000	ML	russet	3	3
Goldrush	ND 450-3R x Lemhi Russet	1992	M	russet	3	3
Kennebec	USDA B 127 x USDA 96-56	1948	M	white	3	3
Pike	Allegany x Atlantic	1996	M	white	4	3
Ranger Russet	Butte x A 6595-3	1991	ML	russet	3	3
Reba	Monona x Allegany	1997	ML	white	2	3
Red Gold	G 68211 x G 6521-4RY	1987	M	red	3	3
Red LaSoda	Clonal selection from LaSoda	1953	M	red	4	3
Red Pontiac	Clonal selection from Pontiac	1945	ML	red	3	3
Reeves Kingpin	CS 7981-7 x CF 7608-19	2004	M	russet	2	3
Russet Burbank	Early Rose x ? (sport of Burbank)	1914	L-VL	russet	3	3
Russet Norkotah	ND 9526-4R x ND 9687-5R	1987	EM	russet	4	3
Shepody	Bake-King x F58050	1980	ML	white	4	3
Snowden	B5141-6 (Lenape) x Wischip	1990	L	white	4	3
Superior	USDA 96-56 x MN59.44	1961	EM	white	3	3
Viking	Nordak x Redskin	1963	M	red	2	2
Yukon Gold	W5279-4 x Norgleam	1980	M	white	3	3

[a] Includes cultivars evaluated from 2004-06 and the 6 standard cultivars that were also evaluated in 2007 field trials that had been included in the previous 3 years (2004-06).
[b] An online potato pedigree database. URL: www.plantbreeding.wur.nl/potatopedigree/.
[c] Cultivar maturity class designations were as follows: E = Early; EM = Early-Medium; M = Medium; ML = Medium-Late; L = Late; VL = Very-Late.
[d] Most information for Frito-Lay (FL) cultivars is not available for public disclosure.

Table 2.4. Potato cultivars evaluated for their response to *P. erythroseptica* in 2007 field trials[a]

Cultivar	Parentage	Release Date	Maturity Class[c]	Type	Field Years Tested (no.)
AF 1758-7	AF 303-5 x CF 7608-19 [b]	n/a	ML	russet	1
Allegany	M 297-17 x GN bulk pollenmixture	1989	VL	white	1
Andover	Allegany x Atlantic	1996	E	white	1
Atlantic	Wauseon x B5141-6 (Lenape)	1976	M	white	4
Delta Gold	USDA 45208 x Earlaine	1978	M	white	1
FL-1879	FL-1207 x Snowden	…[d]	EM	white	1
Innovator	Shepody x RZ 84-2580	1999	ML	russet	1
Katahdin	USDA 40568 x USDA 2462	1932	M	white	1
Keuka Gold	Steuben x Norwis	1999	ML	white	1
Lehigh	Keuka Gold x Pike	2007	ML	white	1
Lenape	USDA B 3672-3 x Delta Gold	1967	ML	white	1
Marcy	Atlantic x Q155-3	2002	L	white	1
Monona	USDA B 1268-46 x USDA B 1299-15	1964	M	white	1
Pike	Allegany x Atlantic	1996	M	white	4
Red LaSoda	Clonal selection from LaSoda	1953	M	red	4
Russet Norkotah	ND 9526-4R x ND 9687-5R	1987	EM	russet	4
Shepody	Bake-King x F58050	1980	ML	white	4
Snowden	B5141-6 (Lenape) x Wischip	1990	L	white	4
Somerset	USDA 6097-9 x USDA B 6516-5	1989	M	white	1
Sunrise	Wauseon x USDA B 6563-2	1984	EM	white	1
Wischip	WIS 55-306.58 x W 231	1973	ML	white	1

[a] Includes cultivars evaluated only in 2007 and the 6 standard cultivars that were also evaluated in the previous 3 field years (2004-06).
[b] An online potato pedigree database. URL: www.plantbreeding.wur.nl/potatopedigree/.
[c] Cultivar maturity class designations were as follows: E = Early; EM = Early-Medium; M = Medium; ML = Medium-Late; L = Late; VL = Very-Late.
[d] Most information for Frito-Lay (FL) cultivars is not available for public disclosure.

Field inoculations with *P. erythroseptica*

Lambert had previously developed artificial soil inoculation methodology and rates to evaluate fungicidal control of *P. erythroseptica* under field conditions (Lambert, unpublished). Applying artificial *P. erythroseptica* inoculation to soil helps to overcome the variability in any resident pathogen population (Johnson, 1998). Each year isolates were tested using the described *in-vitro* assay to test for mefenoxam sensitivity. Only isolates phenotypically classified as mefenoxam sensitive were used as field trial inoculum sources. *P. erythroseptica* pathogen diversity was incorporated into the inoculum as isolates were sourced from spatially distant geographic areas of Aroostook County, Maine from growers employing different cultural practices, rotation crops, and other management factors. Using fresh isolates from the most recent crop year allowed the isolates to stay viable, rather than repeated transfers on agar media. Repeated transfers can lead to isolate loss through contamination and declining virulence. There is no evidence that there is a range of virulence between *P. erythroseptica* isolates from different regions of North America or those mefenoxam sensitive and resistant (Peters *et al*., 2005b).

The vermiculite inoculum mix was scattered in-furrow into rows that were mechanically opened immediately prior to planting. Vermiculite inoculum mix was applied in-furrow at planting and again at hilling at a rate of 24 Petri dishes of *P. erythroseptica* mycelium and oospores in 4.9 liters of vermiculite per 3 m split between planting and hilling. The vermiculite inoculum was measured and applied in opened rows using containers holding 198 grams. After inoculum was evenly scattered in the furrow of the opened row at planting, hand hoes were used to lightly

cover the inoculum with soil prior to placing seed in the furrow. Past experiences indicated that not having seed pieces directly in contact with inoculum improved emergence rates. Each year trials were re-inoculated the same day as mechanical hilling. The mechanical hilling incorporated the additional inoculum into the row. The lower root zone and the upper root and tuber zone are both effective locations for inoculum placement (Lambert, unpublished).

Tuber inoculations with *P. erythroseptica*

Healthy tubers of the desired size profile that were harvested from the field trials were used for tuber inoculations. Each year those healthy tubers were stored in a controlled atmosphere storage for 2-5 months at 4º C and 90% relative humidity. Tubers for inoculations were removed from storage and placed at room temperature 2-3 days prior to inoculations. Tubers were not washed or wounded prior to tuber inoculations. Previous research had found that the incidence of infection on tubers inoculated with *P. erythroseptica* was similar on tubers sterilized with 0.5% NaOCl to those that were not surface sterilized (Salas *et al*., 2000). Tubers were not wounded prior to inoculation as any degree of wounding had been shown to greatly increase the incidence of *P. erythroseptica* infection, regardless of the inoculum source or technique (Salas *et al*., 2000; Clayson and Miller, 2006). Tubers used for inoculations were free from most adhering soil due to the handling of the tubers several times.

The trials were set up on wooden pallets, (1.2 x 1.0 m) which were covered with two layers of black plastic topped by two layers of moistened paper towels. Immediately prior to inoculations, one set of 10 tubers for each cultivar was placed in

a row on a pallet and below that row a different cultivar set of ten tubers with a different skin color. Each year only one mefenoxam sensitive *P. erythroseptica* isolate was used for tuber inoculations. The mefenoxam sensitivity of the isolate was confirmed using the same *in-vitro* assay used for screening the field trials inoculum. Each tuber had three apical lateral eyes inoculated. The inoculation rate per eye was a single 10 µl zoospore suspension drop which contained approximately 300 motile zoospores. Control tubers were inoculated with 10 µl of autoclaved Haynesville bog water. After the inoculum droplets were applied, tubers were left undisturbed for a minimum of five minutes. Lastly, inoculated tubers were covered with two layers of moistened paper towels. Inoculated tubers were stored at the Maine Potato Research Storage in a controlled atmosphere locker at 18º C and 95% relative humidity for 12-14 days.

Field inoculations disease assessment

Field trials were mechanically lifted and picked by hand, at which time the *P. erythroseptica* rot was separated from the healthy tubers and both were weighed in the field. To confirm the presence of *P. erythroseptica,* random symptomatic tubers were selected, and the presence of *P. erythroseptica* growth was identified using the key of Stamps (1978). Healthy tubers from harvest were placed in storage and re-evaluated twice at approximately two week intervals. Tubers that developed *P. erythroseptica* symptoms in storage were weighed at each evaluation and added to the total diseased weight for each cultivar. The amount of *P. erythroseptica* rot associated with each cultivar was expressed as the total diseased weight per cultivar

and total percentage of rot per cultivar (total diseased weight / ((total diseased weight + total healthy weight)) x 100.

Tuber inoculations disease assessment

In all trial years, tubers were evaluated 12 to 14 days after inoculations. Tubers were removed from the storage locker and placed at room temperature and were cut longitudinally through the inoculation points. To incubate the cut tubers they were covered with two layers of moist paper towels and allowed to set for approximately 45-60 minutes to allow internal infected tissues to develop characteristic *P. erythroseptica* symptoms. The incidence of *P. erythroseptica* infection was recorded as (number diseased tubers/number of inoculated tubers) x 100 for each cultivar. For tubers that developed *P. erythroseptica* symptoms, both the depth and width (in mm) of disease lesions beneath the inoculation points were measured. The maximum length (D) and width (W) measurements were used to calculate disease penetration based on an equation previously reported by Salas *et al*., (2003) and originally published by Lapwood *et al*., (1984). The severity of *P. erythroseptica* rot or penetration was determined by penetration = (W/2 + [D-5])/2. In all years of the tuber inoculations, no rots caused by secondary organisms were noted. In 2004, an external tuber necrosis rating was assessed on all infected tubers. For the necrosis rating, whole tubers were washed, cut longitudinally through the inoculation points and allowed to dry. The percentage of tuber surface area necrosis affected was then estimated.

Field inoculations experimental design and statistical analysis

A randomized complete block design with five replicates per cultivar was used in the field inoculation trials. For each cultivar, 10 seed pieces were planted per replicate. In the field trials at planting, separation of cultivars was achieved by alternating cultivar skin color. Buffer rows at the plot margins were included in all years to eliminate edge effects.

The cultivar number evaluated varied each year, but there were five replications of all treatments in each year. Data for each trial year was analyzed separately by analysis of variance (ANOVA) using the General Linear Model of SAS (PROC GLM, SAS Institute, version 9.1, Cary, NC). After testing the homogeneity of error mean squares the data for cultivars evaluated for three years (2004-06) were pooled and analyzed using ANOVA to compare *P. erythroseptica* rot incidence over three years. Data for the 6 standard cultivars that were evaluated in all four field trial years (2004-07) were also pooled for ANOVA. Means separation was differentiated for individual trial years as well as combined data sets using Fisher's least significant difference test (LSD) at P = 0.05 (SAS Institute, version 9.1, Cary, NC).

