

SURVEY AND MANAGEMENT OF POSTHARVEST DISEASES OF POTATO

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ABSTRACT

Postharvest management of potato tubers is essential for keeping up with consumer demands for fresh and processed potato products. The following studies were conducted for improved management of Michigan potato storages: (1) identification of storage rot pathogens present on tubers obtained from lower-peninsula Michigan, (2) efficacy of a potential management tool, SaniDate-5.0, on four major postharvest rots, and (3) varietal resistance in commercial and research potato germplasm. Twelve chip processing potatoes fields across six Michigan counties were included in the survey of tuber-associated abiotic and biotic factors. During the tuber survey, mechanical injuries (wounds and scrapes) (60-61%) and disease signs and symptoms (97%) were observed. Putative rot pathogens frequently isolated from tissue samples were species of *Fusarium* and *Pythium*. Out of 86 *Fusarium* isolates characterized to species, the most frequently collected species was *F. oxysporum* and the most virulent species on potato slices was *F. graminearum*. This differed from previous studies where *F. sambucinum* was the most virulent species causing dry rot. These findings suggest management and screening efforts should consider current population compositions for effective disease control. Next, an evaluation of the peroxyacetic acid sanitizer SaniDate-5.0 for control of four major rot diseases, *Fusarium* dry rot (FDR), bacterial soft rot (BSR), pink rot, and *Pythium* leak was performed in storage bins under commercial conditions. Across two years of repeated experiments, SaniDate-5.0 did not significantly affect FDR in either year or pink rot in year two. Due to insufficient development of BSR and *Pythium* leak in these studies, inoculation protocols were optimized for future studies. Lastly, an assessment of varietal response to these four storage diseases was conducted on chipping, red-skinned, and yellow-flesh germplasm entries. Significant resistance reactions were observed on chipping varieties for FDR in 2020 and 2021, and for pink rot in 2020. Findings indicate that (1) Michigan pathogen isolates may cause variable results to those in other states and may provide valuable information to the screening process and (2) certain varieties may be more resistant to one or more storage diseases but also may vary widely in response across diseases. These screening efforts will further inform potato breeding and variety selection efforts to improve storage disease management. Combined, these studies have helped to identify prevalent diseases and evaluate potential chemical and varietal management strategies for disease impacting potato storages.

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CHAPTER 1: LITERATURE REVIEW

HISTORICAL AND PRESENT SIGNIFICANCE OF THE POTATO

Origin and domestication

The cultivated potato (*Solanum tuberosum* L.) is indigenous to the Andes Mountains in South America and was domesticated over 10,000 years ago (Ames & Spooner, 2008; Glendinning, 1983). Pre-Columbian Andean farmers domesticated 70 plant species including potato, as well as an estimated 400 distinct indigenous-cultivated (landrace) potato varieties currently grown in the Andes (Reader, 2009). Not all wild potato species produce tubers, and those that do are small and are rich in toxic glycoalkaloids (Friedman, 2006; Jadhav et al., 1997). The edibility of present-day potato is due to selective breeding by early indigenous farmers and those who followed to produce modern cultivars with improved productivity and palatability (Smith, 2011).

Although potatoes were brought to Europe as early as the 16th century, widespread potato cultivation was not practiced until the early 19th century (Smith, 2011). Early introductions were short-day-adapted Andean landraces (*S. tuberosum* group Andigena) that failed to tuberize properly in the British climate's long days and short growing seasons (Gutaker et al., 2019). Conversely, Chilean landraces (*S. tuberosum* group Chilotanum) were adapted to the long days of Chilean coastal lowlands, similar to Britain, and thus exhibited superior growth (Glendinning, 1983). First introduced into European breeding stock in 1811, over 99% of modern European and North American cultivars now possess Chilean cytoplasm (Ames & Spooner, 2008).

European and North American cultivars developed prior to the 21st century have a narrow gene pool and share an estimated 80% of alleles between varieties (Glendinning, 1983). This genetic homogeneity is likely due to the limited number of imported breeding stock into Europe and the loss of cultivars during the late blight epidemic of the mid 1800s (Love, 1999). Traditional breeding efforts were time-intensive, taking up to 50 years to develop and constrained by biological factors including sexual incompatibility and infertility of interspecific hybrids (Austin et al., 1988; Haverkort et al., 2009; Spooner et al., 2014).

Fortunately, development of novel biotechnology techniques and the full sequencing of the potato genome have facilitated rapid varietal development (Ghislain & Douches, 2019). Wild *Solanum* species are a source of diverse genetic material for improvement of breeding stock, with an estimated 40% possessing useful resistances to pathogens and abiotic stresses (Ghislain

& Douches, 2019). Introgression of resistance (R) genes of several foliar diseases, including late blight (*Phytophthora infestans*) (Haverkort et al., 2009; Ghislain & Douches, 2019) and potato leaf roll virus (PLRV) (Helgeson, 1989), from wild *Solanum* species into breeding stock has been successful.

Current production and significance

Potato is the third largest carbohydrate crop produced worldwide, following maize, wheat, and rice (FAOSTAT, 2022). Potatoes are grown in more than 100 countries, with leading producers including China, India, the Russian Federation, the Ukraine, and the United States (Beals, 2019; van Niekerk et al., 2016). In 2021, the U.S. harvested over 935 thousand acres and produced over 41 billion pounds of potatoes with an estimated value of \$4.06 billion (National Potato Council, 2021). Potato is a dietary staple for 1.3 billion people, with the majority of potatoes produced worldwide sold as fresh tablestock (Campos & Ortiz, 2019). However, the processing sector has become increasingly important in the U.S. since the emergence of the frozen processed potato market (1942-1966) (Sparks, 1991). In 2021, the majority of U.S. potatoes were sold for processing (70%), followed by table stock (24%) and other sales including livestock feed and seed (5%) (USDA-NASS, 2022). Michigan is the largest producer of chipping potatoes in the U.S. and grows over 70% of tubers for use in the state's chip industry each year (Whitmore, 2020), providing 25% of chips consumed in the country, more than 3,200 jobs, and an estimated \$1.24 billion annually (Falinski, 2022; "Potato progress", 2016).

Potato has become significant for global food security as a nutritious and energy-dense crop capable of growing in diverse regions (Campos & Ortiz, 2019). Potato tubers are a rich source of vitamins, protein, minerals, and macronutrients including potassium, dietary fiber, and vitamin C (Wood et al., 2017). Potato crops have high land-use efficiency, returning an estimated three to four times as much return as other major food crops (Connell, 1951). Approximately 85% of the potato plant is edible by humans, compared to only 50% of cereal plants (Lutaladio & Castaldi, 2009). The water productivity of potato also exceeds other crops in energy and protein content per unit water, which is especially valuable for regions with limited water availability (Renault & Wallender, 2000).

POSTHARVEST POTATO MANAGEMENT

Overview of tuber storage

Demand for fresh tubers and processed goods year-round has motivated the industry to optimize storage management to promote long-term tuber quality (Sparks, 1991). Tubers may be stored for up to ten months under optimal conditions, but shrinkage and decay cause significant losses each year (Wustman & Struik, 2007). During the storage period of December 2018 to June 2019, an estimated 22.0 million hundredweight (cwt) was lost across 13 major states, accounting for 4.97% total production (USDA-NASS 2019). Over 18 million cwt were produced in Michigan with an estimated value of \$191.5 million. An estimated 680,000 cwt were lost in Michigan potato storages from 2018-2019, with an estimated loss of \$7 million (USDA-NASS 2019).

Commercial storages in Michigan and elsewhere maintain tubers in indoor bulk piles (Geyer & Gottschalk, 2008). Several factors significantly affect the storability of tuber, including intended market use and variety, disease pressure from entering inoculum and infected tubers, and conditions during the growing season (Celis-Gamboa et al., 2003; Gould et al., 1979; Wustman, 2007). Temperature, relative humidity, and ventilation are monitored to extend tuber dormancy and reduce pathogenic activity (Heltoft et al., 2016; Sparks, 1973, 1991).

Temperature influences tuber quality as well as disease development. Tubers must be cooled to a uniform temperature prior to loading (± 0.5 °C) or natural convection will result in condensation on cool areas of storage (Geyer & Gottschalk, 2008; Pringle et al., 2009). Seed tubers are stored between 38-40 °F/3-4 °C, whereas fresh market tubers are stored between 40-50 °F/3.3-10 °C and chipping tubers are stored between 50-55 °F/10-13 °C (Driskill Jr. et al., 2007; Magdalena & Dariusz, 2018). Relative humidity in storage (> 80%) facilitates wound healing to protect tubers from infection by pathogens that cannot penetrate the periderm (Lulai, 2007; Nolte et al., 1987; Sabba & Lulai, 2002). The commercial standard (95% RH) promotes periderm wound-healing without significantly affecting rot development (Sparks, 1973). Ventilation removes excess heat when tubers are first brought into storage and manages heat generated by respiration throughout the storage period (Pringle et al., 2009), prevents free moisture buildup and tuber wetting (Pringle & Robinson, 1996), and reduces carbon dioxide accumulation and other conditions that favor reproduction of pathogens such as *Dickeya* and *Pectobacterium* species (Burton & Wigginton, 1970).

Major postharvest rot pathogens

An estimated 22% of postharvest losses are caused by bacterial, fungal, oomycete, and viral pathogens (Czajkowski et al., 2011). Notable tuber rot diseases include Fusarium dry rot (*Fusarium* spp.), soft rot (*Pectobacterium* spp. and *Dickeya* spp.), leak (*Pythium ultimum*), and pink rot (*Phytophthora erythroseptica*) (Lambert & Salas, 2001; Powelson & Franc, 2001; Salas & Secor, 2001; Secor & Salas, 2001; Stevenson et al., 2001).

Fusarium dry rot

Fusarium dry rot (FDR) is a major disease that causes significant tuber decay in storage, affecting 6-25% of tubers annually with up to 60% of stored tubers affected (Chelkowski, 1989). Some *Fusaria* produce mycotoxins with adverse health problems in humans if directly ingested or exposed through contaminated livestock produce (Azil et al., 2021; Desjardins & Plattner, 1989). Infection in seed lots is common and reduces quality by contributing to seedpiece decay, introducing inoculum, and reducing emergence (< 50%) as cited by Kirk et al. (2013).

FDR is characterized by dark brown lesions, hollow or mycelium-filled internal cavities, and sunken periderm of the tuber (Salas & Secor, 2001). There are 13 known FDR pathogens in the United States, of which *F. sambucinum* Fuckel (syn. *F. sulphureum* Schlechtendahl; teleomorph *Gibberella pulicaris* [Fr.:Fr.] Sacc.), *F. oxysporum* Schlechtend (Fries), and *F. solani* (Mart) Sacc. var. *coeruleum* (Lib. Ex Sacc) C. Booth (or *F. coeruleum*; teleomorph *Nectria haematococca*) have historically been the most aggressive in the northern U.S. (Chelkowski, 1989; Gachango et al., 2012; Hanson et al., 1996; Latus-Ziętkiewicz et al., 1987). Other pathogenic species that have been identified in Michigan seed lots include *Fusarium acuminatum*, *F. avenaceum*, *F. cerealis*, *F. equiseti*, *F. sporotrichioides*, *F. torulosum*, and *F. tricinctum* (Gachango et al., 2012).

Soilborne *Fusarium* species persist in the absence of hosts as dormant thick-walled and nutrient-rich chlamydospores (Couteaudier & Alabouvette, 1990). A variety of asexual spore types are associated with *Fusaria*, including macroconidia, microconidia, and chlamydospores, although not all types are produced by each species (El-Ani, 1988). Microconidia and macroconidia are numerous and prolific in established infections and chlamydospores are highly infectious and durable soilborne overwintering structures (Akhter et al., 2016). Infection within storage has been observed to “[increase] throughout the storage period” as cited by Carnegie et al. (1990).

Current management of FDR incorporates reduction of soilborne inoculum by crop rotation and removal of symptomatic tubers, soil and plant residue entering storages (Secor & Salas, 2001). *Fusaria* are unable to penetrate the periderm and infection may be reduced by performing vine-kill two to three weeks prior to harvest (Lulai, 2007), as well as reducing wounding by careful handling, limiting drops and contact with abrasive surfaces, and conditioning tubers prior to loading into storage (Gudmestad et al., 2007; Pringle et al., 2009; Schmidt et al., 2012; Secor & Gudmestad, 1999).

The majority of commercial varieties grown in the 20th century are moderately to highly susceptible to tuber decay by *F. sambucinum* and *F. solani* (Ayers, 1956). Some research germplasm exhibit moderate resistance to one or more pathogenic *Fusarium* species (Corsini & Pavek, 1986; Leach & Webb, 1981). Thiabendazole is a benzimidazole fungicide used on both seed and stored tubers; however, resistant isolates of *Fusarium sambucinum* has been observed in both Europe and the United States (Desjardins & Plattner, 1989; Jeger et al., 1996).

Bacterial soft rot

Bacterial soft rot (BSR) of potato tubers is caused by *Dickeya* and *Pectobacterium* spp. (formerly genus *Erwinia*), which are ubiquitous in potato-producing regions (Pérombelon, 2002). *Pectobacterium carotovorum* ssp. *carotovorum* (PCC) is considered one of the top ten bacterial plant pathogens (Mansfield et al., 2012). In addition to PCC, *Pectobacterium carotovorum* ssp. *atrosepticum* (PCA), *P. chrysanthemi* and *Dickeya dianthicola* are major potato pathogens (Czajkowski et al., 2009).

Soft rot bacteria (SRB) have a broad host range that includes an estimated 35% of angiosperm orders and cause an estimated 15-30% loss of all harvested crops each year (Bisht et al., 1993; Secor et al., 2021). They are ubiquitous in the air, water, and soils of most potato-producing regions (Czajkowski et al., 2015). Infectious propagules can travel large distances via moist air currents, free water, insect vectors, and precipitation (Naas et al., 2018; Powelson & Franc, 2001). Tuber infection commonly occurs during harvesting and handling due to the distribution of contaminated plant residue and soil debris by equipment (Czajkowski et al., 2011). Populations can remain dormant on the periderm or within internal tissues for months, making them particularly insidious in seed tuber production (Czajkowski et al., 2011; Pérombelon, 2002). Stand losses of up to 90% have been previously observed in field trials (Pérombelon, 2021). Latent infections are common on harvested tubers and widespread in most

commercial seed stocks (Pérombelon, 2002). SRB spread via the vascular system from infected seed pieces to the stem and vine (blackleg and aerial stem rot) and into progeny tubers through the stolon (Czajkowski et al., 2011).

Warm (77 °F/25 °C) and moist conditions facilitate BSR pathogenesis (Powelson & Franc, 2001). The characteristic symptom of BSR is wet decay and maceration of tissue caused by exudation of pectolytic cell wall degrading enzymes (Barras & Chatterjee, 1994; Morse, 1917). Maceration is induced only after the population of SRB reach a threshold of 10^7 cells/g peel, which requires extended exposure to moisture (Pérombelon, 1979). Once this threshold has been achieved, a single cell can give rise to as many as 20 million progeny cells in 12 hours (Czajkowski et al., 2011, 2015; Lee et al., 2013). Severely decayed tubers produce watery exudate that dispenses inoculum down through a storage pile (Pérombelon, 2002). BSR increases susceptibility to secondary infection by other pathogens and secondary colonizers (Kushalappa & Zulfiqar, 2001). Contamination in seed lots can lead to downgrading and rejection from certified seed programs (van der Wolf et al., 2017). Infected seed suffers reduced emergence and stand and are primary sources of inoculum into new fields (Powelson & Franc, 2001).

Management of BSR relies on avoidance of warm and wet conditions that induce pathogenesis by avoiding planting in poorly-draining or low-lying fields, performing vine-kill two to three weeks before harvest to ensure proper skin-set (Lulai, 2007), disinfecting equipment especially if bacterial ooze is present (Pérombelon, 1974), harvesting during dry conditions when temperatures are below 77 °F/25 °C and pulp temperatures are below 68 °F/20 °C, and conditioning tubers to storage temperatures before entering bins to prevent temperature gradients subsequent condensation accumulation (Pringle et al., 2009). Proper ventilation dries tuber skins and reduces carbon dioxide accumulation and anaerobic conditions that favor *Pectobacterium* and *Dickeya* spp. population growth (Burton & Wigginton, 1970; Pringle & Robinson, 1996). No effective chemical controls are available for effective control of BSR of potato (Youdkes et al., 2020). Developing resistant cultivars is therefore especially important for SRB diseases. Low to moderate resistance to BSR has been identified in interspecific diploid clones and research is ongoing (Lebecka, 2018; Lebecka et al., 2021).

Pink rot

Pink rot is a prominent storage disease primarily caused by *Phytophthora erythroseptica* Pethyb., although other *Phytophthora* species including *P. cryptogea*, *P. dreschleri*, and *P.*

nicotianae have been identified as minor pathogens (Lambert & Salas, 2001; Mostowfizadeh-Ghalefarsa et al., 2010; Peters & Sturz, 2001). The first report of pink rot in the U.S. was in Maine and affected 20% of tubers harvested from infested fields (Bonde, 1938). Subsequent studies estimate that 10-75% of tubers may be affected the field level and can cause complete yield loss (Goss, 1949; Salas et al., 2003).

Colloquially called ‘watery rot’ alongside Pythium leak, pink rot-affected tubers remain firm but release watery exudate under pressure (Cairns & Muskett, 1933; Taylor et al., 2004). The distinguishing symptom is pink-to-black discoloration of infected tissue within 30 minutes of exposure of symptomatic tissue to air, as well as wrinkling and discoloration of the lenticels and skin, which may slough off (Goss, 1949; Lambert & Salas, 2001; Salas et al., 2000). In most cases, tubers are asymptomatic coming from the field, but after harvest, symptoms first develop at stolon end before rapidly advancing to the entire tuber (Goss, 1949). *Phytophthora erythroseptica* is favored by high moisture, warm temperatures (50-86 °F/10-30 °C), and poor aeration (Goss, 1949).

Infection of tubers occurs through natural openings, such as the stolon, eyes and lenticels, or through injuries (Lambert & Salas, 2001). Although infection in bulk piles during the storage period is rare, ‘pockets’ of disease have been observed when tubers are maintained in moist and warm (77 °F/25 °C) conditions (Goss, 1949). Latent pink rot infection is common coming from the field but contact between infected and asymptomatic tubers in seed lots has been observed to result in transmission and subsequent infection (Cunliffe et al., 1977).

Phytophthora erythroseptica produces three reproductive structures: the sexual oospore and asexual sporangium and zoospore (Walker & van West, 2007). Oospores develop on the haulm, stolon, and root of potato plants and generally act as resting spores due to the poor saprophytic capacities of *P. erythroseptica* mycelium in soil (Cairns & Muskett, 1933; Lonsdale, 1975; Vujičić & Park, 1964). The sporangium is a nonmotile, multinucleate structure containing zoospores that is capable of infecting tubers (Grenville-Briggs & Van West, 2005; Samson, 2015). Sporangium production is induced by increased moisture (Vujičić & Park, 1964). Zoospores are biflagellate, unicellular propagules that are integral for infection due to their prolific production and motility in water-saturated soils (Lonsdale et al., 1980). Zoospores are attracted to potential hosts via chemotaxis and electrotaxis and adhere through encystment,

wherein they lose their flagella and produce a mucilaginous polysaccharide to bind to the root surface (Longman & Callow, 1987; Walker & van West, 2007).

Management during the growing season is integral for minimizing pink rot entry into storage, so agronomic practices such as crop rotation to reduce pink rot pressure in soils, planting away from low-lying areas with poor drainage, and reducing damage to tubers are commonly implemented (Lambert & Salas, 2001; Salas et al., 2000). Zoospore activity is reduced below temperatures of 69 °F/21 °C, so harvesting in cool temperatures reduces infection risk (Hollingshead, 2020). Application of the phenylamide fungicide metalaxyl (mefenoxam) is commonly practiced for control of oomycetes; however, resistance in *P. erythroseptica* has been observed in North America since the mid-1990s (Lambert, 1993; Peters et al., 2001). The majority of cultivars are susceptible to pink rot, but recent studies have identified moderate resistance to pink rot (Peters & Sturz, 2001; Salas et al., 2003; Triki & Priou, 1997).

Pythium leak

Pythium leak (*Pythium* spp.), or “leak,” is a potato tuber disease characterized by grey discoloration of tissue, clear leaking exudate (cellular contents), and a black margin separating symptomatic and asymptomatic tissue (Taylor et al., 2004). *Pythium ultimum* Trow var. *ultimum* is the primary causal agent of Pythium leak in the U.S. (Salas et al., 2003), and *Pythium aphanidermatum* and other *Pythium* species have been identified as rare leak pathogens (Triki & Priou, 1997). Leak causes rot of tubers in storage, as well as damping off in seed pieces and other crops, and is especially problematic in cooler regions (Hollingshead et al., 2020).

Pythium species are generally unable to penetrate the periderm and require wounding to infect (Taylor et al., 2002). However, when conditions are warm (77- 86 °F/25-30 °C) and wet in the field, infection can occur through the stem end (Salas et al., 2003). Potatoes planted in low-lying areas of fields, where runoff is collected and water-disseminated sporangia accumulate, are most vulnerable to infection (Salas et al., 2003). Zoospores of *P. ultimum* are nonmotile and have not been reported to spread significantly between tubers in storage; however, moisture from leaking exudate can increase risk of secondary infections (Salas & Secor, 2001).

Management of leak largely relies on limiting excess moisture by avoiding planting in low-lying and/or poorly-draining areas and careful irrigation management (Taylor et al., 2004; Hollingshead, 2020). Fields with recent history of disease are typically rotated to another crop to reduce inoculum density (Salas et al., 2003). Cultural practices that promote good skin-set, such

as vine-kill 10-25 days before harvest, reduce tuber susceptibility to mechanical injury and subsequent infection (Kempenaar & Struik, 2007). Harvesting when temperatures are below 69 °F/21 °C reduces infection risk by oomycetes because zoospore activity significantly decreases (Hollingshead, 2020). Conditioning tubers to storage temperatures prior to bin loading reduces condensation accumulation (Pringle et al., 2009). The phenylamide fungicide metalaxyl (mefenoxam) is commonly applied for control of oomycetes including leak pathogens; however, resistance has been observed in *Pythium* populations since the 1980s (Sanders, 1984). Recent studies have identified some cultivars with moderate resistance to *Pythium* leak (Peters & Sturz, 2001; Priou et al., 1997; Salas et al., 2003; Taylor et al., 2008; Thompson et al., 2007).

IDENTIFIED KNOWLEDGE GAPS

This study aims to address critical knowledge gaps in postharvest management and storage of potato in Michigan. Large, accumulated piles of rot have been observed in Michigan storage facilities (Michigan Winter Potato Conference, 2018; *personal communication by Dr. Jaime Willbur with local growers*), but primary pathogens have not been identified from secondary pathogens, nor their relative frequency to other storage rots. Identification of major rot pathogens entering bins, as well as the subsequent damages, remains to be quantified. Developing effective disease management strategies is an ongoing objective for agricultural sustainability, and so investigation of novel chemical controls remains a priority for postharvest research. Postharvest disease resistance is still scarce in commercial cultivars and evaluation of variety response in untested germplasm may identify clones with moderate to high resistance.

