AN ABSTRACT OF THE THESIS OF

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Title: Improving Best Management Practices for Potato Production in the Columbia Basin: An Evaluation of Essential Oils for Control of Verticillium Wilt and the Fate of Chloride in the System.

Abstract approved:

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Dan M. Sullivan Philip B. Hamm

Although the potato (*Solanum tuberosum* L.) is a global crop, few growing regions rival the high yields of the Columbia Basin of Eastern Oregon and Washington. Two research projects were conducted in Hermiston, OR to contribute to best management practices for the region. The first project evaluated the efficacy of essential oils to manage *Verticillium dahliae* Kleb., a persistent soilborne pathogen of potato that when untreated leads to significant yield loss. The objectives of this research were to: 1) evaluate if essential oils inhibit *V. dahliae* growth *in vitro;* 2) evaluate whether essential oils adversely impacted plant growth; and 3) determine whether an integrated management approach using essential oils and selective fertilizer application could be an effective approach in mitigating crop loss from *V. dahliae in vivo*.

Twelve treatments including carvacrol (an extract of *Origanum vulgare*), clove (*Eugenia spp.*), lemongrass (*Cymbopogon spp.*), and garlic (*Allium sativum*) were evaluated by transferring from an actively growing *V. dahliae* VCG 4A colony on Sorensen's NP-10 media to similar media amended with varying concentrations of essential oils. Hyphal growth was measured after two time periods. Carvacrol, clove, garlic, cinnamon, thymol, and lemongrass were most effective in the laboratory assay. *V. dahliae* growth was reduced by 100% with at least one dilution of these

treatments when compared to the untreated controls. These six treatments, as well as salicylic acid, were then used as potato seed treatments in replicated greenhouse trials to determine efficacy in reducing *V. dahliae* infection. Calcium chloride and ammonium phosphate, which reduced *V. dahliae* infection of potato in previous unpublished work, as well as four combination treatments of both fertilizer and essential oil applications, were also evaluated in greenhouse trials. No differences were observed among treatments in emergence, plant height, or number of nodes in the greenhouse trials. Treatment impact on *V. dahliae* infection *in vivo* was limited but *in vitro* results suggest that it may be possible to reduce *V. dahliae* infection with an integrated management plan using essential oils. Further research is required to evaluate best application methods and rates to achieve consistent disease reduction.

The second project evaluated the effects of different potassium (K) fertilizer applications on nutrient levels in the potato production system. Petiole sampling is used to make decisions about in-season nitrogen (N) application. Past research has documented an antagonism in uptake between nitrate-N and chloride (Cl), which suggests that N recommendations should be adjusted to take Cl application into account. The objectives of this research were to evaluate: 1) where Cl moves in the system from time of soil application to uptake in plant; and 2) the effects of different K fertilizer applications on nutrient concentrations in plant matter, including potato petioles, with particular emphasis on the effect of the accompanying anions (Cl vs. sulfate).

In this experiment, two years of field trials were conducted in a field with high soil test K (0.79 cmol kg^{-1} exchangeable K; 0-20.3 cm depth) so that differences in yield were minimized across treatments. The source of K (KCl, K_2SO_4 (SOP), or K_2SO_4*2$MgSO_4$ (Kmag)), rate (0, 112, 224, 448 kg K_2O/ha), and time of application (seven months pre-plant, two weeks pre-plant, or in-season) were evaluated. Plant Cl levels were elevated when K source was KCl, with increased KCl application rate, and as applications were made closer to the time of plant uptake. Plant Cl concentrations for KCl treatments applied in September were 1.1 g kg^{-1} in tubers and 15 g kg^{-1} in tops; for treatments applied preplant were 2.2 g kg^{-1} in tubers and 22 g kg^{-1} in tops; and for treatments applied in-season were 1.9 g kg^{-1} in tubers and 24 g kg^{-1} in tops. Petiole Cl levels were highest with KCl treatments as compared to SOP and Kmag. This data supports the conclusion that Cl can be taken up unhindered by potato plants in large quantities when available, and that Cl availability is increased when KCl is applied at higher rates or later in the growing season.

Improving Best Management Practices for Potato Production in the Columbia Basin: An Evaluation of Essential Oils for Control of Verticillium Wilt and the Fate of Chloride in the System.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Sarah Elizabeth Light, Author

CONTRIBUTION OF AUTHORS

Philip B. Hamm provided guidance for research and reviewed Chapter 2. The greenhouse trial was designed following protocols from Dr. Lyndon Porter, who also provided guidance for this research. Dr. Robert Cating offered training and advice for lab work conducted in Chapter 2. Dr. Kenneth Frost assisted with the greenhouse trial and with statistical analysis.

Dr. Don A. Horneck proposed the research presented in Chapter 3 and was involved in all aspects of data collection. Dr. Dan M. Sullivan recommended plant tissue analysis methods and was involved in data interpretation and review for this chapter.

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GENERAL INTRODUCTION

Sarah Elizabeth Light

The potato (*Solanum tuberosum* L.) is the third most important food crop in the world behind rice (*Oryza sativa*) and wheat (*Triticum spp.*) and more than a billion people worldwide consume potatoes on a daily basis (Camire et al., 2009; Birch et al., 2012; Obidiegwu et al., 2015). In 2014 more than 385,000,000 Mg of potato were harvested worldwide (FAO, 2014). Potatoes originated in Peru, where they have been cultivated for 8,000 years, and were first introduced in Western Europe during the second half of the 16th century (Brown, 1993; FAO, 2008; Camire et al., 2009; Birch et al., 2012). Potatoes can be cultivated in a wide range of climates including temperate, tropical, and subtropical regions, and are now produced in more than 100 countries, and on all continents except Antarctica (Walker et al., 1999; FAO, 2008; Birch et al., 2012; Obidiegwu et al., 2015). In addition to tolerance to diverse growing conditions, potatoes are desirable crops because they are nutritionally rich. Potatoes are high in carbohydrates, starch, proteins, fiber, potassium, phosphorous, magnesium, vitamin C, and several forms of vitamin B, as well as other essential minerals (FAO, 2008; Camire et al., 2009; White et al., 2009; Birch et al., 2012; Kleinwechter, 2014; Obidiegwu et al., 2015).

Although the potato is a global crop, few growing regions rival the high yields of the Columbia Basin of Eastern Oregon and Washington. Yields in this region are generally above 51 Mg ha^{-1} but can be as high as 78 Mg ha^{-1} (Lang et al., 1999; Dung et al., 2015). The majority of potatoes produced in Oregon (primarily Morrow and Umatilla Counties) are for the high quality processing market, which includes French fries and chips (Hopkins et al., 2007; Dung et al., 2015). In Morrow and Umatilla Counties, 683,698 Mg of potatoes were produced on over 8,000 ha and 860,643 Mg on over 10,000 ha, in 2011 and 2012, respectively (USDA, 2012). While yield is important, research conducted on 14 grower fields in Oregon, Washington, and Idaho demonstrated that when net crop value (after factoring input costs) is evaluated, following research based best management practices is more economically advantageous than managing for maximum yield (Hopkins et al., 2007). The cost of growing marketable processing potatoes is high and so is their value at harvest, selling for \$109.03 Mg^{-1} (Hopkins et al., 2007). With so much at stake, it can be difficult to persuade growers to modify management practices unless there is compelling evidence that profits will not be reduced. For that reason, two research projects were conducted at the Hermiston Research & Extension Center, Hermiston, OR to provide additional evidence to support best management potato production in the region. The impetus for, and objectives of, each project are briefly outlined below.

The first project focused on management of *Verticillium dahliae* Kleb., a persistent soilborne pathogen with devastating impacts on potato production. This fungus is the causal agent of Verticillium wilt in warmer climates such as the Columbia Basin (Johnson and Dung, 2010). Verticillium wilt is a vascular wilt disease whose symptoms are characterized by chlorotic and necrotic leaves, followed by general necrosis and wilting, and finally premature plant death four to six weeks earlier than healthy plant maturity (Rowe and Powelson, 2002; Johnson and Dung, 2010). If fields are left untreated, 30-50% yield loss may occur (Rowe and Powelson, 2002). This pathogen is notoriously difficult to manage in large part because it has a broad host range and produces high numbers of microsclerotia that can persist in the soil for over ten years making management with crop rotation unrealistic (Rowe and Powelson, 2002; Johnson and Dung, 2010). Growers in the region typically follow a 3 to 4 year crop rotation sequence when growing potatoes. Additionally, a high number of certified potato seed lots have been found to have seed infected with this pathogen (Omer et al., 2000), and inoculum is easily introduced in the tare-dirt found on the surface of seed (Dung et al., 2013). For these reasons, *V. dahliae* is ubiquitous in fields with a history of potato cultivation.

Potato producers in the Columbia Basin remain heavily reliant on soil fumigation to help manage Verticillium wilt (Johnson and Dung, 2010). Application of the soil fumigant metam sodium is the most common management practice for this disease due to its high level of effectiveness (Rowe and Powelson, 2002; Tsror et al., 2005). Although metam sodium has been demonstrated to reduce *V. dahliae* populations and lead to increased yield (Hamm et al., 2003), there is a need to investigate alternative management options as the use of this chemistry may have adverse effects on human health (Pruett and Myers, 2001), is detrimental to non-host soil organisms (Toyota et al., 1999; Collins et al., 2006; Omirou et al., 2011), and is increasingly regulated (MacRae and Noling, 2010). Despite these concerns, no alternative has emerged that is as consistently effective or as easy to incorporate into production practices as metam sodium. For these reasons, potato producers in the Columbia Basin continue to utilize soil fumigation.

Although essential oils and plant products have been used as biocides for hundreds of years, these products have rarely been used for commercial agricultural production (Bakkali et al., 2007). Essential oils have been found to be efficacious against a wide range of microorganisms including fungi (Maruzzella and Liguori, 1958; Maruzzella and Balter, 1959; Kishore and Pande, 2007; Mvuemba et al., 2009; Lanzotti, 2012) and bacteria (Deans and Ritchie,

1987; Hammer et al., 1999; Dorman and Deans, 2000). Although much of the research has been done *in vitro*, there are multiple studies that have found that the fungicidal effects of essential oils are also measurable *in vivo* against the pathogens *Phytophthora nicotianae* (Bowers and Locke, 2004)*; Fusarium oxysporum* (Bowers and Locke, 2000)*; Rhizoctonia solani* (McMaster et al., 2013); and the storage pathogens *Fusarium sambucinum* and *Pythium sulcatum* (Mvuemba et al., 2009). In addition to developing alternative treatments to inhibit pathogen growth, there may be an opportunity to invoke resistance in potatoes against *V. dahliae*. Salicylic acid is associated with potato defense signaling genes in response to *V. dahliae* infection (Derksen et al., 2013) and has been demonstrated to reduce disease severity from potato purple top phytoplasma in tomato (Wu et al., 2012).

The project was designed to provide more information on the efficacy of a broader group of essential oils specifically toward *V. dahliae* VCG 4A, the strain that is most virulent to potato (Joaquim and Rowe, 1991; Strausbaugh, 1993). The objectives of this research were to 1) evaluate if essential oils inhibit *V. dahliae* growth *in vitro;* 2) evaluate whether essential oils adversely impacted plant growth; and 3) determine whether an integrated management approach using essential oils and selective fertilizer application could be an effective approach in mitigating crop loss from *V. dahliae in vivo*. The aim of this research was not to determine if an essential oil could replace soil fumigation, but rather to identify products that have the potential to reduce the disease severity from infection by *V. dahliae,* and that could ultimately contribute to an integrated management approach to reduce grower dependence on metam sodium.