Tuber inoculations experimental design and statistical analysis

For the tuber inoculations, a completely randomized design with five replications was used. Each replicate consisted of one set of 10 tubers per cultivar. Ten tubers per cultivar were inoculated with autoclaved local Haynesville bog water and served as controls. *P. erythroseptica* did not develop in any of the control tubers and that data was not included in the statistical analysis. Data for each trial year was analyzed separately by ANOVA using the General Linear Model of SAS (PROC

GLM , SAS Institute, version 9.1, Cary, NC). After testing the homogeneity of error mean squares, the data for cultivars evaluated in all three years were pooled and analyzed as combined experiments using ANOVA to compare *P. erythroseptica* rot incidence over three years. Means separations were differentiated for individual trial years as well as for combined data using Fisher's least significant difference test (LSD) at P = 0.05 (SAS Institute, version 9.1, Cary, NC).

The width and depth of disease lesions measurements that were collected from individual tubers were analyzed separately. The width and depth data points containing zeroes for tubers in which infection did not occur were omitted for each cultivar in all years. These data sets with the zero data excluded were used to determine the strength of the relationship between the width and depth of the lesions within each cultivar. The disease lesion width and depth measurements for each cultivar were subjected to Pearson's correlation (PROC CORR, SAS Institute, version 9.1, Cary, NC). Pearson's correlation was done only on cultivars evaluated at least two years, which included a total of 23 cultivars, of which 18 were evaluated for three years and 4 were evaluated two years.

Statistical analysis associated with additional data sets

The cultivar screening for susceptibility to *P. erythroseptica* resulted in the generation of seven sets of data from Maine. Three sets of data were generated from Maine field trials conducted from 2004-06 and three sets of data were generated in Maine tuber inoculation studies from 2004-06. The 2007 Maine field inoculations data was not included in the correlation matrix, because the data included mostly cultivars tested only in 2007. Also available from Maine was a 1997 field inoculation

trial data set including 11 cultivars (Lambert, unpublished). The generation of these data sets allowed for the comparison of the Maine field and tuber susceptibility results with recent *P. erythroseptica* cultivar evaluations from other researchers. These additional trials comprised one tuber inoculation data set from North Dakota (Salas *et al*., 2003), which included 18 of the cultivars evaluated in the Maine tuber inoculations, one field incidence data set from Idaho (Miller *et al*., 2003), and one greenhouse microplantlet inoculation data set from PEI (Peters and Sturz, 2001). The correlation matrix included ten data sets of *P. erythroseptica* cultivar susceptibility, including seven from Maine.

In the correlation matrix, the mean *P. erythroseptica* incidence of rot for cultivars from all ten data sets were analyzed rather than data for individual replicates. In the correlations, only cultivars common to the two sets being compared were included in the analysis for the correlation matrix. The correlation matrix was used to analyze the strength of relationships between different data sets and to determine how well the laboratory tests corresponded to field results. Pearson's correlation test (PROC CORR, SAS Institute, version 9.1, Cary, NC) was used to determine the strength of the correlation between the mean incidences of *P. erythroseptica* rot in the ten different data sets.

Results

Plant emergence data

In field trial years 2005-06 most cultivars averaged greater than 90% plant emergence, though there were exceptions. Two of the Frito-Lay cultivars were among the lowest in terms of emergence especially FL-1533, which had the lowest stand (73%), and was statistically different from the other cultivars. Butte was the only cultivar with 100% emergence (Table 2.5).

Table 2.5. Plant emergence means separation of cultivars evaluated in 2005-06 *P. erythroseptica* cultivar susceptibility field trials[a]

Cultivar	% Stand
Butte[b]	100 a
Reba	99 a
Snowden	98 a
Shepody	99 a
FL-1833	**98**
Pike	98 a
Superior	98 a
Red Pontiac	98 a
Red LaSoda	99 a
Kennebec	98 a
Dark Red Norland	98 a
Goldrush	97 a
Yukon Gold	97 a
Atlantic	96 ab
Russet Norkotah	96 ab
Russet Burbank	96 ab
Red Gold	96 ab
Viking	95 ab
A9304-3	**94**
Ranger Russet	94 ab
Gem Russet	85 ab
Reeves Kingpin	83 ab
FL-1867	78 ab
FL-1533	73 b
LSD (P = 0.05)	**23.64**

[a] Two cultivars and means in bold were evaluated in one year only and were not included in the means separation analysis. FL-1833 and A9304-3 were evaluated in 2006 only.

[b] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Of the cultivars evaluated in 2007, six had 100% plant emergence, while seven other cultivars had better than 95% emergence. The cultivars Allegany (80%) and Somerset (82%) had significantly lower percent emergence than many other cultivars (Table 2.6).

Table 2.6. Plant emergence means separation of cultivars evaluated in 2007 *P. erythroseptica* cultivar susceptibility field trials

Cultivar	**% Stand**
Atlantic[a]	100 c
Delta Gold	100 c
Innovator	100 c
Keuka Gold	100 c
Lenape	100 c
Monona	100 c
Pike	100 c
Russet Norkotah	100 c
Wischip	100 c
Andover	98 bc
FL-1879	98 bc
Katahdin	98 bc
Lehigh	98 bc
Marcy	98 bc
Shepody	98 bc
AF 1758-7	96 abc
Red LaSoda	96 abc
Sunrise	96 abc
Somerset	82 ab
Allegany	80 a
LSD (P = 0.05)	**1.67**

[a] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Plant senescence ratings data

There was a tendency for more susceptible cultivars to senesce earlier. Red cultivars had high senescence ratings as well as high incidences of rot. The senescence scores for Red Gold (6.3%) and Dark Red Norland (6.1%) were the highest, while Red Pontiac (4.4%) was also high. The other two red cultivars, Red LaSoda (4%) and Viking (3.9%), were in the middle in terms of senescence ratings compared to the other cultivars. Russet Norkotah, a cultivar highly susceptible to *P. erythroseptica* in field trials, was in the middle in terms of senescence, while some cultivars, including Atlantic (3.4%) and Russet Burbank (1.8%) that demonstrated resistance to moderate resistance in the field, also performed better in senescence ratings. When cultivars were assigned a numeral ranking based upon maturity class and a multiple regression analysis was preformed maturity class had a significant effect on senescence. The earlier maturing cultivars had higher average senescence scores than later maturing cultivars. The maturity classification was not a significant predictor in terms of the incidence of rot. In general, for most cultivars, excluding red types there did not appear to be a strong relationship between the incidences of *P. erythroseptica* rot in the field and average senescence ratings (Tables 2.6 and 2.7).

Table 2.7. Plant senescence ratings means separation of cultivars evaluated in 2005-06 *P. erythroseptica* cultivar susceptibility field trials[a]

Cultivar	Average Senescence Rating	Maturity Class[b]
Red Gold[c]	6.3 i	M
Dark Red Norland	6.1 i	E
FL-1833	**5.8**	**M**
Superior	5.1 h	EM
Yukon Gold	4.7 gh	M
Red Pontiac	4.4 fg	ML
Goldrush	4.4 fg	M
Shepody	4.3 fg	ML
Russet Norkotah	4.3 fg	EM
Snowden	4.2 fg	L
Reba	4.1 fg	ML
Red LaSoda	4.0 ef	M
Viking	3.9 ef	M
FL-1867	3.8 ef	M
Pike	3.4 de	M
Atlantic	3.4 de	M
Kennebec	3.4 de	M
Ranger Russet	2.8 cd	ML
FL-1533	2.7 c	EM
Gem Russet	2.6 bc	ML
Butte	2.0 ab	ML
A9304-3	**2.0**	**ML**
Reeves Kingpin	2.0 ab	M
Russet Burbank	1.8 a	L-VL
LSD (P = 0.05)	**0.60**	

[a] Two cultivars and means in bold were evaluated in one year only and were not included in the means separation analysis. FL-1833 and A9304-3 were evaluated in 2006 only.
[b] Cultivar maturity class designations were as follows: E = Early; EM = Early-Medium; M = Medium; ML = Medium-Late; L = Late; VL = Very-Late.
[c] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

In the 2007 senescence ratings there were some relationships between higher incidence of *P. erythroseptica* rot and more senescence, but for some cultivars the relationship was not apparent. Two of the most susceptible cultivars Somerset and AF 1758-7 had two of the lower senescence scores. Consequently, the indications of greater incidence of *P. erythroseptica* rot were not always evident in the foliage health (Table 2.8).

Table 2.8. Plant senescence ratings means separation of cultivars evaluated in 2007 *P. erythroseptica* cultivar susceptibility field trials

Cultivar	Average Senescence Rating	Maturity Class[a]
Sunrise[b]	6.9 i	EM
Russet Norkotah	6.8 i	EM
Andover	6.4 hi	E
Innovator	6.2 ghi	ML
Monona	5.8 fgh	M
FL-1879	5.6 fgh	EM
Lenape	5.3 efg	ML
Lehigh	5.1 ef	ML
Red LaSoda	5.0 ef	M
Katahdin	4.6 de	M
Shepody	4.6 de	ML
Pike	4.1 cd	M
Keuka Gold	4.1 cd	ML
Atlantic	3.6 bc	M
Snowden	3.5 bc	L
Wischip	3.4 bc	ML
Marcy	3.2 abc	L
Somerset	3.2 abc	M
Allegany	2.9 ab	VL
AF 1758-7	2.3 a	ML
Delta Gold	2.3 a	M
LSD (P = 0.05)	**0.99**	

[a] Cultivar maturity class designations were as follows: E = Early; EM = Early-Medium; M = Medium; ML = Medium-Late; L = Late; VL = Very-Late.
[b] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Assessment of *P. erythroseptica* incidence in field inoculations (2004-06)

Differences among cultivars evaluated for incidence of *P. erythroseptica* rot in the field for individual trial years from 2004-06 were each highly significant (P = 0.0001). The 2007 field trial data was still highly significant, but at a slightly lower level (P = 0.0016). The field trial data for each trial year was analyzed individually as well as combined for multiple years and all were highly significant (P = 0.0001). For the 17 cultivars evaluated in all three years (2004-06), both the year and cultivar variables were highly significant (P = 0.0001) as well as the year by cultivar interaction (P = 0.0001) (Tables 2.9, 2.10, and 2.11).

Table 2.9. Combined analysis of variance of incidence of *P. erythroseptica* rot in cultivars evaluated in field trials from 2004-06[a]

Sources of Variation	DF	SS	MS	F Value	Pr > F
Year	2	6625.3	3312.7	59.7	<0.0001
Replicate	4	173.9	43.5	0.78	0.5377 NS
Cultivar	16	11569.8	723.4	13.03	<0.0001
Year x Cultivar	32	4576.4	143.0	2.58	<0.0001
Replicate x Year	8	480.4	60.1	1.08	0.3796 NS
Replicate x Cultivar	64	3757.6	58.7	1.06	0.3877 NS
Error	128	7102.1	55.5		
Total	254	34285.6			
Coefficient ofVariation	80.49				
R-Square	0.79				

[a] Values followed by NS = nonsignificant at P = 0.05.