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CHAPTER 2: SURVEY OF POSTHARVEST POTATO DISEASES IN MICHIGAN STORAGES, 2019-2020

INTRODUCTION

Effective long-term storage is integral for Michigan's chipping potato industry. To provide potatoes during the off-season, storage facilities with regulated climate conditions are used to maintain tuber health until shipped to consumers. In Michigan, tubers are held in indoor, climate-controlled bulk piles for up to ten months (ASAE, 2018; Olsen, 2014). Michigan produced over 18 million hundredweight (cwt) of potato tubers in 2017 and stored approximately 64% of the crop by December, with an estimated 3.4% of total production lost during the storage period (USDA-NASS, 2017). However, during harvest, transportation, and bin loading, mechanical injuries are commonly inflicted upon tubers, resulting in an estimated 9-40% of harvested tubers suffering wound-related defects (Lulai, 2007; Peters, 1996).

Wounding increases infection risk, respiration rate, weight loss, and disease damage (Heltoft et al., 2016; Rymuza et al., 2014; Wustman & Struik, 2007). Internal defects such as bruises and tissue discoloration are especially important for processing potatoes because they reduce product appearance and quality and can result in rejection (Djaman et al., 2019; Falinski, 2022). While tubers with external defects may be removed during grading, some internal defects are only readily visible after cutting or peeling (McGarry et al., 1996).

An estimated 22% of postharvest tuber loss is caused by bacterial, fungal, and viral pathogens (Czajkowski et al., 2011). To minimize damage and preserve tuber quality, pathogens present in storages must be properly identified so management strategies can effectively reduce disease development below economically damaging levels (Secor & Gudmestad, 1999). Rot diseases cause degradation of tuber tissue, making them unacceptable for consumption, production, or seed (Boyd, 1972; Stevenson et al., 2001).

Soft rot bacteria (SRB) (*Dickeya* and *Pectobacterium* spp., formerly *Erwinia*) produce pectolytic enzymes that degrade plant cell walls and release cellular contents, resulting in tissue maceration and bacterial soft rot (BSR) of the potato tuber (Hadizadeh et al., 2019; Pérombelon, 2002). Due to their ubiquity worldwide and extensive host range estimated to include over 35% of angiosperm orders, SRB-caused diseases are a major concern (Charkowski, 2018). A survey given to bacterial pathologists identified *Dickeya* and *Pectobacterium* spp. as the 9th and 10th top plant pathogenic bacteria of concern (Mansfield et al., 2012). Postharvest infection commonly

occurs during harvesting and handling due to the distribution of contaminated plant residue and soil debris by equipment (Czajkowski et al., 2011). BSR increases susceptibility to secondary infection by other pathogens and secondary colonizers (Kushalappa & Zulfiqar, 2001). In addition to postharvest losses, contamination in seed lots can lead to downgrading and rejection from certified seed programs (van der Wolf et al., 2017). Infected seed suffers reduced emergence and stand and are primary sources of inoculum into new fields. SRB spread from the seed piece to the stem and vine (blackleg and aerial stem rot) and into progeny tubers via the vascular system through the stolon (Boyd, 1972; Czajkowski et al., 2011).

Fusarium dry rot (FDR) is a major disease of potato estimated to cause 6-25% annual loss in storages, with reports of over 60% of tubers in storage affected (Carnegie et al., 1990; Chelkowski, 1989). Symptoms include brown lesions on the periderm that appear after a month in storage, which expand radially on the periderm and into internal tissue, resulting in sunken skin and mycelium-filled cavities (Secor & Salas, 2001). There are 13 known pathogenic *Fusarium* spp. associated with FDR, which are present in soils of all potato-producing regions (Hanson et al., 1996). Distribution of pathogenic species is dependent on geographic location and season (Azil et al., 2021). In Michigan, *Fusarium* spp. have been detected in over 50% of seed lots, 11 species were identified and *Fusarium sambucinum* was the most virulent species (Gachango et al., 2012; Hanson et al., 1996).

Pink rot (*Phytophthora erythroseptica*) and Pythium leak (*Pythium ultimum* Trow var. *ultimum* and other species) are watery rots of potato and have been reported to cause up to 50% of losses postharvest (Secor & Gudmestad, 1999). Pink rot and Pythium leak are commonly observed at harvest and in storage, especially in crops grown in fields with excessive soil moisture (Taylor et al., 2004). *Phytophthora erythroseptica* and *Pythium ultimum* var. Trow are soilborne oomycetes found in most potato-producing regions (Secor & Gudmestad, 1999). They may persist in fields for many years by surviving as oospores in soil and on plant debris, as well as on other solanaceous and non-solanaceous alternate hosts (Cairns & Muskett, 1933; Lonsdale, 1975; Vujičić & Park, 1964). Additionally, infected seed may also carry *P. erythroseptica* and *P. ultimum* into uninfected fields (Taylor et al., 2008).

Tuber blemish diseases including black scurf (*Rhizoctonia solani*), early blight (*Alternaria solani*), silver scurf (*Helminthosporium solani*), and common scab (*Streptomyces* spp.) are not the focus of the present study but are significant in potato production. They affect

the periderm, resulting in reduced visual appeal and irregular periderm formation, shape deformation, and reduced processing efficiency (Jeger et al., 1996; Secor & Gudmestad, 1999; Thirumalachar, 1967). Appearance is a major factor in fresh market tuber sales and blemishes can cause significant economic loss (Stefaniak et al., 2021). Infection occurs at all stages of production, but tubers are especially likely to suffer damage when handled during harvest and transportation to storage facilities (Kempenaar & Struik, 2007; Nolte et al., 1987; Peters, 1996). Whenever tubers are handled, they are at risk of mechanical injury that penetrates or abrades the periderm, and these openings may be entry sites for pathogens (Nolte et al., 1987; Pérombelon, 2002; Secor & Gudmestad, 1999).

This survey was conducted after concerns of postharvest rots were reported by Michigan growers (Michigan Winter Potato Conference, 2018; *unpublished survey conducted by Dr. Jaime Willbur*), and therefore prioritized pathogens of the genera *Dickeya*, *Fusarium*, *Pectobacterium*, *Phytophthora*, and *Pythium*. The objective of this study was to evaluate abiotic and biotic factors entering and persisting in Michigan potato storages and collect representative pathogen samples. Tubers were visually assessed for symptoms and signs of disease, and putative pathogens were isolated from internal and external tuber tissues. Quantifying symptomatic tubers provided preliminary estimates of inoculum entering bins, while isolation of microorganisms was performed to detect putative pathogens on asymptomatic tubers. Findings will be used to provide localized information when developing storage disease management options for Michigan.

MATERIALS AND METHODS

Tuber collection and preparation

This study used tubers grown during the year 2019, obtained from grower cooperators from six counties in Michigan (**Table 2.1**). Twelve commercial fields were included in the study and 10-18 tubers were collected during harvest from five arbitrarily selected locations per field. Two sets of samples were obtained for at-harvest (AH) and post-storage (PS) evaluation (10-18 tubers x 5 within-field locations x 12 fields x 2 timepoints). Collection occurred between September and October 2019, and tubers were arbitrarily sampled by personnel in the field and transported to Michigan State University Potato and Sugar Beet Pathology program facilities within a week of harvest. AH samples were stored at commercial storage temperatures (48 °F/8.9 °C; 95% RH) and destructive sampling was performed no more than eight weeks after arrival. PS samples were held in the MPIC Cargill Potato Demonstrations Storage Facility at commercial

storage conditions for 42-52 weeks (48 °F/8.9 °C; 95% RH). PS samples were bagged and arbitrarily placed in single-layer piles within plastic crates to simulate pile conditions while permitting access to tubers for external assessment during the storage period. Processing of PS samples was delayed due to mandated restrictions to laboratory access, following COVID-19 quarantine guidelines.

Dirt and other debris were wiped away by hand and samples of 10-18 tubers from the same location and field were weighed. Tubers were washed using tap water and dish soap and air-dried for approximately ten minutes on paper towel. Severity ratings for signs and symptoms of diseases as well as abiotic mechanical damage were graded by visual estimation of percent of surface area affected (0-100%). For internal evaluation, tubers were laterally cut from apical to basal ends and halves were evaluated. Postharvest samples were externally assessed at three timepoints during the storage period, and the final assessment included internal and external damage ratings, disease ratings, and destructive sampling for putative pathogen isolation.

Abiotic damage categories included internal and external mechanical injuries and physiological disorders. Internal categories included brown spot, bruise, hollow heart, and vascular discoloration. Wounding was initially recorded as “scrape” for shallow cuts less than 1-cm deep and “wound” for cuts exceeding 1-cm but was consolidated to “wound” during the 2019-2020 post-storage evaluation due to subjectivity of evaluators. The category “eye discoloration” describes inflamed eyes with pink discoloration; however, the characteristic fluorescence symptom was not checked in all samples, so this symptom is not necessarily the ‘pink eye’ physiological disorder (Lulai et al., 2007). External and internal tissue was examined for macroscopic disease symptoms or pathogen signs (**Table 2.2**).

Putative pathogen isolation and identification

At-harvest evaluation of 625 tubers was performed no more than eight weeks after sample harvest (**Table 2.1**). Post-storage evaluation of 584 tubers was performed between 42-52 weeks after harvest. Tubers exhibiting putative signs or symptoms of BSR were sampled at the site of infection using a sterile inoculation loop and streaked onto crystal violet pectin agar (CVP; 1.0mL of 0.075% aqueous crystal violet solution in 500 mL pectate solution; Fisher Chemical, Fair Lawn, New Jersey; Cuppels and Kelman, 1973; **Table 2.2**). Putative SRB were incubated at 82 °F/28 °C for 24-48 hours after inoculation and then examined for cavity development. Four tissue samples from each tuber were collected for fungal and oomycete

pathogen isolation after visual evaluation. Symptomatic tuber tissue was sampled at the border of symptomatic and asymptomatic tissue. Tubers without symptoms and signs were arbitrarily sampled at apical and basal sides of the tuber external and internal tissue. Approximately 1 cm³ was excised using a sterile razor blade, and blades were replaced after each tuber. Tissue samples were surface-disinfested by submersion into 10% bleach (0.825% sodium hypochlorite in deionized water; Clorox Professional Products Company, Oakland, California) for 60 seconds, followed by three rinses in sterile deionized water. Samples were blotted on sterile paper towel and air-dried under a laminar flow hood for 60 seconds. Surface-disinfested tissue was placed onto 1.5%-water agar (Hanson et al., 1996; Salas et al., 2003; Taylor et al., 2002).

Cultures were maintained at ambient room temperature (68 °F/20 °C). After 4-7 days, resulting growth was examined for putative pathogens. Putative fungal and oomycete pathogens were identified by morphological characteristics including colony appearance and pigmentation aid, as well as hyphal growth and spore-bearing structures using a dissection scope (7-30x magnification, Leica Zoom 2000, LEICA Microsystems) and compound light microscope (50-200x magnification, Olympus BX41, Olympus Co.) (Barnett & Hunter, 2006). If multiple pathogens were suspected on a single tuber, up to four hyphal transfers were made for each tuber to isolate putative pathogens. In subsequent transfers, each morphologically unique isolate was maintained for further characterization. In the case of multiple morphologically similar isolates, one was arbitrarily selected.

Putative *Fusarium* species isolation and long-term storage

Putative *Fusarium* isolates were identified based on morphological characteristics described by Leslie and Summerell (2006), and isolated from tuber tissue cultures using a flame-sterilized metal pin to transfer hyphal tips onto 1.5% water agar. Morphologically distinct *Fusarium* isolates from the same tuber were identified as separate isolates. Single-spore cultures were prepared by transferring a diluted spore suspension (50-μL of concentrated spore suspension from 7-to-14-day-old culture diluted in 1 mL in distilled water) onto potato dextrose agar (PDA; 24 g L⁻¹ in distilled water) and distributed evenly using a flame-sterilized glass cell spreader. Cultures were maintained at ambient room temperature (68 °F/20 °C) under a light bank with 16 hours of light, followed by 8 hours of darkness (16:8 photoperiod). Based on colony morphology on PDA, microconidia presence, macroconidia size and shape as well as

apical or basal cell shape, isolates were further identified to putative *Fusarium* species (Leslie & Summerell, 2006).

To prepare *Fusarium* isolates for long-term storage, a protocol by Fong et al. (2000) was modified to accommodate for alternate available equipment. Glass-fiber filter paper (Whatman International Ltd; Little Chalfont, Buckinghamshire, UK) was quartered and sterilized in the autoclave for 15 minutes at 250 °F/121 °C. In a laminar flow hood, 95% ethanol and flame-sterilized forceps were used to evenly position 10-14 quarter slices on the surface of PDA. A 5-mm mycelial plug was transferred from pure single-spore culture onto the filter paper culture. Cultures were grown under ambient room temperature conditions (68 °F/20 °C). After 7-10 days, when mycelial growth fully covered the quarter slices, forceps were used to move slices into a sterile petri dish to dry overnight, and then placed into sterile paper envelopes under aseptic conditions in a laminar flow hood. Envelopes were enclosed in a sterile magenta box with chemical desiccant (anhydrous indicating drierite, W.A. Hammond Drierite Company, Ltd.) and stored at -4 °F/20 °C.

Molecular characterization of isolated *Fusarium* species

To prepare tissue for molecular characterization, pure cultures of *Fusarium* isolates were grown on PDA. After 7-10 days, in a laminar flow hood, colonized PDA agar plugs were taken from the actively growing perimeter using a sterile 5-mm cork-borer and transferred to potato dextrose broth (PDB; 24 g/L in deionized water). Liquid cultures were grown in the dark for 5 days at ambient room temperature (20-24 °C/ 68-75 °F) before collection of mycelial masses in sterile 2-mL tubes. Mycelial mass samples were stored at -4 °F/-20 °C until DNA extraction, no more than 7 days after collection.

DNA extraction was performed on 42 representative putative *Fusarium* isolates using the QIAGEN DNeasy® Plant Mini Kit (QIAGEN, Germany). Mycelial masses were thawed out at ambient room temperature (68 °F/20 °C) for no more than 1 hour before DNA isolation and mechanically lysed using Lysing Matrix A with 6.35-mm ceramic spheres (MP Biomedicals, Solon, OH) and the TissueLyserII (QIAGEN, Germany) for 30 seconds twice at 30-hz. DNA was amplified via polymerase chain reaction (PCR) using the QIAGEN PCR kit, targeting the *Fusarium* TEF1 translocation elongation factor 1- α gene with primer set EF1 (forward primer; 5'-ATGGGTAAGGA(A/G)GACAAGAC-3') and EF2 (reverse primer; 5'-GGA(G/A)GTACCAGT(G/C)ATCATGTT-3') (O'Donnell et al., 1998; Geiser et al., 2004).

PCR parameters were modified from the protocol described by Du (2012): initial denaturation at 94 °C for 60s, 35 cycles of denaturation (95 °C for 45s), annealing (58 °C for 45s), and extension (72 °C for 60s), and final extension (72 °C for 10 minutes). Amplified DNA was then purified using the Qiaquick PCR Purification Kit (QIAGEN, Germany) for a target final DNA content of 10-40 ng. To verify amplification of the correct region (approximate 680-bp product), amplicons were visualized using the FlashGel™ system (LONZA, Rockland, ME). Sanger DNA sequencing was performed by the MSU Research Technology Support Facility Genomics Core (East Lansing, MI). Species were confirmed by sequence alignment using Fusarium-ID (Geiser et al., 2004) and blastn in NCBI (>90% identities).

To confirm species identification, bootstrapping phylogenetic analyses were performed using The Molecular Evolutionary Genetics Analysis software, MEGA11 (Tamura et al., 2011). Sequence alignment of the TEF region was performed on 42 representative *Fusarium* spp. isolates and 10 known *Fusarium* spp. sequences, obtained from the downloadable version at the official FUSARIUM-ID GitHub (<https://github.com/fusariumid/fusariumid>). NRRL sequences were obtained from the USDA-ARS Culture Collection (NRRL, <https://nrml.ncaur.usda.gov/>). FRC sequences were obtained from the Fusarium Research Center (FRC, <https://plantpath.psu.edu/facilities/fusarium-researchcenter>) (**Table 2.3**). *Sarocladium kiliense*_R3PS(A)_MK752489 was selected as an outgroup (Azil et al., 2021). A bootstrap maximum parsimony tree was generated using the outgroup *Sarocladium kiliense* (MK752489) and performing 1,000 replicates with a cut-off threshold of 50%. Evolutionary history was inferred using the neighbor-joining method and distances computed using the maximum composite likelihood method (Saitou and Nei, 1987; Tamura et al., 2011).

Fusarium species virulence assay on potato tuber slices

Eighty-six confirmed *Fusarium* spp. isolates were grown on potato slices and resulting mycelial growth of *Fusarium* spp. colonies and lesion development on tubers was measured to determine relative virulence. A known pathogenic *Fusarium sambucinum* isolate obtained from Dr. Raymond Hammerschmidt (Professor Emeritus of Plant Pathology & Faculty Coordinator of MSU Plant and Pest Diagnostics; Department of Plant, Soil and Microbial Sciences) was used as the positive control, and a sterile non-colonized PDA plug was used for the negative control. A total of four replicates were performed in two independent repeated experiments, with two replicates each (1 isolate x 2 tuber slice x 2 timepoints). Isolates were grown from filter paper

storage 14 days prior to the assay by plating quarter slices onto PDA. After seven days, single-spore cultures used for mycelial plug inoculum were prepared using protocols as described by Leslie & Summerell (2006), maintained at ambient room temperatures under a light bank set to an 18:6-hour photoperiod, and grown for seven days.

Healthy potato tubers cv. Lamoka harvested in 2021 were obtained from Kalkaska County, Michigan. Dirt and other residue were removed from the surface of tubers with dish soap and tap water and 5-10 mm thick slices from the center of the tuber were selected with minimal (<1-5%) internal defects and no visual disease incidence. Slices were surface disinfested by submerging in a 10% bleach solution for 1 minute, followed by three rinses with sterile deionized water, and then air-dried. Eight to ten slices were placed into humid chambers comprised of ethanol-sterilized plastic trays and plastic mesh, sterile paper towel, and 30 mL sterile deionized water. Mycelial plugs were transferred under aseptic conditions onto the center of tuber slices using a 10-mm cork-borer, with the mycelium side down. Humid chambers were wrapped with parafilm, placed into dark conditions in a loosely sealed cardboard box, and incubated at ambient room temperature for four days. Measurements were performed 2- and 4-days post-inoculation (dpi) using a digital caliper.

Data Analysis

SAS v.9.4 (SAS Institute Inc., 2013) and SAS OnDemand for Academics (SAS Institute Inc., Cary, NC: SAS Institute Inc.) were used to analyze data. Damage and disease incidence was recorded as a binary response. Mean incidence (I) (number of damaged/symptomatic tubers per sample) was calculated as the percentage of tubers affected for each location sample, using the function $I = 100 \times A/T$, where A = affected tubers and T = total tubers per location sample.

For the virulence assay analysis, FDR lesion length and width (mm) four days after inoculation were used for analyses, and statistical significance was evaluated at $\alpha = 0.05$. Symptomatic area was also calculated by the equation: $\text{area} = \pi \times (0.5 \times \text{length}) \times (0.5 \times \text{width})$. The generalized linear mixed model (GLIMMIX) procedure was performed to determine the effects of the regressor variable of isolate entry (entnum) on the dependent variables of growth length and width by analysis of variance (ANOVA) (SAS Institute Inc., 2013). Replicate (rep) was included as a random effect. Studentized residuals were generated to test for normality by confirming normal distribution using the produced histogram and linear relationship of theoretical and sample percentiles using the normal probability plot. A one-way ANOVA was

performed to determine whether there was significant variation among *Fusarium* spp. isolates. The LSMEANS statement was used to compute least squares means of fixed effects and means comparisons were generated using Fisher's protected LSD for symptom (lesion) length and width (Piepho, 2012; Taylor et al., 2008).

RESULTS

Damage observations

A total of 1,017 tubers were evaluated for abiotic damage (**Table 2.4**). The frequency of damaged tubers at-harvest and post-storage (60-61%) were numerically similar. Major mechanical injuries were shallow scrapes (31-40% incidence; average 4-12% surface area) and wounds (19% incidence; average 2-9% surface area). Internal bruising was the least common injury (7-10%). All mechanical injuries (scrape/wound/bruise) were observed at-harvest and post-storage. The physiological disorders vascular discoloration, internal brown spot, and hollow heart were overall observed at lower frequencies than mechanical damage. Hollow heart, internal brown spot, and vascular discoloration were only observed at-harvest at numerically low rates and severities (1% incidence; average length ≤ 0.1 -1% surface area). Eye discoloration was only observed post-storage (4% incidence). Severity was numerically greater for all types of damage except hollow heart in post-storage samples.

Disease observations

A total of 1,209 tubers were evaluated for disease signs and symptoms (**Table 2.5**). Disease signs and symptoms were observed in the majority of tubers at all time points. Out of the 625 tubers evaluated at-harvest, 604 (97%) exhibited at least one disease sign or symptom. Blemish diseases were the most commonly observed type of disease and were observed at numerically higher frequencies post-storage. Common scab was the most common disease at-harvest and the only disease to affect the entire tuber exterior at-harvest. Within the "blemish" category, black dot was more common (25- 51%) than silver scurf (2-9%) at-harvest and post-storage. Average severity of silver scurf was higher at-harvest (41% surface area impacted) than black dot (22%), whereas post-storage silver scurf severity (17%) was lower than black dot (39%). At-harvest, the most commonly observed rot was soft rot (53%) followed by dry rot (33%). While leak was observed in a relatively low number of tubers (1- 3%), it was the rot disease with the greatest severity observed at-harvest (10- 44%). Dry rot was observed at greater

frequencies at-harvest, but average severity of post-harvest samples was greater (18%). Pink rot was only observed post-storage and exhibited a high average symptom severity (45%).

Genus observations

Seven fungal, oomycete, and bacterial genera were identified from isolated organisms during the two-year period: *Alternaria*, *Colletotrichum*, *Fusarium*, *Geotrichum*, *Pythium*, *Rhizoctonia*, and *Streptomyces* spp. (**Table 2.6**). Fungal genera were the most frequently identified organisms during both sampling points, and the three most frequently identified genera were *Rhizoctonia* (41-45%), *Fusarium* (40-43%), and *Alternaria* (25-40%). The only oomycetes isolated were putative *Pythium* isolates (27-34%). The only genus of bacterium collected was putative *Streptomyces*, which were collected at numerically low frequencies (1-5%) relative to scab incidence. No pectolytic pitting bacteria (*Pectobacterium* or *Dickeya* spp.) were successfully isolated. No significant trends in genus representation were observed comparing at-harvest to post-storage samples ($P > 0.05$; *data not shown*).

Fusarium identification and virulence assay

Fusarium dry rot symptoms were observed in all samples (5-10%) (**Table 2.5**) and FDR was the second most severe rot disease during both destructive sampling periods, AH behind soft rot and PS behind pink rot. Desiccated lesion symptoms ranged from covering 1-100% of the internal and external surfaces of bisected tubers, with average coverage ranging from 7-18 mm. Mycelium on tuber tissue was frequently observed on and within lesions.