The second project evaluated the effect of potassium (K) fertilizer application on potato production systems. Nitrogen (N) and K are the two nutrients that plants need in most abundance (Ren et al., 2015), and potato plants in the Columbia Basin can accumulate over 650 kg K ha^{-1} in one growing season (Horneck and Rosen, 2008). This nutrient is the most abundant cation found in plant tissue and is pivotal for optimum photosynthesis (Cakmak, 1994; Kanai et al., 2007), for translocation of sugars (Haeder et al., 1973; Cakmak et al., 1994; Kanai et al., 2007), and for regulation of osmotic potential and turgidity of cells (Hsiao and Läuchli, 1986). Potato crops that are deficient in K can result in reduced marketable yield (Grzebisz et al., 2015).

Although K is supplied as either chloride (KCl) or sulfate salts (K_2SO_4), KCl comprises more than ninety percent of the K applied to cropping systems in the United States due to its low cost and ease of application (IFA, 2013; Ren et al., 2015). After application, K is readily

adsorbed to soil particles whereas the accompanying anion is more likely to leach out of the system if applied far in advance of root uptake (Ren et al., 2015) and chloride (Cl), relative to other possible anions, leaches readily following major soil drainage (Saffigna et al., 1977; Hill, 1986). Both Cl and sulfur (taken up as sulfate-S) are essential for plant physiology; Cl is important for stomatal regulation and is a component of the water-splitting reaction in photosystem II (Westermann, 2005; Marschner, 2012), and S is a component of two essential amino acids and of other necessary organic compounds (Droux, 2004; Westermann, 2005).

Application of K can have an effect on plant uptake of other nutrients and on plant tissue nutrient concentrations. Previous research has documented both a positive uptake interaction between N and K (Singh and Lal, 2012) and a mutual antagonism between nitrate-N and Cl uptake (James et al., 1970a; James et al., 1970b; Saffigna and Keeney, 1977; Kafkafi et al., 1982; James et al., 1994). Reduced concentrations of petiole nitrate-N, above ground biomass nitrate-N and total N, and tuber total N have been documented as a result of elevated Cl concentrations following KCl application in potato production systems (Murarka et al., 1973; Saffigna and Keeney, 1977; James et al., 1994). In contrast, there is not the same competition for uptake between sulfate and nitrate (James et al., 1994).

The change in plant nitrate-N concentrations as a result of KCl application has consequences for potato production because growers use petiole tissue nitrate-N as a metric for mid-season nitrogen fertilizer application. Current fertilizer recommendations do not take into account soil Cl, or K application source, rate, or timing (Lang et al., 1999; Stark et al., 2004; Pavek, 2013), although some researchers have suggested that they should be adjusted based on petiole Cl concentrations (Saffigna and Keeney, 1977; James et al., 1994). In addition to the potential cost savings to growers from reduced fertilizer use, there are also environmental considerations for reevaluating these recommendations. Nitrate leaches readily under potatoes grown in soils with high sand content (Hill, 1986; Neumann et al., 2012) and annual nitrate leaching in potato production systems has been estimated to range from 70 kg N ha^{-1} to upwards of 200 kg N ha^{-1} (Davenport et al., 2005). Growers may be applying excess in-season N due to a perceived deficiency where none exists because petiole nitrate-N concentrations are depressed following KCl application.

This experiment was designed to track the fate of Cl in a potato production system where nutrients are not limited. Experimental design minimized tuber yield differences

between treatments so that nutrient uptake and translocation could be evaluated without regard to plant nutrient partitioning and physiological source-sink relationships which can be affected by K application and deficiency (Beringer et al., 1990; Gerardeaux et al., 2010). In this research, the quantity of Cl taken up by potato plants was measured, and the movement of Cl in the plant after uptake was evaluated. Nutrient concentration was measured in aboveground biomass, harvested tubers, and petioles collected during the growing season. This data can help better understand the role of Cl in the potato production system. The objectives of this research were to evaluate: 1) where Cl moves from time of soil application to uptake in plant; and 2) the effects of different K fertilizer sources and application rates on nutrients in plant tissue with particular emphasis on the effect of the accompanying anions (Cl vs. sulfate).

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EVALUATION OF ESSENTIAL OILS ON MYCELIAL GROWTH OF *VERTICILLIUM DAHLIAE* AND CONTROL OF VERTICILLIUM WILT OF POTATO IN THE GREENHOUSE

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ABSTRACT:

*Verticillium dahlia*e Kleb. is a persistent soilborne pathogen of potato (*Solanum tuberosum* L.) that, when untreated, leads to significant yield loss. Though expensive, soil fumigation is the most common management practice for this fungus. Alternatives to soil fumigation are needed. Although not commonplace in commercial agriculture production today, essential oils have been used as biocides for hundreds of years. The objectives of this research were to: 1) evaluate if essential oils inhibit *V. dahliae* growth *in vitro;* 2) evaluate whether essential oils adversely impacted plant growth; and 3) determine whether an integrated management approach using essential oils and selective fertilizer application could be an effective approach in mitigating crop loss from *V. dahliae in vivo*. Twelve treatments including carvacrol, clove, lemongrass, and garlic were initially evaluated by measuring growth of *V. dahliae* vegetative compatibility group 4A colonies on Sorensen's NP-10 media that had been amended with varying concentrations of essential oils. Six essential oils were effective in limiting growth *in vitro*. These six, as well as salicylic acid, were then applied as seed treatments in two replicated greenhouse trials where potato plants were inoculated with *V. dahliae*. Calcium chloride and ammonium phosphate, which reduced *V. dahliae* infection of potato in previous unpublished work, as well as four combination treatments of both fertilizer and essential oil applications, where also evaluated in greenhouse trials.

Carvacrol, cinnamon, clove, garlic, lemongrass, and thymol were most effective in the laboratory assay. Carvacrol reduced growth at all dilutions, and completely inhibited growth at 250 ppm and above after 17 days and 500 ppm and above after 36 days. For both measurement dates, growth was completely inhibited at 500 ppm and above with cinnamon, clove, and thymol, and at 2500 ppm with garlic and lemongrass. Greenhouse trials resulted in no differences in emergence, plant height, or number of nodes on plant stems by treatment. Treatment impact on *V. dahliae* infection *in vivo* was limited but *in vitro* results suggest that it may be possible to reduce *V. dahliae* infection with an integrated management plan using essential oils. Further research is required to evaluate best application methods and rates to achieve consistent disease reduction. Additionally, product costs and in field implementation need to be fully vetted before commercial applications are considered.

Key words: ammonium polyphosphate, calcium chloride, plant physiology*, in vivo*, *in vitro*.

INTRODUCTION:

Verticillium dahliae Kleb. is a persistent soilborne pathogen with devastating impacts on potato (*Solanum tuberosum* L.) production. This fungus is the causal agent of Verticillium wilt in warmer climates like the Columbia Basin in Eastern Oregon and Washington (Johnson and Dung, 2010) and is the major component of the potato early dying complex (PED). Verticillium wilt and PED are vascular wilt diseases whose symptoms are characterized by chlorotic and necrotic leaves, followed by general necrosis and wilting, and finally premature plant death four to six weeks earlier than healthy plant maturity (Rowe and Powelson, 2002; Johnson and Dung, 2010). If untreated, 30-50% yield loss may occur (Rowe and Powelson, 2002). Additional losses can occur through the interaction with root lesion nematodes, *Pratylenchus penetrans,* resulting in the highest levels of PED (Botseas and Rowe, 1994). Although there are several vegetative compatibility groups (VCGs) within the species, VCG 4A has been identified as the most virulent to potato (Joaquim and Rowe, 1991; Strausbaugh, 1993).

This pathogen is especially difficult to manage. The life cycle of *V. dahliae* is monocyclic and the germination of microsclerotia in soil is initiated by potato root exudates. After initial infection through direct penetration of plant roots, the fungus colonizes the root cortex, grows into the xylem, and then produces conidia that move throughout the vascular tissue to infect the entire potato plant (Rowe and Powelson, 2002). These microsclerotia are found in senesced plant tissue and are released into the soil when plant matter decays. More than 90,000 microsclerotia can be introduced into soil by a single infected stem and these microsclerotia can then be spread throughout the field by cultivation (Johnson and Dung, 2010). Microsclerotia can persist for more than 10 years (Rowe and Powelson, 2002) and over 200 dicotyledonous species are known hosts of *V. dahliae* (Johnson and Dung, 2010). Growers in the region typically follow a 3 to 4 year crop rotation sequence when growing potatoes. Management through crop rotation is not a viable option due to these factors. Soil inoculum concentrations may be inconsistent throughout a field which poses an additional challenge for effective management (Johnson et al., 1988). Furthermore, a high number of certified potato seed are infected with this pathogen (Omer et al., 2000) and inoculum is easily introduced to a field in the tare-dirt

found on the surface of seeds (Dung et al., 2013). For these reasons, *V. dahliae* is ubiquitous in fields with consistent potato cultivation.

Potato producers remain heavily reliant on soil fumigation to help manage Verticillium wilt (Johnson and Dung, 2010). Application of the soil fumigant metam sodium, though expensive, is the most common management practice for this disease due to its high level of effectiveness and demonstrable results in increasing tuber yield where *V. dahliae* is present (Rowe and Powelson, 2002; Hamm et all, 2003; Tsror et al., 2005). However, the use of this chemistry may have adverse effects on human health (Pruett and Myers, 2001), is detrimental to non-target soil organisms (Toyota et al., 1999; Collins et al., 2006; Omirou et al., 2011), and is increasingly regulated, causing applications to be more difficult to achieve (MacRae and Noling, 2010). There is a need for alternative management options. Despite evidence that it may be possible to reduce the impact of this pathogen using cultural practices such as soil solarization (Katan, 1981), cover cropping (Davis et al., 1996; Subbarao and Hubbard, 1996), and modified irrigation management (Cappaert et al., 1992; Cappaert et al., 1994), no alternative has emerged that is as consistently effective or easily incorporated into production practices as metam sodium. For these reasons, potato producers remain heavily reliant on soil fumigation.

Other alternatives to manage Verticillium wilt are needed and may be possible to develop. Although essential oils have been used as biocides for hundreds of years, these products have rarely been evaluated for their benefit in commercial agricultural production (Bakkali et al., 2007). Many plant derived products (essential oils and plant extracts) have been found to be efficacious against a wide range of microorganisms including fungi (Maruzzella and Liguori, 1958; Maruzzella and Balter, 1959; Kishore and Pande, 2007; Mvuemba et al., 2009; Lanzotti, 2012) and bacteria (Deans and Ritchie, 1987; Hammer et al., 1999; Dorman and Deans, 2000). Although much of the work has been done *in vitro*, there are multiple studies that have found that the fungicidal effects of essential oils and plant extracts were measurable *in vivo.* Some of the plant derived products that have demonstrated efficacy include: cinnamon, cassia, and a chili pepper-mustard formula on *Phytophthora nicotianae* (Bowers and Locke, 2004); clove, cassia, and a chili pepper-mustard formula on *Fusarium oxysporum* (Bowers and Locke, 2000); cinnamon and ginger on the storage pathogens *Fusarium sambucinum* and *Pythium sulcatum*, respectively (Mvuemba et al., 2009); and clove and thyme on *Rhizoctonia solani* (McMaster et al., 2013).