Data for the 17 cultivars evaluated in three years of field trials (2004-06) were analyzed as individual years and pooled and analyzed as combined experiments with means separations to differentiate trends among the three years. Red LaSoda (21.4%) and Russet Norkotah (19.9%) were the most susceptible and not statistically different. Goldrush (16.9%), Red Gold (16.8%), Shepody (16.3%), and Red Pontiac (12%) were all highly susceptible and statistically equal. Ranger Russet (9.6%), Russet Burbank (6.9%), Yukon Gold (7.4%), and Superior (6.9%) were all statistically the same and moderately resistant, while the cultivars Kennebec (4.8%) and FL-1867 (4.4%) were equal and demonstrated decent levels of resistance. Snowden (1.5%), Gem Russet (1.1%), Atlantic (0.8%), and Pike (0.3%) all were the most resistant to incidence of rot and statistically equal (Table 2.10).

Data for cultivars evaluated for two years that were not included in the analysis of cultivars evaluated three years in the field also showed trends. Reba (28.6%) and Viking (28%) showed high levels of susceptibility in two years of testing. Reeves Kingpin (10.2%) was moderately resistant and Butte (3%) demonstrated resistance. Two Frito-Lay cultivars, FL-1533 and FL-1833 were evaluated in two years, while FL-1867 was evaluated in the field for three years. In comparing the Frito-Lay cultivars evaluated, FL-1533 was the most susceptible (10.9%), but considered moderately resistant in comparison to all other cultivars evaluated, while the other two Frito-Lay selections FL-1833 (4.5%) and FL-1867 (4.4%) had about half of the incidence of rot of FL-1533 (Table 2.10).

In 2004, Red Gold (12.1%), Red LaSoda (8.3%), and Russet Norkotah (4.4%) were highly susceptible. There were not statistical differences between FL-1833

(3.2%), Russet Burbank (2%), Goldrush (1.9%), Red Pontiac (1.7%), Shepody (1.4%), Ranger Russet (1.2%), Superior (0.7%), Pike (0.5%), and FL-1867 (0.4%). Rot was not detected in any of the replicates of Atlantic, Gem Russet, Kennebec, Snowden, or Yukon Gold (Table 2.10).

In 2005, Russet Norkotah (29.8%) was the most susceptible, followed by Red LaSoda (28.8%), Viking (28.4%), and Shepody (25.9%), which were all statistically the same. The cultivars statistically the same and considered moderately resistant included Red Gold (11%), FL-1533 (6.9%), and Reeves Kingpin (6.7%). Snowden (1.3%) and Atlantic (0.6%) demonstrated resistance, while Gem Russet (0.3%) and Pike (0.2%) had lower incidences of rot and were statistically equal (Table 2.10).

In 2006 Reba (34.3%) was the most susceptible, while Viking (27.7%) and Red Gold (27.3%) were both highly susceptible and statistically equal. Those considered moderately susceptible and statistically equal included Kennebec (8.9%), Superior (8.4%), FL-1867 (6.9%), FL-1833 (5.8%), Russet Burbank (4.6%), and Butte (3.9%). Cultivars demonstrating resistance, but different statistically included Atlantic (1.6%) and Pike (0.3%) (Table 2.10).

Table 2.10. Analysis of variance and means separation of incidence of *P. erythroseptica* tuber rot in cultivars evaluated in field trials from 2004-06[a]

Cultivar[b]	Years Tested (no.)	2004-06[c] Rot (%)	2004 Rot (%)	2005 Rot (%)	2006 Rot (%)
Dark Red Norland[d]	3	10.41 c	0.42 ab	17.46 i-f	13.34 b-f
Red Gold	3	16.79 de	12.07 d	11.01 a-f	27.28 ijk
Red LaSoda	3	21.38 e	8.28 cd	28.84 ij	27.03 h-k
Red Pontiac	3	11.97 de	1.67 ab	13.44 d-h	20.80 e-j
Viking	2			28.36 ij	27.65 jk
A9304-3	1				15.60 d-i
Butte	2			2.09 a-d	3.90 a-d
Gem Russet	3	1.14 a	0.00 a	0.28 a	3.12 abc
Goldrush	3	16.90 de	1.86 ab	23.65 hij	25.19 f-k
Ranger Russet	3	9.55 bc	1.22 ab	12.02 b-h	15.40 d-h
Reeves Kingpin	2			6.71 a-f	13.63 c-f
Russet Burbank	3	6.89 bc	2.00 ab	14.06 e-h	4.61 a-d
Russet Norkotah	3	19.94 e	4.38 bc	29.76 j	25.69 g-k
Atlantic	3	0.75 a	0.00 a	0.64 ab	1.61 ab
FL-1533	2			6.92 a-f	14.91 c-g
FL-1833	2		3.15 ab		5.84 ad
FL-1867	3	4.40 ab	0.39 ab	5.88 a-f	6.92 ad
Kennebec	3	4.80 ab	0.00 a	5.47 a-e	8.92 ad
Pike	3	0.34 a	0.52 ab	0.18 a	0.32 a
Reba	2			22.78 g-j	34.33 k
Shepody	3	16.31 de	1.35 ab	25.87 ij	21.70 f-j
Snowden	3	1.48 a	0.00 a	1.33 abc	3.11 abc
Superior	3	6.86 bc	0.74 ab	11.45 a-g	8.40 a-d
Yukon Gold	3	7.42 bc	0.00 a	12.43 d-h	9.84 a-e
LSD (P = 0.05)		**5.38**	**4.25**	**11.65**	**11.86**
Replicate		**0.538 NS**	**0.073 NS**	**0.572 NS**	**0.483 NS**
Cultivar (Cv)		**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Year (Yr)		**<0.0001**			
Yr x Cv Interaction		**<0.0001**			

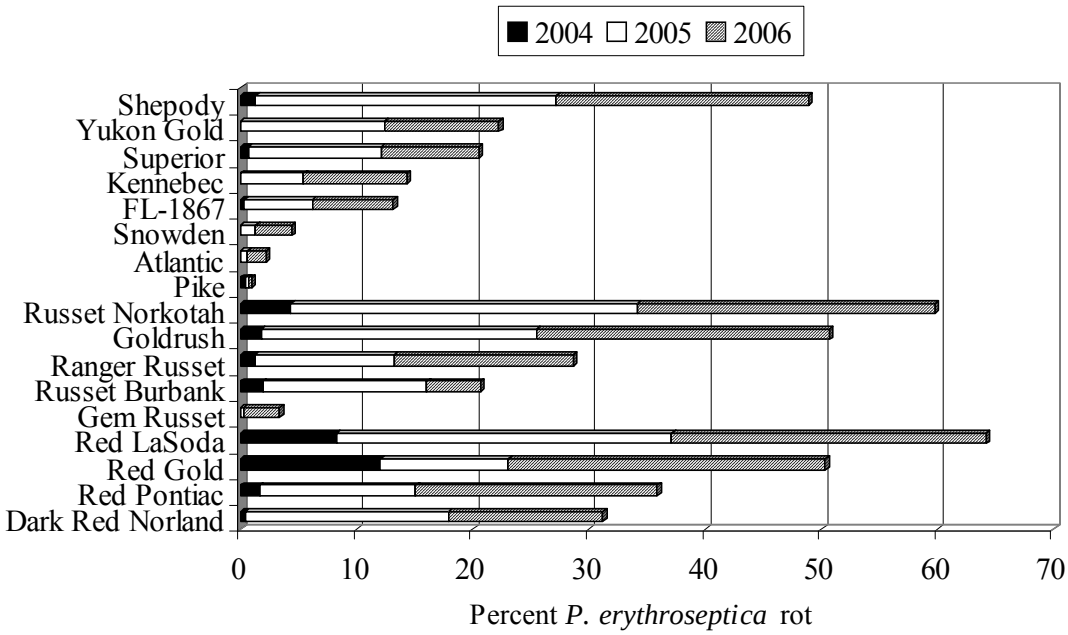
[a] Values followed by NS = nonsignificant at P = 0.05.

[b] Includes all cultivars evaluated in the field 2004-06.

[c] Combined analysis of variance and means separation for cultivars evaluated in all three years (2004-06).

[d] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Figure 2.1. *P. erythroseptica* percent rot of cultivars grouped by type for each year and 3-year cumulative rot percentages for cultivars evaluated in field years (2004-06)



Assessment of *P. erythroseptica* incidence in field inoculations in six standard cultivars (2004-07)

For the 6 standard cultivars evaluated in all four field trial years the incidence of rot was highly significant for year, cultivar, and the year by cultivar interaction (P = 0.0001). Overall, in four years of testing the cultivars the most susceptible were Russet Norkotah (17.59%), Red LaSoda (17.56%), and Shepody (14.5%), which were all statistically equal. While, those the least susceptible did not differ statistically and included Snowden (1.5%), Atlantic (0.9%), and Pike (0.4%) (Table 2.11.).

Table 2.11. Analysis of variance and means separation of incidence of *P. erythroseptica* rot in six standard cultivars evaluated in field trials from 2004-07[a]

Cultivar	Years Tested (no.)	2004-07 Rot (%)
Red LaSoda[b]	4	17.56 b
Russet Norkotah	4	17.59 b
Atlantic	4	0.87 a
Pike	4	0.39 a
Shepody	4	14.45 b
Snowden	4	1.48 a
LSD (P = 0.05)		**3.97**
Replicate		**0.2906 NS**
Cultivar (Cv)		**<0.0001**
Year (Yr)		**<0.0001**
Yr x Cv Interaction		**<0.0001**

[a] Values followed by NS = nonsignificant at P = 0.05.
[b] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Assessment of *P. erythroseptica* incidence in field inoculations (2007)

The cultivars evaluated in 2007 were all different than those evaluated in the previous three years other than the 6 standard cultivars. The results and discussion of the field results obtained in 2007 are presented separately as the cultivars evaluated were selected mostly based upon their lineage and relation to cultivars that had demonstrated resistance in the previous three field years. Maine field trials (2004-06) had identified good genetic resistance in four cultivars- Atlantic, Snowden, Pike, and Gem Russet, which were all in the recent genetic background of Lenape (B5141-6). The four cultivars were all 1st to 3rd generation progeny of Lenape. Lenape is a parent of both Atlantic and Snowden. Lenape is a grandparent of Pike via Atlantic and Lenape is a great grandparent of Gem Russet via Atlantic. Lenape and several progeny of Lenape were included in 2007 field trials to verify the source of resistance for the four cultivars demonstrating substantial resistance. Other cultivars were included which were believed to be highly susceptible or resistant based on grower communication and other researchers.