A total of 503 putative *Fusarium* isolates were obtained from AH and PS destructive sampling (**Table 2.6**). *Fusarium* was the second-most frequently observed genus from tissue samples, accounting for 42% of all collected putative pathogens. From these putative *Fusarium*, 83 morphologically-distinct isolates were selected for collection and storage (**Table 2.7**). Diffused purple pigmentation was commonly observed on water agar and hyphal growth was rapid, spreading to the edges of 100-mm petri dishes within 7-10 days. When grown on potato tuber slices, growth was diverse and included white, pink, red, orange, and yellow coloration. Colony texture was either clumped, woolly, or floccose. Due to restricted laboratory access during March to July 2020 and contamination of AH cultures by unidentified fungivorous organisms, pure cultures of putative *Fusarium* isolates were only obtained from PH samples.

Eighty-six identified *Fusarium* spp. isolates were obtained from tubers sampled from four Michigan counties post-storage (**Table 2.7**). The most frequently isolated species was *Fusarium*

oxysporum (68%), and the following species were also identified: *F. incarnatum-equiseti* (10%), *F. graminearum* (7%), *F. solani* (7%), *F. lateritium* (1%), and *F. proliferatum* (1%). Of the seven *F. graminearum* isolates evaluated, four exhibited significantly greater virulence than the positive control (**Table 2.7**), with mycelial growth ranging from 39.7- 43.7 mm after four days of growth on cv. Lamoka tuber slices. One *F. oxysporum* isolate, 21SR14-9, was statistically similar to the top-performing group and exhibited mean mycelial growth of 33.4 mm. Across the four represented counties, *F. oxysporum* was the most prevalent species (67-71%) (**Table 2.8**). Of the other prevalent species, *F. incarnatum-equiseti* and *F. graminearum* were isolated in Mecosta and St. Joseph Counties but not from Montcalm or Cass County samples.

DISCUSSION

Tuber disease observations and pathogen isolation

The original objective of this survey was to identify signs and symptoms of all storage diseases present on sampled tubers. However, individual cultures were not able to be regularly maintained due to the quantity of isolates collected from tissue samples. During the Covid-19 quarantine from March to July of 2020, laboratory access was limited, and putative pathogen samples were further contaminated. We prioritized isolation of postharvest rot pathogens after considering grower concerns, as described in the Introduction, but were only able to recover putative *Fusarium*.

Limiting abiotic damage is a common practice in disease management (Lulai, 2007; Nolte et al., 1987; Storey, 2007), because of the increased susceptibility of wounded tubers to infection by various potato pathogens, as previously discussed in the “Literature Review.” Disease-associated blemishes identified as signs and symptoms of early blight, black dot, black scurf, silver scurf, and common scab were also observed during tuber evaluations. Organisms identified to genus as *Alternaria*, *Colletotrichum*, and *Rhizoctonia* were also frequently observed.

Although they are not the focus of the present study, blemishes caused by abiotic damage and non-rot tuber disease signs and symptoms were observed during tuber evaluations. Blemishes are a significant problem for fresh market potatoes due to consumer rejection of tubers imperfect appearance, resulting in the culling of an estimated 15-20% of harvested tubers (Robinson & Secor, n.d.). Additionally, blemishes may also reduce processing efficiency and form imperfections on finished products (Hunger & McIntyre, 1979; Lees & Hilton, 2003).

Bacterial pathogens

Two bacterial diseases were observed in this survey: bacterial soft rot (*Pectobacterium* and *Dickeya* spp.) and common scab (*Streptomyces* spp.). Common scab was the most common disease symptom observed at-harvest (88%) (**Table 2.5**) and post-storage (46%); frequencies do not reflect changes within a tuber sample over time due to destructive sampling at each timepoint. Average symptom severity was 20- 27% of the tuber periderm but ranged from 1- 100% (**Table 2.5**). Geographic location, agronomic practices, field history, and cultivar resistance response significantly affect scab incidence and severity (Clarke et al., 2019). A five-year U.S. variety evaluation of 23 research germplasm including round, white-skinned and long, russet-skinned varieties reported a wide range of incidences and symptom severity with significant variation between clone x location interactions (Clarke et al., 2019). To compare symptom severity to these and other studies, future observations should utilize a rating scale that includes lesion pitting in addition to symptomatic area percentage, such as the Merz 0 to 6 scale (Merz, 2000; Clarke et al., 2019).

A total of 40 putative *Streptomyces* spp. isolates were observed, accounting for 1% of collected putative pathogen organisms. Common scab and other blemish diseases were not prioritized in this survey and *Streptomyces* was not isolated for species characterization or long-term storage. A disparity between scab incidence and *Streptomyces* isolation was observed in the current study; therefore, a future study using targeted isolation methods, such as heat treatment of tuber tissue as described by Faucher et al. (1992) would provide more information on pathogenic *Streptomyces* spp. of Michigan.

Pectobacterium and *Dickeya* species are known as soft rot bacteria (SRB) and secrete pectolytic enzymes that can result in rapidly developing (3-5 days) watery rots (Pérombelon, 1974, 2002; Charkowski, 2018). Tuber soft symptoms were commonly observed at-harvest; however, the severity of symptoms was frequently low. Of the 53 symptomatic tubers at-harvest, 37% had severity ratings below 5% and these small symptoms appeared either at or just beneath the periderm (57%).

No pectolytic bacteria were successfully isolated. Both *Pectobacterium* and *Dickeya* spp. are found in potato-producing regions and have wide host ranges, making natural infection of seed tubers common (Czajkowski et al., 2009). The primary causal agent of potato BSR in Europe and the United States has historically been *Pectobacterium* spp., but outbreaks of

Dickeya dianthicola and other species were reported in Maine seed lots in 2015 (Jiang et al., 2016). *Dickeya* species thrive in warm temperatures (<77 °F/25 °C) and rising global temperatures and reports of novel infection in 22 states suggest that *Dickeya dianthicola* may soon become a major pathogen of potato at all stages of production (Charkowski, 2018; Toth et al., 2011). Infected seed tubers are the primary source of inoculum in modern potato farming (Pérombelon, 1974).

Crystal violet pectin (CVP) media was used for putative soft rot samples for its selective properties against gram-positive bacteria often present on soil and tuber surfaces, as well as for its diagnostic cavity formation (Cuppels & Kelman, 1973). No putative soft rot bacteria were collected from tissue sampled from evaluated tubers. Use of a more selective isolation method, for example to enhance soft rot development by incubating tubers in humid and anaerobic conditions (Pérombelon, 1979), or to isolate using a thioglycolate medium (Obi, 1981), may increase likelihood of isolating soft rot bacteria.

Oomycete-caused diseases

Pink rot (*Phytophthora erythroseptica*) and Pythium leak (*Pythium ultimum*) were rarely observed during this survey but when present, affected a greater average area than other diseases individually (**Table 2.5**). Pink rot was only observed post-storage (0.7%), with complete internal and external infection of one tuber and average symptom severity of 45% tuber coverage. Pythium leak incidence and severity was higher at-harvest (2.7% incidence, 44% severity) than post-storage (0.3% incidence, 10% severity). The incidence of these symptoms was low, perhaps as a consequence of cultural practices that resulted in low disease pressure in the fields or tubers may have not entered storage due to harvest and sorting methods standard for commercial storages. These factors may have also contributed to the lack of observations of *Phytophthora* species and moderate observations of *Pythium* species (27-34%) in the isolations in the current study.

A study of symptomatic tubers from 16 U.S. states and two Canadian provinces isolated *P. erythroseptica* and *P. ultimum* at 47% and 37% incidences, respectively (Taylor et al., 2002). Sampling from tubers with moderate to severe pink rot and Pythium leak symptoms and minimal secondary infection, as well as using the selective medium P₅ARPH (Taylor et al., 2002) may promote oomycete isolation. The primary objective of the Taylor et al. (2002) study was to test fungicide resistance on a wide range of water rot pathogens, and so isolation methods were

specifically selective for oomycetes. Conversely, the current study used a single generalized culturing technique in an attempt to collect and observe as many putative pathogenic organisms as possible (Whipps, 1987; Adams and Lapwood, 1978). In future surveys, it might be prudent to utilize selective culturing techniques as well as general in order to select for as many organisms of interest as possible.

Fungal diseases

This survey observed several fungal diseases and putative pathogens of their respective genera. Black dot (caused by *Colletotrichum coccodes*) and silver scurf (*Helminthosporium solani*) were observed at both sampling points, and early blight (*Alternaria solani*) was observed in post-storage samples (**Table 2.5**). However, as blemish diseases were not the primary focus of the study, further discussion will be limited to storage rot diseases.

Geotrichum rubbery rot (caused by *G. candidum*) has been reported affecting several Michigan counties over multiple years and was detected in samples submitted to the MSU Plant and Pest Diagnostic Services and the Potato and Sugar Beet extension program (Willbur et al., 2022). *Geotrichum candidum* also was recently reported causing disease in produce including rubbery rot of potato in Idaho (Duellman et al., 2021) and sour rot in peach and nectarine (Yaghmour et al., 2012). While no tubers collected for this survey exhibited rubbery rot symptoms, the Willbur lab received nine symptomatic tubers from Cass and St. Joseph counties from 2018 to 2019. Further studies are necessary to understand the prevalence, risk, and effective management practices for potato rubbery rot in Michigan.

Fusarium identification and virulence assessment

The relative distribution and virulence of species in *Fusarium* populations is variable and dependent on factors including geographic location, temperature conditions, and host tuber cultivar (Corsini and Pavek, 1986; Latus-Ziętkiewicz et al., 1987; Du et al., 2012). There are several hundred species in the genus *Fusarium* and at least thirteen have been identified as causal agents of Fusarium dry rot of potato tubers (Cullen et al., 2005). Of these species, eleven have been reported to cause dry rot in North America (Ayers and Robinson, 1956; Desjardins and Plattner, 1989; Hanson et al., 1996; Ocamb et al., 2007; Gachango et al., 2012). Surveys in North America implicate the following three species as primary dry rot pathogens: *F. sambucinum* Fuckel (syn. *F. sulphureum* Schlechtendahl; teleomorph *Gibberella pulicaris* [Fr.:Fr.] Sacc.), *F. oxysporum* Schlechtend (Fries), and *F. solani* (Mart) Sacc. var. *coeruleum* (Lib. Ex Sacc) C.

Booth (syn. *F. coeruleum*; teleomorph *Nectria haematococca*) (Corsini and Pavek, 1986; Desjardins and Plattner, 1989; Hanson et al., 1996; Ocamb et al., 2007; Gachango et al., 2012). In addition, Peters et al. (2008) has reported *F. avenaceum* (Fr.) Sacc as a prevalent FDR pathogen. This survey identified 97 isolates of seven *Fusarium* species from symptomatic and asymptomatic chipping-variety tubers grown in lower Michigan, of which four species were most frequently collected: *F. oxysporum* (68), *F. incarnatum-equiseti* (10), *F. solani* (7), and *F. graminearum* (7) (**Table 2.6, 2.7**).

Fusarium oxysporum (FOX) was identified as the second-most commonly isolated species (20%) in the northeast U.S. in 1996 and first (30%) in Michigan in 2012 (Hanson et al., 1996; Gachango et al., 2012). Though frequently isolated from temperate potato-producing regions, FOX has consistently exhibited less virulence than FSC and FSO (Latus- Ziętkiewicz et al., 1987; Loria, 1993; Gachango et al., 2012; Du et al., 2012). Out of 68 FOX isolates in this study, one (21SR14-9) was not significantly different from two of four of the most virulent isolates, both of which were *F. graminearum* (FGR). Despite low aggressivity, FOX is currently the most common dry rot pathogen in Michigan and should not be disregarded when considering disease management.

Fusarium sambucinum (FSC) has historically been among the most aggressive dry rot pathogens in North America. In 2007, FSC was identified as the most prevalent and most virulent *Fusarium* sp. in Oregon and Washington (Ocamb et al., 2007) and seed lots from Prince Edward Island (Ayers and Robinson, 1956) and Michigan (Hanson et al., 1996). The absence of FSC in the current survey is an unexpected and intriguing result that begs the question of whether there might be a population shift and if such a shift might persist in Michigan, or whether it is just a transient population fluctuation.

Fusarium graminearum (FGR) has historically been regarded as a minor pathogen due to low incidence. No FGR isolates were found in fresh market, tablestock, or seed lot tubers from northeastern states or Canada (Hanson, 1996), and only comprised 0.4% of *Fusarium* spp. isolated from symptomatic tubers sampled from Michigan seed lots in 2009 and 2010 (Gachango et al., 2012). In recent years, FGR has been implicated in dry rot outbreaks in potato storages in Poland and North Dakota (Latus-Ziętkiewicz et al., 1987; Ali et al., 2005). It is noted in the current study that of the eight *Fusarium* spp. isolates exhibiting significantly higher virulence

than the *F. sambucinum* used as a positive control in the tuber slice assay, seven were FGR (**Table 2.8**).

Members of the *Fusarium incarnatum-equiseti* species complex (FEQ) are common wheat pathogens (Theron & Holz, 1989) and were collectively the second most prevalent *Fusarium* type collected in the current survey. Though identified at low incidences in the northeast U.S. in 1996 (Hanson et al., 1996), FEQ has only recently been reported in Michigan and was the second most common species collected in 2009 and 2010 (Gachango et al., 2012). Further identification of species belonging to the *F. incarnatum-equiseti* complex identified in the current study requires further sequencing using other characterized gene regions, such as bTub2 (β -tubulin 2 gene) or RPB2 (subunit of RNA polymerase II) (Azil et al., 2021). A better understanding is needed as some members of the FEQ species complex have been reported as major pathogens in South Africa where mycotoxin production has been reported on potatoes (Theron & Holz, 1989).

In Michigan, potato is commonly rotated with cereal crops such as corn, wheat, rye, and oats, as well as other crops including alfalfa, dry bean, sugar beet, soybean, and peas (Chris Long; MSU Potato Outreach Program, *personal communication*). Several species of *Fusarium* are FDR pathogens, including FGR, FSC, and FEQ, are also pathogens of rotated crops including barley, wheat, alfalfa, corn, and soybean (Broders et al., 2007; Nganje et al., 2002; O'Donnell et al., 2008; Peters et al., 2008). Inclusion of multiple host crops in rotations may pose a risk over consecutive years in fields with history of pathogenic *Fusarium* spp. populations, as well as reduce efficacy of inoculum reduction.

One isolate of *Fusarium proliferatum* (FPR) was collected in this study. This species is relatively new to potatoes in Michigan (Merlington et al., 2013). The presence of FPR is a concern because it is a known producer of mycotoxins (Chelkowski et al., 1989; Latus-Ziętkiewicz et al., 1987) and there has been one case of a mycosis with this species in humans, as cited by Potekhina et al. (2023). Michigan grows potato in regions with loamy soil that favor FPR with several alternative hosts, including asparagus, wheat, corn, and peas (*personal communication with Chris Long*). In the present survey, FPR was infrequently isolated and exhibited minimal growth on potato slices (**Table 2.7**); however, it has been reported as a FDR pathogen in other studies (Merlington et al. 2013, Tiwari et al. 2022). Another species that was

only isolated once is *F. lateritium*, which is reported as pathogen of woody shrubs and trees, but not humans or potato (Leslie & Summerell, 2006).

Pathogenic *Fusarium* species previously identified in Michigan, but not in this survey include *F. avenaceum* (Fr.) Sacc., which is a major dry rot pathogen in Great Britain (Estrada Jr. et al., 2010), and reported as the causal agent of 10% of FDR incidences in Canadian storages by Peters et al. (2008). Gachango et al. (2012) identified isolates from seed lots as *F. avenaceum* in 2009 (11.1%) and 2010 (17.1%). Other known dry rot pathogens not identified in this survey include *F. crookwellense* L.W. Burgess, P.E. Nelson, and T.A. Toussoun, *F. acuminatum* Ellis & Everh., *F. culmorum* (W.G. Smith) Sacc., *F. sporotrichioides*, and *F. torulosum* (Hanson et al., 1996; Peters et al., 1996; Theron and Holz, 1989).

In the current study, relative frequencies of collected *Fusarium* species were variable from previous reports. There are differences in methodology from studies conducted by Hanson et al. (1996) and Gachango et al. (2012) that should be considered. In the current study, tubers were round-white chipping varieties grown exclusively in Michigan. Hanson et al.'s (1996) samples included processing, seed, and table stock tubers from three states including Michigan and the Canadian province of New Brunswick. Additionally, the objectives for isolation were different. Both studies collected symptomatic and asymptomatic tubers, but to maximize isolate collection, Hanson encouraged disease development in asymptomatic tubers with simulated bruising and incubation at favorable temperatures (68-75 °F/24-28 °C). While Gachango's samples originated from Michigan, they were maintained in seed overwintering conditions and only symptomatic tubers were collected. The current survey minimized handling damage to quantify organisms present on tubers and did not promote disease progression. Additionally, season and temperature may have affected results. Gachango's seed tubers were collected in April to May, whereas the current survey's post-storage tubers were sampled from June to October, as a result of laboratory access restrictions mandated by the COVID-19 quarantine.

In conclusion, the current survey of potato tubers at-harvest and post-storage evaluated postharvest rots of concern, as reported in Michigan in 2017 and 2018: *Fusarium* dry rot, pink rot, and *Pythium* leak. While soft rot bacteria isolation was limited due to isolation methods used, frequent observations of tuber soft rots indicate that bacterial soft rot should be considered in potato storage disease management. Differing from previous surveys, *F. graminearum* was characterized to be a highly virulent genus associated with potato tubers in Michigan, albeit at

relatively levels compared to other surveys, and warrants further investigation. Future post-harvest disease research, such as potato breeding screening or management studies, should consider using representatively virulent *F. graminearum* isolates.

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APPENDIX

Table 2.1: Sampling location information for potato tubers collected from six counties in Michigan in 2019. Two samples of 10-18 tubers were collected from five locations per field and destructively sampled at one of two time-points: at-harvest or post-storage.

Origin	County	Variety	Field	Harvested	At-harvest ^a	Stored ^b	Post-storage ^c
Andersen Farms	Montcalm	Lamoka	AB 3	10/8/2019	10/15/2019	10/8/2019	8/24/2020
Main Farm	Mecosta	Lamoka	DF-02	10/17/2019	12/6/2019	10/17/2019	10/6/2020
Sackett Potatoes	Mecosta	Mackinaw	SP 25	10/8/2019	10/15/2019	10/8/2019	8/3/2020
Sackett Potatoes	Montcalm	Lamoka	SP 150	9/24/2019	10/15/2019	10/18/2019	9/30/2020
Sackett Potatoes	Mecosta	Lamoka	SP 25	9/24/2019	10/15/2019	9/8/2019	n.s. ^d
Sackett Ranch	Montcalm	FL2137	SR 93-94	9/24/2019	12/6/2019	9/24/2019	7/20/2020
Thorlund Brothers	Montcalm	FL2137	TB PT-GR	9/19/2019	9/24/2019	9/20/2019	6/29/2020
Thorlund Brothers	Montcalm	Lamoka	TB PT-GR	9/19/2019	9/24/2019	9/20/2019	n.s.
Walthers Farms	St. Joseph	Lamoka	SJ 300	10/9/2019	10/29/2019	10/17/2019	8/30/2020
Walthers Farms	St. Joseph	Lamoka	SJ 325	10/9/2019	10/30/2019	10/17/2019	9/22/2020
Walthers Farms	Cass	Lamoka	C114 (Bin 43)	10/9/2019	11/4/2019	12/6/2019	9/15/2020
Walthers Farms	Cass	Lamoka	C114 (Bin 44)	10/9/2019	11/4/2019	12/6/2019	9/15/2020
Walthers Farms	Tuscola	Lamoka	Cass City	10/9/2019	10/30/2019	12/6/2019	10/13/2020

^a At-harvest tuber samples were stored at commercial storage temperatures (48 °F/8.9 °C; 95% RH) until destructive sampling.

^b Post-storage tuber samples were stored at commercial storage conditions (48 °F/8.9 °C; 95% RH) for 42-52 weeks in the MPIC Cargill Potato Demonstrations Storage Facility.

^c Post-storage analysis was delayed due to laboratory access restrictions implemented during the 2020 COVID-19 quarantine.

^d Tubers were not sampled (n.s.) for post-storage evaluation due to insufficient collection from the field of Sackett Potatoes SP 25 (cv. Lamoka) or Thorlund Farms PT-GR (cv. Lamoka).

Table 2.2: Summary of tuber symptoms and morphological characteristics (of colonies and spores) used for genus-level identification.

Genus ^a	Tuber Symptom	Colony and Spore Morphology ^b	Citation
<i>Alternaria</i>	Buff to tan lesions	Dark pigmented conidiophores; brown-to-black, pigmented, obclavate to elliptical to ovoid conidia; septate; may have branch appendages	Barnett and Hunter (2006)
<i>Colletotrichum</i>	Grey to brown lesions; visible black sclerotia	Disc-shaped, or cushion-shaped waxy acervuli typically with pigmented setae; 1-celled hyaline ovoid or oblong conidia	Barnett and Hunter (2006); Mattupalli et al. (2013)
<i>Fusarium</i>	Dry brown lesions; white or colorful mycelial growth may be present	Floccose yellow, pink, white, or red mycelium; pigment production; sporodochia; chlamydospores; hyaline, oblong to curved, 2-5 celled macroconidia; sometimes also microconidia; phialides	Toussoun and Nelson (1968); Leslie and Summerell (2006)
<i>Geotrichum</i>	Sweet vinegar odor; loose mycelial clumps	White, septate mycelium; conidiophores absent; short, hyaline, 1-celled arthrospores	Barnett and Hunter (2006)
<i>Helminthosporium</i>	Circular tan to grey lesions with silvery appearance when wet	Dark to hyaline septate mycelium; unbranched, erect conidiophores with 3-10 celled conidia, pigmented, often appearing in whorls; pleurogenous conidia development on conidiophores	Stevenson et al. (2001); Barnett and Hunter (2006); Mattupalli et al. (2013)
<i>Phytophthora</i>	Formaldehyde odor; pink-to-black tissue discoloration; wet exudate; rubbery texture ^c	White mycelium, sparse growth; ovoid to ellipsoid sporangia; hyphal swelling; coenocytic hyphae	Stevenson et al. (2001); Gallegly and Hong (2005)
<i>Pythium</i>	Grey internal discoloration with black margin; wet grey exudate;	Cottony white mycelium; coenocytic hyphae; hyphal swelling; smooth-walled, round aplerotic oogonia	Stevenson et al. (2001)
<i>Rhizoctonia</i>	Brown-to-black flat sclerotia	Hyaline to brown, bi- or multi-nucleate hyphae; branches form at acute or right angle and are constricted where they join main hyphae; conidia absent; may have pigmented sclerotia not divided into rind and medula	Barnett and Hunter (2006); Sneh et al. (1991)
<i>Streptomyces</i>	Buff-to-tan corky lesions that may be corky, raised, or pitted; sooty appearance; disrupted periderm; scabbing	Aerial vegetative filaments approx. 1 µm in diameter, straight to corkscrew spore chains, brown to black pigmentation on some media.	Schaad (1988); Stevenson et al. (2001)

^a Additional genera that were searched for but not observed were *Pectobacterium* and *Dickeya* (Cuppels & Kelman, 1973) and *Phoma* and *Spongospora* (Barnett & Hunter, 2006).