V. dahliae is a fungus in the class Sordariomycetes, subphylum Pezizomycotina, and phylum Ascomycota. Previous research has established that certain essential oils and plant extracts are efficacious in inhibiting growth of other Sordariomycetes fungi including: *Origanum vulgare*—oregano against *Fusarium proliferatum* (Velluti, et al., 2003), *Fusarium oxysporum* (Lee et al., 2007), and *Colletotrichum gloeosporioides* (Lee et al., 2007); *Plantago lanceolata*—plantain against *Colletotrichum gloeosporioides* (Silva et al., 2008); *Thymus vulgaris*—thyme against *Fusarium oxysporum* (Barrera-Necha et al., 2009), *Fusarium solani* (Zambonelli et al., 1996), and *Colletotrichum lindemuthianu* (Zambonelli et al., 1996); *Calendula officinalis*—calendula against *Fusarium solani* (Hussain et al., 2012); *Curcuma longa*—turmeric against *Colletotrichum coccodes* (Cho et al., 2006); *Allium cepa* L.—onion against *Myrothecium verrucaria, Claviceps purpurea,* and *Ophiostoma ulmi* (Maruzzella and Balter, 1959); *Cymbopogon spp.*—lemongrass against *Nigrospora panici* (Maruzzella and Liguori, 1958); *Allium sativum*—garlic against *Myrothecium verrucaria* and *Claviceps purpurea* (Maruzzella and Balter, 1959); *Cinnamomum zeylanicum*—cinnamon against *Fusarium sambucinum* (Mvuemba et al., 2009), *Fusarium oxysporum* (Barrera-Necha et al., 2009), *Fusarium proliferatum,* and *Colletotrichum musae* (Ranasinghe et al., 2002); and *Eugenia spp.*—clove against *Fusarium oxysporum* (Bowers and Locke, 2000; Barrera-Necha et al., 2009), *Fusarium proliferatum*, and *Colletotrichum musae* (Ranasinghe et al., 2002). Additionally, a protein isolated from *Zingiber officinale*—ginger was found to be effective against *Fusarium oxysporum* and *Physalospora piricola* (Wang and Ng, 2005).

Investigators have reported that certain biological control methods and plant-derived treatments may be efficacious specifically toward *V. dahliae.* Various *Origanum* and *Thymus* species were found to inhibit the growth of *V. dahliae in vitro*. Although three VCGs were tested, VCG 4A, the most virulent to potato, was not included (Arslan and Dervis, 2010). *Larrea tridentate* (creosote bush), clove, and garlic inhibited *V. dahliae* growth most effectively in another *in vitro* study, however this study only measured growth for 144 hours of incubation suggesting the need for a longer-term evaluation is needed given the nature of the pathogen (López-Benítez et al. 2005). Several studies found that bacterial isolates effectively inhibited *V. dahliae* growth *in vitro*. These results suggest that it is possible to develop an alternative to soil fumigation to effectively manage this pathogen (Alström, 2001; Uppal et al., 2007; Uppal et al., 2008; El Hadrami et al., 2011). In addition to inhibiting pathogen growth, there may be an

opportunity to invoke resistance in potatoes against *V. dahliae*. Salicylic acid is associated with potato defense signaling genes in response to *V. dahliae* infection (Derksen et al., 2013) and has been demonstrated to reduce disease severity from potato purple top phytoplasma in tomato, another crop in the Solanaceae family (Wu et al, 2012).

This research was designed to provide more information on the efficacy of a broader group of essential oils specifically towards *V. dahliae* VCG 4A. The objectives of this research were to: 1) evaluate if essential oils inhibit *V. dahliae* growth *in vitro;* 2) evaluate whether essential oils adversely impacted plant growth; and 3) determine whether an integrated management approach using essential oils and selective fertilizer application could be an effective approach in mitigating crop loss from *V. dahliae in vivo*. The intention was not to determine if an essential oil could be used as a replacement for soil fumigation but rather to identify products that might have potential to aid in disease management of *V. dahliae* that would ultimately reduce dependence on metam sodium.

MATERIALS AND METHODS:

Laboratory assay:

Twelve treatments were evaluated for their ability to inhibit *V. dahliae* growth *in vitro* (Table 2.1). Eleven essential oils and compounds derived from essential oils were selected due to their demonstrated anti-fungal efficacy *in vitro* against other fungi in the class Sordariomycetes. Methyl salicylate, an ester of salicylic acid was also included. Sorensen's NP-10 medium (Sorensen et al., 1991), a semi-selective agar that is conducive to *V. dahliae* growth was prepared in 0.125 L batches without antibiotics. After the medium was autoclaved (15 PSI and 121°*C for 15 minutes*) and cooled to ~45°*C.*, dilutions of each essential oil treatment were added by volume at varying concentrations (Table 2.2 and Table 2.3) and thoroughly mixed using a stir plate. Some of the extracts were in solid form and were first solubilized in ethanol following the product specification sheet. Sorensen's NP-10 medium without antibiotics and with varying amounts of ethanol were also prepared as controls to evaluate the effect of the ethanol on inhibiting *V. dahliae* growth. Contents of each medium were then poured into seven *Petri* plates. Therefore for each treatment/ethanol concentration there were 7 replicated *Petri* plates. Once cooled, an agar plug from the edge of an actively growing colony of V. dahliae (VCG-4A isolate 653, source D.A. Johnson) grown on Sorensen's NP-10 medium with antibiotics

was transferred to the center of each plate. *Petri* plates were placed in plastic bags, in the dark, at room temperature (~22℃). To evaluate the efficacy of each treatment in inhibiting *V. dahliae* growth over an extended period of time, colony growth was measured and recorded after 17 and 36 days. Due to laboratory constraints in a few instances, colony growth was measured a day before or a day after day 17 or 36. In this case, growth rate was calculated per day and then multiplied by either 17 or 36 to generate measurements. This experiment was repeated.

Greenhouse trials:

The effect of the six best performing essential oils from the laboratory assay, plus salicylic acid, ammonium polyphosphate (P1034: 10-34-0), and calcium chloride ($CaCl_2$) (Table 2.1) were evaluated for their effect on the development of Verticillium wilt in potato in two separate greenhouses trials at the Hermiston Agricultural Research and Extension Center (HAREC) in Hermiston, OR. Methods for both greenhouses were similar. Virgin soil, classified as an Adkins fine sandy loam (coarse-loamy, mixed, superactive, mesic Xeric Haplocalcids was collected from a previously unplanted buffer region at HAREC. Field-moist soil was then steam sterilized in a soil aeration cart (Model: ST 2.0, Siebring M.F.G., Inc., George, IA). By this process hot steam from a steam generator (Model: SF15, Siebring M.F.G., Inc., George, IA) was pushed into the wagon using an aeration blower (Model: AB28, Siebring M.F.G., Inc., George, IA). This process was continued until internal soil temperature was maintained above 63°C for at least one hour. Soil was then dried on clean tarps in a hothouse. Equal quantities (11.4 kg) of dried soil were then weighed in sterilized buckets and transferred to bleach-sterilized pots (24.1 cm tall by 25.4 cm diameter). Pots and measuring implements were sterilized with a 10% bleach solution and rinsed thoroughly with water before use.

Treatments were prepared one day prior to planting. Essential oils were diluted to 2500 ppm in 40 ml of water and kept in suspension with 10 µl of Tween-80. Thymol, which is soluble in ethanol, was dissolved the day prior and diluted in water immediately prior to application. To reduce the introduction of seed borne pathogens with the seed piece, an uncut nuclear potato seed with initial sprout development was planted in each pot. Essential oils were evenly applied at a rate of 2 ml of treatment per 100 g of tuber spread evenly on the exterior of the seed pieces. Seed was planted in the center of the pot, 12.7 cm from the bottom. P1034 treatments were applied at 9.3 ml/pot (224 kg P_2O_5/ha) in a 2.5 cm by 7.6 cm (1” by 3”) band placed 5.1 cm (2”)

below and 5.1 cm to the side of the seed piece. $CaCl_2$ treatments were applied at 6.5 g per pot (112 kg Ca/ha) by diluting 6.5 g of $CaCl_2$ into 200 ml water and pouring it evenly around the soil surface after watering. After planting, all pots were watered with 1500 ml of water. Greenhouse 1 (GH1) was planted on April 23, 2015 and Greenhouse 2 (GH2) on April 27, 2015.

Greenhouse temperatures were set at 17.8 °C at night and 21.1°C during the day and soil and external temperatures were recorded using a soil temperature sensor (Spectrum Technologies, Inc., Aurora, IL) and micro station (Model: Watchdog 1000 Series, Spectrum Technologies, Inc., Aurora, IL). Water and in-season fertilizer applications were consistent for all pots. Prior to plant emergence, water was applied sparingly to prevent seed piece decay. Following emergence, water was applied as needed. An easily soluble 24-8-16 all-purpose fertilizer was applied weekly following plant emergence in all pots. If plants developed multiple stems, the less vigorous stem(s) was/were pruned at 1.3 to 2.5 cm above soil line. All main stems were staked with bleach-sterilized stakes and pre-cut plastic twists ties for support. To quantify plant vigor, plant height and number of nodes on plant stems were measured weekly beginning on the day of inoculation (42 days after planting) in GH1. In GH2 the same metrics were measured weekly but measurements began one week prior to inoculation (56 days after planting).

Inoculum for GH1 was started one week after full emergence. In GH2, two pots had delayed emergence so inoculum was started one week after 97.5% emergence. Concentrated conidial suspensions of *V. dahliae* VCG-4A isolate 653 were grown for 9 to 10 days prior to inoculation in multiple 250 ml flasks containing 125 ml Czapek-Dox broth (Simko et al., 2004). Nine to twelve 1-cm^2 mycelial-agar plugs from the edge of an actively growing colony on Sorensen's NP-10 were added to flasks, then kept at room temperature (~22 °*C*) in the dark on a horizontal shaker (Joaquim and Rowe, 1991). On the day of inoculation, flasks were combined into a single large flask and conidia quantified using a hemocytometer. Inoculum was diluted to a 1 x 10^6 conidial solution using sterile deionized water. While actively stirred, 50 ml of inoculum was measured into individual sterile tubes. Individual tubes were vortexed for 30 seconds to re-suspend conidia then poured into a single pot at the base of each plant. Following inoculation, plants were watered with 500 ml to push conidia into the root zone. Greenhouse air temperature ranged from 22-25 °C during inoculation in GH1 and 27-28°C in GH2.