In the 2007 trials, 6 standard cultivars from the previous three years' trials (Table 2.11) were included for benchmarking against the different cultivars evaluated in 2007. The 2007 results for the standard cultivars included three susceptible selections Russet Norkotah (10.5%), Shepody (8.9%), and Red LaSoda (6.1%) and the three cultivars with resistance Snowden (1.5%), Atlantic (1.2%), and Pike (0.5%). For the new cultivars included in 2007, the results were mixed and at times difficult to interpret in terms of relating incidence of *P. erythroseptica* rot to cultivar lineage. The most susceptible cultivar was Sunrise (15.3%), which was evaluated because of

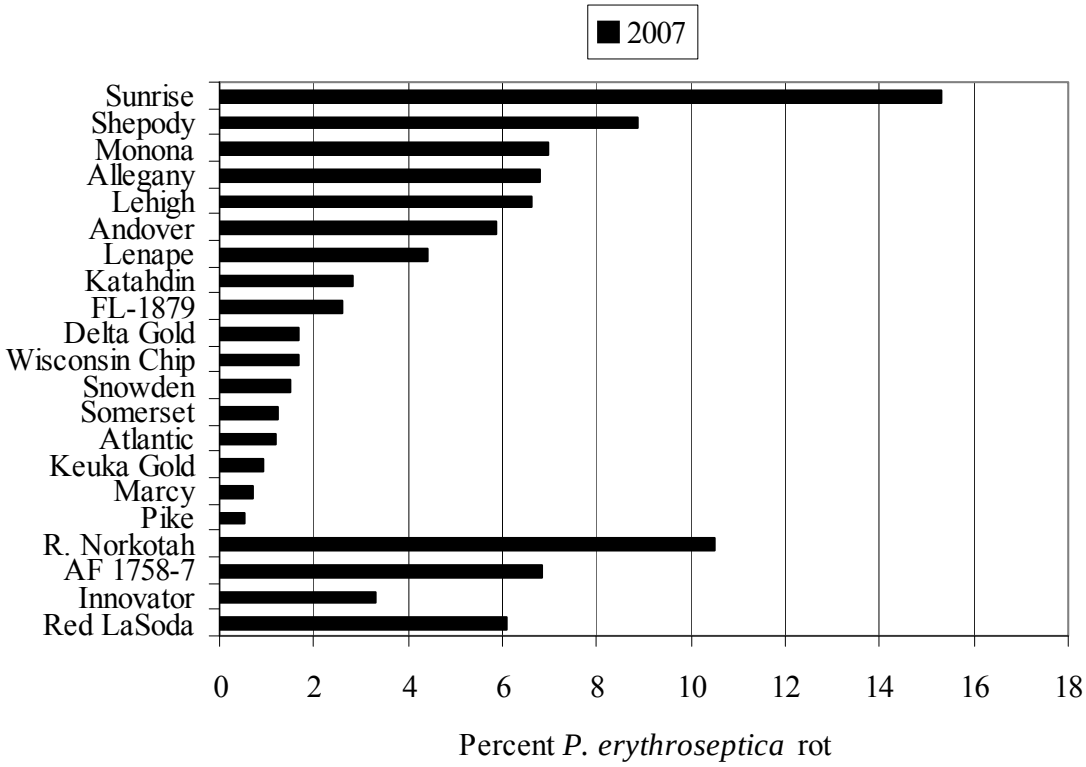
grower reports of substantial *P. erythroseptica rot* incidence. The incidence of rot for both parents of Lenape, Delta Gold (1.7%) and Somerset (1.3%) were statistically equal and indicated resistance. Lenape's parents are Delta Gold and a numbered Beltsville line. Lenape is a parent of both of Somerset's parents – a double grandparent. The rot incidence of Lenape (4.4%) itself indicated moderate susceptibility. A Snowden (1.5%) parent, Wischip (1.7%) had low tuber rot incidence. In terms of the 2007 cultivars evaluated, the second most resistant cultivar after Pike (0.5%) was Marcy (0.7%), which was first generation progeny of Atlantic. Several cultivars with Lenape in their recent genetic background showed considerable levels of susceptibility. Those included Allegany (6.8%), Lehigh (6.6%), Andover (5.9%), and Lenape (4.4%), which were all statistically the same. The moderately resistant cultivar FL-1879 (2.6%) is the progeny of Snowden (1.5%) and FL-1207. Snowden has identified resistance, while FL-1207 was one of the most susceptible white type cultivars in the tuber inoculations of Salas *et al*., (2003). An advanced breeding selection from Aroostook Farm, AF 1758-7 (6.8%) was as susceptible as Red LaSoda (6.1%). Recent grower experiences with the cultivar had indicated high levels of post harvest *P. erythroseptica* rot. In addition, field screening in Idaho had found AF 1758-7 to be one of the most susceptible cultivars (Table 2.12).

Table 2.12. Analysis of variance and means separation of incidence of *P. erythroseptica* rot in cultivars evaluated in 2007 field trials

Cultivar	**Rot (%)**
Red LaSoda[a]	6.08 abc
AF 1758-7	6.82 abc
Innovator	3.30 ab
Russet Norkotah	10.52 cd
Allegany	6.80 abc
Andover	5.87 abc
Atlantic	1.21 a
Delta Gold	1.69 a
FL-1879	2.62 ab
Katahdin	2.84 ab
Keuka Gold	0.91 a
Lehigh	6.63 abc
Lenape	4.41 abc
Marcy	0.72 a
Monona	6.95 abc
Pike	0.52 a
Shepody	8.88 bcd
Snowden	1.48 a
Somerset	1.25 a
Sunrise	15.31 d
Wisconsin Chip	1.66 a
LSD	**6.75**
Replicate	**0.0183**
Cultivar	**0.0016**

[a] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Figure 2.2. *P. erythroseptica* percent rot of cultivars grouped by type for cultivars evaluated in 2007 field trials



Influence of irrigation on field cultivar susceptibility

Differences in the susceptibility and subsequent incidence of *P. erythroseptica* rot in some cultivars may be significantly influenced by the application of irrigation, especially later in the growing season. Irrigation was not applied to field trials in 2004, which may have contributed to the overall lower incidence of rot. The cultivar Red Gold was evaluated in three years of field trials (2004-06) as well as the 1997 Maine field trial. Red Gold was among the highest in terms of incidence of rot in the 1997 screening trial with greater than 30% *P. erythroseptica* rot. In the 2004 field trial Red Gold (12.1%) was the most susceptible compared to next most susceptible cultivar Russet Norkotah (4.4%), under non-irrigated conditions. While, in 2005 and 2006 under irrigated trial conditions Red Gold was still susceptible, but to a lesser extent compared to the same cultivars evaluated in 2004. In 2005 Russet Norkotah (29.8%) was the most susceptible, while Red Gold (11%) demonstrated moderate resistance compared to other cultivars evaluated in the same year. In 2006 Red Gold (27.3%) was somewhat less susceptible, compared to the most susceptible cultivar, Reba (34.3%) and the susceptible Russet Norkotah (25.7%). Overall in three years of field trials Russet Norkotah (19.9%) incidence of rot was among the highest, while Red Gold (16.8%) was high, but less susceptible when the incidence of rot was averaged over the three years.

In 2007 one single 27 meter row was inoculated and planted according to the described materials and methods and planted with Russet Norkotah and Red Gold to compare the incidence of *P. erythroseptica* rot between the two cultivars under non-irrigated conditions. The single row was planted with four different sets of five

whole seed pieces of each cultivar alternating by cultivar every five hills. The disease pressure was high, but Red Gold (32.7%) without irrigation was much higher in rot incidence than Russet Norkotah (17.4%).

Assessment of *P. erythroseptica* incidence in tuber inoculations

Differences in incidence of infection among the potato cultivars evaluated for *P. erythroseptica* susceptibility in tuber inoculations for individual trial years were highly significant in each year (P = 0.0001). In 2005 and 2006 the replicate variable was highly significant (P = 0.0001). Also in 2005 and 2006 the interaction of replicate by cultivar was highly significant (P = 0.0001). The 2004 tuber data was still highly significant for the replicate by cultivar interaction, but at a slightly lower level (P = 0.0009). For the 18 cultivars evaluated in all three years the data was pooled and analyzed for all sources of variation including, replicate, year, cultivar, the interactions of replicate by cultivar, replicate by year, and year by cultivar, which were all highly significant (P = 0.0001) (Table 2.13).

Table 2.13. Combined analysis of variance of incidence of *P. erythroseptica* rot in 18 cultivars evaluated in tuber inoculation trials from 2004-06

Sources of Variation	DF	SS	MS	F Value	Pr > F
Year	2	498.7	249.4	13.71	<0.0001
Replicate	4	1632.1	408.0	22.43	<0.0001
Cultivar	17	6949.2	408.8	22.47	<0.0001
Year x Cultivar	34	1326.6	39.0	2.14	0.0001
Replicate x Year	8	5450.2	681.3	37.45	<0.0001
Replicate x Cultivar	68	2965.3	43.6	2.40	<0.0001
Error	2566	46684.5	18.2		
Total	2699	65506.5			
Coefficient Variation	103				
R-Square	0.29				

Overall, in three years of tuber inoculations the cultivar Red LaSoda (78%) was the most susceptible and statistically different. The next most susceptible cultivar was Dark Red Norland (60%), while the cultivars Russet Norkotah (56.7%), Red Pontiac (54%), and Red Gold (52.7%) were classified susceptible. Those cultivars considered moderately susceptible included Kennebec (38.7%), Russet Burbank (37.3%), Goldrush (36.7%), Yukon Gold (35.3%), and Pike (34.7%). Cultivars demonstrating levels of resistance in the tuber inoculations included Atlantic (23.3%) and Reeves Kingpin (20%) that were statistically the same. The most resistant cultivar evaluated in three years was Gem Russet (7.3%), which was statistically different (Table 2.14).

The incidence of rot in all cultivars evaluated in two or three years was reasonably consistent without large variations in incidences observed between years. In comparing the means separation on cultivars tested in all three years Red LaSoda (78%) was the statistically more susceptible than the next most susceptible selection Dark Red Norland (60%). The other susceptible cultivars Russet Norkotah (56.7%), Red Gold (52.7%), and Red Pontiac (54%) were all statistically equal. Those with moderate resistance included Kennebec (38.7%), Goldrush (36.7%), Yukon Gold (35.3%), and Pike (34.7%) (Table 2.14).

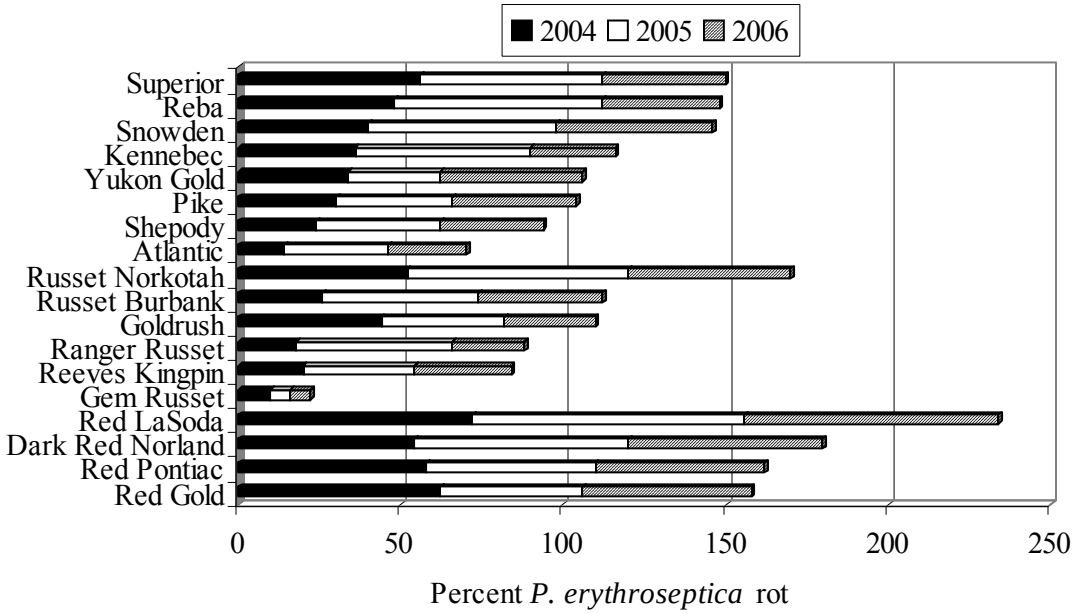
Results obtained from the visual tuber necrosis data collected in 2004 included a range of necrosis from 1% - 43.8%. In general the red skinned cultivars had the highest percentage of tuber necrosis (31.9%). The cultivar Snowden was susceptible in tuber inoculations (40%), but had a higher surface necrosis (27.5%) compared to other cultivars demonstrating similar incidence of rot (Appendix B).