^b Samples used for preliminary morphological characterization were grown on non-selective water agar (fungi and oomycetes) or crystal violet pectin (bacteria).

Table 2.2 (cont'd)

° Observation of pink rot (*Phytophthora erythroseptica*) on potato were performed using species-specific disease signs and symptoms and morphological traits.

Table 2.3: NCBI Gene Bank accession and database information for nine *Fusarium* species. Reference sequences were obtained from the USDA-ARS Culture Collection (NRRL, <https://nrnl.ncaur.usda.gov/>) and the Fusarium Research Center (FRC, <https://plantpath.psu.edu/facilities/fusarium-researchcenter>).

Name	<i>Fusarium</i> -ID database entry ^a	Accession No.
NRRL 36238 oxysporum potato USA	TEF1 NRRL_36238 FOOSC 'oxysporum' Solanum_tuberosum USA gb=FJ985336.1	FJ985336.1
NRRL 26033 oxysporum Solanum lycopersicum	TEF1 NRRL_26033 FOOSC 'oxysporum' Solanum_lycopersicum USA_FL fsp=radicis_lycopersici	AF008507
NRRL 22101 solani cotton Panama	TEF1 NRRL_22101 FSSC_21a solani_melongenae Cotton_cloth Panama	AF178333.1
NRRL 36466 equiseti potato Denmark	TEF1 NRRL_36466 FIESC_14_b equiseti potato_peel Denmark gb=GQ505653.1	GQ505653.1
NRRL 26228 sambucinum wheat	TEF1 NRRL_26228 FSAMSC_sambucinum venenatum Halmbase_of_winter_wheat Austria gb=MW233085	MW233085.1
FRC R738 sambucinum potato USA	TEF1 FRC_R738 FSAMSC_sambucinum sambucinum potato USA_NY gb=MW233142	MW233142.1
NRRL 53436 langsethiae Hordeum vulgare Russia	TEF1 NRRL_53436 FSAMSC_sporotrichioides langsethiae Hordeum_vulgare Russia gb=GCA_001292635.1	HM744688.1
NRRL 13721 graminearum potato Poland	TEF1 NRRL_13721 FSAMSC_graminearum cerealium potato Poland gb=MW233068	MW233068
NRRL 28336 graminearum wheat	TEF1 NRRL_28336 FSAMSC_graminearum graminearum wheat USA_OH	AF212459.1

^a Database information structure: locus name | isolate specific identifier | *Fusarium* species complex | species name | host/substrate | geographic locality | additional metadata.

Table 2.4: Incidence, frequency, and severity of abiotic damage in tuber samples evaluated at-harvest and post-storage. Tubers were rinsed with dish soap and tap water and evaluated after 10-30 minutes of airdrying. Damage ratings were performed by visual estimation of percentage of tuber tissue affected.

Damage	At-harvest					Post-storage				
	Incidence	Frequency	Severity (%)			Incidence	Frequency	Severity (%)		
	#	%	Average ^a	Max	Min	#	%	Average	Max	Min
Scrape	196	31%	3.8	50	1	157	40%	11.8	50	1
Wound	119	19%	1.8	60	1	74	19%	9.4	50	1
Hollow Heart	4	1%	<0.1	1	1	0	0%	0.0	0	0
Internal Brown Spot	6	1%	<0.1	5	1	3	1%	5.7	15	1
Internal Bruise	48	8%	0.1	5	1	38	10%	3.5	10	1
Eye Discoloration	0	0%	0.0	0	0	14	4%	6.9	20	1
Vascular Discoloration	7	1%	1.1	1	1	0	0%	0.0	0	0
Total	625					392 ^b				

^a Average severity rating (0-100%) excludes undamaged tubers and was determined separately for each damage category.

^b Damage observations were not taken for all tubers in post-storage destructive sampling.

Table 2.5: Incidence, frequency, and severity of disease signs and symptoms in tuber samples evaluated at-harvest and post-storage. Tubers were rinsed with dish soap and tap water and evaluated after 10-30 minutes of airdrying. Internal and external signs and symptoms were rated by percentage of tissue per tuber affected.

Damage	At-harvest						Post-storage					
	Incidence	Frequency	Severity (%) ^a			Incidence	Frequency	Severity (%)				
	#	%	Average	Max	Min	#	%	Average	Max	Min		
Blemish ^b	237	38%				489	84%					
Black Dot	158	25%	21.7	70	1	297	51%	39.2	100	5		
Early Blight	0	0%	0.0	0	1	241	41%	24.2	80	1		
Silver Scurf	54	9%	40.8	80	10	12	2%	17.1	40	5		
Black Scurf	59	9%	8.9	50	1	32	5%	19.6	70	1		
Dry Rot	33	5%	7.0	40	1	59	10%	18.1	100	1		
Scab	548	88%	26.6	100	1	270	46%	19.6	80	1		
Soft Rot	53	8%	7.5	40	1	3	<1%	10.3	20	1		
Pink Rot	0	0%	0.00	0	0	4	<1%	45.0	100	10		
Leak	17	3%	43.8	60	15	2	<1%	10.0	10	5		
Total	625					584						

^a Average severity (0-100%) excludes asymptomatic tubers and was determined separately for each disease category.

^b The “blemish” category was introduced in 2020 to prevent misidentification due to limited experience of evaluators diagnosing postharvest tuber diseases. Although black scurf and common scab are also considered blemish diseases, their symptoms were more readily identifiable and thus the “blemish” category only includes the diseases black dot, early blight, and silver scurf.

Table 2.6: Incidence and frequency of genera of isolated organisms from potato tubers. Tuber tissue was excised (approximately 1 cm³) and surface-disinfested before plating onto 1.5% water agar. Resulting colony and spore morphology was examined after growth at ambient room temperatures (68 °F/20 °C) and a 16:8 photoperiod.

Genus	At Harvest ^a		Post-Storage ^b	
	Incidence #	Frequency % ^c	Incidence #	Frequency %
<i>Alternaria</i>	158	25%	232	40%
<i>Colletotrichum</i>	74	12%	109	19%
<i>Fusarium</i>	250	40%	253	43%
<i>Geotrichum</i>	0	0%	0	0%
<i>Phytophthora</i>	0	0%	0	0%
<i>Pythium</i>	170	27%	197	34%
<i>Rhizoctonia</i>	254	41%	263	45%
<i>Sclerotinia</i>	0	0%	0	0%
<i>Streptomyces</i>	32	5%	8	1%
Total	625		584	

^a At-harvest cultures were examined 4-7 days after plating.

^b Post-storage cultures were not examined until 4-12 weeks after plating due to restricted lab access following COVID-19 quarantine guidelines.

^c Frequency reflects the percentage of affected tubers out of the total sample due to concurrent infection of multiple pathogens on single tubers.

Table 2.7: Relative species incidence for 97 *Fusarium* spp. isolates collected from asymptomatic and symptomatic potato tubers from four Michigan counties and sampled after approximately eight months in storage. *Fusarium* isolates were grown on potato dextrose agar at ambient room temperature (20-24 °C/ 68-75 °F) under a 16:8 photoperiod and identified based on morphological characteristics described by Leslie and Summerell (2006). Molecular characterization was performed to confirm species identity using *Fusarium* TEF1 translocation elongation factor 1- α gene (O'Donnell et al., 1998) by the MSU Research Technology Support Facility Genomics Core (East Lansing, MI).

Species	# Collected	Incidence (%) ^a
<i>F. oxysporum</i>	66	68.0
<i>F. incarnatum-equiseti</i>	8	8.2
<i>F. graminearum</i>	7	7.2
<i>F. solani</i>	7	7.2
<i>F. equiseti</i>	2	2.1
<i>F. lateritium</i>	1	1.0
<i>F. proliferatum</i>	1	1.0
Unidentified ^b	5	5.2
Total	97	

^a Relative *Fusarium* species incidence out of 86 representative isolates collected from post-storage isolates

^b Species not confirmed due to lack of amplification during sequencing

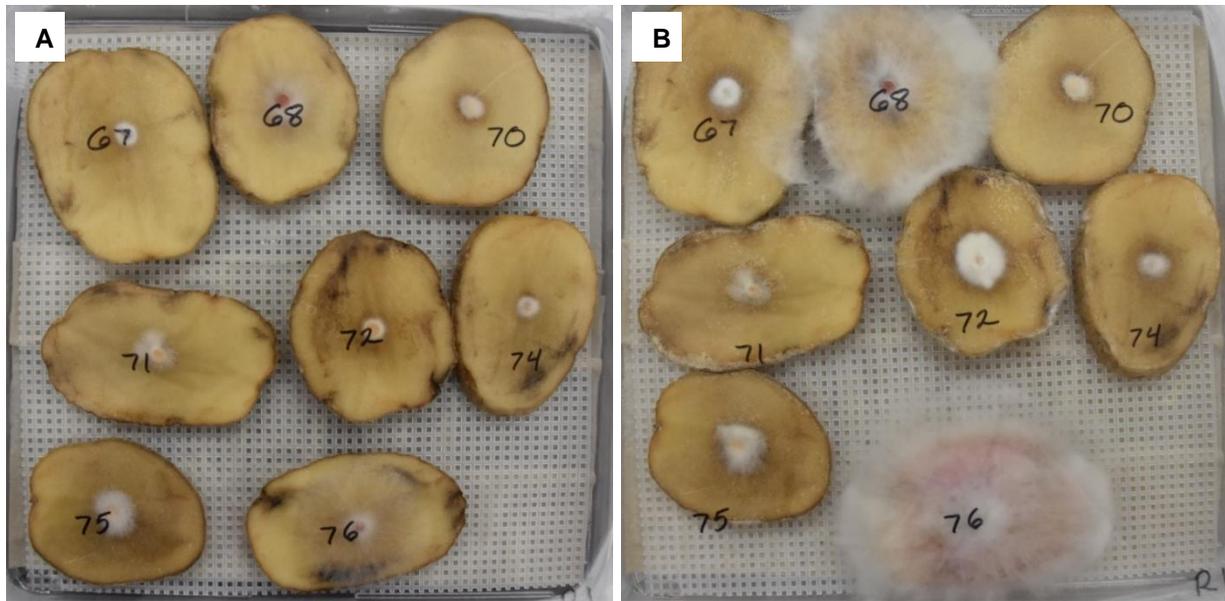


Figure 2.1: Virulence assay of *Fusarium* spp. isolates collected in 2020 on cv. Lamoka potato tuber slices. Mycelial plugs of *Fusarium* isolates used for inoculum were grown on potato dextrose agar for seven days under a 16:8 photoperiod at ambient room temperature (20-24 °C/ 68-75 °F). Inoculum plugs were placed on surface-disinfested tuber slices and incubated in darkened humid chambers at ambient room temperature. Virulence was measured by mycelial growth and tuber discoloration (lesion development) at (A) 2 and (B) 4 days-post-inoculation. Mycelium extending beyond the tuber slice perimeter was not included in measurements.

Table 2.8: County of origin and symptomatic area (mm) for 87 *Fusarium* species isolates evaluated for virulence in susceptible potato cv. Lamoka. *Fusarium* dry rot lesions were measured after 4 dpi and area was calculated by the equation: area = $\pi \times (0.5 \times \text{length}) \times (0.5 \times \text{width})$.

Isolate	ID	County	Area (cm ²) ^a	CI	95%	Species	
21TL9-9	F086	Montcalm	177.8	a	14.1	<i>F. graminearum</i>	*b
21SR12-1	F008	Mecosta	169.7	ab	14.1	<i>F. graminearum</i>	*
21SR14-9	F012	Mecosta	158.3	a-c	14.1	<i>F. oxysporum</i>	
21WF13-8	F068	St. Joseph	156.2	bc	14.1	<i>F. graminearum</i>	*
21SR18-10	F053	Montcalm	155.1	bc	14.1	<i>F. graminearum</i> (ITS)	
21SR6-5	F040	Mecosta	154.5	bc	14.1	<i>F. graminearum</i>	*
21SR13-6	F011	Mecosta	154.0	bc	14.1	<i>F. graminearum</i>	*
21MF4-8	F076	Mecosta	150.7	bc	14.1	<i>F. graminearum</i>	*
21WF13-9	F069	St. Joseph	146.9	c	14.1	<i>F. graminearum</i>	*
21SR13-4	F048	Mecosta	67.8	d	14.1	<i>F. graminearum</i> (ITS)	
Ctrl+ ^c	Ctrl+	-	46.2	e	10.0	<i>F. sambucinum</i>	
21SR20-5	F054	Montcalm	27.1	f	14.1	<i>F. incarnatum-equiseti</i>	*
21AB2-7	F093	Montcalm	25.1	fg	14.1	- ^d	
21SR13-7	F049	Mecosta	14.7	f-h	14.1	<i>F. oxysporum</i>	
21AB4-1#1	F016	Montcalm	14.2	f-h	14.1	<i>F. solani</i>	*
21WF13-4	F066	St. Joseph	13.9	f-h	14.1	<i>F. incarnatum-equiseti</i>	*
21MF4-9	F077	Mecosta	13.3	f-h	14.1	<i>F. incarnatum-equiseti</i>	*
21AB1-7	F092	Montcalm	10.5	f-h	14.1	<i>F. oxysporum</i>	
21WF12-10	F064	St. Joseph	10.4	f-h	14.1	<i>F. oxysporum</i>	
21SR21-5	F055	Montcalm	10.4	f-h	14.1	<i>F. incarnatum-equiseti</i>	*
21WF1-4	F056	Cass	10.3	f-h	14.1	<i>F. oxysporum</i>	
21WF13-10	F070	St. Joseph	9.5	f-h	14.1	<i>F. incarnatum-equiseti</i>	*
21MF1-4	F071	Mecosta	9.3	f-h	14.1	<i>F. incarnatum-equiseti</i>	*
21WF9-6	F058	St. Joseph	8.9	f-h	14.1	<i>F. oxysporum</i>	
21AB3-2	F094	Montcalm	8.4	f-h	14.1	<i>F. oxysporum</i>	*
21SR13-8	F050	Mecosta	8.4	f-h	14.1	<i>F. oxysporum</i>	*
21SR12-4	F009	Mecosta	8.2	f-h	16.2	<i>F. oxysporum</i>	
21WF10-5	F059	St. Joseph	8.2	f-h	14.1	<i>F. incarnatum-equiseti</i>	*
21AB3-8	F095	Montcalm	7.9	f-h	14.1	<i>F. oxysporum</i>	
21WF10-7	F060	St. Joseph	7.7	f-h	14.1	<i>F. oxysporum</i>	
21MF2-1	F072	Mecosta	7.2	gh	14.1	<i>F. oxysporum</i>	
21SR9-7#2	F006	Mecosta	7.1	gh	14.1	<i>F. oxysporum</i>	
21TL1-2	F079	Montcalm	7.0	gh	14.1	<i>F. oxysporum</i>	
21WF13-7	F067	St. Joseph	6.8	gh	14.1	<i>F. oxysporum</i>	*
21MF4-5	F075	Mecosta	6.8	f-h	16.2	<i>F. oxysporum</i>	
21AB4-1#2	F029	Montcalm	6.6	gh	14.1	<i>F. solani</i>	*
21SR9-7#1	F097	Mecosta	6.4	gh	14.1	<i>F. oxysporum</i>	
21SR8-2	F045	Mecosta	6.3	gh	14.1	<i>F. oxysporum</i>	
21MF3-7	F091	Mecosta	5.9	gh	14.1	<i>F. oxysporum</i>	
21SR12-10	F046	Mecosta	5.9	gh	14.1	<i>F. oxysporum</i>	*
21WF11-9	F063	St. Joseph	5.8	h	10.0	<i>F. oxysporum</i>	*
21SR5-5	F037	Montcalm	5.7	g-h	14.1	<i>F. oxysporum</i>	
21AB2-1	F026	Montcalm	5.6	gh	14.1	<i>F. equiseti</i>	*

Table 2.8 (cont'd)

21MF2-1#1	F089	Mecosta	5.5	gh	14.1	<i>F. oxysporum</i>	
21WF11-4	F062	St. Joseph	5.5	gh	14.1	<i>F. oxysporum</i>	
21SR5-9	F038	Montcalm	5.5	g-h	14.1	<i>F. oxysporum</i>	
21AB5-13	F033	Montcalm	5.4	gh	14.1	<i>F. oxysporum</i>	*
21SR3-11	F007	Mecosta	5.2	h	14.1	<i>F. oxysporum</i>	*
21WF12-1	F024	St. Joseph	5.2	h	14.1	<i>F. oxysporum</i>	
21SR2-11#2	F003	Montcalm	5.2	h	14.1	<i>F. oxysporum</i>	
21SR1-5	F034	Montcalm	5.2	h	14.1	<i>F. oxysporum</i>	
21SR6-2	F039	Mecosta	5.2	h	14.1	<i>F. oxysporum</i>	
21TL3-1	F083	Montcalm	5.1	h	14.1	<i>F. solani</i>	*
21MF2-1#2	F090	Mecosta	5.1	h	14.1	<i>F. oxysporum</i>	*
21AB2-10	F027	Montcalm	5.0	h	14.1	<i>F. oxysporum</i>	
21SR9-10	F101	Mecosta	4.9	h	14.1	<i>F. oxysporum</i>	
21SR2-11#1	F004	Montcalm	4.9	h	14.1	<i>F. oxysporum</i>	
21AB5-7	F096	Montcalm	4.8	h	14.1	<i>F. solani</i>	*
21SR13-3	F047	Mecosta	4.8	h	14.1	<i>F. oxysporum</i>	
21TL1-5	F080	Montcalm	4.8	h	14.1	<i>F. oxysporum</i>	
21SR7-14	F005	Mecosta	4.8	h	10.0	<i>F. oxysporum</i>	
21WF11-5	F100	St. Joseph	4.8	h	14.1	<i>F. oxysporum</i>	*
21SR8-10	F044	Mecosta	4.7	h	14.1	<i>F. oxysporum</i>	
21SR16-10	F052	Mecosta	4.5	h	14.1	<i>F. incarnatum-equiseti</i>	*
21SR7-11	F041	Mecosta	4.4	h	14.1	<i>F. oxysporum</i>	
21AB5-1	F032	Montcalm	4.2	h	14.1	<i>F. solani</i>	*
21TL2-6	F081	Montcalm	4.2	h	14.1	<i>F. oxysporum</i>	
21AB4-13	F031	Montcalm	4.0	h	14.1	<i>F. equiseti</i>	*
21AB2-8	F014	Montcalm	3.9	h	14.1	<i>F. oxysporum</i>	*
21WF13-1	F065	St. Joseph	3.8	h	14.1	<i>F. oxysporum</i>	
21SR1-7	F035	Montcalm	3.6	h	14.1	<i>F. oxysporum</i>	
21SR13-2	F010	Mecosta	3.5	h	14.1	<i>F. proliferatum</i>	*
21TL10-3	F087	Montcalm	3.5	h	14.1	<i>F. oxysporum</i>	
21MF3-10	F074	Mecosta	3.2	h	14.1	<i>F. oxysporum</i>	
21TL5-3	F084	Montcalm	2.9	h	14.1	<i>F. oxysporum</i>	*
21WF2-4	F020	Cass	2.8	h	14.1	<i>F. oxysporum</i>	
21WF3-5	F057	St. Joseph	2.7	h	14.1	<i>F. lateritium</i>	*
21AB4-6	F017	Montcalm	2.6	h	14.1	<i>F. oxysporum</i>	
21AB3-12	F013	Montcalm	2.5	h	11.5	<i>F. oxysporum</i>	
21SR7-5	F043	Mecosta	2.4	h	14.1	<i>F. oxysporum</i>	*
21WF3-1	F021	Cass	2.2	h	14.1	<i>F. oxysporum</i>	
21TL2-8	F082	Montcalm	1.9	h	14.1	<i>F. oxysporum</i>	
21WF3-1#2	F019	Cass	1.5	h	14.1	<i>F. oxysporum</i>	
21MF8-7	F078	Mecosta	1.4	h	14.1	-	
Ctrl- ^c	Ctrl-	-	0.0	h	11.5	-	
<i>P-value</i>			<0.0001				

^a Mean symptom areas followed by the same letter are not significantly different based on Fisher's protected Least Significant Difference ($\alpha = 0.05$).

^b Isolates designated with an asterisk (*) were included in the phylogenetic analysis.

^c Isolates designated with a dash (-) were not successfully identified to species after molecular characterization.

Table 2.8 (cont'd)

^d A positive control (known virulent isolate of *F. sambucinum*) and a mock-inoculated (sterile potato dextrose agar) were included for comparison.

Table 2.9: County distribution for 97 *Fusarium* isolates collected from asymptomatic and symptomatic potato tubers (from four Michigan counties) sampled after approximately eight months in storage.

Species	Montcalm		Mecosta		Cass		St. Joseph	
	#	%	#	%	#	%	#	%
<i>F. incarnatum-equiseti</i>	0	0	3	9	0	0	3	19
<i>F. graminearum</i>	0	0	4	12	0	0	2	13
<i>F. lateritium</i>	0	0	0	0	1	17	0	0
<i>F. oxysporum</i>	27	100	24	71	4	67	11	69
<i>F. proliferatum</i>	0	0	1	3	0	0	0	0
<i>F. solani</i>	0	0	0	0	1	17	0	0
Unidentified ^a	0	0	2	6	0	0	0	0
Total	27		34		6		16	

^a Species not confirmed due to lack of amplification during the sequencing process.