Pots were destructively sampled and harvested three weeks after inoculation. Soil *V. dahliae* concentrations were determined by taking three 2.5 cm wide by 5.1 cm deep (1" by 2") soil cores from each pot in a triangle pattern around the base of the stem. Soil was moist (field capacity) and cores were bulked into one composite sample per pot. The soil probe was sterilized using 10% bleach solution and rinsed with water between pots. Soil from each pot was then mixed and 1 g was plated onto five plates of Sorensen's NP-10 media (0.2 g per plate). As conidia were used to inoculate the pots, wet soil was assayed to capture concentrations of both conidia and microsclerotia because conidia numbers are reduced in dry soil (Menzies and Griebel, 1967). The number of colony forming units (CFU g^{-1} wet soil) was determined using morphological features 26-28 days after plating (Smith, 1965). Tubers and stems were harvested and separated, and tubers were counted and individually weighted.

Disease severity was assessed using an assay adapted by Jordan Eggers from Hoyos et. al (1991). Twenty centimeters (8") of total stem was used (10 cm below soil line and 10 cm above). Stems were washed, soaked in a 10% bleach solution for three minutes, rinsed thoroughly in water, and then sprayed with ethanol and passed over a flame to burn off excess. The stems were cut into 3 sections and placed in a quart sized Ziploc bag. Stem sap was extracted using a specialized device in which samples are placed between two metal surfaces and crushed using a hand lever. The Ziploc bag prevented sap from contaminating the crushing tool. The corner of each Ziploc bag was then cut with ethanol sterilized scissors and sap was transferred into a 1.5 ml DNAse free tube. Extracted sap was diluted to 10^{-1} and 10^{-2} in tubes with deionized water. An aliquot of 250 µl of sap solution from each dilution was then added to each of four replicated Sorensen's NP-10 *Petri* plates containing antibiotics using a sterilized L-shaped cell spreader. Plates were stored in the dark at room temperature (~24 °C) for 14-16 days. *V. dahliae* CFU ml^{-1} stem sap were determined by counting colonies growing on plates which were identified using morphological features (Smith, 1965).

Statistical analysis:

Statistical analysis was conducted using the program R Studio. All data was analyzed using a one way ANOVA at alpha = 0.05. Tukey's HSD mean comparison tests were only conducted when the f-test was statistically significant. The Tukey's HSD test was selected over

others because of the large number of treatments and subsequent risk of making Type I errors. P-values from the ANOVA, as well as significant HSD results are reported.

As all 7 *Petri* plates for each treatment in the laboratory assay were poured from the same flask, they are pseudoreplicates and cannot be considered discrete measurements. Two flasks were made per treatment (14 total *Petri* plates) and the difference between growth in plates from one flask is minimal when compared to the difference in growth between plates of distinct flasks of the same treatment. Thus for the laboratory growth data, measurements from the 7 plates were averaged and the average value for each flask was used for analysis (two flasks were made of each treatment therefore n=2). Greenhouse studies were analyzed separately as they are discrete repetitions of the *in vivo* evaluation. *V. dahliae* CFUs from soil and stem crush counts were averaged by pot and average values were used for statistical analysis (5 replications were planted per greenhouse therefore n=5). Stem crush measurements were log transformed prior to analysis.

RESULTS:

Laboratory Assay:

Carvacrol, cinnamon, clove, garlic, lemongrass, and thymol were most effective in reducing growth of *V. dahliae in vitro* (Table 2.2 and Table 2.3). Carvacrol reduced growth at all dilutions for both measurement dates, completely inhibiting growth at 250ppm and 500 ppm and above at 17 and 36 days, respectively. Cinnamon and clove completely inhibited growth at 500ppm and above at both 17 and 36 days. Cinnamon also reduced growth at 250 ppm for both dates whereas clove was not tested at lower dilutions. Thymol significantly reduced growth at 500ppm and above after 36 days when compared to control plates with the same amount of ethanol added (6.25ml). Garlic reduced growth at 500ppm and completely inhibited growth at 2500ppm for both measurement times. Lemongrass completely inhibited growth at 2500ppm at both times and reduced growth at 500ppm at 17 days. These six treatments, because of their effectiveness in reducing growth *in vitro*, were used in subsequent greenhouse trials.

Calendula, curcumin, ginger, onion, plantain, and salicylic acid were the least effective at inhibiting *V. dahliae* growth *in vitro* (Table 2.2 and Table 2.3). Calendula, ginger, plantain, and salicylic acid were ineffective at any dilution. Curcumin appeared to inhibit growth at higher dilutions however, when these dilutions (500ppm and 750ppm) were compared to the control

plates with the same amount of ethanol (6.25ml and 9.375ml respectively), there were no differences. Onion oil was effective at partially inhibiting growth at 1000ppm and above after 17 days but only at 2500ppm after 36 days.

Greenhouse trials:

External and soil temperatures were recorded in both greenhouses throughout the course of the experiment. External temperature ranged from 15.2°C to 36.6°C (average 22.2 °C) and 10.2 °C to 45.9°C (average 22.8 °C) in GH1 and GH2, respectively. Soil temperatures ranged from 14.1 °C to 37.1 °C (average 22.0°C) and 10.2 °C to 41.6°C (average 23.3°C) in GH1 and GH2, respectively. Differences in temperature and light gradients made it difficult to maintain uniform soil moisture throughout each greenhouse.

Plant emergence was not affected by treatment in either greenhouse however there was variability between replicates within a treatment (Table 2.4 and Table 2.5). Treatment averages for plant emergence date ranged from 19.2 to 22.4 days after planting (DAP) and 25.8 to 31 DAP in GH1 and GH2, respectively. There was considerable variation in emergence date between pots within individual treatments, with individual pot emergence dates ranging from 18 to 26 DAP in GH1 and 22 to 46 DAP in GH2.

In both greenhouses, differences in plant height and number of nodes were insignificant by treatment but significant by replication at all measurement dates (ranging from 42-63 DAP in GH1 and 49-77 DAP in GH2). On the day of inoculation (42 DAP) in GH1, average measurements of plant height by treatment ranged from 31.5 to 37.9 cm and average number of nodes from 9.8 to 11.4 (Table 2.4). When plants were destructively sampled in GH1 three weeks later, average plant height and number of nodes ranged from 83.5 to 92.1 cm and from 24.0 to 25.8, respectively (Table 2.4). On the day of inoculation in GH2 (56 DAP) average plant height and number of nodes by treatment ranged from 40.3 to 49.0 cm and from 15.0 to 18.0, respectively (Table 2.5). When sampled three weeks later, average plant height in GH2 ranged from 88.8 to 99.8 cm and number of nodes ranged from 29.0 to 32.0 (Table 2.5). High variation between replicates of each treatment reduced the opportunity to measure differences between treatments for yield data—number of tubers per pot and sum of tuber weights (Table 2.6). Weekly height and node measurements were also analyzed using net growth difference (weekly measurement minus measurement at inoculation). This did not change the results.

V. dahliae concentrations in potato sap (CFU ml^{-1}) revealed no differences between treatments and the inoculated control in either greenhouse (Table 2.7). Variability occurred between replicates within treatments where some stems had no countable colonies and others had very high concentrations. As there was no correlation between stem sap and soil CFUs of *V. dahliae* in either greenhouse ($R^2 \leq 0.001$), soil data is not reported. In GH2, there were differences ($p=0.002$) where eight of the treatments had more infection than the un-inoculated controls (Table 2.7).

DISCUSSION:

Six of the 12 treatments (carvacrol, cinnamon, clove, garlic, lemongrass, and thymol) evaluated in the laboratory completely inhibited *V. dahliae* growth in at least one dilution for 36 days (Table 2.3). Growth measurements were taken at 17 and 36 days to evaluate the effect of the treatments over a sustained period of time. With few exceptions, treatment effects that were measurable after 17 days continued for 36 days. Given these results, future work comparing *in vitro* efficacy of essential oils may only require comparisons up to 17 days. Clearly essential oils provide an opportunity to limit pathogen growth for a sustained period of time in a controlled environment. While curcumin treatments did reduce *V. dahliae* growth at higher dilutions, this reduction was attributed to the ethanol used to dissolve the treatment, based on the ethanol controls. Several of the treatments (calendula, ginger, plantain, and salicylic acid) evaluated in the laboratory had no efficacy against *V. dahliae* growth. The results reported here indicate that only certain essential oils effectively reduce growth of *V. dahliae in vitro*. This result is consistent with previous findings that some essential oils are effective at inhibiting growth of specific microorganisms *in vitro* and not others (Maruzzella and Liguori, 1958; Hammer et al., 1999).

Two of the most effective treatments in decreasing *V. dahliae* infection *in vitro* were carvacrol and thymol, which are phenolic compounds extracted from oregano and thyme, respectively. Other researchers have isolated specific compounds in these oils and evaluated their efficacy as compared to the complete oil (Müller-Riebau et al., 1995; Daferera et al., 2000; Kishore and Pande, 2007; Lanzotti, 2012; Taweechaisupapong et al., 2012). If components prove to be effective, a greater opportunity to reduce damage due to *V. dahliae* may be possible.

Once identified these components could be synthesized and used commercially. Clearly more work in this area is needed.

The work reported here compared growth of *V. dahliae in vitro* on essential oil amended media. Other researchers have evaluated the affect of essential oils on fungal morphology. Multiple studies report degeneration or disintegration of fungal hyphae, modified hyphal morphology, and/or reduction in number of conidia produced (Zambonelli et al., 1996; Soylu et al., 2006; Soylu et al., 2007; Soylu et al., 2010). One study reported a modification in the morphology of the sclerotia of *Sclerotinia sclerotiorum,* a pathogen that like *V. dahliae*, produces long-lived soil resting structures (Soylu et al., 2007). These reports elucidate some of the potential biological impacts of essential oils on fungi. *V. dahliae* produces long-lived microsclerotia which germinate in response to host root exudates. The fungus then produces hyphae and infects the actively growing portion of the potato root. If any part of this infection process, either at the microsclerotia or hyphal stage is disrupted, infection may be reduced or eliminated. A quantification of the impact of essential oils on *V. dahliae* morphology could reveal optimum application time and method required to reduce disease.

Direct contact with the essential oil was evaluated during the *in vitro* growth studies as *V. dahliae* was plated on media with treatments added. Other researchers have compared essential oil vapor on fungal growth. These reports found that the volatile phase of essential oils was consistently more effective than the direct contact phase (Soylu et al., 2006; Soylu et al., 2007; Soylu et al., 2010). The challenge with direct contact is the need to use enough product in a soil drench application to impact either microsclerotia or actively growing hyphae in the soil. However given that previous work has found the volatile phase to be effective in inhibiting the growth of other fungal species, the use of vapor may provide opportunities for field application that are feasible for potato producers. Future work evaluating the effect of essential oil vapor toward *V. dahliae* could provide new effective uses.

The essential oils that were effective *in vitro* were not generally effective *in vivo*. There were light and temperature gradients in both greenhouses that may have contributed to high variability by replication, and which may have diminished the ability to measure treatment differences *in vivo.* Although salicylic acid was not effective in inhibiting *V. dahliae* growth *in vitro* at any dilution, the product was included in subsequent greenhouse trials. Previous reports suggest that the salicylic acid pathway is involved in potato defense against *V. dahliae*

(Derksen et al., 2013) and application of salicylic acid, via foliage spray and root-drench, prior to inoculation, has been demonstrated to reduce disease severity from potato purple top phytoplasma in tomato (Wu et al, 2012). For these reasons, salicylic acid was used *in vivo*, however no effect was observed (Table 2.7).