Table 2.14. Analysis of variance and means separation of incidence of *P. erythroseptica* rot in cultivars evaluated in tuber inoculation trials 2004-06[a]

Cultivar[b]	Years Tested (no.)	2004-06[c] Rot (%)	2004 Rot (%)	2005 Rot (%)	2006 Rot (%)
Reeves Kingpin[d]	3	20.2 b	20.0 a-d	34.0 bcd	30.0 b-e
Atlantic	3	23.3 b	14.0 a-c	32.0 bc	24.0 bcd
Goldrush	3	36.7 c	44.0 f-j	38.0 b-e	28.0 bcd
Kennebec	3	38.7 c	36.0 e-h	54.0 f-i	26.0 bcd
Red Pontiac	3	54.0 de	58.0 j-m	52.0 e-h	52.0 hi
Shepody	3	31.3 bc	24.0 b-e	38.0 b-e	32.0 b-f
Ranger Russet	3	29.3 bc	18.0 a-d	48.0 d-g	22.0 bc
Snowden	3	48.7 d	40.0 c-g	58.0 ghi	48.0 ghi
Dark Red Norland	3	60.0 e	54.0 i-l	66.0 hi	60.0 i
Superior	3	50.0 d	56.0 i-m	56.0 ghi	38.0 e-i
Russet Burbank	3	37.3 d	26.0 b-e	48.0 d-g	38.0 e-i
Yukon Gold	3	35.3 c	34.0 d-g	28.0 b	44.0 e-h
Red LaSoda	3	78.0 f	72.0 m	84.0 j	78.0 j
Reba	3	49.3 d	48.0 g-k	64.0 hi	36.0 d-h
Russet Norkotah	3	56.7 de	52.0 h-l	68.0 i	50.0 ghi
Red Gold	3	52.7 de	62.0 k-m	44.0 c-g	52.0 hi
Pike	3	34.7 c	30.0 c-f	36.0 b-d	38.0 d-h
Gem Russet	3	7.3 a	10.0 ab	6.0 a	6.0 a
Viking	2		68.0 lm	28.0 b	
FL-1533	2			46.0 c-g	28.0 bcd
Butte	2			40.0 c-g	18.0 ab
FL-1867	2			46.0 c-g	26.0 bcd
FL-1833	1				46.0 fghi
A9304-3	1				6.0 a
LSD (P = 0.05)		**0.97**	**1.73**	**1.56**	**1.50**
Replicate		**<0.0001**	**0.7713 NS**	**<0.0001**	**<0.0001**
Cultivar (Cv)		**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Year (Yr)		**<0.0001**			
Yr x Cv Interaction		**<0.0001**	**0.0009**	**<0.0001**	**<0.0001**

[a] Values followed by NS = nonsignificant at P = 0.05.
[b] Includes all cultivars evaluated in tuber inoculations 2004-06.
[c] Combined analysis of variance and means separation for cultivars evaluated in all three years (2004-06).
[d] Means followed by the same letter are not significantly different according to Fisher's LSD (P = 0.05).

Figure 2.3. Incidence of *P. erythroseptica* tuber infection of cultivars grouped by type for each year and 3-year cumulative rot incidences for cultivars evaluated in tuber inoculation trials from 2004-06



Assessment of *P. erythroseptica* disease lesion severity in tuber inoculations

The severity of *P. erythroseptica* tuber infection was assessed by the depth and width of lesion penetration. Lesion penetration was determined using the following calculation; penetration = (W/2 + [D-5])/2 (Lapwood *et al*., 1984). Cultivars with shallower lesions were more positively correlated (P = 0.01) for depth and width. While, cultivars with deeper disease lesions were negatively correlated for depth and width. There were only weak associations between lesion size and incidence of *P. erythroseptica* rot. Depth and width of the individual lesions was weakly correlated (P = 0.031). Within specific cultivars there was a wide range of correlations between depth and width. The depth and width of cultivar means were negatively and significantly correlated (P = 0.001). That negative correlation suggests that cultivars tend to do one thing at the expense of the other. The penetration calculation was closely related to the depth measurement with a coefficient of 0.99. Of the 22 cultivars that were analyzed using Pearson's correlation, 12 cultivars were positively correlated and 10 were not significant. The cultivar Atlantic had a low incidence of tuber infection (23.3%) and did not have a significant depth and width correlation (P = 0.4743). While, the cultivar Dark Red Norland was found to be highly susceptible with a high tuber rot incidence (60%). The depth and width correlation for Dark Red Norland was not significant (P = 0.2175). Red LaSoda was the most susceptible in terms of tuber incidence (78%) with a highly positive depth and width correlation (P = 0.0062). While, the cultivar Pike had a much lower incidence of tuber infection incidence (34.7%). Despite the

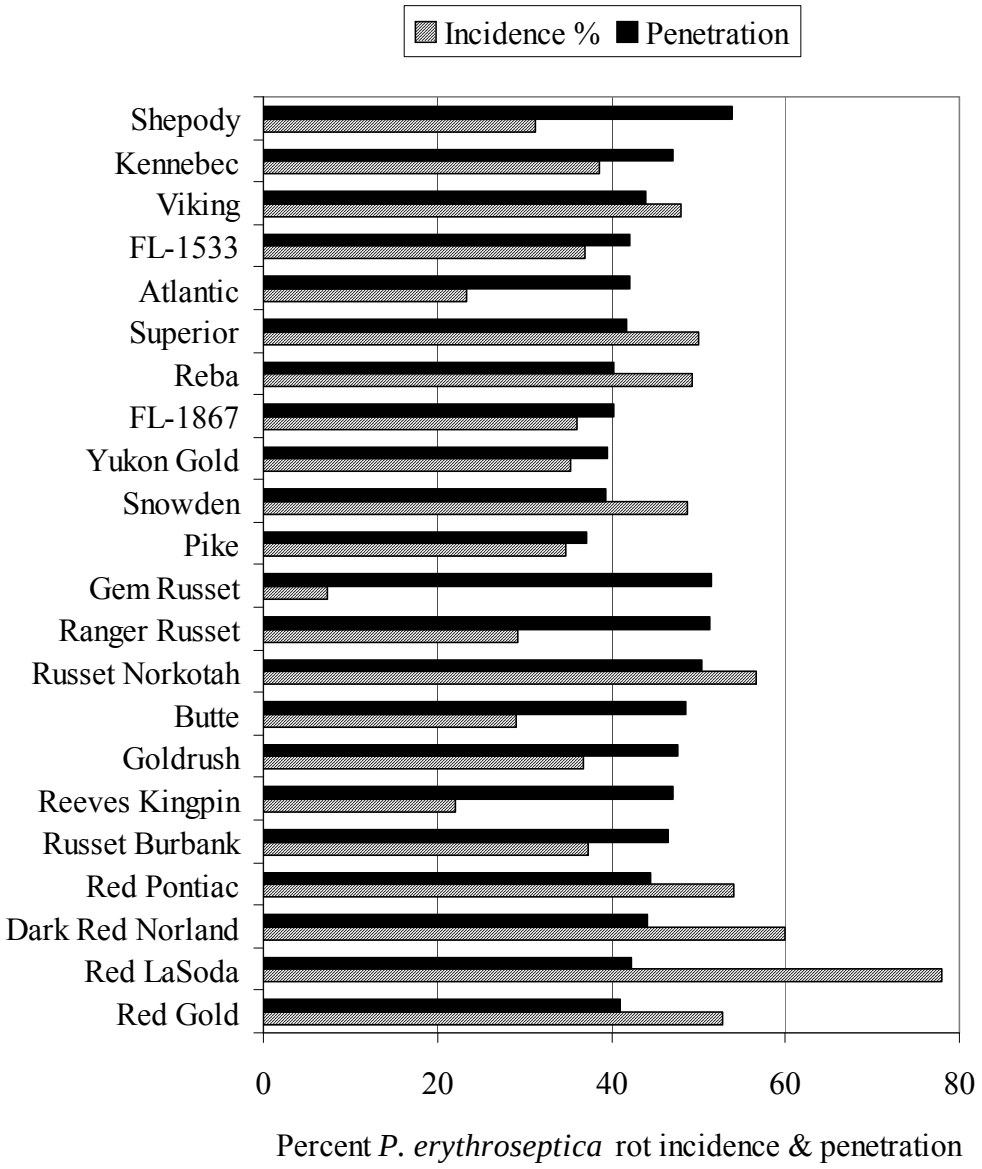
lower incidence of infection Pike had a positive depth and width correlation (P = 0.0012) (Table 2.15).

Table 2.15. Incidence, depth, width, penetration, and the significance of Pearson's correlation for pink rot disease lesion colonization caused by *P. erythroseptica* in tuber inoculations[a]

Cultivar	Years Tested (no.)	Incidence (%)	Depth (mm)[b]	Width (mm)[c]	Penetration[d]	Depth-Width Correlation[e]
Reeves Kingpin	3	22.00	47.65	75.15	47.01	0.4538 NS
Atlantic	3	23.30	58.87	59.77	42.12	0.4743 NS
Goldrush	3	36.70	50.35	75.12	47.67	0.9707 NS
Kennebec	3	38.70	49.94	74.13	47.07	0.0005
Red Pontiac	3	54.00	55.25	66.26	44.46	0.0114
Shepody	3	31.30	50.18	87.50	53.82	0.3399 NS
Ranger Russet	3	29.30	83.21	48.44	51.24	0.0052
Snowden	3	48.70	54.00	56.74	39.39	0.2605 NS
Dark Red Norland	3	60.00	53.34	66.54	44.12	0.2175 NS
Superior	3	50.00	51.21	62.86	41.75	0.0340
Russet Burbank	3	37.30	49.21	73.56	46.60	0.4079 NS
Yukon Gold	3	35.30	51.72	58.31	39.61	0.0275
Red LaSoda	3	78.00	54.47	62.39	42.33	0.0062
Reba	3	49.30	56.29	57.31	40.25	0.7451 NS
Russet Norkotah	3	56.70	53.18	79.21	50.43	0.0010
Red Gold	3	52.70	53.83	60.01	40.98	0.0059
Pike	3	34.70	54.22	52.13	37.13	0.0012
Gem Russet	3	7.30	49.97	82.88	51.45	0.8579 NS
Viking	2	48.00	54.46	65.76	44.02	0.7508 NS
FL-1533	2	37.00	49.91	64.29	42.14	0.0006
Butte	2	29.00	43.72	80.10	48.51	0.0189
FL-1867	2	36.00	52.14	59.38	40.24	0.0003

[a] Values followed by NS = nonsignificant at P = 0.05.
[b] Depth of individual disease lesions measured from point of inoculation.
[c] Width of individual disease lesions measured from point of inoculation.
[d] Lesion penetration determined by (W/2 + [D-5])/2.
[e] Significance (P) of Pearson's correlation between depth and width variables.