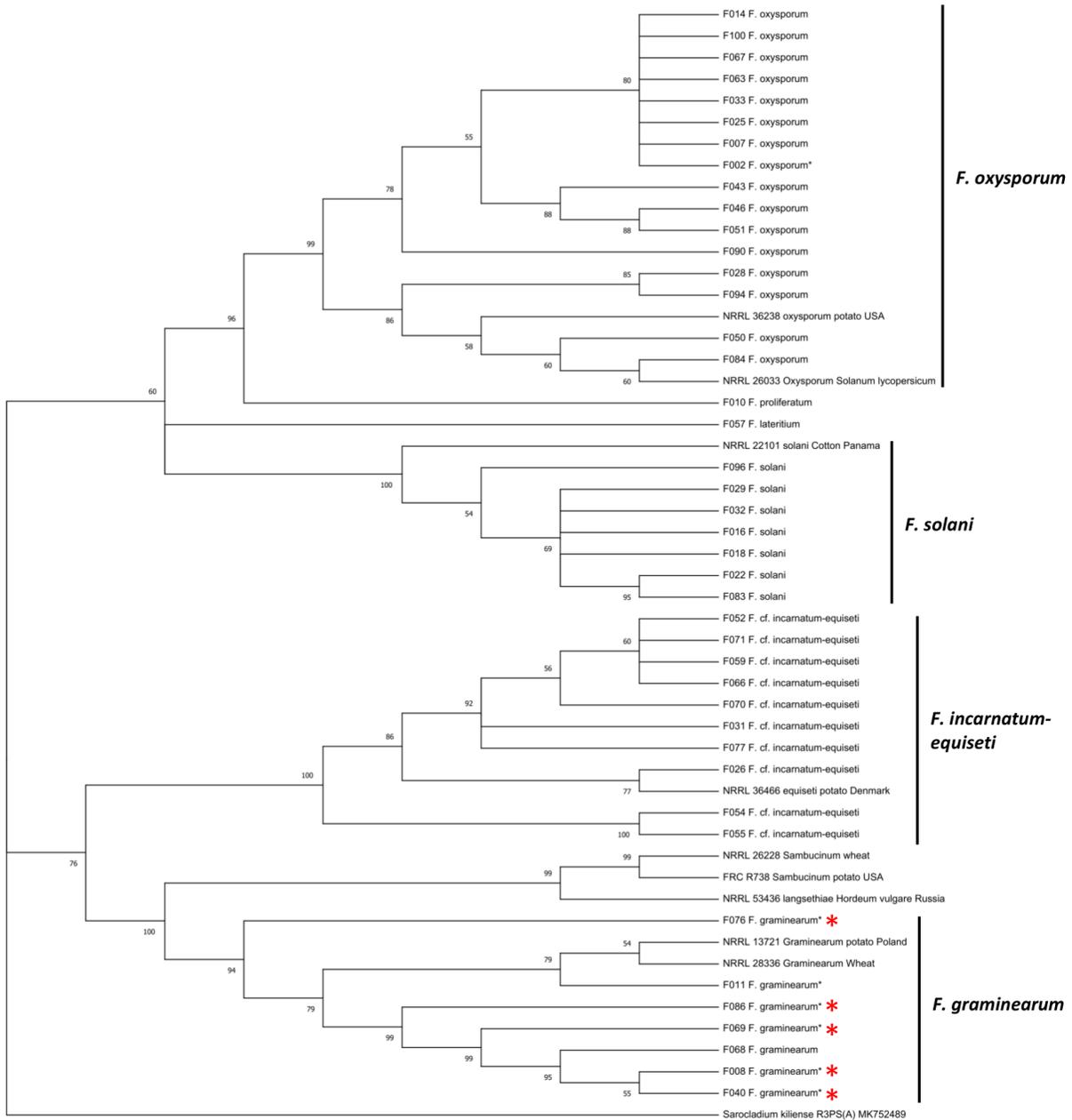


Figure 2.2: Bootstrap phylogenetic analysis obtained using *translation elongation factor 1- α* gene sequences of 42 representative *Fusarium* species isolates and nine known reference sequences. Tree was generated using the outgroup *Sarocladium kiliense* (MK752489) and performing 1,000 replicates with a cut-off threshold of 50%. Evolutionary history was inferred using the neighbor-joining method and distances computed using the maximum composite likelihood method in MEGA11. Major species are summarized in bolded labels. Isolates denoted by red asterisks had significantly greater lesion development than the *Fusarium sambucinum* positive control on potato slices, as determined by Fisher's protected Least Significant Difference ($\alpha = 0.05$).

CHAPTER 3: EVALUATION OF SANIDATE-5.0 (PEROXYACETIC ACID) EFFICACY ON CONTROL OF FOUR POSTHARVEST POTATO DISEASES

INTRODUCTION

Potato storage

The cultivated potato (*Solanum tuberosum*) is a dietary staple worldwide due to its high yield and versatile growing conditions, dense energy and nutrition content, and high satiety and palatability provided by both fresh and processed goods (Deveaux et al., 2020; Haase, 2007; Wood et al., 2017). Maintaining potato tuber quality after harvest is essential to meet the year-round demand for fresh and processed goods (Pringle et al., 2009). Postharvest disease management is integral, especially for states such as Michigan that primarily produce potatoes for processing and require extended holding periods (Michigan Potato Industry Commission, 2020; *personal communication with Chris Long*). An estimated 70% of potatoes produced in Michigan are sold for potato chip processing (Falinski, 2022). Storage losses are especially damaging because production costs have already been incurred (Hanson et al., 1996; Potato Marketing Board, 1970). In 2018, Michigan reported postharvest losses of 680,000 cwt with an estimated value of \$7 million (USDA-NASS, 2019).

Major postharvest diseases

Pathogens in storage are diverse and include bacteria, fungi, and oomycetes, collectively causing an estimated 22% of postharvest loss each year (Secor & Gudmestad, 1999; Wustman & Struik, 2007). Soft rot bacteria (SRB) (*Pectobacterium* and *Dickeya* spp.) are among the most important bacterial pathogens worldwide and estimated to cause the loss of 15-30% of all harvested crops annually (Mansfield et al., 2012; Pérombelon, 2021). Bacterial soft rot (BSR) of potato tubers is a major contributor to postharvest potato losses and in addition to storage decay, infected seed has been reported to cause as much as 90% stand loss (Pérombelon, 2021). Fusarium dry rot (FDR) (*Fusarium* spp.) causes an estimated loss of 6-25% annually and has been reported to affect up to 60% of stored tubers (Carnegie et al., 1990; Chelkowski, 1989). Oomycete-caused tuber rots such as pink rot (*Phytophthora erythroseptica*) and Pythium leak (*Pythium ultimum* and other spp.) cause an estimated 10-50% loss in-field and in-storage annually, with up to 70% of tubers affected. (Salas et al., 2003; Secor & Gudmestad, 1999; Taylor et al., 2006, 2008).

Postharvest chemical controls

Effective disease management strategies utilize a variety of tactics including cultural, physiological, biological, and chemical controls (Schmidt et al., 2012). Some pesticides used for postharvest rots include thiabendazole (benzimidazole) and fludioxonil (phenylpyrrole) for FDR (Brandhorst & Klein, 2019; Hanson et al., 1996; Satyaprasad et al., 1997) and metalaxyl (phenylamide) for oomycete-caused rots (Peters & Sturz, 2001; Taylor et al., 2002).

The repeated usage of pesticides with common modes of action risks resistance development in pathogen populations (Brent & Holloman, 1995; Russell, 2006), which affects management of postharvest diseases including BSR, FDR, pink rot, and Pythium leak (Desjardins et al., 1993; Gachango et al., 2012a; 2012b; Lambert, 1993). Reduced pesticide efficacy, non-target toxicity, and high usage rates that increase cost are all prohibitive consequences to repeated pesticide usage (Adaskaveg & Förster, 2010; Russell A. D., 2003; Russell P. E., 2006). Identification of novel chemical controls for disease management is therefore a research priority.

SaniDate-5.0

SaniDate-5.0 is a broad-spectrum disinfectant containing two powerful oxidizing active ingredients: hydrogen peroxide (23.0%; H₂O₂) (HP) and peroxyacetic acid (5.3%; CH₃CO₃H; syn. peracetic acid) (PAA) (Antonelli et al., 2006). It is currently used in food and water processing due to its rapid and strong antimicrobial properties and breakdown into environmentally-benign compounds: acetic acid, hydrogen peroxide, oxygen, and water (Alvaro et al., 2009; Rutala & Weber, 2015).

This study assessed the efficacy of SaniDate-5.0 fog application for control of the following postharvest diseases in Michigan potato storages: BSR (*Pectobacterium carotovorum* ssp. *carotovorum*), FDR (*Fusarium sambucinum*), pink rot (*Phytophthora erythroseptica*), and Pythium leak (*Pythium ultimum*). Application of SaniDate-5.0 by spray and direct injection into humidification water are registered for control of these diseases on potato tubers, but not fog application (BioSafe Systems LLC., 2019; EPA, 2019). Michigan growers have requested a study on the efficacy of fogging (Michigan Winter Potato Conference, 2018; *personal communication by Dr. Jaime Willbur with local growers*), because fog-applied SaniDate-5.0 was hypothesized to provide a rapid application method with low exposure to handlers and uniform

coverage throughout the bins (Austerweil & Grinstein, 1997), as well as reduce wetting of tubers that otherwise increases risk of disease development (Afek et al., 1999).

METHODS

Tuber collection and preparation

Potato tubers cv. Mackinaw were commercially sourced from Mecosta, MI and mechanically harvested, placed into plastic mesh bags for transport, and washed two days later (10 tubers x 5 disease treatments x 2 chemical treatments x 4 replicates). Harvest occurred on October 13th in 2020 and October 15th in 2021. Symptomatic and undersized tubers (< 3 inches) were arbitrarily removed. Tubers were placed into metal baskets and rinsed twice in tap water, surface disinfested in bleach solution (0.825% sodium hypochlorite in deionized water; Chlorox Professional Products Company, Oakland, California) for 30 seconds, and rinsed once in deionized water. Tubers for inoculation were separated into four disease treatments: BSR, FDR, pink rot, and *Pythium* leak. Non-inoculated potato dextrose broth (PDB; 24 g L⁻¹ in distilled water) was used as a negative control. In 2021, the number of inoculated tubers was increased from 3 to 10.

Pathogen maintenance and inoculation method

Virulent isolates of *Fusarium sambucinum*, *Pectobacterium carotovorum* ssp. *carotovorum* (PCC), and *Phytophthora erythroseptica* were obtained from the MSU Plant and Pests Diagnostics. *Pythium ultimum* was obtained by the MSU Potato and Sugar Beet Pathology Program in 2019 from tubers grown from Michigan exhibiting leak symptoms, and identification was confirmed by amplification of the internal transcribed spacer (ITS4/5) region and Sanger sequencing at the Research Technology Support Facility Genomics Core (East Lansing, MI, USA). All culture maintenance was performed in a laminar flow hood surface-disinfested with 70% ethanol before and after use. Culturing tools were flame-sterilized for 60 seconds using 95% ethanol and cooled between uses.

Fusarium sambucinum storage cultures were maintained on sterile 25-mm glass microfiber filter paper (Whatman International Ltd, Little Chalfont, Buckinghamshire, UK) in sterile 2 ¼ x 3 ½ paper envelopes enclosed in a sterile magenta box with DRIERITE® chemical desiccant (Avantor Performance Materials LLC, Radnor, PA), following a modified protocol by Fong et al. (2000). Filter paper and paper envelopes were wrapped in aluminum foil and autoclaved for 60 minutes (250 °F/121 °C, 15 psi). Fourteen days prior to inoculation, *F.*

sambucinum was grown from filter paper storage on potato dextrose agar (PDA; 39 g/L in distilled water). Seven days before inoculation, a 5-mm mycelial plug was transferred onto fresh PDA. Approximately one hour before inoculation, mycelium was scraped using an ethanol and flame-sterilized glass cell spreader, and the resulting suspension was collected in a sterile 15-mL falcon tube. Inoculum concentration was adjusted to approximately 1×10^4 macroconidia mL^{-1} using either sterile distilled water (2020) or potato dextrose broth (PDB; 24 g L in distilled water) (2021). Inoculation was performed using a 100- μl Hamilton syringe inserted to a depth of 1 cm (Taylor et al. 2002, 2004; Salas et al. 2003).

Phytophthora erythroseptica and *Pythium ultimum* were stored on carrot agar slants in sterile mineral oil at room temperature (68 °F/20 °C) (Humber, 1997). Twenty-one days before inoculation, a scalpel was used to place a 5-mm³ section of mycelium-colonized agar onto green pea agar (GPA) (Leonian, 1934; Vujičić & Park, 1964). Hyphal tips were transferred onto GPA and incubated for at least 14 days under a 16:8 photoperiod. Sporulating cultures were selected for inoculum preparation, and mycelium was agitated using a glass cell spreader. The resulting suspension was collected in a sterile 15-mL falcon tube no more than 1 hour before tuber inoculation. Initial inoculum concentration was quantified using a hemacytometer (Hausser Scientific, Bright-Line hemacytometer, Horsham, PA) and compound light microscope (50-200x magnification, Olympus BX41, Olympus Co.) and adjusted to approximately 1×10^4 sporangia/ mL^{-1} using sterile distilled water (2020) or PDB (2021). In 2021, released zoospores were used for the preparation of *P. ultimum* inoculum, with a final concentration of 1.4×10^6 zoospores/ mL^{-1} .

Pectobacterium carotovorum ssp. *carotovorum* (PCC) was stored at 25 °F/-4 °C in 20% glycerol Luria-Bertani broth (LB) (Luria Bertani, L3152 SIGMA) (Celeste Dmytryszyn; *personal communication*). Seven days before inoculation, bacteria were revived onto crystal violet pectin agar (CVP; 1.0 ml of 0.075% aqueous crystal violet solution in 500 mL pectate solution; Fisher Chemical, Fair Lawn, NJ) (Cuppels & Kelman, 1973). CVP cultures were incubated for 48 hours (82 °F/28 °C) (Thermo Fisher Scientific Inc., Thermo Scientific Heratherm IMC18 Incubator, Waltham, MA) to confirm pectolytic activity and screen for contaminants. Five days before inoculation, a full single pectolytic colony was transferred into 500 ml PDB and placed into a controlled environment incubator shaker (New Brunswick Scientific Co. Inc., New Brunswick, NJ) (82 °F/28 °C; 180 RPM).

In 2020, PCC inoculation was performed via vacuum infiltration using a modified protocol by van der Wolf et al. (2017) and Taylor et al. (2021). Tubers were washed with tap water, surface disinfested in 10% bleach solution for 1 minute, and rinsed in sterile deionized water. In a stainless-steel milk jug, tubers were fully immersed in 4 L of PCC inoculum suspension (prepared as described below) and infiltrated for 5 minutes using a vacuum motor (0.6-0.8 bar).

Due to low disease incidence, PCC inoculation was performed by syringe injection in 2021. In 2021, two days before inoculation, 100 μ L of PCC stock was evenly pipetted onto PDA. Approximately 15 hours before inoculation, an overnight culture was prepared by transferring a single colony into 10 mL PDB using a plastic pipette tip and placed into an incubator-shaker. Approximately 6 hours before inoculation, 100 μ L of overnight PCC stock was transferred to 10 mL PDB and placed in the incubator-shaker. One hour before inoculation, the optical density of the grow-out culture was measured at 600 nm using a spectrophotometer (final target $OD_{600} = 0.4-0.5$), and a serial dilution in PDB to a final dilution factor of 8×10^6 colony forming units (cfu) per mL^{-1} was performed (Azadmanesh et al., 2016; Lebecka, 2018).

To retroactively calculate concentration, five replicates of 100- μ L PCC final inoculum suspension were spread uniformly onto PDA plates immediately after inoculum preparation, colonies were counted after 48 hours, and cfu concentration was calculated using the following equation: average # colonies x final dilution factor = cfu mL^{-1} . The final concentration of PCC inoculum was 1.1×10^2 cfu mL^{-1} in 2020 and 7.3×10^3 cfu mL^{-1} in 2021.

Fungal and oomycete spore suspensions were filtered through stainless steel sieves to remove excess mycelia and solid media and minimize the risk of clogging. Suspensions were adjusted to a concentration of approximately 1×10^4 spores ml^{-1} with either sterile distilled water (2020) or PDB (2021). Sterile distilled water was used in 2020 following the modified protocol by Fong et al. (2000). In 2021, PDB was used in attempts to increase disease incidence and was kept standard across all pathogens tested. All inoculum suspensions were prepared no more than 1 hour before tuber inoculation and were regularly agitated by hand during tuber inoculation to keep propagules homogenous within the suspension.

Incubation and data collection

Inoculated tubers (3 in 2020, 10 in 2021) were placed in plastic ‘inner’ mesh bags with an outer plastic mesh bag containing ten non-inoculated satellite tubers. Each chemical-disease

treatment was replicated four times during 2020 (12 inoculated tubers, 40 satellite tubers) and 2021 (40 inoculated tubers, 40 satellite tubers). Sample bags were secured using plastic zip-ties and stored at the MPIC Cargill Potato Demonstrations Storage Facility (95% relative humidity, 48 °F/9 °C), in Bin 8 (non-treated) and Bin 9 (treated).

Bin loading occurred two days-post-inoculation (dpi) on October 14th in 2020 and October 16th in 2021. Bin 9 was treated with SaniDate-5.0 at 0.95 fl. oz. per ton of potatoes by fog application (Gun Valley Ag. & Industrial Services, Inc.) on October 20th in 2020 (8 dpi) and on November 24th in 2021 (41 dpi). Samples were collected during bin emptying and closure on June 14 in 2021 (244 dpi; 237 days-post-SaniDate-5.0-application [dpa]) and July 6 in 2022 (264 dpi; 224 dpa). Symptom length and width were measured immediately after. Tubers were cut laterally through apical and basal inoculation sites and symptomatic tissue length and width were measured using digital calipers. Mean measurements (length and width) were then calculated across subsample tubers within each replicate timepoint (two per year).

Data analysis

All data analysis was performed in SAS 9.4 (SAS Institute Inc., 2013) and SAS OnDemand for Academics (SAS Institute Inc., Cary, NC: SAS Institute Inc.). Analyses were performed separately for chemical treatment (trt; SaniDate-5.0 or non-treated). Fixed effect of SaniDate-5.0 treatment (trt) was performed separately for each inoculation treatment (fus, pcc, pyth, pery, control) and tuber end (apical and basal), using mean symptom measurements. Years were evaluated separately due to differences in inoculation treatments and protocols. Replicate (rep) was included as a random effect (Salkind, 2012; Williams & Abdi, 2010).

To confirm normality, studentized residuals were generated and normal distribution in histograms and linear relationships using the normal probability plot were observed. The generalized linear mixed model (GLIMMIX) procedure was performed to detect significant variation of symptom development between chemical x disease interactions. The LSMEANS statement was used to compute least squares means of fixed effects, and means comparisons were generated using Fisher's protected least significant difference (LSD) for symptom (lesion) length and width. Analysis of variance (ANOVA) was conducted using the generalized linear mixed model (GLIMMIX) procedure in SAS v. 9.4 and means were compared using Fisher's protected LSD ($\alpha=0.05$) via the 'mult' macro (Williams and Abdi, 2010; Salkind, 2012). The significance threshold of $\alpha = 0.05$ was used for all tests.

RESULTS

2020

In 2020, a total of 12 inoculated and 40 satellite cv. Mackinaw tubers were evaluated for symptom development after overwintering following chemical treatment (SaniDate-5.0 treated/not treated) and one of four disease treatments (FDR, BSR, pink rot, or Pythium leak). SaniDate-5.0 treatment had no significant impact on symptom length development for FDR, BSR, pink rot, or Pythium leak ($P < 0.05$; *data not shown*).

Symptom length development of FDR on non-treated tubers was significantly greater than that of BSR, pink rot, or Pythium leak ($P_{dis} = 0.0015$) (**Fig. 3.1**). Mean FDR lesion lengths of treated tubers were 6.0 mm (non-treated) and 3.9 mm (treated) (**Table 3.1**). FDR lesions were corky, dark-brown, and dry in appearance and present on 27% of treated tubers and 23% of non-treated tubers (**Fig. 3.1A**). Out of the 80 uninoculated satellite tubers, two non-treated tubers (3%) and one treated tuber (2%) developed internal lesions from apical to basal injection sites. Mean symptom lengths for BSR, pink rot, and Pythium leak ranged from 0.0-3.9 mm (**Table 3.1**).

2021

In 2021, a total of 40 inoculated and 40 satellite cv. Mackinaw tubers were evaluated for symptom development following overwintering after chemical and disease inoculation treatments. Development of FDR lesions on treated tubers was significantly greater than that of BSR, pink rot, or Pythium leak ($P_{dis} < 0.001$) (**Fig. 3.1B**). In non-treated tubers, mean FDR lesion length 13.2 mm, while means for BSR, pink rot, and Pythium leak symptoms ranged from 1.2-9.1 mm (**Table 3.1**). In SaniDate-5.0 treated tubers, mean lesion length of tubers inoculated with FDR was 9.1 mm, and mean lengths of BSR, pink rot, and Pythium leak ranged from 1.2-7.1 mm. SaniDate-5.0 treatment did not significantly affect symptom development of FDR, BSR, pink rot, or Pythium leak ($P < 0.05$; *data not shown*). FDR was present on 17% of non-treated and 20% of treated tubers, and no tubers in 2021 exhibited full-length lesions.

DISCUSSION

SaniDate-5.0 fog-application on potato tubers

Conventional postharvest chemical treatments are applied onto potato tubers via spray or roller brush prior to loading or by direct injection into the humidification system of loaded bins (Olsen & Miller, 2006). Washing with aqueous solutions is the conventional method of

application for some crops, especially those consumed without heat processing, but efficacy is variable due to cross-contamination in rinsewater and sometimes fragility of the produce (Burton & Wigginton, 1970; Murray et al., 2017; Simons & Sanguansri, 1997). One issue caused by free moisture is the formation of water films around tubers, which inhibits gas diffusion and may produce low-oxygen or anaerobic spaces within the tuber (Burton & Wigginton, 1970). Soft rot bacteria (*Pectobacterium* and *Dickeya* spp.) are an example of pathogens favored by free moisture and anaerobic conditions; Cromarty & Easton (1973) reported increased incidence and severity of BSR on surface-wetted tubers and further increased when incubated at low-oxygen conditions (4% oxygen level). Another complication of free moisture is that tuber wetness induces swelling of lenticels, through which pathogens including soft rot bacteria may infect (Fox et al., 1971).

We hypothesized that fog application would benefit in-storage potato disease management because fogging allows for uniform distribution of pesticides throughout loaded bulk piles of tubers (Lindquist, 2011). Another advantage is that the generated fog introduces very little moisture into storages (3-7 μL per droplet) compared to other methods such as spray or dunk-immersion (Afeke et al., 1999). During the current study, however, fog applications of SaniDate-5.0 did not significantly affect FDR lesion development for syringe-inoculated tubers in either year. This indicates that fog application of SaniDate-5.0 may not be effective for management of FDR in loaded potato bins.

One hypothesis for the low efficacy observed in the present study is that contact duration may be insufficient between SaniDate-5.0 and the targeted pathogens. Afeke et al. (1999) previously demonstrated the efficacy of 10% Compound C (stabilized hydrogen peroxide), continuously applied for 10 hours, for control of PCC in potato storages. Conversely, the contact duration registered for fogging SaniDate-5.0 onto produce is 20-30 seconds (BioSafe Systems, 2019). In the future, *in vitro* fungicide efficacy screening such as an inverted plate assay (Förster et al., 2004; Lin et al., 2022; Morris et al., 1979) may be useful for evaluating the efficacy of SaniDate-5.0 at different durations for controlling the postharvest rots focused on in the present study.

Another factor that may reduce efficacy was hypothesized to be the number of applications performed during the storage period. In the present study, SaniDate-5.0 was applied once but is currently registered for repeated application on stored tubers as frequently as once per month (BioSafe Systems, 2019). Afeke et al. (2001) previously demonstrated the efficacy of vaporized

10% hydrogen peroxide plus (HPP) as a control of silver scurf (*Helminthosporium solani*) on potatoes in storage. The silver scurf pathogen *H. solani* is known to spread to nearby tubers in storage as well as increase severity of lesions, even at commercial storage temperatures (< 48 F/9 °C) (Rodriguez et al., 1996). The study by Afek et al. (2001) performed monthly 10-hour fogging applications of HPP for a total of five treatments over a six-month period. Afek et al. (2001) observed significantly reduced *H. solani* growth on infected tuber surfaces, as well as reduced infection incidence (2%) compared to the non-treated control (38%). While the present study did not test frequency or duration of application, future research involving these factors may provide more insight on fog-applied SaniDate-5.0 and its control of the postharvest rot diseases.