Whereas in the laboratory assay, essential oils were in direct contact with *V. dahliae* mycelium growing on amended media, in the greenhouse conidial suspensions were applied as a root drench at the plant base. Plants were inoculated weeks after the essential oils were applied to the seed piece. This inoculation method was successful in achieving consistent infection in previous experiments (Hu et al., 1993; Uppal et al., 2008; Porter, unpublished data, 2013). There are, however, some issues with this technique. The greenhouse is a modified environment and the use of a conidial suspension is not a replication of the true host-pathogen relationship that exists in a managed potato production system. In a field scenario, microsclerotia germinate as a result of root exudates. In addition, germinating potato seed in the soil may be immediately exposed to microsclerotia in the soil. Essential oils were applied to the seed piece because, if efficacious, this method could be easily replicated prior to planting on a large scale. However, given the difference in date of the essential oil application to the seed and the date of inoculation, it is unclear if at the time of inoculation the essential oil residue persisted in the soil around the root zone, or if the oil had volatized or leached out of the root zone. Other factors may have impacted the amount of oil residue in the pots, including variation in soil moisture or plant root growth and subsequent evapotranspiration. The variation in CFUs from the stem crush assay between replicates of each treatment might be partially explained by these, or other factors. Microsclerotia germinate in response to exudates from actively growing roots, and thus may be triggered to germinate progressively throughout the growing season (Johnson and Dung, 2010). If sustained essential oil levels around the root zone are required for effective disease management, this intermittent germination throughout the growing season would prove problematic, as it would be challenging to maintain consistent essential oil concentrations in the soil throughout the growing season. Additionally, *V. dahliae* microsclerotia exist at differing concentrations throughout a field (Johnson et al., 1988) so roots may grow into areas with higher amounts of microsclerotia, which would increase disease pressure later in the season when treatment options are not available. Studies similar to those

reported here need to be conducted using microsclerotia as the inoculum source to determine if essential oils would have an impact to that spore structure for a sustained period of time.

Despite the fact that no treatment had less infection than the inoculated control in either greenhouse, possible trends did emerge in best and worst performing treatments. It should also be noted that a stem with zero measurable *V. dahliae* might not actually be indicative of zero infection in the stem. As sap was diluted prior to being plated, it is possible that there was *V. dahliae* present in stems but it was at such low amounts that it was not distinguishable in the stem crush assay. Salicylic acid, garlic, carvacrol + P1034, salicylic acid + $CaCl_2$, and salicylic acid + P1034 had higher disease levels, whereas cinnamon, carvacrol, and P1034 alone had the least infection based on CFUs ml^{-1} stem sap. Interestingly, although P1034 and carvacrol were components in treatments with the lowest CFUs ml^{-1}, when applied together they were among the treatments with highest amount of disease. Why this is the case is unknown. P1034 and $CaCl_2$ have been shown to be effective in the greenhouse and field situations, respectively (Porter, personal communication, 2013). Although similar disease reduction was not observed in the trials reported here, the use of these materials warrants further investigation. The application of salicylic acid to the surface of the seed piece did not reduce disease levels despite previous research demonstrating that this pathway is a component of potato defense against *V. dahliae* (Derksen et al., 2013). This result would suggest that the application of salicylic acid to the seed piece either did not trigger the defense pathway, or did not trigger the defense pathway at the level needed to reduce disease incidence.

While the salicylic acid treatment did not reduce disease in this research, there may be an opportunity to induce resistance to *V. dahliae* in potato plants through application of a plant-based treatment. Although they did not use essential oils, one research group in Canada observed that applying extracts from *Astragalus canadensis* L. (Canada milk vetch) as a seed treatment in greenhouse trials reduced disease severity of *V. dahliae* and increased potato plant accumulation of rutin (El Hadrami et al., 2011). In that research, disease severity was evaluated both visually throughout the course of the experiment, and quantitatively after destructive sampling (by counting microsclerotia and using molecular techniques). They quantified plant rutin concentration using HPLC and measured an increase in plant rutin concentration with seed treatment application. To better understand this observation they conducted an *in vitro* experiment in which they observed that *V. dahliae* sporulation was reduced following the

addition of paper disks containing rutin to *Petri* plates where fungal colonies were actively growing (El Hadrami et al., 2011). They determined that the Canada milk vetch seed treatment increased plant production of rutin which appears to inhibit *V. dahliae* growth. Despite the promising nature of this observation, they also concluded that the relationship is more complex as the pathogen appears to be able to respond to, and counteract, increased plant rutin levels in some cases.

When this same group of researchers repeated the experiment in a field trial, they again measured reduced disease severity of *V. dahliae* infection with application of a pre-plant Canada milk vetch seed treatment (Uppal et al., 2008). The reduction was greater in the Kennebec variety of potato than in Russet Burbank, which are highly and moderately susceptible, respectively. Additionally, they did not measure an increase in yield compared to the untreated control despite lower disease levels. The relationship between improved disease management and successful crop production is complicated and more work is needed to understand mechanisms of resistance *in planta*. Much research, including that reported here, has focused on essential oils and plant extracts as anti-fungal or anti-microbial agents (Zambonelli et al., 1996; Bowers and Locke, 2000; Bowers and Locke, 2004; Barrera-Necha et al., 2009; Mvuemba et al., 2009; McMaster et al., 2013) but few have evaluated the effect of treatments on the physiology of the host itself. Focusing on inducing resistance in the host plant may be particularly important if essential oil use is to be implemented in a field setting due to some of the constraints with application on a large scale.

One objective of this work was to evaluate if the use of essential oils impacted plant growth. Much of the past work with essential oils has focused on the *in vitro* effect (Zambonelli et al., 1996; Hammer et al., 1999; López-Benítez et al. 2005; Arslan and Dervis, 2010) but less is known about the effect on the plant when essential oils are applied directly to the seed piece. One study that evaluated the use of essential oils *in vivo* found that origanum and clove oils were phytotoxic to broccoli seedlings at high application rates (McMaster et al., 2013). In this research, multiple metrics were used to evaluate plant growth including plant emergence, plant height, number of nodes on a single plant stem, and yield (number of tubers and total tuber weight at harvest). At the rate applied *in vivo* (2500ppm), there was no negative impact on potato growth characteristics regardless of treatment (Table 2.4, Table 2.5, and Table 2.6). These results are encouraging because they demonstrate that the essential oils were not

phytotoxic when applied to potato seed, and allow for the potential use of higher rates of application to further investigate management of *V. dahliae*. Trends emerged in yield data; treatments where P1034 was applied resulted in reduced tuber weights. Since P1034 is currently used in commercial potato production without negative yield impacts (Rhue et al., 1981; Stark et al., 2004), these trends were likely the result of the artificial growing environment in the greenhouse.

Although the results of the *in vivo* work reported here were inconsistent, essential oils and modified soil fertility practices may prove useful as a component of an integrated management plan targeted toward *V. dahliae,* especially since several treatments clearly reduced or eliminated growth *in vitro*. More work is needed to determine if essential oils impact different life stages of *V. dahliae*. If specific compounds or essential oils can be demonstrated to be effective against microsclerotia, others against hyphal growth, and still others influence a plant's natural defense response, these compounds could potentially be combined into a single seed treatment. While there may be benefits to the use of essential oils, further work is required to ensure there are no detrimental effects to their use.

Despite increased regulation, metam sodium remains the most used active ingredient in commercial potato production. More comprehensive research is needed on the use of essential oils or other alternative products before growers' will reduce chemical application. Only an integrated alternative management plan that is reasonable to implement, comparable or lower in cost to metam sodium, effective at reducing disease, and does not negatively impact yield or net income, will be widely adapted by growers.

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Table 2.1. Common and Latin names of treatments evaluated *in vitro* and *in vivo* to reduce growth of *V. dahliae*.*

Treatment	Latin Name	*In vitro* †	*In vivo* ‡	*In vivo* (rate per pot)
Plantain	*Plantago lanceolata*	yes	no	-
Calendula	*Calendula officinalis*	yes	no	-
Ginger	*Zingiber officinale*	yes	no	-
Curcumin	extract of *Curcuma longa* (turmeric)	yes	no	-
Onion §	*Allium cepa* L.	yes	no	-
Carvacrol	extract of *Origanum vulgare* (oregano)	yes	yes	2500 ppm
Lemongrass	*Cymbopogon spp.*	yes	yes	2500 ppm
Garlic §	*Allium sativum*	yes	yes	2500 ppm
Thymol	extract of *Thymus vulgaris* (thyme)	yes	yes	2500 ppm
Salicylic Acid ¶		yes	yes	2500 ppm
Cinnamon	*Cinnamomum zeylanicum*	yes	yes	2500 ppm
Clove	*Eugenia spp.*	yes	yes	2500 ppm
Ammonium Polyphosphate		no	yes	9.32 ml
Calcium Chloride		no	yes	6.51 g

* Controls with no treatment added were included in both experiments
† tested in lab assay (rates in Table 2.2)
‡ tested in greenhouse assays
§ artificial
¶ methyl salicylate was used

Table 2.2. Results of *in vitro* evaluation of essential oils at various concentrations to reduce growth of *V. dahliae* after 17 days.*

Treatment	**EtOH added**	**----------Concentration----------**					
	ml	0 ppm	100 ppm	250 ppm	500 ppm	1000 ppm	2500 ppm
Calendula			16.1 ab†	15.7 abc	14.5 abcde	16.1 ab	15.6 abc
Carvacrol			5.3 ghij	0.0 j	0.0 j	0.0 j	0.0 j
Cinnamon			14.0 abcdef	1.1 ij	0.0 j	0.0 j	0.0 j
Clove			nm‡	nm	0.0 j	nm	0.0 j
Control	0	16.2 ab					
Control	6.25	6.9 fghij					
Control	9.375	0.0 j					
Curcumin	1.25; 3.125; 6.25; 9.375 §		13.1 abcdef	9.8 abcdefg	1.5 hij	3.8 ghij ¶	
Garlic			nm	nm	1.1 ij	nm	0.0 j
Ginger			nm	nm	16.7 a	nm	16.7 a
Lemongrass			nm	nm	8.2 defghi	nm	0.0 j
Onion			14.5 abcde	13.4 abcdef	9.3 bcdefg	7.2 efghij	1.2 ij
Plantain			14.7 abcd	15.1 abcd	13.6 abcdef	15.2 abcd	14.2 abcde
Salicylic Acid			16.7 a	16.1 ab	14.5 abcde	16.2 ab	12.8 abcdef
Thymol	0.25; 0.625; 1.25; 2.5; 6.25		8.8 cdefgh	0.5 j	0.0 j	0.0 j	0.0 j
Significance (α = 0.05)		p-value					
Treatment		<0.0001					

* Values represent mean *V. dahliae* growth (cm) in 14 *Petri* plates from 2 replicated experiments (7 plates per experiment).

† Values followed by the same letter are not significantly different in a Tukey's HSD test at alpha = 0.05.

‡ Assessment of selected treatments indicated that 500 ppm and 2500 ppm were sufficient to evaluate efficacy so some dilutions were not measured (nm).

§ These are added respectively, with the lowest amount of EtOH going into the lowest dilution.

¶ Dilution is 750 ppm. No 1000 or 2500 ppm were made for this treatment because of the high volume of EtOH.