Figure 2.4. Average *P. erythroseptica* percent rot incidence and disease lesion penetration in tuber inoculation trials from 2004-06 grouped by cultivar type



Overall, cultivar width, depth, and penetration had little to do with incidence of tuber infection (Table 2.16). The relationships between incidence and depth, width, and penetration are too weak to be used as predictors of cultivar susceptibility. There was significant variation among cultivars in the degree of lesion spread one way or the other within a tuber. The value of slower rotting cultivars highly depends on the location. With slow rotting cultivars the degree of *P. erythroseptica* present in the field may be underestimated at harvest. Growers may harvest those potatoes and place them in storage when they should have been left in the field. Slower rotting cultivars in storage would be generally good in a storage situation. If the rot occurred at a slower rate it would give the grower additional time to market and deliver those potatoes before the rot comprised the entire storage.

Table 2.16. Correlation probabilities among cultivar depth, width, penetration, and volume of disease lesion colonization

	Incidence	**Width**	**Depth**	**Penetration**	**Volume**[a]
Incidence	…	0.49	**-0.057**[b]	**-0.087**	0.924
Width		…	**-0.001**	**-0.015**	
Depth			…	0.000	

[a] Volume was equal to D x W x W.
[b] Numbers in bold were negative correlations.

Assessment of Pearson's correlation matrix including additional data sets

The most significant (P = 0.000) disease assessment correlations were between the 2005 and 2006 Maine field data sets. There was less significance when comparing the 2004 field results with the 2005 and 2006 Maine field results. The P values for the 2004 Maine field data compared to the 2005 and 2006 Maine field results were P = 0.008 and P = 0.036, respectively. The 1997 Maine field data set was significantly correlated with the Maine 2004 field (P = 0.007) and 2006 Maine field (P = 0.005) and but not with the Maine 2005 field (P = 0.208). The Idaho field data compared to the average Maine field data was significant (P = 0.001). In comparing the average North Dakota tuber inoculations with the three Maine field years there was limited significance. The North Dakota tuber inoculations compared to 2006 Maine field results (P = 0.115) and 2005 Maine field results (P = 0.122) were not significant, but were significant when compared to the 2004 Maine field results (P = 0.036). The only data sets that the PEI greenhouse data showed significance with was when compared to the 2006 Maine field results (P = 0.007), 2005 Maine field results (P = 0.047), and the average Maine field results (P = 0.042).

The 2004 Maine tuber inoculations were significantly correlated to both the 2005 and 2006 Maine tuber inoculations (P = 0.000), while the 2005 and 2006 tuber inoculation data probability was also significant (P = 0.003). In comparing the North Dakota average tuber inoculations with the average Maine tuber inoculations there was significance (P = 0.027). In comparing the North Dakota average lab results with individual years there was significance in 2004 (P = 0.022) and 2005 (P = 0.024), but not in comparison to 2006 Maine tuber inoculations (P = 0.053). The Idaho field data

was significantly correlated to the average North Dakota tuber inoculations (P = 0.008). Comparisons between the three years of Maine field results and the complete Maine lab results varied in significance. The 2004 Maine tuber inoculations were more significantly correlated with other Maine field data sets than the other years. There was significance in comparing the 2004 Maine tuber inoculations with the 2004 Maine field data (P = 0.009), 2005 Maine field data (P = 0.030), and 2006 Maine field data (P = 0.028).

The highest level of significance was found when comparing the field data sets, not the tuber inoculations and greenhouse data. It is important to evaluate cultivar susceptibility using a method that can be repeated with comparable results (Table 2.17).

Table 2.17. Correlation matrix of *P. erythroseptica* cultivar susceptibility including Maine trials and other available data sets

	2006 ME Field[a]	2005 ME Field[b]	2004 ME Field[c]	ME Avg Field[d]	2006 ME Lab[e]	2005ME Lab[f]	2004 ME Lab[g]	ME Avg Lab[h]	ND Lab[i]	PEI Grnh[j]	1997 ME Field[k]	ID Field[l]
2006 ME Field	…	0.000	0.036	…	0.206	0.141	0.028	0.068	0.115	0.007	0.005	
2005 ME Field		…	0.008	…	0.033	0.015	0.030	0.013	0.122	0.047	0.208	
2004 ME Field			xxx	…	0.011	0.121	0.009	0.014	0.036	0.632	0.007	
ME Avg Field				…	0.048	0.035	0.011	0.014	0.114	0.042	0.015	0.001
2006 ME Lab					…	0.003	0.000	…	0.053	0.807		
2005 ME Lab						…	0.000	…	0.024	0.305		
2004 ME Lab							…	…	0.022	0.270		
ME Avg Lab								…	0.027	0.836		0.082
ND Lab									…	0.449		0.008
PEI Grnh										…	0.346	
1997 ME Field											…	

[a] 2006 Maine field inoculation trial.
[b] 2005 Maine field inoculation trial.
[c] 2004 Maine field inoculation trial.
[d] Average of cultivars evaluated in Maine field inoculations trials three years 2004-06.
[e] 2006 Maine lab tuber inoculation trial.
[f] 2005 Maine lab tuber inoculation trial.
[g] 2004 Maine lab tuber inoculation trial.
[h] Average of cultivars evaluated in Maine lab tuber inoculation trials three years 2004-06.
[i] North Dakota lab tuber inoculation data.
[j] Prince Edward Island greenhouse microplantlet inoculation.
[k] 1997 Maine field inoculation trial.
[l] 2002 Idaho field screening trial.

Discussion

In both field and tuber screening methods and in all cultivars, none were immune to *P. erythroseptica*, but varying levels of susceptibility were demonstrated. The tuber inoculation data is valuable, but it is the field inoculation data and incidence of *P. erythroseptica* that is the most important. Screening detached tubers excludes the stem stolon infection pathway by which a majority of *P. erythroseptica* infections occur. In a 2006, *P. erythroseptica* fungicide trial using Russet Norkotah the incidence of infection that occurred through the stolon was assessed for all twelve treatments. In each treatment, *P. erythroseptica* infections occurred via the stolon 92% to 100% of the time and averaged 96%. Therefore, a majority of the *P. erythroseptica* infection occurred via the stolon. Overall, it is the resistance to this type of infection that is the most important factor in *P. erythroseptica* cultivar susceptibility. It is the incidence of infection in the field that is the important factor, not so much what happens following harvest.

Overall, according to our field results and other published results Russet Norkotah is likely the most susceptible cultivar produced in significant commercial production (Lambert unpublished, Peters and Sturz, 2001; Miller *et al*., 2003; Salas *et al*., 2003). Russet type cultivars vary in terms of susceptibility with two of the most important commercially, Russet Burbank and Ranger Russet demonstrating moderate resistance. One of the most resistant cultivars was a russet type, Gem Russet. The red type cultivars were classified as the most susceptible or highly susceptible in comparison to the other cultivars evaluated. A total of five red cultivars including Dark Red Norland, Red Gold, Red LaSoda, Red Pontiac, and Viking were evaluated

from two to four years and were mostly susceptible with an average rot incidence of 17% and ranging from 10.4% to 28%. The white type cultivars, though variable, demonstrated the most resistance, particularly Atlantic, Pike, and Snowden. Shepody considered a long white was highly susceptible.

In comparing the Maine field data generated with previous tuber inoculation data the most significant differences were seen in the evaluation of the cultivar Snowden. In five years of Maine field trials Snowden was one of the most resistant cultivars, while previous tuber inoculations had identified Snowden as one of the most susceptible (Salas *et al*., 2003).

Evaluating the parentage of commonly grown potato cultivars provides some information on the sources of *P. erythroseptica* disease resistance demonstrated in certain cultivars. The cultivar Lenape is in the pedigrees of four of the cultivars that demonstrated the most *P. erythroseptica* resistance. The 2004-06 field results indicated substantial conservation of *P. erythroseptica* cultivar resistance in 1st to 3rd generations from Lenape with continuous variation for resistance among the more susceptible cultivars. These susceptibility results suggested that resistance is likely not conferred by only one or a few major genes from Lenape, but by genes of lesser effect, quantitative trait loci (QTL) in cultivars with intermediate resistance. Further investigation is needed to determine the validity of Lenape as a major source of *P. erythroseptica* resistance. The evaluation of various cultivars that share lineage and comparisons of their *P. erythroseptica* responses may provide information on sources of resistance.

In conducting field trials there exists variability related to environmental factors that are most often beyond the control of those conducting the research. In 2004 field trials, irrigation was not applied and the *P. erythroseptica* disease incidence was considered low with a mean rot incidence of 2.1%. While, in 2005 and 2006 using the same inoculation rate at planting, but applying late season irrigation the disease levels were considered moderate to high averaging 12.8% and 14.1%, respectively. *P. erythroseptica* disease was heavier in 2005 and 2006 and those years were highly correlated. Lower disease pressure in 2004 resulted in less separation of cultivars and poorer relationship to 2005 and 2006 data. When incidence of rot comparisons were done between Red Gold and Russet Norkotah under non-irrigated conditions in 2007, Red Gold was more susceptible to disease than Russet Norkotah. The incidence of rot associated with certain cultivars may be more impacted by irrigation applications than other cultivars. Susceptibility of Red Gold in particular, was dramatically affected by irrigation or moisture availability. In 2007 *P. erythroseptica* disease levels were lower with a mean rot of 4.6%. In 2007 for the 6 standard cultivars tested the three previous years the percent rot for the three most susceptible cultivars was considerably lower than the 2005 and 2006 rot levels. The lower incidence of rot in 2007 was partially attributed to soil tests that indicated that soil pH levels, were very acidic (pH 4.7). Soil analysis from samples in the fall recommended the application of 3362 kg/ha of lime to reach a pH of 5.2.

In the correlation matrix among the ten data sets there were highly significant correlations between the 2005 and 2006 Maine field years (P = 0.000). In those years the disease pressure was the greatest compared to the lesser significance in comparing

those two same years 2005 (P = 0.008) and 2006 (P = 0.036) with the 2004 data where the incidence of rot was much less. The high level of significance indicates that it is necessary to have adequate disease pressure to detect greater variability in cultivar susceptibility. The average of the Maine field data were better correlated (P = 0.014) with average tuber inoculations from Maine than the average of tuber inoculations conducted in North Dakota (P = 0.114).

The 1997 evaluation of 11 cultivars in Maine agreed with the most recent Maine data in that the cultivars Red Gold and Russet Norkotah were both highly susceptible, with greater than 30% *P. erythroseptica* tuber rot. Russet Burbank and FL-1533 were moderately resistant with less than 10% rot. The two cultivars with the most resistance were Snowden and Atlantic with less than 5% rot, which correlates well with the field data, generated in subsequent Maine trials (Lambert, unpublished). In the correlation matrix comparisons between the three Maine field years (2004-06) and the 1997 Maine field data involving the same cultivars there was significance in 2004 and 2006. The P values for comparing three Maine field years (2004-06) with the 1997 Maine field data were P = 0.005, P = 0.208, and P = 0.007, respectively.