Chemical treatment in other crop systems

Common active ingredients in food-grade sanitizers include chlorine and peroxide compounds (Russell, 2003). They are biocidal on a wide range of bacteria, fungi, oomycetes, and vegetative spores including common food-spoilage and rot pathogens found on fruits and vegetables (Baur et al., 2005; Rodgers et al., 2004; Singh et al., 2018). Chlorine compounds, such as free chlorine and chlorine dioxide, are the most common food-grade sanitizers (Galal, 2017). However, these disinfectants have drawbacks including corrosive properties, inactivation due to binding with organic matter and breakdown into carcinogenic compounds (Hoigné & Bader, 1988; Richardson et al., 2007; Simons & Sanguansri, 1997).

Hydrogen peroxide (HP) and peroxyacetic acid (PAA) are effective sanitizers widely used for treatment of food and water (Alvaro et al., 2009; Antonelli et al., 2006). Studies on fresh produce including lettuce, melon, and tomato reported that peroxide-based sanitizers demonstrated greater efficacy than chlorine-based sanitizers at reducing food spoilage bacteria (*Escherichia coli*, *Salmonella*, and *Listeria monocytogenes*) (Alasri et al., 1992; Baur et al., 2005; Singh et al., 2018; Wang et al., 2022). Conversely, in another stored root crop, a study on dump-tank immersion of sweet potato roots found that SaniDate did not significantly affect black rot (*Ceratocystis fimbriata*) of sweet potato (Stahr & Quesada-Ocampo, 2021).

Fog application has been considered for crops that cannot withstand wetting periods and has been effective in several studies including vapor-phase HP against food-spoilage microbes on prunes (Simmons et al., 1997). Vardar et al. (2012) reported that treatment of strawberries with high concentrations of HP (1500 and 2000 $\mu\text{L L}^{-1}$) was more effective than chlorine dioxide, sodium hypochlorite, citric acid, or ethanol for control of food-spoilage bacteria and fungi

including gray rot (*Botrytis cinerea*) and Rhizopus rot (*Rhizopus stolonifer*). Studies such as Vardar et al. (2012), as well as those on potato pathogens by Afek et al. (1999, 2001), suggest that further evaluation of oxidizing disinfectants may be warranted to determine potential efficacy and optimize fog application of oxidizing agents for control of postharvest potato rots.

Low disease incidence

Of the four tested diseases, only FDR had sufficient disease development for statistical analysis. Low disease development for BSR, pink rot, and Pythium leak provided inconclusive results for both years. Potential factors of these observation were hypothesized to include low favorability of environments for disease progression or suboptimal inoculum preparation.

As described in the “Literature Review,” the commercial storage environment is controlled to create less favorable conditions for disease development. Rather than performing fungicide efficacy testing under commercial storage conditions, increasing humidity during incubation may promote increased soft rot, pink rot, and Pythium leak development (Barras & Chatterjee, 1994; Byers et al., 2002). For experiments on disease development in controlled laboratory settings, this could be achieved by supplying wetted paper towels for experiments conducted.

For those conducted in loaded bins such as the present study, inoculum preparation could be optimized. This could include the use of higher-nutrient media, such as those containing peptone, yeast extract, or tryptone which have previously been found to promote *P. carotovorum* sbsp. *carotovorum* growth (Pérombelon, 1979; Sezonov et al., 2007; Smith & Bartz, 1990). To increase incidence of pink rot and Pythium leak, inducing zoospore release and germination of *P. erythroseptica* and *P. ultimum* with a “chilling period” followed by acclimation to warmer temperatures (Grenville-Briggs & Van West, 2005; Vujičić & Park, 1964), as well as reducing potential *P. ultimum* encystment by refraining from agitation of inoculum has been reported in some studies (Jones et al., 1991; Longman & Callow, 1987) and could be worth testing. Further testing for inoculum concentration and methods is necessary for future studies conducted by the MSU Potato and Sugar Beet Pathology Program and is discussed in greater detail in Chapter 4.

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APPENDIX

Table 3.1: Mean symptom length on tubers inoculated with one of four pathogens and incubated in SaniDate-5.0-treated/non-treated bins in 2020 (244 days-post-inoculation [dpi]) and 2021 (265 dpi) under commercial storage conditions (95% relative humidity, 48 °F/9 °C). SaniDate-5.0 treatment was performed post-bin loading via fog application at 0.95 fl. oz. per ton of potatoes (Gun Valley Ag. & Industrial Services, Inc.) 6 dpi in 2020, and 39 dpi in 2021.

Bin	SaniDate-5.0 Treatment	Pathogen Treatment	Mean Length (mm)	
			2020	2021
8	No	Syringe-delivered PDB (-)	1.28	1.34
8	No	<i>Fusarium sambucinum</i>	6.04	13.25
8	No	<i>Pythium ultimum</i>	0.51	1.19
8	No	<i>Phytophthora erythroseptica</i>	2.72	9.16
8	No	Vacuum Infiltration PDB (-)	1.29	. ^a
8	No	<i>Pectobacterium carotovorum</i>	0.15 ^b	4.78
9	Yes	Syringe-delivered PDB (-)	2.78	1.71
9	Yes	<i>Fusarium sambucinum</i>	3.89	9.1
9	Yes	<i>Pythium ultimum</i>	1.48	1.22
9	Yes	<i>Phytophthora erythroseptica</i>	1.90	7.10
9	Yes	Vacuum Infiltration PDB (-)	0.45	.
9	Yes	<i>Pectobacterium carotovorum</i>	0.00 ^c	3.31

^a No vacuum infiltration negative control was performed in 2021.

^{bc} PCC inoculation was performed via vacuum infiltration in 2020 and via syringe delivery in 2021.

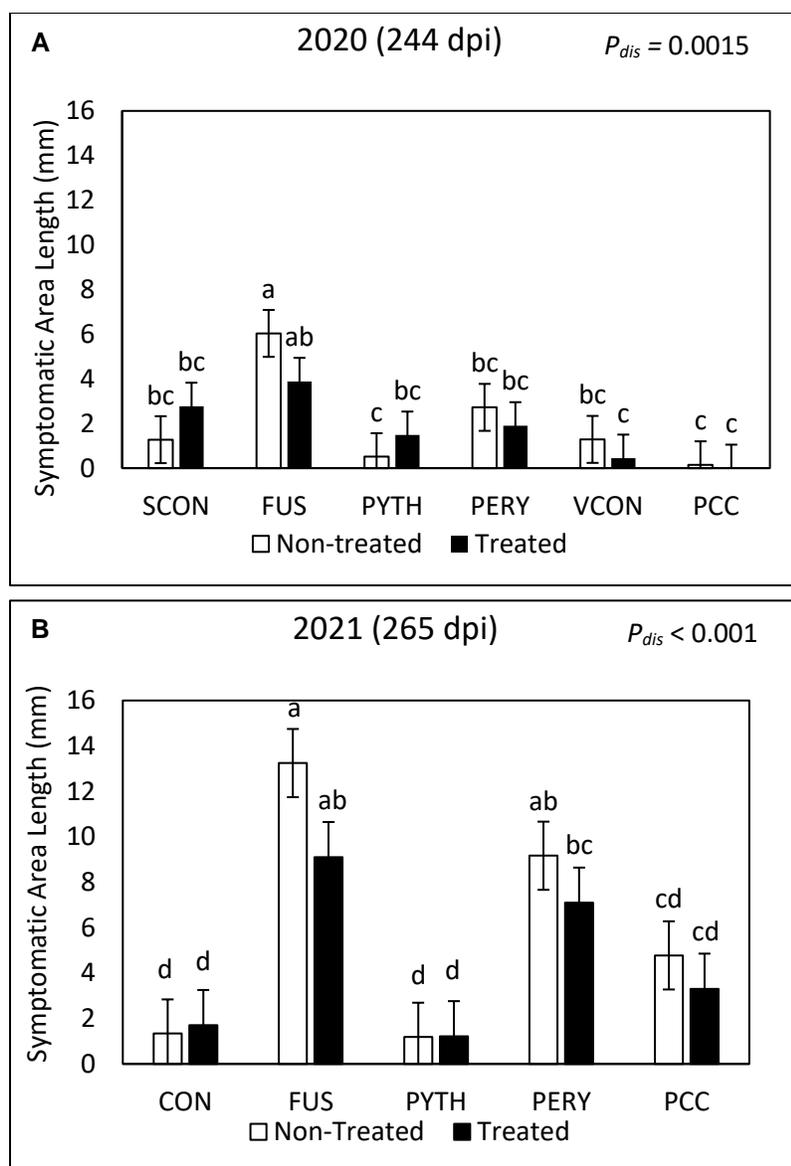


Figure 3.1: Mean apical symptom lengths measured on tubers were analyzed using mixed model ANOVA and Fisher's protected Least Significant Difference ($\alpha = 0.05$) after incubation in loaded storage bins. ANOVA was performed to detect correlations between SaniDate-5.0 treatment (non-treated or treated) and the following disease treatments separately: Fusarium dry rot (FUS), Pythium leak (PYTH), pink rot (PERY), bacterial soft rot (PCC), or vacuum infiltrated (VCON) and syringe-delivered (SCON) non-inoculated potato dextrose broth. (A) In 2020 (244 dpi), SaniDate-5.0 treatment did not significantly impact disease development in ($P > 0.05$). Fusarium dry rot developed at a significantly higher rate than Pythium leak and bacterial soft rot ($P = 0.0015$). (B) In 2021 (265 dpi), SaniDate-5.0 treatment did not affect disease development ($P > 0.05$). Fusarium dry rot developed at significantly higher rates than bacterial soft rot and Pythium leak ($P < 0.001$).

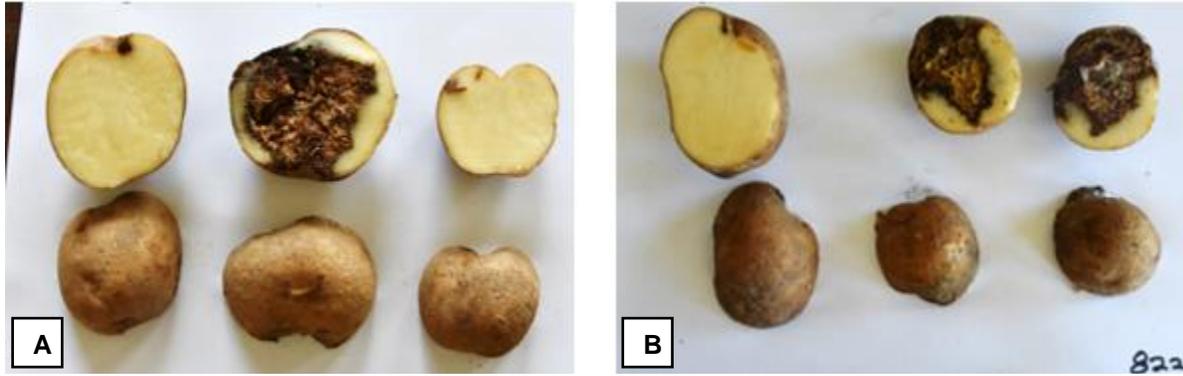


Figure 3.2: Symptoms of *Fusarium* dry rot (*Fusarium sambucinum*) on potato (cv. Mackinaw) tubers 244 days post-inoculation (dpi) at the apical (A) or basal (B) ends via syringe (1×10^4 macroconidia mL^{-1}). Tubers were incubated in loaded bins under commercial storage conditions (95% relative humidity, 48 °F/9 °C). Upper row are internal symptoms and lower row are external characteristics of the same tubers.

CHAPTER 4: ASSESSMENT OF POTATO GERMPLASM RESISTANCE TO FOUR POSTHARVEST DISEASES

INTRODUCTION

Global importance of potato and postharvest disease

The cultivated potato, *Solanum tuberosum* L., is the product of generations of concentrated effort to produce a desirable tuber resistant to disease and stresses (Carputo et al., 2005). Potato is the fourth largest carbohydrate crop, behind corn, rice, and wheat, and has become a staple food providing agricultural stability and food security (van Niekerk et al., 2016; Beals, 2019). It is tolerant to a diverse range of geographic regions and rich in energy and nutrients (McGill et al., 2013), serving as a staple food to 1.3 billion people worldwide (Campos & Ortiz, 2019). Michigan is the eighth largest potato producing state in the United States and approximately 70% of potatoes are grown for processing with an estimated \$1.2 billion annual contribution to Michigan's economy (Falinski, 2022).

Year-round demand for potato and processed goods requires overwinter storage that preserves tuber quality by minimizing postharvest disease severity and incidence as well as tuber weight loss and sprouting (Grubben et al., 2019). Rot diseases degrade potato tubers, making them unacceptable for consumption, production, or seed (Boyd, 1972; Stevenson et al., 2001). Infection can occur at all stages of production, including during harvest and in storage, and bacteria enter through natural openings and wounds (Secor and Gudmestad, 1999; Stevenson et al., 2001). An estimated 22% of postharvest losses are caused by bacterial, fungal, oomycete, and viral pathogens (Czajkowski et al., 2011). A 2018 survey completed by Michigan growers identified four major postharvest rot pathogens of concern: bacterial soft rot (*Pectobacterium* and *Dickeya* spp.), Fusarium dry rot (*Fusarium* spp.), pink rot (*Phytophthora erythroseptica*), and Pythium leak (*Pythium* spp.) (Michigan Winter Potato Conference, 2018; *unpublished survey conducted by Dr. Jaime Willbur*). Selection of breeding materials resistant to postharvest diseases would improve the quality and storability of potato tubers prior to processing.

Breeding for disease resistance

The incredible diversity of potato species, known as *Solanum* section *Petota*, includes seven cultivated and 228 wild species originating from South America (Spooner et al., 2014). Resistance genes are present in approximately 40% of wild potato species and are an invaluable source of biodiversity (Spooner et al., 2014). However, there is limited diversity in traditional

cultivars grown in the 1900s, which were estimated to share up to 80% of genetic material (Glendinning, 1983). Low biodiversity endangers potato production and food security because the majority of domesticated cultivars are susceptible to postharvest diseases including bacterial soft rot (Lapwood & Read, 1986), Fusarium dry rot (Leach & Webb, 1981), pink rot (Cairns & Muskett, 1933), and Pythium leak (Jones, 1935; Taylor et al., 2002; 2008). Hybridization of wild *Solanum* species with domestic cultivars to introduce genetic resistance into superior germplasm will greatly benefit the potato industry by providing an additional control against disease (Zimnoch-Guzowska & Lojkowska, 1993).

Overview of postharvest diseases

Bacterial soft rot

Bacterial soft rot of potato tubers (BSR) is caused by pectinolytic soft rot bacteria (SRB) (*Pectobacterium* and *Dickeya* spp., formerly classified in genus *Erwinia*). The diagnostic symptom of BSR is a creamy, moist rot caused by cell-wall degrading enzymes that macerate tissue (Powelson & Franc, 2001). The most prevalent in the United States has historically been *P. carotovorum* ssp. *carotovorum*; however, in recent years *Dickeya dianthicola* has been identified as an emerging BSR pathogen in the U.S. (Czajkowski et al., 2009; 2015). There are no chemical controls that effectively manage BSR on potato tubers, as reported by Youdkes et al. (2020). Development of resistant cultivars is therefore especially important for soft rot bacterial diseases, which cause an estimated 15-30% loss of harvested crops worldwide (Bisht et al., 1993; Pérombelon, 2021).

The majority of cultivars grown prior to the 21st century were susceptible to BSR, although significant variation in response was observed in 28 cultivars challenged with *P. atrosepticum* (Bisht et al., 1993; Lapwood and Read, 1986; Reeves et al., 1999). Currently, resistance to BSR in commercial cultivars is low to moderate (Lebecka et al., 2021). Research is ongoing, but hybridization of the domestic potato (*Solanum tuberosum*) with *Solanum brevidens*, a diploid, non-tuber-bearing species, has successfully produced diploid germplasm with improved resistance to BSR (Austin et al., 1988; Lebecka et al., 2021).

Fusarium dry rot

Fusarium dry rot (FDR) is a major postharvest disease characterized by dry tuber-penetrating lesions, which cause an estimated 6-25% loss of harvested tubers annually in storage (Chelkowski, 1989). Thirteen *Fusarium* species are known to cause FDR in the northeastern

United States (Hanson et al., 1996; Gachango et al., 2012). The most aggressive FDR pathogen in North America has historically been *Fusarium sambucinum*, followed by *F. solani* (Hanson et al., 1996; Gachango et al., 2012; Ocamb et al., 2007); however, *F. graminearum* has recently been identified as an emerging concern for Michigan and other states (Ali et al., 2005; Estrada Jr. et al., 2010). Historically, all commonly grown cultivars in the U.S. have been susceptible to FDR, although moderate resistance to one or more pathogenic *Fusarium* species has been observed (Corsini & Pavek, 1986; Leach & Webb, 1981). While effective chemical controls such as fludioxonil and thiabendazole have been used commercially, reports of frequent resistance development in wild *Fusarium* populations are a concern and additional management strategies have been a research priority for decades (Gachango et al., 2012; Hanson et al., 1996).

Pink rot and Pythium leak

Pink rot (*Phytophthora erythroseptica*) and Pythium leak (*Pythium* spp.) are watery rot diseases characterized by tuber discoloration and exudate leakage. Tuber losses range from 10-50% annually, and losses of up to 70% have been reported in the field and storage (Secor & Gudmestad, 1999; Salas et al., 2003; Taylor et al., 2006; 2008). *Phytophthora erythroseptica* Pethybr. is the primary causal agent of pink rot (Cairns & Muskett, 1933); however, *P. nicotianae* and other *Phytophthora* species have been reported to rarely cause pink rot (Lambert & Salas, 2001). *Pythium* species may cause seed piece and sprout decay in the field that reduces emergence and stand count (Salas et al., 2003). The most common leak pathogen in temperate regions is *Pythium ultimum* var. *ultimum* Trow (syn. *P. debaryanum* R. Hesse) (Salas & Secor, 2001). While *Phytophthora erythroseptica* infects through natural openings and mechanical wounds, *Pythium* spp. require wounding to enter the tuber because they cannot penetrate the periderm, as reported by Taylor et al. (2008). Both oomycetes are ubiquitous in the soil and water of potato-producing regions and are favored in warm (>72 °F/22 °C), wet, and poorly-ventilated conditions (Jones, 1935; Lambert & Salas, 2001).

Common management strategies avoid environmental conditions conducive to *Phytophthora erythroseptica* and *Pythium* spp. growth and minimize tuber injury (Lambert & Salas, 2001; Salas & Secor, 2001; Secor & Gudmestad, 1999). Pink rot and leak have been controlled in the U.S. using phenylamide fungicides (mefenoxam and metalaxyl) since the 1980s (Lambert, 1993; Secor & Gudmestad, 1999). However, resistance has been observed in *Pythium aphanidermatum* (Sanders, 1984) and in *Phytophthora erythroseptica* Pethybr. in Maine

(Lambert, 1993), and has since been frequently observed throughout North America (Peters et al., 2001). Although significant variation between cultivar x pathogen interactions has been observed, the majority of commercial cultivars are susceptible to pink rot and Pythium leak (Cairns & Muskett, 1933, Lennard, 1980; Yellareddygaru et al., 2019). Recent studies, however, have identified cultivars with moderate resistance to pink rot and Pythium leak (Peters & Sturz, 2001; Priou et al., 1997; Salas et al., 2003; Taylor et al., 2008; Thompson et al., 2007).

Integrating genetic resistance into germplasm with superior traits benefits the potato industry as an additional management option for control of diseases and pests (Stephen, 1999). This study was performed to assess variety response to four postharvest diseases: bacterial soft rot (*Pectobacterium carotovorum* ssp. *carotovorum*), Fusarium dry rot (*Fusarium sambucinum*), pink rot (*Phytophthora erythroseptica*), and Pythium leak (*Pythium ultimum*). Tubers of red-skinned yellow-flesh and chipping germplasm and commercial cultivars were inoculated with virulent strains of the aforementioned pathogens. After 47 days of incubation, symptom development was measured, and relative resistance of germplasm was analyzed. This study includes two yearly replicates for chipping lines and one for red-skinned yellow-flesh lines, with a second iteration in-progress.

METHODS

Tuber collection and preparation

In this study, 39 total varieties of chipping potato germplasm and standard commercial cultivars were evaluated for disease resistance to four postharvest diseases. For 14 of these varieties, the experiment was repeated over two years (2020-2021). In 2021, red-skinned and yellow-flesh varieties were evaluated from up to three field studies. Tubers were sourced from Montcalm and Kalkaska counties courtesy of Michigan commercial growers, the Michigan Potato Outreach Program, and the Potatoes USA-SNAC International Trial, and were harvested in fall 2020. Agronomic and integrated pest management practices were managed and applied commercially and were standard of the Michigan potato growing region; healthy, disease-free tubers were collected and used in storage experiments. Varieties obtained from more than one location were treated as separate entries for data analysis. Two replicate timepoints were performed per year for each entry. Tuber quantity for each replicate was dependent on availability (typically 3-5 tuber subsamples inoculated per pathogen). After harvest, tubers were

stored at the MSU Agronomy Farm in plastic mesh bags under commercial storage conditions (48 °F/9 °C; 95% RH) until inoculation.

One day prior to inoculation, tubers were washed twice using tap water to remove soil and debris, followed by submersion for 30 seconds in 10% bleach (0.825% sodium hypochlorite in distilled water; Clorox Professional Products Company, Oakland, California) and a final rinse in distilled water, and then air-dried overnight at ambient room temperatures in the MSU Agronomy Farm (68 °F/20 °C).

Pathogen maintenance and inoculation method

Fusarium sambucinum, *Pectobacterium carotovorum* and *Phytophthora erythroseptica* isolates were obtained from MSU Plant and Pests Diagnostics (originating from symptomatic samples) and *Pythium ultimum* was obtained from the MSU Potato and Sugar Beet Pathology Program collection (isolated from symptomatic potato tubers in 2019). *Pythium ultimum* identification was confirmed by amplification of the internal transcribed spacer (ITS4/5) region and Sanger sequencing at the Research Technology Support Facility Genomics Core (East Lansing, MI, USA). Cultures were prepared from stored isolates 7-21 days before tuber inoculation. Isolate storage and inoculum preparation for each pathogen is described below. All culture maintenance was performed under a laminar flow hood after sterilization with 70% ethanol for ten minutes. All culturing tools were flame-sterilized for 1 minute with 95% ethanol and cooled between uses.

Fusarium sambucinum storage cultures were maintained on sterile 25-mm glass microfiber filter paper (Whatman International Ltd, Little Chalfont, Buckinghamshire, UK) in sterile 2 ¼ x 3 ½ paper envelopes (Cenveo Inc., Printmaster Envelope, USA) enclosed in a sterile magenta box with DRIERITE® chemical desiccant (Avantor Performance Materials LLC, Radnor, PA), following a modified protocol by Fong et al. (2000). Prior to use, filter paper and paper envelopes were wrapped in aluminum foil and autoclaved for 60 min (250 °F/121 °C, 15 p.s.i.).

Fourteen days prior to inoculation, *F. sambucinum* was grown from filter paper storage on potato dextrose agar (PDA; 39 g L⁻¹ in distilled water). Seven days prior to inoculation, a 5-mm mycelial plug was transferred onto fresh PDA. Mycelium was scraped using an ethanol and flame-sterilized glass cell spreader and the resulting solution was collected in a sterile 15-ml falcon tube. Inoculum concentration was checked by quantifying macroconidia using a

hemacytometer (Hausser Scientific, Bright-Line hemacytometer, Horsham, PA) and compound light microscope (50-200x magnification, Olympus BX41, Olympus Co.). Concentration was adjusted by diluting the suspension to approximately 1×10^4 macroconidia ml^{-1} using either sterile distilled water (2020) or in potato dextrose broth (PDB; 24 g L^{-1} in distilled water) (2021).