Table 2.3. Results of *in vitro* evaluation of essential oils at various concentrations to reduce growth of *V. dahliae* after 36 days.*

Treatment	**EtOH added**	**Concentration**					
	ml	0 ppm	100 ppm	250 ppm	500 ppm	1000 ppm	2500 ppm
Calendula			33.8 a	33.7 a	32.7 ab†	33.8 a	32.4 ab
Carvacrol			15.4 bcdefg	0.7 g	0.0 g	0.0 g	0.0 g
Cinnamon			30.2 ab	7.2 defg	0.0 g	0.0 g	0.0 g
Clove			nm‡	nm	0.0 g	nm	0.0 g
Control	0	34.8 a					
Control	6.25	19.2 abcdef					
Control	9.375	2.6 fg					
Curcumin	1.25; 3.125; 6.25; 9.375 §		28.1 abc	22.8 abcd	5.0 defg	11.2 cdefg ¶	
Garlic			nm	nm	5.5 defg	nm	0.0 g
Ginger			nm	nm	34.3 a	nm	36.6 a
Lemongrass			nm	nm	20.9 abcde	nm	0.0 g
Onion			33.0 ab	31.5 ab	26.0 abc	22.3 abcd	11.1 cdefg
Plantain			34.3 a	34.3 a	33.0 ab	34.6 a	32.3 ab
Salicylic Acid			35.2 a	35.1 a	31.5 ab	35.5 a	30.8 ab
Thymol	0.25; 0.625; 1.25; 2.5; 6.25		22.7 abcd	3.4 efg	0.0 g	0.0 g	0.0 g
Significance (α = 0.05)		p-value					
Treatment		<0.0001					

* Values represent mean *V. dahliae* growth (cm) in 14 *Petri* plates from 2 replicated experiments (7 plates per experiment).

† Values followed by the same letter are not significantly different in a Tukey's HSD test at alpha = 0.05.

‡ Assessment of selected treatments indicated that 500 ppm and 2500 ppm were sufficient to evaluate efficacy so some dilutions were not measured (nm).

§ These are added respectively, with the lowest amount of EtOH going into the lowest dilution.

¶ Dilution is 750 ppm. No 1000 or 2500 ppm were made for this treatment because of the high volume of EtOH.

Table 2.4. Effect of treatment on emergence, plant height, and number of nodes in Greenhouse 1.*

Treatment		Emergence DAP*	Height 42 DAP cm	Nodes 42 DAP	Height 49 DAP cm	Nodes 49 DAP	Height 56 DAP cm	Nodes 56 DAP	Height 63 DAP cm	Nodes 63 DAP
Non-inoculated		20.2	37.9	11.2	51.8	15.8	71.3	21.2	92.1	25.8
Inoculated		19.8	35.8	10.8	50.5	15.0	69.4	21.2	88.6	25.8
Inoc. + tween 80		21.6	34.5	10.6	49.2	15.0	66.6	20.8	89.4	24.6
Cinnamon		21.4	34.0	10.8	48.5	15.0	68.2	20.0	88.0	24.2
Clove		22.4	34.2	10.6	47.4	14.2	66.2	19.2	87.1	24.2
Lemongrass		20.6	35.1	11.0	50.2	14.8	69.8	21.4	86.8	24.4
Carvacrol		21.4	34.0	10.8	47.9	13.8	66.8	20.8	88.5	25.0
Thymol		19.2	36.8	11.2	50.7	15.6	69.5	21.0	88.7	25.0
Salicylic Acid		20.4	35.1	11.0	48.7	14.8	67.3	21.4	86.5	24.0
Garlic		21	36.3	10.4	48.8	14.8	68.2	20.4	87.4	24.4
CaCl alone		19.4	36.1	11.4	50.6	15.0	69.3	21.4	87.8	25.0
P1034 alone		21.4	31.5	9.8	45.0	13.8	63.3	19.6	83.5	24.2
Carvacrol + CaCl		22.2	33.5	10.4	47.2	14.4	67.6	20.2	90.6	25.6
Carvacrol + P1034		21	34.7	10.4	49.0	15.0	67.8	21.4	86.6	24.2
Salicylic Acid + CaCl		21.6	32.6	10.6	46.7	14.8	68.0	20.0	88.8	24.2
Salicylic Acid + P1034		21.6	35.2	10.4	49.2	15.2	69.1	21.0	90.2	24.8
Significance (α= 0.05)	DF	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value
Replication	4	<0.001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.001	<0.0001	<0.0001
Treatment	15	0.343	0.157	0.365	0.398	0.283	0.489	0.037†	0.536	0.160

* DAP = days after planting. Experiment was planted on April 23, 2015. Plants were inoculated 42 DAP and destructively sampled 63 DAP. Weekly height and node measurements were also analyzed using net growth difference (weekly measurement minus measurement at inoculation). This did not change the results.

† The Tukey's HSD mean comparison did not find differences between treatment means.

Table 2.5. Effect of treatment on emergence, plant height, and number of nodes in Greenhouse 2.*

Treatment		Emergence DAP*	Height 49 DAP cm	Nodes 49 DAP	Height 56 DAP cm	Nodes 56 DAP	Height 63 DAP cm	Nodes 63 DAP	Height 70 DAP cm	Nodes 70 DAP	Height 77 DAP cm	Nodes 77 DAP
Non-inoculated		28.6	27.6	11.4	46.3	16.4	63.6	20.6	78.9	26.0	97.1	29.6
Inoculated		27.6	29.2	11.6	48.4	18.0	66.6	22.4	82.1	28.4	99.8	31.4
Inoc. + tween 80		28.6	27.0	11.0	46.5	16.2	65.2	20.2	81.2	25.8	98.0	29.8
Cinnamon		27.2	27.4	11.6	46.8	17.4	64.3	22.0	79.1	26.6	96.9	31.0
Clove		28	29.7	12.6	48.5	18.0	66.1	21.8	80.8	27.2	97.0	31.0
Lemongrass		29.6	25.8	11.6	43.9	16.2	63.3	21.6	80.6	26.8	98.6	31.2
Carvacrol		27.8	28.8	11.8	49.0	17.6	67.7	21.2	82.6	27.4	97.4	31.4
Thymol		30.4	24.1	10.8	41.9	15.6	60.9	20.6	76.3	26.0	94.2	29.4
Salicylic Acid		29.8	24.3	9.4	42.9	15.6	61.6	19.8	77.7	26.0	93.9	30.2
Garlic		29.8	26.8	11.2	45.4	16.2	63.4	21.2	79.1	26.4	96.1	30.4
CaCl alone		28.8	25.0	10.4	42.4	15.4	59.6	18.6	77.3	26.4	94.0	30.0
P1034 alone		31	25.0	10.4	42.6	15.8	60.3	20.8	77.5	25.4	94.3	29.6
Carvacrol + CaCl		25.8	28.5	11.4	47.1	17.2	65.5	21.4	82.0	27.8	98.6	31.4
Carvacrol + P1034		27.6	29.5	11.6	47.9	17.8	64.0	21.0	80.7	27.6	97.0	32.0
Salicylic Acid + CaCl		30.4	22.4	9.2	40.3	15.0	55.6	18.8	72.0	23.6	88.8	29.0
Salicylic Acid + P1034		27.8	29.3	11.6	47.6	17.4	65.2	22.4	80.7	27.4	97.1	30.6
Significance (α= 0.05)	DF	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value	p-value
Replication	4	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.001	<0.0001	<0.0001	<0.0001	<0.0001
Treatment	15	0.691	0.484	0.445	0.377	0.191	0.285	0.038†	0.517	0.061	0.559	0.379

* DAP = days after planting. Experiment was planted on April 27, 2015. Plants were inoculated 56 DAP and destructively sampled 77 DAP. Weekly height and node measurements were also analyzed using net growth difference (weekly measurement minus measurement at inoculation). This did not change the results.

† The Tukey's HSD mean comparison did not find differences between treatment means.

Table 2.6. Treatment effect on number of tubers and total tuber weight in Greenhouse 1 and Greenhouse 2.*

		----------Greenhouse 1----------		----------Greenhouse 2----------	
Treatment		**Tuber Count**	**Sum of Tubers g pot^{-1}**	**Tuber Count**	**Sum of Tubers g pot^{-1}**
Non-inoculated		12.6	99.8	8.0	76.4
Inoculated		9.2	93.3	6.8	85.0
Inoc. + tween 80		10.4	86.0	6.2	80.9
Cinnamon		11.4	77.4	6.6	81.7
Clove		9.2	72.1	6.6	105.9
Lemongrass		11.6	101.6	10.6	77.8
Carvacrol		9.8	73.4	9.4	86.8
Thymol		10.2	102.7	8.2	57.0
Salicylic Acid		12.0	93.4	6.6	72.7
Garlic		8.4	73.4	8.0	69.4
CaCl alone		12.8	92.1	6.0	88.5
P1034 alone		10.6	47.3	6.8	30.0
Carvacrol + CaCl		9.0	54.3	5.4	106.4
Carvacrol + P1034		11.2	65.2	6.8	66.8
Salicylic Acid + CaCl		12.0	74.5	7.4	91.4
Salicylic Acid + P1034		8.6	57.8	9.4	84.3
Significance (α= 0.05)†	DF	p-value	p-value	p-value	p-value
Replication	4	0.727	<0.0001	0.003	<0.0001
Treatment	15	0.575	0.024‡	0.446	0.178

* Greenhouse 1 was planted on April 23, 2015 and destructively sampled 63 days after planting (DAP). Greenhouse 2 was planted on April 27, 2015 and destructively sampled 77 DAP.

† Statistical analyses for Greenhouse 1 and Greenhouse 2 were conducted separately.

‡ The Tukey's HSD mean comparison did not find differences between treatment means.

Table 2.7. Concentration of *V. dahliae* in potato stem sap following destructive sampling of plants three weeks after inoculation in greenhouse trials.*

Treatment		Greenhouse 1 ***V. dahliae in sap*** **log CFU ml^{-1}**	Greenhouse 2 ***V. dahliae in sap*** **log CFU ml^{-1}**
Non-inoculated		0	0 b
Inoculated		3.72	6.48 ab
Inoc. + tween 80		3.52	8.26 a
Cinnamon		2.47	6.64 ab
Clove		2.72	7.43 a
Lemongrass		6.16	6.87 ab
Carvacrol		2.34	7.17 ab
Thymol		6.69	6.75 ab
Salicylic Acid		4.01	9.12 a
Garlic		5.02	8.83 a
CaCl alone		4.87	6.26 ab
P1034 alone		3.71	6.10 ab
Carvacrol + CaCl		2.24	10.32 a
Carvacrol + P1034		5.22	8.37 a
Salicylic Acid + CaCl		4.72	9.50 a
Salicylic Acid + P1034		8.10	9.73 a
Significance (α= 0.05)	DF	p-value	p-value
Replication	4	0.253	0.414
Treatment	15	0.088	0.002

*Stems were sterilized and crushed to extract stem sap, which was then plated on Sorensen's NP-10 media. *V. dahliae* colonies were visually quantified 14-16 days after sap plating using morphological features. Values followed by the same letter are not significantly different in a Tukey's HSD test at alpha = 0.05.