The *P. erythroseptica* cultivar susceptibility documented in an Idaho powdery scab screening trial correlated well with results obtained from recent Maine field trials. In the Idaho trial Russet Norkotah, Shepody, and AF 1758-7 were all highly susceptible in comparison to other cultivars evaluated, with greater than 10% *P. erythroseptica* tuber rot. Cultivars that demonstrated resistance in Maine trials, including Atlantic and Russet Burbank also had the least amount of rot in the Idaho

screening. Similar to Maine Gem Russet demonstrated resistance in Idaho as no *P. erythroseptica* rot was found (Miller *et al*., 2003).

There were both negative and positive correlations between the resistance of the nontuber potato germplasm screened in the greenhouse (Peters and Sturz, 2001) and the Maine *P. erythroseptica* field and tuber inoculation susceptibility data of the same cultivars. There were positive correlations seen in Shepody between the susceptibility demonstrated when screening microplantlets and the subsequent high susceptibility demonstrated in four years of Maine field trials. The evaluation of nontuber germplasm is not necessarily an indicator of tuber resistance, but provides a source of information on the importance of root, stolon, and stem infections associated with *P. erythroseptica* infections.

Differences detected in tuber inoculations among years, may be partially attributed to differences between growing seasons. Environmental conditions varied, including monthly precipitation amounts, growing degree days, crop maturity at harvest, among others between field trials in the 2004-06 growing seasons. Annual differences in environmental conditions would invariably alter the tubers both physiologically and chemically, which would likely affect tuber responses to inoculation with *P. erythroseptica* or other pathogens. In addition, other possible factors affecting tuber disease susceptibility are physiological changes that occur as tubers age. The physiological age of the tubers at the time of inoculation in the Maine trials should not have been a major factor. Each year (2004-06) the tuber inoculations were carried out within the same time period from January to March. Recent research involving *P. erythroseptica* has mentioned differences in endophytic

microflora found in potatoes produced in different regions and the subsequent impact on tuber susceptibility to various pathogens (Peters *et al*., 2005a).

Pearson's correlations on width and depth measurements of disease lesions from tuber inoculations found limited trends. The positively correlated depth and width variables indicated that the width and depth increased together. The negatively correlated depth and width variables indicated the likelihood that the depth of the disease lesion increased at the expense of the width of the lesion. The development and colonization of lesions more rapidly in the field is marginally helpful, but not in storage. Overall, there were weak associations comparing lesion colonization with incidence and variability in lesion development among cultivars. Tuber inoculations reported by other researchers found no correlation between the incidence of infection and penetration of *P. erythroseptica* rot (Salas *et al*., 2003; Thompson *et al*., 2007). The relationship between lesion size and disease incidence would likely not be a useful indicator of cultivar resistance. *P. erythroseptica* resistance needs to be expressed as resistance to infection, not resistance to severity of penetration.

Each year during tuber inoculation assessments of all replicates general comments were recorded. In reviewing three years of comments there were certain trends prevalent in all three tuber inoculation trial years. Most often in tuber inoculations if the tuber developed *P. erythroseptica* when the tuber was cut longitudinally through the inoculation points all internal tissues were unmistakably discolored pink. In all three years the cultivar Pike was noted as having a pink discoloration of internal tissues that was much lighter in color than other cultivars. Additionally, the disease lesions associated with Pike tended to spread distinctively

more around the perimeter of the tuber in a thin line. Other cultivars responded to inoculation by developing disease lesions that uniformly traveled downward and outward from the inoculation points throughout the tuber. The penetration calculation derived from the width and depth measurements for Pike (37.1%) were the lowest. While, the depth and width correlation for Pike was highly significant (P = 0.0012). In three years disease lesion penetration in Ranger Russet (51.2%) and Reeves Kingpin (47%) were observed to often not move downward the entire length of the tuber from the inoculation points. Despite those observations the average lesion penetration for Ranger Russet and Reeves Kingpin were not lower than many cultivars. Those differences may be partially attributed to the oblong nature of those two russet type cultivars. The disease colonization and consequently the rot did not penetrate the entire tuber depth or length, as was most often the scenario in other cultivars. The depth and width correlation for Ranger Russet (P = 0.0052) was highly significant, while the relationship for Reeves Kingpin (P = 0.4538) was not significant. Tuber disc assays evaluating the *P. erythroseptica* susceptibility of Russet Burbank and Russet Norkotah found considerable differences between lesion responses and appearances in the two cultivars (Johnson, 1998). The disease lesion penetration for Russet Burbank (46.6%) and Russet Norkotah (50.4%) were similar. The depth and width correlation for the two cultivars were much different for Russet Burbank (P = 0.4079) and Russet Norkotah (P = 0.0010).

Direction of future *P. erythroseptica* research

The validation of alternative cultivar susceptibility evaluation techniques that require less resources and time is needed. The field trials require available land for conducting trials and the option of incorporating *P. erythroseptica* inoculum into the soil. For tuber inoculations the production of zoospores is both time and labor intensive. Zoospores are short lived, thus the inoculation and storage procedures must be optimized for infection and experimental efficiency. The use of greenhouse pot trials is a possible alternative, and its validity can now be verified against known field results. An additional option in the future may include cultivar susceptibility screening using field stem inoculations.

Germplasm of breeding programs could be developed with greater resistance to *P. erythroseptica*, by incorporating cultivars that demonstrate levels of *P. erythroseptica* resistance in screening trials. Breeding programs need to screen current lines used for breeding as well as wild species to identify sources of *P. erythroseptica* resistance for integration into breeding programs. In the near term, the validated field screening method can screen out highly susceptible breeding lines at an early stage in progeny from crosses.

The lack of variability in isolate virulence seen in *P. erythroseptica* isolates from different parts of North America should make the sourcing of inoculum for breeding programs from local *P. erythroseptica* isolates possible for screening resistance in breeding lines. *P. erythroseptica* susceptibility results should be easily extrapolated to other growing regions as the variability in virulence of local *P. erythroseptica* isolates is extremely low.

In 2006 a cultivar highly resistant to *P. erythroseptica*, Atlantic was crossed with a cultivar highly susceptible, Russet Norkotah. The F1 progeny from that cross will be screened for *P. erythroseptica* resistance in field trials in 2008. The highly resistant and susceptible progeny from that cross will be identified. The resistance and/or susceptibility will be verified in 2009 in replicated field trials and in greenhouse pot studies. Resistant and susceptible F1 progeny will be intermated to generate an F2 population and also backcrossed with resistant and susceptible parents. The progeny will be screened for *P. erythroseptica* resistance (Haynes, de los Reyes, Lambert, and Porter, unpublished).

To date precise resistance selection in breeding populations has been limited by the lack of knowledge of the genetics of the trait. Resistance selection efficiency in breeding programs depends largely on developing a precise understanding of the mode of inheritance of the resistance trait and the number of genetic loci that contribute to the trait. The inheritance of *P. erythroseptica* resistance will be investigated by using the progeny from the 2006 Atlantic and Russet Norkotah cross. Amplified Fragment Length Polymorphism (AFLP) will be used to examine the genetics of *P. erythroseptica* resistance. The goals will include defining the mode of inheritance of *P. erythroseptica* resistance and tagging the regions of the potato chromosomes containing the resistance loci with DNA markers. The goal would be to identify those molecular markers and eventually use them as a routine selection tool in breeding programs (Haynes, de los Reyes, Lambert, and Porter, unpublished).

Conclusions

Much of the results found in the Maine field and tuber inoculation trials supports observations by growers, concerning the susceptibility of various cultivars to *P. erythroseptic*a. Potato growers often report that the cultivars Shepody and Russet Norkotah have a large degree of susceptibility. While, on an annual basis *P. erythroseptica* problems associated with cultivars like Russet Burbank grown in significant acreage in Maine (43%) are typically less problematic (Maine Potato Board, 2008). Growers report red cultivars, especially Red LaSoda being problematic, while the cultivar Pike can be harvested and successfully stored when grown in fields with poor drainage.

Potato cultivars differ in their susceptibility to *P. erythroseptica*, but most commercially grown cultivars are moderately or highly susceptible to the disease. The cultivars evaluated varied in their susceptibility or resistance to *P. erythroseptica*, which was measured in terms of reduced incidence in both the field and tuber inoculations. Screening detached tubers excludes the stem stolon infection pathway by which a majority of *P. erythroseptica* infections occur. Typically tuber infection in the field occurs at the stem end, apparently by infection of stolons and subsequent growth of the pathogen into the tuber. Tuber inoculation evaluations did not always correspond closely to field conditions and failed to identify some cultivars having high levels of resistance under normal growing conditions.

When planning a breeding and evaluation program it is important to use the most valid evaluation technique. Both field and tuber inoculations are tedious screening methods and limit the number of entries, which can be tested. Currently

field screening for *P. erythroseptica* cultivar susceptibility is the most reliable evaluation method for detecting valid resistance in potato cultivars.

With the efficacy of the only truly effective fungicide to control *P. erythroseptica*, mefenoxam in jeopardy in the future control of the pathogen will require the employment of alternative strategies. With the limited cultural and chemical management options for *P. erythroseptica* future management of the disease largely depends upon the release of new cultivars with improved resistance. In the absence of new chemistries to adequately and cost-effectively control *P. erythroseptica* it is important to focus efforts on the development of genetic resistance in the germplasm of breeding programs. In the future with greater knowledge of the mechanisms of *P. erythroseptica* resistance inheritance it can be transferred into the backgrounds of breeding populations, such as red or russet types, which is presently absent or uncommon. Ultimately, breeding programs would breed cultivars deliberately for *P. erythroseptica* resistance as part of an integrated management approach.

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APPENDICES

Appendix A

FIELD CULTIVAR SUSCEPTIBILITY TRIALS SUPPLMENTAL IRRIGATION

In all field trial years drip line irrigation as installed in the cultivar susceptibility trial at the time of hilling or shortly after. In field trial years 2004-07 each year Watermark soil moisture sensors (Spectrum Technologies Inc., Plainfield, IL) were installed. The three soil moisture sensors were connected to one WatchDog data logger (Spectrum Technologies Inc., Plainfield, IL). The data logger was programmed to measure soil moisture in kilopascal (kPa) units at timed intervals of fifteen minutes. Three soil moisture sensors were installed in 2005 and 2006, while only two sensors were installed in 2007. In 2005 and 2006 when three soil moisture sensors were installed the lines SMA and SMB in the graphs represent sensors that were installed 20 cm below the top of the planted row. Also in the 2005 and 2006 soil moisture graphs a third sensor, representing SMC in the graphs was installed 41 cm below the top of the row. The 2007 soil moisture graph differs in that only two soil moisture sensors were installed. The SMA line represents only one sensor installed at a depth of 20 cm and SMB represents one sensor installed 41 cm below the top of the row. The WatchDog data loggers were downloaded on a weekly basis using SpecWare 6.02 Build 0035 (Spectrum Technologies, Plainfield, IL). The SpecWare software generated the soil moisture graphs included in this appendix. According to irrigation guidelines developed for Maine potato production conditions (Sexton, unpublished) an irrigation application is recommended at soil moisture levels greater than 55 kPa. In some trial years despite soil moisture readings greater

than 55 kPa irrigation was not applied until at least the second week of August. Each irrigation application was the equivalent to 1.3 cm of water. Irrigation was not applied in 2004, but was applied in field trial years 2005-07.