Phytophthora erythroseptica and *Pythium ultimum* were stored on carrot agar slants in sterile mineral oil at room temperature ($68 \text{ }^\circ\text{F}/20 \text{ }^\circ\text{C}$) (Humber, 1997). Twenty-one days prior to inoculation, a scalpel was used to place 5-mm^3 of stored mycelium onto green pea agar (GPA) (Leonian, 1934; Vujičić & Colhoun, 1966). Hyphal growth was observed using a dissection scope (7-30x magnification, Leica Zoom 2000, LEICA Microsystems). Hyphal tips were transferred onto GPA and incubated for at least 14 days under a 16:8 photoperiod. Sporulating cultures were selected for inoculum preparation and mycelium was agitated using a glass cell spreader. The resulting suspension was collected in a sterile 15-ml falcon tube no more than 1 hour before tuber inoculation. Inoculum concentration was checked using a hemacytometer and diluted to approximately 1×10^4 sporangia ml^{-1} using sterile distilled water (2020) or PDB (2021). In 2021, released zoospores were used for preparation of *P. ultimum* inoculum rather than sporangia for a final concentration of 1.4×10^6 zoospores ml^{-1} .

Pectobacterium carotovorum ssp. *carotovorum* (PCC) was stored at $25 \text{ }^\circ\text{F}/-4 \text{ }^\circ\text{C}$ in 20% glycerol Luria-Bertani (LB broth) (Celeste Dmytryszyn; *personal communication*). Seven days before inoculation, 1 ml of storage culture was transferred onto crystal violet pectin agar (CVP; 1.0 ml of 0.075% aqueous crystal violet solution in 500 ml pectate solution; Fisher Chemical, Fair Lawn, NJ) (Cuppels & Kelman, 1973) using a pipette and glass cell spreader. CVP cultures were placed in an incubator (Thermo Fisher Scientific Inc., Thermo Scientific Heratherm IMC18 Incubator, Waltham, MA) for 48 hours ($82 \text{ }^\circ\text{F}/28 \text{ }^\circ\text{C}$) to confirm pectolytic activity and screen for contaminants. Five days before inoculation, cavity formation was observed and a full single pectolytic colony was transferred into 500 ml PDB using a sterile pipette tip and placed into a controlled environment incubator shaker (New Brunswick Scientific Co. Inc., New Brunswick, NJ) ($82 \text{ }^\circ\text{F}/28 \text{ }^\circ\text{C}$; 180 RPM) (Azadmanesh et al., 2016). Two days before inoculation, 100 μl of PCC stock was evenly pipetted onto PDA using a glass cell spreader. Approximately 15 hours before inoculation, an overnight culture was prepared by transferring a single colony into 10 ml PDB using a pipette tip and placed into the incubator-shaker. Approximately 6 hours before inoculation, 100 μl of overnight PCC stock was transferred to 10 ml PDB and placed in the

incubator-shaker. One hour before inoculation, optical density of the grow-out culture was measured at 600 nm using a spectrophotometer (final target $OD_{600} = 0.4-0.5$) and serial dilution to final dilution factor 8×10^{-6} was performed using PDB (Azadmanesh et al., 2016; Lebecka, 2018; Lebecka et al., 2021). To retroactively calculate concentration, five replicates of 100 μ l final inoculum suspension were spread uniformly onto PDA plates immediately after inoculum preparation, colonies were counted after 48 hours, and the actual concentration calculated using the following equation: average # colonies x final dilution factor = colony forming units ml^{-1} .

Incubation and data collection

Cultures were screened for propagating structures approximately 1 hour before inoculation and the inoculum suspension was prepared by flooding cultures with sterile distilled water (2020) or potato dextrose broth (2021). Sterile distilled water was initially used as a low-nutrient suspension medium to promote disease incidence on inoculated tubers (Fong et al., 2000) and changed to potato dextrose broth (PDB; 24 g L^{-1} in distilled water) in 2021. PDB was used in attempts to increase symptom development for *Pythium* leak and soft rot and was kept standard across all pathogens tested in 2021. Fungus and oomycete inoculum suspensions were filtered through stainless steel sieves to remove excess mycelia and solid media and minimize risk of clogging and adjusted to a concentration of approximately 1×10^4 spores mL^{-1} . All inoculum suspension were prepared no more than 1 hour before tuber inoculation and regularly agitated by hand during tuber inoculation to keep propagules homogenous within suspension.

Tubers were inoculated with 10 μ l of inoculum suspension per injection at two sites, one on each of the apical and basal ends. Inoculation was performed using a 100- μ l Hamilton syringe inserted to a depth of 1 cm (Taylor et al. 2004, 2002; Salas et al. 2003). Samples were incubated in the dark in paper bags stacked in plastic crates for 47 days at ambient room temperature (68 $^{\circ}F/20$ $^{\circ}C$, 30-40% RH). After incubation, tubers were cut laterally through both inoculation sites and symptomatic tissue length and width was measured using digital calipers. Mean measurements (length and width) were then calculated across subsample tubers within each replicate timepoint (two per year).

Data analysis

The following analyses were conducted separately by disease treatment, tuber end, and mean symptom measurements. Data analyses were performed using SAS v.9.4 (SAS Institute Inc., 2013) and SAS OnDemand for Academics (SAS Institute Inc., Cary, NC: SAS Institute

Inc.). Studentized residuals were generated to test for normality by confirming normal distribution using the produced histogram and linear relationship of theoretical and sample percentiles using the normal probability plot. Using the generalized linear mixed model (GLIMMIX) procedure, a one-way analysis of variance (ANOVA) was performed to determine whether there was significant variation of symptom development among varieties. Six standard chipping varieties were evaluated from two growing locations in Montcalm County (fields A and B), Michigan, and were analyzed as separate entries. Variety (including variety x field combinations) were considered fixed effects. The LSMEANS statement was used to compute least squares means of fixed effects and means comparisons were generated using Fisher's protected least significant difference (LSD) for symptom (lesion) length and width. A significance threshold of $\alpha = 0.05$ was used for all tests. Replicate (rep) was included as a random effect (Williams and Abdi, 2010; Salkind, 2012).

RESULTS

Chipping entry responses

Across the 39 chipping entries evaluated in 2020 and 15 entries in 2021, significant variation in the symptom development of FDR and pink rot was observed between potato germplasm and commercial cultivars evaluated in this study ($P < 0.05$) (**Table 4.1**). However, no significant differences in BSR or Pythium leak symptom development were detected at apical or basal sites ($P > 0.05$). Based on potential differences in physiological activity at stem or bud ends of the tubers, apical and basal information was analyzed and presented separately in the following sections.

Fusarium dry rot

In 2020, significant differences in FDR development (*Fusarium sambucinum*) were detected in symptom length and width measurements collected at both apical and basal sites ($P < 0.05$) (**Table 4.1**). In entries evaluated after 47 days ($P = 0.0002$) (**Table 4.2**), FDR symptom average (or mean) lengths ranged from 5.1-50.8 mm (**Figure 4.1A, C, E, and G**). Four entries, MSAFB605-4, MSZ219-13, Petoskey (A), and CO11023-2W, exhibited significantly ($P < 0.001$) greater lesion lengths (38.8-50.8 mm) than 31 other entries (5.1-23.1 mm). Among the standard lines, Lady Liberty, Lamoka, Mackinaw (site B), Petoskey (B), and Snowden (A and B) were grouped with the relatively lower-symptom lines (23.1 mm or less) whereas Mackinaw (A) and Petoskey (A) were grouped with the relatively greater-symptom lines (23.1 mm or more).

Significant differences in entries obtained from multiple fields were observed between Petoskey at sites (A) and (B) ($P < 0.05$), but not between Snowden (A) and (B) or Mackinaw (A) or (B) ($P > 0.05$).

In 2021, significant differences in FDR development were only detected in symptom lengths measured after inoculation at apical sites ($P = 0.0415$) (**Table 4.1**). FDR symptom widths observed at apical sites and lengths and widths observed at basal sites were not significantly different among entries ($P \geq 0.05$). After 47 days, symptom lengths of 15 entries ranged from 7.3-44.4 mm (**Table 4.3**). Three entries, MSAA076-6, NY163 (A), and NY163 (B), exhibited significantly smaller lesion length (7.3-9.9 mm) than the four highest-symptom entries (33.8-44.4 mm) ($P < 0.05$). NY163 was the only cultivar tested from two fields and no significant differences in dry rot responses were observed ($P > 0.05$).

Pink rot

In 2020, significant differences in symptom development were observed in 39 chipping entries evaluated for pink rot (*Phytophthora erythroseptica*) responses at the apical injection site after 47 days ($P = 0.0021$) (**Table 4.4**) (**Figure 4.1B, D, F, and H**). Basal symptoms were not significantly different ($P = 0.29$). Three entries exhibited significantly greater symptom development (22.0-28.0 mm) than 32 other entries (2.2-12.0 mm) ($P < 0.01$). Three commercial varieties were tested from two different fields and no significant differences in symptom development were detected between locations ($P > 0.05$).

In 2021, no significant differences were detected between variety responses to pink rot ($P > 0.05$), with average apical symptom development ranging from 0.0-29.41 mm in length (**Table 4.6**). The majority of symptoms were observed extending beyond the site of inoculation (depth of 10 mm).

Bacterial soft rot and Pythium leak

In 2020, no significant differences were detected between varieties for responses to BSR (*Pectobacterium carotovorum*) or Pythium leak (*Pythium ultimum*) ($P > 0.05$) (**Table 4.5**). For BSR, limited apical symptoms were observed (0.0-5.88 mm lengths). For Pythium leak, limited apical symptoms were again observed (0.0-7.41 mm lengths). Neither pathogen resulted in symptom development beyond the site of inoculation (depth of 10 mm).

In 2021, bacterial soft rot and Pythium leak apical symptom lengths observed were limited and ranged from 0.0-4.20 mm and 0.0-2.53 mm, respectively (**Table 4.6**). Despite the

amendment of PDB to inoculum suspensions, symptoms were again limited to within the site of inoculation and no significant differences were observed between varieties screened against either pathogen ($P > 0.05$).

Red-skin and yellow-flesh entry responses

In 15 entries tested from three repeated field studies (total of 34 entries) in 2021, no significant differences were detected between red-skinned and yellow-fleshed entry responses for any of the four pathogens tested at apical and basal sites of tubers ($P > 0.05$) (**Table 4.7**). However, considerable apical symptom development was observed for FDR and pink rot, and the majority of symptoms extended beyond the site of inoculation ranging from 0.0-37.2 mm and 0.0-61.0 mm lengths, respectively. For soft rot, apical symptom lengths ranged from 0.0-28.8 mm and approximately 15% of symptoms observed extended beyond the site of inoculation. *Pythium* leak apical symptom lengths, however, ranged from 0.0-13.2 mm and only approximately 5% of symptoms observed extended beyond the site of inoculation. No variability was detected between entries originating from the three different field sites.

DISCUSSION

Potato breeding has improved the cultivated potato in many ways, including expanding its production range, increasing yield and storage duration, and numerous other agronomic and processing traits (Stephen, 1999; Ghislain & Douches, 2019). The potato is a staple food for an estimated 1.3 billion people worldwide and has become increasingly important for global food security (Devaux et al., 2019). However, the genetic base of cultivars prior to 1969 is narrow and largely susceptible to disease (Glendinning, 1983; Stephen, 1999). Introgression of resistance genes from wild relatives has successfully given rise to varieties with resistance to late blight and other foliar diseases (Douches et al, 1997), but postharvest disease resistance remains scarce in commercial cultivars (Cairns & Muskett, 1933; Jones, 1935; Lapwood & Read, 1986; Leach & Webb, 1981).

This study was performed to assess the relative susceptibility of germplasm and commercial cultivars to a set of postharvest diseases. Mackinaw, Petoskey, and Snowden are three commercial chipping varieties that have been used for development of germplasm included in the current study, as well as being evaluated during both years. While the current study was unable to evaluate variety response to BSR or *Pythium* leak due to insufficient disease development, some inferences on susceptibility based on pedigrees have been noted below.

Standard chipping variety responses to dry rot and pink rot

Mackinaw (Saginaw Chipper x Lamoka)

Across two years of testing, response of the cultivar Mackinaw to FDR and pink rot was noted to be affected by field location and year. Overall, Mackinaw was not consistently noted to be more resistant or susceptible to FDR or pink rot than other entries evaluated.

Mackinaw was developed by the MSU Potato Breeding and Genetics Program as a long-term chipping variety. In 2017, Mackinaw was noted as one of the three top performing varieties for long-term storage alongside cvs. NY152 and Lamoka (2017 SNAC International Storage Chip Quality Michigan Regional Trials). Studies performed by the Michigan Potato Outreach Program indicate Mackinaw possesses excellent agronomic and processing traits such as high yield, specific gravity, and starch content, in addition to resistance to common scab, *Rhizoctonia* black scurf, and potato virus Y (MSU Potato Outreach Program Database, [Medius.Re](#)). Several varieties in Mackinaw's pedigree have been evaluated for storage disease tolerance. Lamoka, the paternal parent, is susceptible to BSR caused by *Dickeya dianthicola* and *Pectobacterium parmentieri*, whereas Atlantic, a paternal grand-parent of Lamoka, is moderately tolerant (Ge et al., 2021). Megachip, a maternal grand-parent of Mackinaw, is moderately resistant to pink rot, FDR, and BSR (Groza et al., 2007). Pike, a paternal great-grand parent, is highly susceptible to FDR and was the first cultivar reported with dry rot lesions caused by *F. sambucinum* (Wharton et al., 2006).

Petoskey (Beacon Chipper x MSG227-2)

In the current study, Petoskey response to FDR was affected by field location and year of testing. Overall, considerable FDR symptom development was observed in Petoskey tubers from one field location in both years, indicating that FDR susceptibility may be a concern for this variety. In the second year of testing, symptom development in Petoskey was noted to be relatively greater than other entries for FDR than for pink rot, supporting previous research that physiological resistances for these two diseases may not be connected (Salas et al., 2003). Our findings in the present study support previous observations that disease resistance responses were not consistent between different diseases, as shown when comparing Pythium leak and pink rot responses (Salas et al. 2003).

Petoskey was developed by the MSU Potato Breeding and Genetics Program as a long-term storage chip variety, with excellent appearance, processing traits, and low internal defect

incidence (MSU Potato Outreach Program Database, [Medius.Re](#)). Petoskey was noted as one of the top three lines in 2019 for full-season storage alongside cvs. Mackinaw and MSW075-2 (2019-2020 SNAC Trials; MSU Potato Outreach Program Database, [Medius.Re](#)). Resistance to common scab has previously been observed in Petoskey's pedigree with Beacon Chipper, the maternal parent (Douches et al., 2006); however, no resistance to storage diseases have been observed.

Snowden (Wischip x B5141-6)

In the current study, Snowden was noted to be less susceptible to FDR than other entries and this was consistent across years and locations. The Snowden response to pink rot, however, was not noted to be significantly more or less susceptible than the majority of other entries in either year of testing.

Snowden was developed by Dr. Stan Peloquin and Mr. Donald Kichefski at the University of Wisconsin-Madison in 1990 (Andrade et al., 2021). Snowden is a major chip variety used for processed goods, alongside Atlantic and Lamoka, and is currently used as a trial control for long-term storage evaluations (2021 SNAC Michigan Regional Trial; MSU Potato Outreach Program Database, [Medius.Re](#)). Snowden is resistant to external and internal defects and discoloration, as well as common scab and was the top performing variety in 1988, compared to Atlantic and Norchip, with superior specific gravity and chip color (Peloquin et al., 1994). Lenape/B5141-6 (parent to Snowden and Atlantic) was noted for high solids content and chipping quality (Akeley et al., 1968), which supports the selection and use of Snowden for chip processing. With regards to storage performance, Snowden was the result of efforts to develop potatoes acceptable for chipping after being stored at cold temperatures (Love et al., 1998).

Notable chipping germplasm entry responses to dry rot and pink rot

MSAFB635-15 (NYH15-5 x MSS297-3)

In the current study, germplasm entry MSAFB635-15 was noted to exhibit variable response to FDR in the different years of testing. In both years, however, pink rot development resulted in significantly smaller average rot than the six highest varieties in 2020. Pink rot susceptibility has been previously observed in Norchip, a variety included in MSAFB635-15's pedigree (Salas et al., 2000), and these results support disease tolerance in MSAFB635-15. While dry rot symptoms observed in the second year of testing may be a concern, the yield and

specific gravity potential combined with consistently desirable pink rot responses support the continued development of line MSAFB635-15.

MSZ242-13 (MSR169-8Y X MSU383-A)

The response of advanced MSU breeding line MSZ242-13 (since renamed ‘Dundee’) to FDR was variable across two years of screening. The relatively high symptom development observed in the second year of testing indicates FDR susceptibility may be a concern. Interestingly, *F. sambucinum* causing severe FDR of tubers and sprouts was first reported in Michigan on cultivar Pike (grandparent of MSZ242-13/Dundee) in 2006, indicating FDR susceptibility was noted previously in the Dundee pedigree (Wharton et al., 2006).

In the current study, the MSZ242-13 pink rot response was significantly less than the four entries with greatest symptom development and responses were consistent across two locations in the first year of testing. In Potatoes USA National Chip Processing Trials and national, multi-state Potatoes USA SNAC-International Chip Variety Trials, this line has been noted for good specific gravity, high yield (higher than Snowden and Mackinaw), and excellent long-term storage characteristics (MSU Potato Outreach Program Database, [Medius.Re](#)). Combined, the desirable agronomic traits and potential for reduced pink rot development support the continued development of this chipping line for long-term storage.

MSAA260-3 (MSQ086-3 x Atlantic)

Germplasm line MSAA260-3 was noted to exhibit low to moderate dry rot across two years of the current study and was among the 29 entries that were not significantly different from the numerically-lowest disease severity. In a previous study conducted in Maine, storage losses to FDR were higher in Atlantic (parent of MSAA260-03) than either Katahdin or Kennebec though processing quality was equal or slightly better (Leach, 1978). However, in 1976, after several days of heavy rains and wet harvest in Florida and Maine, FDR in Atlantic was relatively low compared to other varieties (Webb et al., 1978). Our findings indicate that breeding efforts may have improved MSAA260-3 storage rot disease performance compared to previous studies of dry rot in at least one member of its pedigree. However, the current study did not provide information about BSR that would be necessary to support comparisons to previous research. In MSU Potato Outreach Program chip variety trials, MSAA260-3 has been noted to have desirable yield and specific gravity characteristics, further supporting the continued development of this line.

Overall, while disease responses for chip varieties and germplasm entries did vary with field and year, some showed significantly and consistently reduced symptom development for dry rot and pink rot. Contrastingly, red-skin and yellow-flesh potato entries appeared to be generally susceptible to FDR and pink rot. Detection of disease resistance in germplasm will help identify useful genetic resources for future breeding efforts. Factors for use as long-term storage chipping varieties and disease responses appear independent of one another, therefore the varieties and lines of interest identified in the current study should be screened for responses to other major postharvest diseases, such as BSR and Pythium leak. As is the case for most diverse diseases studied, variety responses to pink rot and Pythium leak were also not linked in Taylor et al.'s study (2008), so screening is needed for the diseases of interest. Due to the variability of responses observed in the current study, additional years and locations of testing would also be recommended to validate the consistency of these findings and to better inform future management decisions.

Low disease incidence for Pythium leak and soft rot

During both years of the current study, disease incidence and symptom development of Pythium leak and BSR were low, and no significant differences were observed (**Tables 4.5 and 4.6**). The isolates used have previously been observed to produce significant symptoms on cv. Lamoka tubers in preliminary trials, so the low disease development observed in this study may be due to suboptimal inoculum preparation and/or inoculation method. Inoculation methods are known to have varying efficacy depending on the pathogen and host, as well as the physiological age and organ (e.g., leaf, tuber, root, or stem) affected (Choiseul et al., 2001; Czajkowski et al., 2011; Lapwood & Read, 1986).

Bacterial soft rot

Potato dextrose broth was used in this study for cultivation and inoculation of *Pectobacterium carotovorum* sbsp. *carotovorum* (PCC). Due to its site-specific and measured delivery, syringe-inoculation of PCC was chosen over vacuum infiltration (Koppel, 1993). Preliminary tests of cv. Lamoka tubers challenged by syringe-delivered PCC in PDB produced BSR symptoms (*data not shown*); however, the tubers were placed in enclosed plastic containers with a moistened paper towel for high humidity. The incubation conditions used in the main study were not as humid, with tubers held in paper bags at ambient room temperature with no supplemental humidity. Unfortunately, humidity within the sample bags was not monitored,

although conditions were adequate for FDR and pink rot development. Induction of pectolytic enzyme release and subsequent soft rot symptoms is dependent on achieving a minimum bacterial cell density in favorable conditions (Barras & Chatterjee, 1994; Byers et al., 2002). Perhaps low humidity in conjunction with insufficient starting inoculum in the present study prevented PCC from achieving the population density required for exoenzyme production.

Water suspensions of PCC have been successfully used for potato tuber inoculations; however, tuber discs or uncut tubers were often incubated at high relative humidity (Smith & Bartz, 1990; Pérombelon, 1979) or vacuum-infiltrated (Lebecka et al., 2021; van der Wolf et al., 2017) with this material. The consistent reports of BSR development at high humidity supports the hypothesis that increasing humidity would significantly improve inoculation efficacy. In previous studies, *Pectobacterium* spp. strains were maintained on nutrient agar or broth containing peptone and yeast extract to support bacterial growth (Smith and Bartz, 1990), and *Pectobacterium* and *Dickeya* strains were maintained using tryptone soy agar (van der Wolf et al., 2017). Luria-Bertani/Lysogeny (LB) broth contains tryptone, which is commonly used by bacteria as a source of carbon, amino acids, and inorganic nutrients (Sezonov et al., 2007). In future screening efforts, other nutrient or tryptone-containing media could be tested to determine whether they might increase inoculum concentration. If so, it is hypothesized that they should be combined with increased humidity post-inoculation to improve inoculation efficacy of *P. carotovorum* in potato tubers.

Pink rot and Pythium Leak

During the current study, inoculum protocols were designed without consideration of differing infection rates between oomycete asexual structures, including zoospores and sporangia. *Phytophthora* and *Pythium* species are capable of producing two types of asexual propagules: sporangia and zoospores. Sporangia are nonmotile and multinucleate, transferred between hosts primarily through air and rain (Walker & van West, 2007), contain thousands of zoospores, and can directly or indirectly infect hosts (Grenville-Briggs & Van West, 2005; Samson, 2015). Zoospores are motile unicellular propagules that locate compatible hosts via methods such as chemotaxis and electrotaxis and are important for transmission between hosts (Longman & Callow, 1987; Walker & van West, 2007). Once an infection site is located, zoospores release mucilaginous polysaccharide exudate to adhere, or encyst (Jones et al., 1991; Longman & Callow, 1987). Encysted zoospores are immobilized, losing flagella function,

gaining a cell wall, and producing a germ tube or appressorium to penetrate the host (van West et al., 2003; Walker & van West, 2007). In general, sporangial germination is favored in warmer temperatures (>54 °F/12 °C) (Grenville-Briggs & van West, 2005), whereas zoospore release and germination is induced by a “chilling” period followed by acclimation back to warm temperatures (Vujičić and Colhoun, 1966). Zoospore release is dependent on genus and species, and in *Phytophthora*, this can range from five minutes to an hour (Walker & van West, 2007).