THE EFFECT OF POTASSIUM FERTILIZATION AND CHLORIDE UPTAKE ON POTATO CROP NUTRIENT STATUS

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ABSTRACT

Potassium (K) is an essential nutrient for potato (*Solanum tuberosum* L.) and is usually applied as chloride (KCl) or sulfate salts (K_2SO_4). This research evaluated the effects of different K fertilizer applications on nutrient concentrations in potato plant matter, including petioles, with particular emphasis on the effect of the accompanying anions (Cl vs. sulfate), and tracked where Cl moved in the potato production system from time of application in soil to uptake in the plant. Two years of field trials were conducted in Hermiston, OR in an Adkins fine sandy loam with high soil test K (0.79 cmol kg^{-1} exchangeable K; 0-20.3 cm depth) so that differences in yield were minimized across treatments. Potassium source (KCl, K_2SO_4 (SOP), or K_2SO_4*2$MgSO_4$ (Kmag)), rate (0, 112, 224, 448 kg K_2O ha^{-1}), and time of application (seven months pre-plant (September), two weeks pre-plant, or in-season) were evaluated.

Soil Cl was 15 mg kg^{-1}, 53 mg kg^{-1}, and 47 mg kg^{-1} for KCl only treatments applied in September, pre-plant, and in-season, respectively. Plant Cl concentrations for KCl treatments applied in September were 1.1 g kg^{-1} in tubers and 15 g kg^{-1} in tops; for treatments applied preplant were 2.2 g kg^{-1} in tubers and 22 g kg^{-1} in tops; and for treatments applied in-season were 1.9 g kg^{-1} in tubers and 24 g kg^{-1} in tops. Petiole Cl was elevated with KCl treatments (June: 16-18 g kg^{-1} and July: 36-40 g kg^{-1}) as compared to SOP (June: 9.6-10 g kg^{-1} and July: 26 g kg^{-1}) and Kmag (June: 10-11 g kg^{-1} and July: 27-28 g kg^{-1}). Soil and plant tissue K concentrations were affected by application rate, but generally not by source or time of application. Plant N concentrations were largely insignificant among treatments. In contrast to previous studies, an antagonism between N and Cl was not observed. Yield and internal potato quality were not affected by treatment in either 2013 or 2014. Results suggest that potato plants can take up Cl in large quantities when present in the root zone, and that soil Cl increased when K source is KCl, and as KCl is applied at higher rates or applied later in the growing season. Applying KCl far in advance of peak plant growth can help address concerns with elevated plant Cl concentrations as Cl has a chance to leach out of the root zone but K is adsorbed and thus plant available later in the growing season.

Keywords: petiole, sulfate, anion uptake, nutrient management, micronutrients.

INTRODUCTION

Potassium (K) and nitrogen (N) are the two nutrients that plants need in most abundance (Ren et al., 2015). Potato (*Solanum tuberosum* L.) plants can accumulate over 650 kg K ha^{-1} in one growing season (Horneck and Rosen, 2008) and K is the most abundant cation found in plant tissue and is highly mobile in plants. This nutrient is pivotal for optimum photosynthesis (Cakmak, 1994; Kanai et al., 2007), for translocation of sugars (Haeder et al., 1973; Cakmak et al., 1994; Kanai et al., 2007), and for regulation of osmotic potential and turgidity of cells (Hsiao and Läuchli, 1986), which is critical for stomata opening (Roelfsema and Hedrich, 2005). Severe K deficiency in potato can result in glossy, crinkled, and slightly darker younger leaves and scorched leaf margins and necrosis in older leaves (Stark and Westermann, 2008). Marketable tuber yield can be reduced due to reduced tuber growth, decreased stem biomass and tuber number, and cracked tubers (Grzebisz et al., 2015).

Potassium is supplied as either chloride (KCl) or sulfate salts (K_2SO_4) and can be adsorbed to soil particles and thus remain available to plants after application. The accompanying anion (Cl^- or SO_4^-), in contrast, is more likely to leach out of the system if applied far in advance of root uptake (Ren et al., 2015). KCl comprises over 90 percent of the K applied to cropping systems in the United States due to its low cost and ease of application (IFA, 2013; Ren et al., 2015) and chloride (Cl), relative to other possible anions, leaches readily following major soil drainage (Saffigna et al., 1977; Hill, 1986). Specific gravity is a quality evaluation metric used by the potato industry and higher specific gravity increases crop value. Although some studies have been inconclusive (Davenport and Bentley, 2001), it is generally established that KCl leads to a greater reduction in specific gravity than sulfate K sources (Timm and Merkle, 1963; McDole et al., 1978; Laboski and Kelling, 2007).

Both Cl and sulfur (taken up as sulfate-S) are essential for plant physiology. Chloride is important for stomatal regulation and is a component of the water-splitting reaction in photosystem II (Westermann, 2005; Marschner, 2012). Although soil Cl is generally adequate to meet crop need, and Cl deficiency rarely occurs in a field setting (White and Broadley, 2001), a Cl deficiency in plants can manifest as reduced yield, poor root development, and wilting, discoloration, chlorosis, and necrosis of leaves (Broyer et al., 1954; Johnson et al., 1957). In potatoes specifically, Cl deficiency results in discoloration (light green followed by purplish bronze) and curling of younger leaves (Stark and Westermann, 2008). Sulfur is a component of

two essential amino acids (cysteine and methionine) and of other necessary organic compounds (Droux, 2004; Westermann, 2005). Potato plants deficient in S exhibit symptoms in the younger leaves, which turn light green and then yellow (Stark and Westermann, 2008).

Plant uptake of other nutrients, and plant tissue nutrient concentrations, can be affected by K application. Previous research has documented both a positive uptake interaction between N and K (Singh and Lal, 2012) and a mutual antagonism between nitrate and Cl uptake (James et al., 1970a; James et al., 1970b; Saffigna and Keeney, 1977; Kafkafi et al., 1982; James et al., 1994). Reduced petiole nitrate-N concentrations, reduced above ground biomass nitrate-N and total N uptake, and reduced tuber total N uptake have been documented as a result of elevated Cl uptake following KCl application in potato production systems (Murarka et al., 1973; Saffigna and Keeney, 1977; James et al., 1994). In contrast, the competition for uptake between sulfate and nitrate is not as strong (James et al., 1994).

Plant organic acid concentrations can be affected by K application. Plants synthesize organic acid anions if cations have been taken up in excess of anion uptake (Hiatt and Leggett, 1971; Blevins et al., 1974; Marschner, 2012). This occurs in the cytosol where increased cation concentrations result in hydrogen ions being pumped out of the cell, which in turn elevates pH. Organic acid anions are formed for the stabilization of cytosol pH and charge compensation (Marschner, 2012). This difference in organic acid anion concentration is evidenced in plant tissue analysis by the fact that petiole cation concentrations are constant between KCl and K_2SO_4 application despite significantly different petiole anion concentrations by treatment (James et al., 1994). Elevated Cl application has consequences for plant tissue analysis that extend beyond the uptake antagonism between nitrate and Cl.

The change in petiole nutrient concentration as a result of KCl application has applied consequences in potato production. Potato growers use petiole tissue nitrate-N as a metric for mid-season nitrogen fertilizer application. These recommendations do not take into account soil Cl, or K application source, rate, or timing (Lang et al., 1999; Stark et al., 2004; Pavek, 2013). It has been suggested that mid season petiole nitrate-N recommendations should take into account petiole Cl concentration due to the documented antagonism between the two nutrients, but guidelines have not been adjusted (Saffigna and Keeney, 1977; James et al., 1994). In addition to the potential cost savings to growers from reduced fertilizer use, there are also environmental considerations for redoing these recommendations. Nitrate leaches readily

under potatoes grown in soils with high sand content (Hill, 1986; Neumann et al., 2012) and annual nitrate leaching in potato production systems has been estimated to range from 70 kg N ha^{-1} to more than 200 kg N ha^{-1} (Davenport et al., 2005). Growers may be applying excess in-season N due to a perceived deficiency where none exists because petiole nitrate-N concentrations are depressed following KCl application.

This research tracked the fate of Cl in a system where nutrients were not limited and can help better understand the role of Cl in the potato production. The objectives of this research are to evaluate: 1) where Cl moves in the potato production system from time of application in soil to uptake in plant; 2) the effects of different K fertilizer applications on nutrient concentrations in plant matter, including potato petioles, with particular emphasis on the effect of the accompanying anions (Cl vs. sulfate).

MATERIALS AND METHODS:

This research was conducted in 2013 and 2014 under center-pivot irrigation at the Hermiston Agricultural Research and Extension Center in Hermiston, OR. Soil is classified as an Adkins fine sandy loam (coarse-loamy, mixed, superactive, mesic Xeric Haplocalcids). This soil is well-drained with an average pH of 6.0 (0-20 cm). Nutrient management was the same for both years. Total season N application was 392 kg ha^{-1}. Approximately 235 kg N ha^{-1} was applied as in a combination of pre-plant broadcast urea, and at planting side-dress urea and urea ammonium nitrate. The remaining N was applied weekly through the center pivot as urea ammonium nitrate during peak above ground growth (approximately from 35 days after planting (DAP) to 70 DAP). Pesticides were applied following standard regional grower practice both at planting and as needed throughout the growing season to control insects, pathogens, and weeds. All plots both years were planted using a potato planter with cut, commercial grade, Russet Burbank seed pieces at 0.23 m (9”) apart in furrows.

In 2013 KCl (0-0-60-0 S-45 Cl) and K_2SO_4 (0-0-52-18 S), were broadcast applied by hand at rates (0, 112 kg ha^{-1}, 224 K_2O kg ha^{-1}) at two times during the growing season: at planting and in-season (49 DAP) (Table 3.1). Field plots that were three rows wide (0.86 m per row) by 9.14 m long were planted on April 24 in a randomized complete block design with five replicates. At planting, applications were broadcast applied by hand after the field was planted and individual plots were measured and marked. Tubers in 3.0 m from the middle of the center row of each

plot were mechanically dug 135 DAP, and picked up by hand. Tubers were collected from the middle of each plot to ensure that tuber movement from mechanical harvester did not affect collection by plot. Tubers were put into storage at 4°C until sorting seven days later. Harvested potatoes were separated into five categories: culls, <113 g (0-4 oz), 113-170 g (4-6 oz), 170-283 g (6-10 oz), and >283 g (>10 oz) to determine total yield and USDA grade. A subsample of potatoes in the 170-283 g range was used to measure specific gravity. Specific gravity was quantified using the weight in water-weight in air method with a manual hydrometer (similar product: http://martinlishman.com/potato-dry-matter-measurement/). Ten potatoes from this subsample were used to quantify internal defects. These 10 potatoes were cut longitudinally and visually evaluated for hollow heart, vascular discoloration, brown center, or internal brown spot.

Methods were modified in 2014 based on results from the 2013 field season. In 2014, K was broadcast applied by hand at 0, 112, 224 or 448 kg K_2O per hectare via three sources; KCl (0-0-60-0 S-45 Cl), K_2SO_4 (0-0-52-18 S), and $K_2SO4*2MgSO_4$ (0-0-22-22 S-11 Mg), at one of three application timings; 206 days prior to planting (September), 14 days prior to planting (pre-plant), and 35 DAP (in-season); (Table 3.1). Field plots that were four rows wide (0.86 m per row) by 9.14 m were planted on April 11 in a randomized complete block design with five replicates. Four soil cores (0-20 cm) from side of row hills were collected June 18-20, 2014 (68-70 DAP) from the two middle rows of each pot and mixed well in a bucket. A subsample was taken from the field and air dried before analysis. Soil concentrations from control plot were 0.79 cmol kg^{-1} K, 103 mg kg^{-1} P (Mehich III), 16 mg kg^{-1} Cl.