Figure A.1. 2005 cultivar susceptibility trial soil moisture graph

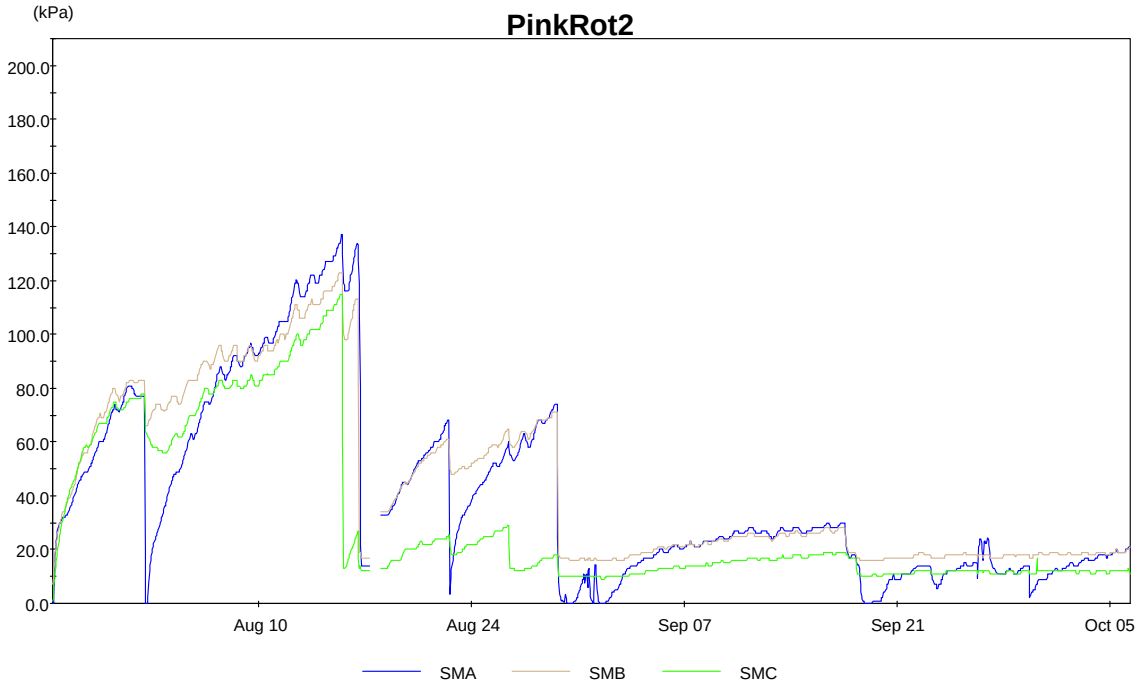


Figure A.2. 2006 cultivar susceptibility trial soil moisture graph

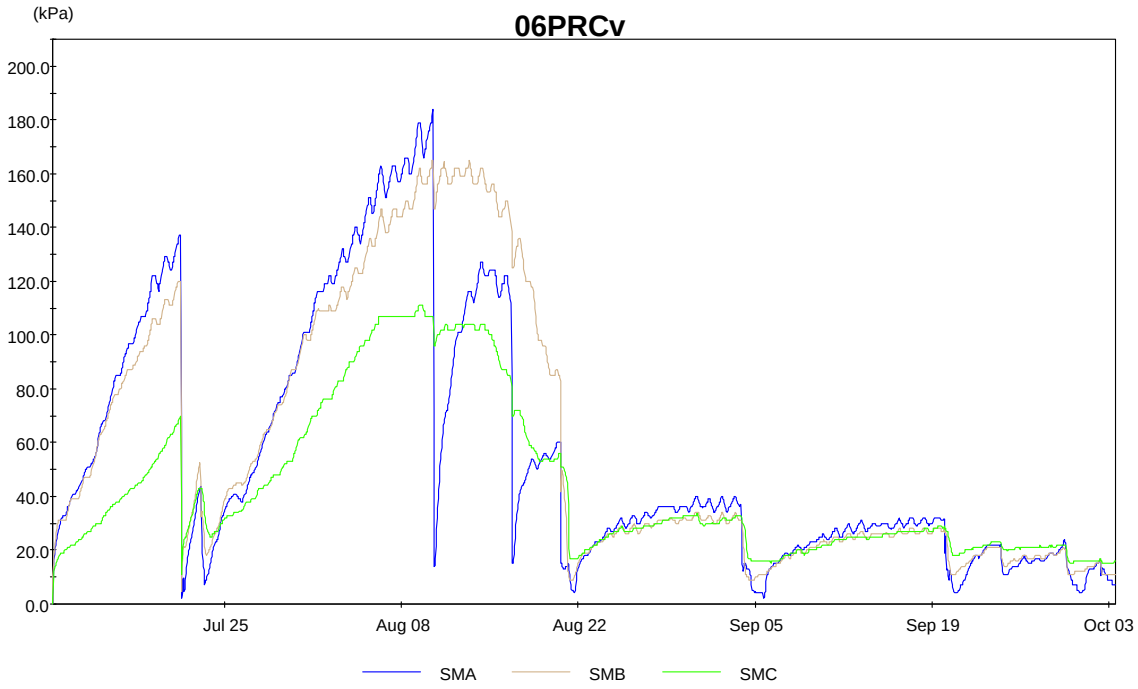
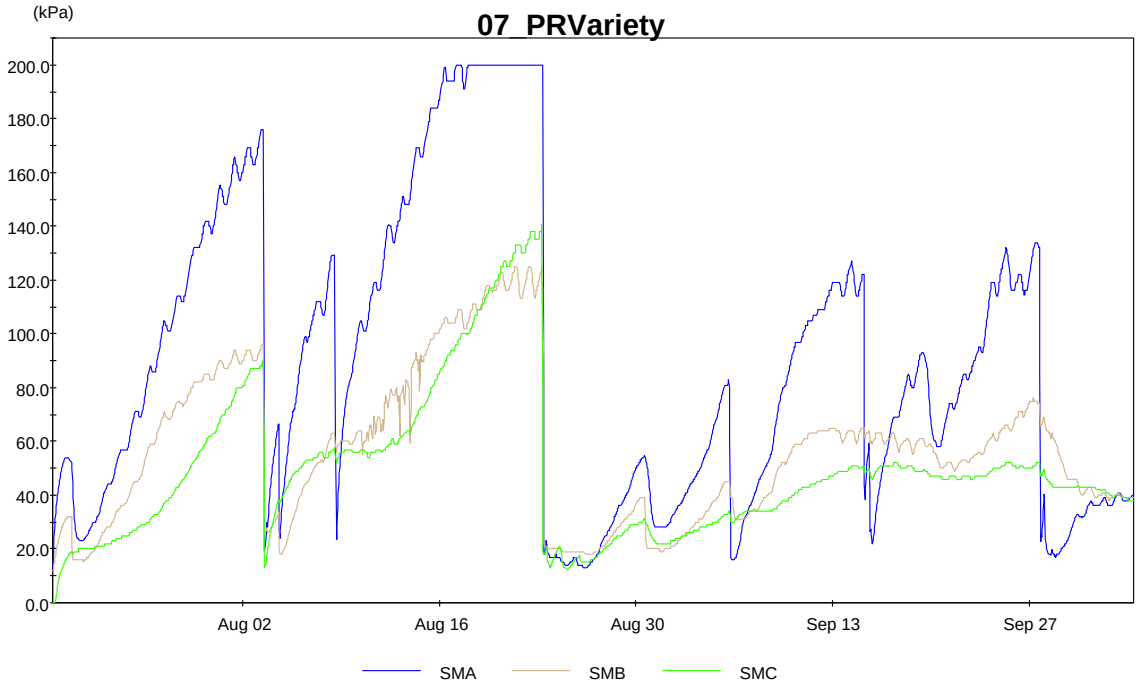


Figure A.3. 2007 cultivar susceptibility trial soil moisture graph



Appendix B

2004 TUBER INOCUALTIONS PERCENT EXTERNAL NECROSIS

In only the first year of tuber inoculations in 2004 an external tuber necrosis rating was done for each tuber that was infected with *P. erythroseptica*. At the time of evaluation all tubers were washed and infected tubers were rated for surface necrosis (percent area) and then sectioned longitudinally from the point of inoculation. The percent external necrosis rating was done in 2004 only, because it was time and labor intensive requiring all tubers be washed and the visual rating estimate was considered somewhat subjective. The results obtained in 2004 included a range of necrosis from 1% - 43.8%. In general the red type cultivars had the highest percentage of tuber necrosis averaging 31.9%. The cultivar Snowden was susceptible in tuber inoculations (40%), but had a higher surface necrosis (27.5%) compared to other cultivars demonstrating similar incidence of rot.

Table B.1. 2004 *P. erythroseptica* cultivar susceptibility tuber inoculations incidence of infection and percent external necrosis

Cultivar	Incidence (%)	Necrosis[a] (%)
Red LaSoda	72.0	43.8
Viking	68.0	22.2
Red Gold	62.0	32.5
Red Pontiac	58.0	28.1
Superior	56.0	38.3
Dark Red Norland	54.0	33.0
Russet Norkotah	52.0	25.0
Reba	48.0	17.0
Goldrush	44.0	12.0
Snowden	40.0	27.5
Kennebec	36.0	17.7
Yukon Gold	34.0	16.1
Pike	30.0	6.5
Russet Burbank	26.0	17.3
Shepody	24.0	19.9
Reeves Kingpin	20.0	1.0
Ranger Russet	18.0	5.9
Atlantic	14.0	8.7
Gem Russet	10.0	8.2

[a] Percentage of tuber surface area necrosis affected was estimated for each infected tuber.

BIOGRAPHY OF THE AUTHOR

Erica Rae Fitzpatrick-Peabody was born in Presque Isle, Maine on May 19, 1980. She was raised in Houlton, Maine on a potato farm and graduated from Houlton High School in 1998. She attended the University of Maine and graduated in May 2003 with a Bachelor of Science degree in Landscape Horticulture. She continued at the University of Maine enrolling in the Department of Plant, Soil and Environmental Sciences in the fall of 2003. In January 2005, prior to completing the research requirements for her degree Erica joined McCain Foods USA, Inc. in Easton, Maine as a potato agronomist. She continued the lab and field aspects of her thesis project at the Aroostook Farm in Presque Isle over the next three years. Erica married R. Barrett Peabody in August 2007 in a potato themed wedding. Erica is a member of the Maine Potato Board, Potato Market Improvement Fund and Potato Association of America. After receiving her degree, Erica will continue her agronomy work for McCain Foods USA, while growing a few acres of potatoes of her own on the side with her father. Erica is a candidate for the Master of Science degree in Plant, Soil, and Environmental Sciences from The University of Maine in May, 2008.