Further optimization of inoculation procedures could consider 1) whether use of sporangia or zoospores promotes infection of *P. erythroseptica* and *P. ultimum*, 2) environmental conditions that are more favorable for sporangia vs. zoospore development, and 3) increasing humidity during the incubation period to promote disease development during the screening period. In the future, germination and infection rates between sporangia and zoospores should be compared to evaluate disease incidence and severity for inoculation with *P. erythroseptica* and *P. ultimum*. Inoculum preparation procedures could be adapted (as described in the above paragraph) to promote production of the structure most likely to infect under the target inoculation conditions. Increased humidity during incubation will also improve disease development; as shown in previous studies, zoospore suspensions were successful when injection sites were incubated under four layers of saturated paper towels (Salas et al., 2003; Taylor et al., 2004; 2006; 2008), whereas no steps were taken to promote high humidity in the current study. To improve *Pythium* leak, manual abrading of the periderm and inoculation with mycelia-colonized agar plugs has also resulted in disease development (Taylor et al., 2008). Based on these studies, propagule preparation, inoculum concentration, delivery method, and incubation conditions may all be factors to adjust in future screening efforts.

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APPENDIX

Table 4.1: One-way analysis of variance (ANOVA) table for symptom development of four diseases in 39 or 15 total chipping potato entries 47 days after inoculation in 2020 and 2021 ($\alpha = 0.05$). Four replicates of approximately five tubers per variety were inoculated with 10 μ L of inoculum suspension at apical and basal ends and incubated at ambient room temperature (68 °F/20 °C) for 47 days in paper bags.

Disease	2020				2021			
	Apical		Basal		Apical		Basal	
	Length	Width	Length	Width	Length	Width	Length	Width
Fusarium Dry Rot	<0.001	<0.01	<0.01	0.02	0.04	0.11	0.05	0.11
Bacterial Soft Rot	0.64	0.64	0.25	0.62	0.53	0.53	0.54	0.54
Pink Rot	<0.01	0.01	0.29	0.24	0.85	0.69	0.83	- ^a
Pythium Leak	0.65	0.65	0.25	0.62	0.61	0.61	0.66	0.61

^a ANOVA did not yield an objective function for *P. erythroseptica* for basal width.

Table 4.2: Means of Fusarium dry rot (*Fusarium sambucinum*) apical symptom length on potato tubers 47 days after inoculation in 2020 analyzed using mixed model ANOVA and Fisher's protected Least Significant Difference ($\alpha = 0.05$). Mean FDR response was significantly different in 39 entries of chipping germplasm and commercial cultivars of potato ($P = 0.0002$).

*a Entry	Location ^b	Fusarium Dry Rot	
		Apical Length (mm) ^c	
MSAA570-3	B	5.10	g
* NY163	B	6.66	fg
MSZ063-2	B	7.94	fg
* Snowden^d	A	8.00	fg
MSW474-1	B	8.13	fg
MSZ242-13	B	8.41	fg
* Petoskey	B	8.44	e-g
ND7519-1	B	8.69	e-g
MSZ063-2	A	8.73	e-g
* Mackinaw	B	9.15	e-g
* Snowden	B	9.21	e-g
* MSAA076-6	B	9.63	d-g
* MSBB058-1	B	9.90	e-g
* MSY156-2	B	10.00	e-g
Lamoka	B	10.21	e-g
* MSZ242-07	B	10.64	e-g
MSAFB635-3	B	11.40	e-g
NY166	B	11.73	e-g
MSBB610-13	B	12.96	e-g
* MSZ242-13	A	13.78	d-g
CO11023-9W	B	14.31	d-g
* MSW474-1	A	15.55	d-g
* MSAFB609-12	B	15.89	d-g
* MSAFB635-15	B	16.87	d-g
NY165	B	20.01	d-g
MSZ120-4	B	20.04	d-g
MSAA260-03	B	20.57	d-g
B2869-29	B	20.65	d-g
* NY163	A	20.87	d-g
Lady Liberty	B	22.04	d-g

Table 4.2 (cont'd)

MSZ242-09	B	23.05	d-g
* Mackinaw	A	26.19	b-e
NYOR14Q9-9	B	27.49	b-e
MSAA373-3	B	28.06	b-e
* MSAA217-3	B	29.89	b-d
MSAFB605-4	B	38.76	a-c
MSZ219-13	B	38.90	ab
* Petoskey	A	40.53	a
CO11023-2W	B	50.84	a

$P = 0.0002$

^a Asterisk (*) denotes included in both 2020 and 2021 variety evaluations.

^b Tubers were grown in fields at two sites in Montcalm County, Michigan in 2020.

^c Mean lesion length is followed by letter grouping; shared letters indicate means were not significantly different based on Fisher's protected Least Significant Difference ($\alpha = 0.05$).

^d Bolded entries indicate commercial potato cultivars.

Table 4.3: Means comparison of *Fusarium* dry rot (*Fusarium sambucinum*) apical symptom length 47 days after inoculation in 2021 were analyzed using mixed model ANOVA and Fisher's protected Least Significant Difference ($\alpha = 0.05$). FDR response was significantly different in 15 research germplasm and commercial cultivars of potato ($P = 0.0415$).

Entry	Location ^a	Fusarium Dry Rot Apical Length (mm) ^b	
MSAA076-6	B	7.35	d
NY163	B	8.62	d
NY163	A	9.87	cd
Snowden ^c	B	13.79	b-d
MSBB058-1	B	14.77	b-d
Mackinaw	B	20.56	a-d
MSAA260-03	B	22.38	a-d
MSAA217-3	B	24.78	a-d
MSW474-1	B	26.77	a-d
MSAFB635-15	B	27.35	a-d
MSAFB609-12	B	29.64	a-c
MSZ242-07	B	33.76	ab
MSZ242-13	B	38.65	ab
MSV093-1Y	B	39.00	ab
Petoskey	B	44.42	a

$P = 0.0415$

^a Tubers were grown in Montcalm County, Michigan at the Montcalm Research Center in 2021.

^b Mean lesion length is followed by letter grouping; shared letters indicate means were not significantly different based on Fisher's protected Least Significant Difference ($\alpha = 0.05$).

^c Bolded entries indicate commercial potato cultivars.

Table 4.4: Means comparison of pink rot (*Phytophthora erythroseptica*) apical symptom length 47 days after inoculation in 2020 were analyzed using Fisher’s Least Significant Difference ($\alpha = 0.05$). Pink rot response was significantly different in 39 research germplasm and commercial cultivars of potato, based on Fisher’s protected least significant difference test ($P = 0.0021$).

*a Entry	Location ^b	Apical Length (mm) ^c	Pink rot
* Petoskey ^d	B	2.19	g
* MSAFB635-15	B	4.31	fg
ND7519-1	B	5.11	e-g
MSAA260-03	B	5.29	e-g
MSAFB605-4	B	6.00	e-g
* MSZ242-13	A	6.04	e-g
* MSBB058-1	B	6.09	e-g
* Petoskey	A	6.30	e-g
* Snowden	B	6.60	e-g
* MSAA076-6	B	6.94	e-g
B2869-29	B	7.04	e-g
CO11023-2W	B	7.12	e-g
MSZ242-09	B	7.46	e-g
Lamoka	B	7.69	d-g
Lady Liberty	B	8.57	d-g
NYOR14Q9-9	B	8.97	d-g
CO11023-9W	B	9.04	d-g
MSY156-2	B	9.09	d-g
NY165	B	9.23	d-g
MSAA373-3	B	9.61	d-g
MSZ242-13	B	9.75	d-g
MSZ242-07	B	9.98	d-g
MSAA570-3	B	10.11	d-g
* MSAA217-3	B	10.24	d-g
MSW474-1	B	10.54	d-g
MSZ063-2	B	10.65	d-g
MSZ063-2	B	11.02	d-g
MSAFB635-3	B	11.15	d-g
* MSAFB609-12	B	11.16	d-g
* Mackinaw	B	11.62	d-f
* NY163	A	11.88	d-f
MSZ120-4	B	11.97	d-f
* Mackinaw	A	13.20	c-f
* Snowden	A	13.47	b-e
* MSW474-1	A	13.66	b-e
* NY163	B	16.63	b-d
NY166	B	21.96	a-c
MSBB610-13	B	22.33	ab
MSZ219-13	B	28.00	a

$P = 0.0021$

^a Asterisk (*) denotes included in both 2020 and 2021 variety evaluations.

^b Tubers were grown in fields at two sites, designated A and B, in Montcalm County, Michigan in 2020. Means represent two replicates of five-tuber subsamples.

^c Mean lesion length is followed by letter grouping; shared letters indicate means were not significantly different based on Fisher’s protected Least Significant Difference ($\alpha = 0.05$).

^d Bolded entries indicate commercial potato cultivars.

Table 4.5: Bacterial soft rot (*Pectobacterium carotovorum*) and Pythium leak (*Pythium ultimum*) apical symptom lengths 47 days after inoculation in 2020, analyzed using mixed model ANOVA ($\alpha = 0.05$). Entry responses were not significantly different in 39 entries of chipping germplasm and commercial cultivars ($P > 0.05$).

* ^a Entry	Location ^b	Apical Length (mm)	
		Bacterial soft rot	Pythium leak
B2869-29	B	1.08	5.19
CO11023-2W	B	1.47	5.93
CO11023-9W	B	1.60	4.15
Lady Liberty ^c	B	0.79	1.77
Lamoka	B	0.70	3.94
*Mackinaw	A	0.56	3.87
*MSAA076-6	B	0.66	3.90
*MSAA217-3	B	0.14	0.18
MSAA260-3	B	1.75	5.85
MSAA373-3	B	1.51	3.98
MSAA570-3	B	0.33	1.64
MSAFB605-4	B	0.95	2.96
*MSAFB609-12	B	0.23	0.83
*MSAFB635-15	B	0.80	2.70
MSAFB635-3	B	1.00	2.72
*MSBB058-1	B	0.47	4.52
MSBB610-13	B	0.36	1.21
MSW474-1	B	0.83	1.23
*MSW474-1	A	0.78	2.37
MSY156-2	B	0.35	1.37
MSZ063-2	B	0.62	2.27
MSZ063-2	A	1.21	3.64
MSZ120-4	B	-	3.32
*MSZ242-07	B	3.00	3.93
MSZ242-09	B	5.88	7.41
MSZ242-13	B	0.86	3.46
*MSZ242-13	A	0.93	4.70
ND7519-1	B	1.02	2.50
*NY163	B	0.73	3.74
*NY163	A	0.72	2.96
NY165	B	2.19	6.13
NY166	B	0.89	4.25
NYOR14Q9-9	B	0.46	2.27
*Petoskey	B	0.00	0.00
*Petoskey	A	0.92	3.11
*Mackinaw	B	0.90	3.40
*Snowden	B	0.00	0.00
*Snowden	A	1.62	4.79
MSZ219-13	B	0.69	3.09
		$P = 0.6395$	$P = 0.6546$

^a Asterisk (*) denotes included in both 2020 and 2021 variety evaluations.

^b Tubers were grown in fields at two sites in Montcalm, County, Michigan in 2020.

^c Bolded entries indicate commercial potato cultivars.

Table 4.6: Bacterial soft rot (*Pectobacterium carotovorum*), pink rot (*Phytophthora erythroseptica*), and Pythium leak (*Pythium ultimum*) apical symptom lengths 47 days after inoculation in 2021, analyzed using mixed model ANOVA ($\alpha = 0.05$). Entry responses were not significantly different in 15 entries of chipping germplasm and commercial cultivars ($P > 0.05$).

Entry	Location ^a	Apical Length (mm)		
		Bacterial soft rot	Pink rot	Pythium leak
Mackinaw ^b	B	0.00	1.77	0.09
MSAA076-6	B	0.00	0.96	0.00
MSAA217-3	B	3.72	17.30	0.00
MSAA260-3	B	0.00	17.37	0.00
MSAFB609-12	B	1.99	14.71	0.00
MSAFB635-15	B	0.00	3.99	2.53
MSBB058-1	B	0.00	14.91	0.00
MSV093-1Y	B	0.00	11.03	0.09
MSW474-1	B	4.20	20.45	0.00
MSZ242-07	B	0.00	18.22	0.00
MSZ242-13	B	0.00	29.41	0.00
NY163	B	0.00	10.70	0.73
NY163	A	0.00	0.00	0.00
Petoskey	B	0.00	16.37	0.00
Snowden	B	2.36	6.60	0.00
		<i>P</i> = 0.5300	<i>P</i> = 0.8488	<i>P</i> = 0.6105
		Standard Error = 1.21	11.05	10.30

^a Tubers were grown in fields at two sites in Montcalm County, Michigan in 2021.

^b Bolded entries indicate commercial potato cultivars.

Table 4.7: Bacterial soft rot (*Pectobacterium carotovorum*), Fusarium dry rot (*Fusarium sambucinum*), pink rot (*Phytophthora erythroseptica*), and Pythium leak (*Pythium ultimum*) apical symptom lengths 47 days after inoculation in 2021, analyzed using mixed model ANOVA ($\alpha = 0.05$). Entry responses were not significantly different in 15 entries of red-skinned and yellow-fleshed germplasm and commercial cultivars ($P > 0.05$).

~ ^a Entry	Location ^b	Apical Length (mm)				
		Bacterial soft rot	Dry rot	Pink rot	Pythium Leak	
Allora	T	0.00	30.17	0.00	0.00	
Allora	P	0.00	12.82	46.79	0.00	
Allora	M	6.81	12.61	0.00	0.00	
C099076-6R	T	28.79	8.63	39.52	8.07	
C099076-6R	M	8.78	10.02	35.62	10.92	
Columba	T	0.00	26.35	0.00	0.11	
Columba	P	0.00	26.50	20.68	0.11	
Constance	M	2.95	29.12	- ^c	0.00	
Constance	P	15.56	0.01	26.25	6.55	
~ Dark Red Norland^d	M	0.00	5.45	22.18	-	
~ Dark Red Norland	P	0.00	2.88	22.70	0.00	
~ Dark Red Norland	T	0.00	11.95	47.47	0.00	
Golden Globe	T	0.00	26.75	23.94	0.00	
Golden Globe	P	0.00	22.73	0.21	0.00	
Golden Globe	M	0.00	-	55.84	1.46	
Gourmandine	M	0.00	12.50	25.74	0.11	
Gourmandine	P	2.95	9.13	6.95	0.00	
MSV093-1Y	M	-	12.71	0.21	0.11	
MSV093-1Y	T	2.95	29.24	20.27	0.11	
MSV093-1Y	P	3.93	3.93	19.13	0.00	
MSW474-1	P	0.00	37.15	-	-	
~ NDA050237B-1R ^e	T	0.00	22.71	37.34	0.00	
~ NDA050237B-1R	M	4.76	9.99	37.23	0.00	
~ NDA050237B-1R	P	9.89	4.07	29.77	0.00	
~ NDAF113484B-1	P	23.18	12.76	28.12	0.00	
~ NDAF113484B-1	M	0.00	15.29	29.33	0.00	
Paroli	T	10.51	22.16	29.11	0.00	
Paroli	M	0.00	3.40	60.97	0.00	
Paroli	P	14.71	0.01	22.16	13.23	
Queen Anne	P	0.00	12.14	42.07	0.00	
Queen Anne	M	-	3.78	24.31	0.00	
W15240-2Y	P	2.95	34.53	33.09	0.00	
Yukon Gold	M	2.95	10.31	23.74	0.00	
Yukon Gold	P	2.95	-	34.21	0.00	
		$P = 0.7219$	0.7787	0.8146	0.4343	
		Standard Error =	8.74	10.46	16.95	3.24

^a Red-skinned potato entries denoted by ~; all unmarked entries were of the yellow-fleshed market class.

^b Tubers were grown in fields at three MSU Potato Outreach Program variety trial sites in the following Michigan counties: (**P**) Presque Isle Co., (**M**) Monroe Co., (**T**) Tuscola Co.

^c Samples that were unable to be recovered due to excessive secondary contamination are indicated with the “-” symbol.

^d Bolded entries indicate commercial standard potato cultivars.

^e NDA050237B-1R has since been renamed cv. Becca Rose.

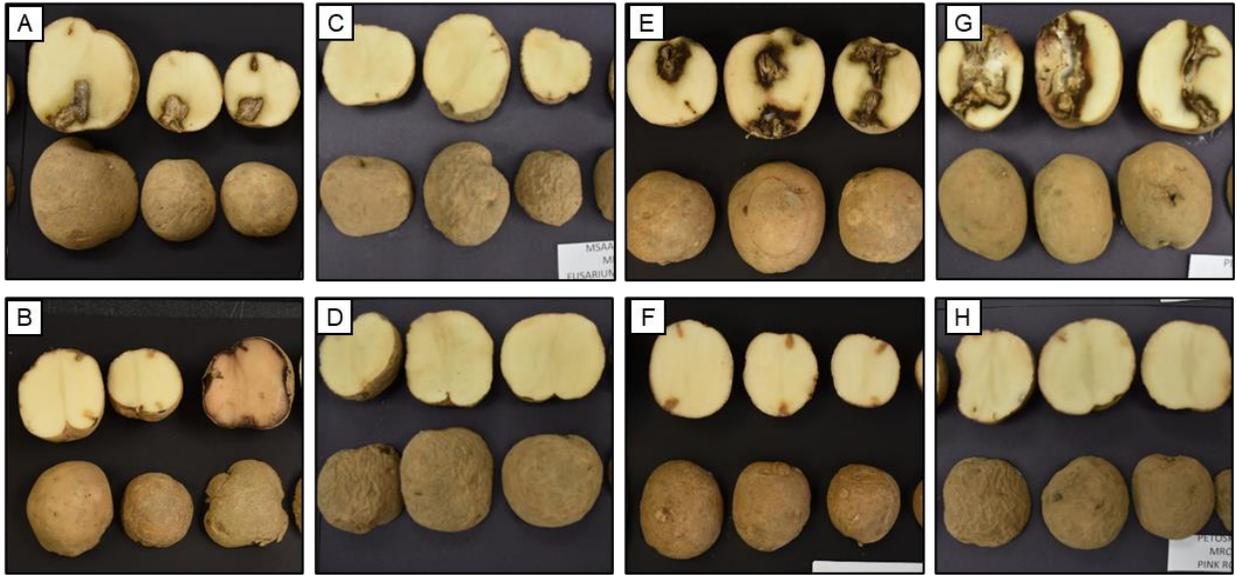


Figure 4.1: Resistance response of four chipping potato lines 47 days to Fusarium dry rot (FDR) or pink rot after inoculation with *Fusarium sambucinum* or *Phytophthora erythroseptica*. MSZ242-13 treated with (A) FDR and (B) pink rot; MSAA076-6 treated with (C) FDR and (D) pink rot; MSAA217-3 treated with (E) FDR and (F) pink rot; Petoskey treated with (G) FDR and (H) pink rot.

CHAPTER 5: FUTURE DIRECTIONS

Fusarium graminearum is an emerging *Fusarium* dry rot pathogen that has been previously detected in Michigan seed lots (Gachango et al., 2012), and while detected at low frequency in the current studies (Chapter 2), virulent isolates were collected during the 2019-2020 tuber survey. This and other prevalent, virulent species could be utilized alongside the current *F. sambucinum* inoculum for *Fusarium* dry rot studies, such as chemical control evaluations.

During the course of the 2019-2020 survey, abiotic damages (mechanical injury and physiological disorders), disease symptoms, and putative pathogen incidence were observed, but were not the focus of the study. Further analysis of interactions between these categories, as well as other factors such as field parameters, may yield valuable information to support management efforts of the potato industry.

In Chapter 3, vaporized SaniDate-5.0 was found to have no significant effect on FDR on stored potatoes. Although the present study was unable to provide conclusive results for bacterial soft rot (BSR), oxidizing sanitizers have previously been reported to effectively control BSR with extended application duration (Afek et al., 1999) and may still have utility in potato postharvest management. Future chemical efficacy studies could be conducted on tubers in bins or smaller-scale growth chamber trials, or *in vitro* using filter paper-disc or vapor diffusion plate techniques (Lin et al., 2022; Marais, 1990; Morris et al., 1979). For the latter, the procedure could be adapted to include inoculated tuber slices and whole tubers to evaluate efficacy of vaporized SaniDate-5.0 and other chemical controls against surface-infesting versus internal pathogens.

Bacterial soft rot (BSR) (*Pectobacterium* and *Dickeya* spp.) symptoms were observed on sampled tubers; however, no soft rot bacteria (SRB) were successfully isolated. Difficulty with SRB isolation has previously been noted in the present study, but crystal violet pectin medium supplemented with NaNO₃ was reported to recover 77-79% of *P. carotovorum* from soils (Cuppels & Kelman, 1973). Isolating from soil may provide localized data specific to sampled fields that could inform participating growers of high-risk growing areas for soft rot development. Kushalappa & Zulfiqar (2001) described a protocol for assessing BSR pathogenicity on tubers wherein inoculated tubers are maintained in high-humidity trays in a growth chamber under controlled conditions, followed by measurement of symptomatic areas.

Additionally, Kushalappa & Zulfiqar (2001) utilized periodic misting to promote disease development, which could be useful for testing pathogenicity under different temperature conditions. It is suggested that a similar method of raising humidity during incubation might be useful for variety screening.

Following identification of pathogens associated with tubers grown in Michigan, correlating present species with field environment parameters may be of interest. Variable virulence of SRB strains on different parts of the potato has been previously observed (Czajkowski et al., 2015; Pérombelon, 2002), and identifying which strains are most prevalent in Michigan regions may be useful to develop relevant management strategies. If possible, periodic grading of blackleg and aerial stem rot in sample fields during the growing season prior to harvest in conjunction with randomized at-harvest and post-storage tuber sampling may provide a more comprehensive survey of SRB-associated diseases throughout potato production.

Pink rot (*Phytophthora erythroseptica*) was rarely observed during the survey. Previous reports indicate that asymptomatic infections coming from the field are common (Cunliffe et al., 1977; Goss, 1949), so lack of disease observations may not indicate risk. It may be more efficient to sample from symptomatic tubers and use a selective medium, similar to methodology described by Taylor et al. (2002). The modified cornmeal-based medium P₅ARP (5 mg/L pimarinic acid + 250 mg/L ampicillin + 10 mg/rifampicin) developed by Jeffers and Martin (1986) has been used for selective isolation of both *Phytophthora* and *Pythium* species from plant tissues and soils.

Inoculation methods used for pink rot and *Pythium* leak in the present study did not investigate potential differences using sporangia and zoospores (Walker & van West, 2007). Future inoculum preparation may incorporate techniques that promote sporangia formation and zoospore release, as discussed in Chapter 4. As an alternative, Taylor et al. (2004) demonstrated that manual abrasion of the periderm in addition to syringe-delivered inoculation to the eyes results in significant and rapid disease development without need for surface disinfestation of tubers. Similar methods could be investigated in future studies.

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