Thirty petioles per plot were collected twice during the growing season (70 DAP and 97 DAP) from the middle of the two center rows of each plot. The fifth petiole from the top of the stem (fourth fully developed petiole) was collected and leaflets were stripped off petiole immediately after collection (Lang et al., 1999; Stark et al., 2004). Above ground biomass was collected 116 DAP from a 0.91 m length of an outside row of each plot. Outside row data was adequate for sample collection, as plots were carefully marked and measured prior to planting and treatment application. By this time of sampling, severe infection by *Sclerotinia sclerotiorum* (white mold) and general necrosis were observed in the field so the greenest part of the middle of the row was sampled.

Tubers in 4.6 m from the middle of one of the center row of each plot were mechanically dug, and picked up by hand 137 DAP. Tubers were collected from the middle of each plot to ensure that tuber movement from mechanical harvester did not affect collection by plot. Tubers were graded and weighed the following day. Harvested potatoes were separated into five categories: culls, <113 g, 113-170 g, 170-283 g, and >283 g to determine total yield and USDA grade. A subsample of tubers in the 170-283 g category was used to measure specific gravity. Specific gravity was quantified using the weight in water-weight in air method with a manual hydrometer (similar product: http://martinlishman.com/potato-dry-matter-measurement/). Ten tubers from this subsample were cut longitudinally and used to visually quantify internal defects (hollow heart, vascular discoloration, brown center, or internal brown spot). Half of 3 of these cut tubers were used for nutrient analysis.

Laboratory Analysis:

Soil and plant samples were prepared for analysis at HAREC and nutrient analyses were conducted at Brookside Laboratories in New Bremen, OH. Soil samples were air dried prior to analysis. With the exception of soil Cl, soil nutrient were extracted using the Mehlich III method (Mehlich, 1984). Soil Cl was extracted using 0.1M $Ca(NO_3)_2$. Soil Cl concentrations were quantified using mercuro-thiocynate flow injection on a colormetric autoanalyzer (model: FIAlab 1000, FIAlab Instruments Inc., Seattle, WA).

Plant samples (petioles, above ground biomass, tubers) were dried at 60°C and ground prior to analysis. Plant sample Cl was extracted using a 2% acetic acid extraction using 0.25 g of material. Plant Cl concentrations were quantified using mercuro-thiocynate flow injection on a colormetric autoanalyzer (model: FIAlab 1000, FIAlab Instruments Inc., Seattle, WA). Petiole NO_3-N was extracted using a 2% acetic acid extraction with 0.25g of material and quantified using cadmium reduction flow injection on a colormetric autoanalyzer (model: FIAlab 1000, FIAlab Instruments Inc., Seattle, WA). Above ground biomass and tuber total N were determined using the combustion method—Carlo Erba Carbon-Nitrogen analyzer with 10 mg of ground sample (model: NA1500, CE Elantech, Inc., Lakewood, NJ). Other nutrient analyses of plant samples were digested from 0.25g of material using a nitric acid and hydrogen peroxide microwave digestor (model: Mars 6, CEM Corporation, Matthews, NC). Nutrients in digest were

quantified using an inductively coupled plasma spectrophotometer (ICP-MS) (Model: iCAP 6500 Duo, Thermo Fisher Scientific, Waltham, MA).

Statistical Analysis:

To compare effects of rate, time of application, and K source for Year 2, treatments were divided into three factorials for analysis. In each factorial, one variable (rate, source, or timing) was kept constant to allow comparison of the other two variables (Table 3.1). Factorials will be referred to as Source x Timing, Rate x Timing, and Rate x Source. In some instances, treatments were used in multiple factorial comparisons. Zero K added control plots were not used in statistical analysis and will not be discussed in the results, but treatment means are included in data tables for reference. Statistical differences were analyzed at alpha = 0.05. Any differences by treatment that are reported were statistically significant at this level. P-values will not be mentioned in text but can be found in data tables. Statistical analysis was conducted using the program R Studio. Least Significant Difference (LSD) mean comparison tests were conducted when the results of the F-test were statistically significant at alpha = 0.05.

RESULTS

Yield and specific gravity data for both years will be presented first. Data collected in 2014 only (soil analysis and plant nutrient concentrations) will then be discussed. The presentation of 2014 data will be structured by the three factorials used in statistical analysis (Source x Timing, Rate x Timing, and Rate x Source).

Yield and Specific Gravity:

Yield and specific gravity were generally not affected by timing, rate, or source of K application in either 2013 or 2014 (Table 3.2). USDA Number 1 tubers ranged from 57 to 60 Mg ha^{-1} in 2013 and from 43 to 49 Mg ha^{-1} in 2014. Specific gravity ranged from 1.077 to 1.083 in 2013. In 2014, specific gravity ranged from 1.064 to 1.071 and was reduced as rate of K application increased. When comparing rates and times of KCl application in the Rate x Timing factorial, specific gravity was higher for September application than for planting or in-season applications.

Source x Timing Factorial:

Soil and plant Cl were affected by K source in the Source x Timing factorial (Table 3.3). Soil Cl was highest when K source was KCl (42 mg kg^{-1}) than when source was Kmag or SOP (both 14 mg kg^{-1}). Tuber, tops, and petiole Cl concentrations followed the same trend. Tuber Cl concentration was 1.7 g kg^{-1} with KCl application, 1.2 g kg^{-1} with Kmag, and 1.1 g kg^{-1} with SOP. Tops Cl concentration was 19 g kg^{-1} with KCl application and 14 g kg^{-1} with both Kmag and SOP. For the June sampling date, petiole Cl was 16 g kg^{-1} for KCl application and 10 g kg^{-1} for both Kmag and SOP (Table 3.4). A similar pattern was measured for the July sampling date (Table 3.5).

Some other differences were measured by treatment in this factorial. Total anion concentrations in both the June and July petiole collections were elevated for KCl treatments when compared to other K sources (Table 3.4 and Table 3.5). Soil Cl and soil S were both affected by time of application with lowest measurements of each recorded for treatments applied in September as compared to treatments applied preplant or in-season (Table 3.3). Soil S was also affected by K source. Highest soil S was measured with Kmag application (76 mg kg^{-1}) compared to KCl (23 mg kg^{-1}) or SOP (39 mg kg^{-1}). No consistent differences emerged by treatment for soil K measurements or K plant concentrations in this factorial. Similarly, plant N concentrations were not consistently affected by treatment.

Rate x Timing Factorial:

Soil and plant Cl were affected by both rate and time of KCl application in the Rate x Timing factorial (Table 3.6). Soil Cl increased with elevated rates of KCl application and when KCl was applied later in the grower season. Soil Cl was 15 mg kg^{-1} when treatments were applied in September, 53 mg kg^{-1} for treatments applied preplant, and 47 mg kg^{-1} for treatments applied in-season. Tuber, tops, and petiole Cl concentrations followed similar trends (Table 3.6, Table 3.7, and Table 3.8). For the July collection, for example, petiole Cl was 32 g kg^{-1} when 112 kg K_2O ha^{-1} was applied, 36 g kg^{-1} with 224 kg K_2O ha^{-1} applied, and 38 g kg^{-1} with 448 kg K_2O ha^{-1} applied (Table 3.8). Petiole Cl concentration for samples collected in July was lowest for September treatment application (27 g kg^{-1}) compared to treatments applied preplant (39 g ka^{-1}) or in-season (40 g kg^{-1}). Petiole total anion concentrations were also affected by time of treatment application, with highest total anions measured as treatments were applied later in the growing season (Table 3.7 and Table 3.8).

Soil K and plant K concentrations were consistently elevated as KCl was applied at higher rates (Table 3.6, Table 3.7, and Table 3.8). Plant N concentrations in tops, tubers, and petioles were generally not affected by treatment.

Rate x Source Factorial:

Soil and plant Cl concentrations were consistently higher with KCl application than with application of other K sources (Table 3.9). Soil Cl was 47 mg kg^{-1} for KCl treatments compared to 14 mg kg^{-1} for Kmag treatments and 12 mg kg^{-1} for SOP treatments. In plant tops, Cl concentration was 24 g kg^{-1} for KCl treatments, 15 g kg^{-1} for Kmag treatments, and 13 g kg^{-1} for SOP treatments. Similar measurements were observed for tuber and petiole Cl concentrations (Table 3.9, Table 3.10, and Table 3.11).

Other differences were observed by treatment in this factorial. Petiole anions were affected by K source with highest anion concentrations measured for KCl treatments as compared to other K sources (Table 3.10 and Table 3.11). Soil S was highest when K source was Kmag (105 mg kg^{-1}) compared to KCl (21 mg kg^{-1}) or SOP (56 mg kg^{-1}) (Table 3.9). Soil K and plant K concentrations were consistently higher as treatments were applied at elevated rates. Plant N was unaffected by K source. Petiole nitrate-N was inversely related to K rate for both collection dates, with the highest petiole nitrate-N measured for the lowest rate of K application.

DISCUSSION

Plant and Soil Nutrient Concentrations:

The experiment was designed to minimize yield differences between treatments so that nutrient movement could be evaluated without regard to plant nutrient partitioning and physiological source-sink relationships, which can be affected by K application and deficiency (Beringer et al., 1990; Gerardeaux et al., 2010). Previous research determined that potato plants accumulate high concentrations of nutrients throughout the growing season. Work conducted in the Hermiston area measured uptake of over 448 kg ha^{-1} total N and over 672 kg ha^{-1} total K in one growing season and a study in Minnesota measured total uptake of 392 kg ha^{-1}, 577 kg ha^{-1}, and 38 kg ha^{-1} N, K, and S, respectively (Horneck and Rosen, 2008). Total uptake in this study was not as high. These inconsistencies in uptake can be partially attributed to the white mold that prematurely killed potato plants, although that did not infect the field until

after the majority above ground growth and uptake had occurred. It is likely that differences in experimental design, in addition to the disease, contributed to these large discrepancies.

These data indicate that potato plants accumulate large concentrations of Cl when available due to higher rates of application and/or applications later in the growing season. Other researchers have confirmed this finding that potatoes (Corbett and Gausman, 1960) and other plant species including tomato (*Solanum lycopersicum*) (Kafkafi et al., 1982), tobacco (*Nicotiana tabacum*) (Fuqua et al., 1987), and sugarbeet (*Beta vulgaris)* (James et al., 1970a; Moraghan, 1987) luxury consume Cl when available. September KCl treatments, which were applied the furthest in advance of planting and peak plant uptake, resulted in the lowest soil and plant Cl concentrations when compared to other times of K application. This data suggests that Cl is less available if applied far in advance of peak plant growth and is consistent with other research findings that Cl leaches readily out of the soil profile (Saffigna et al., 1977; Hill, 1986).

In this research, tops and tubers were collected three weeks apart (tops 116 DAP and tubers 137 DAP) and Cl concentration in tops was higher than in tubers. Plant partitioning of Cl more heavily into tops compared to roots is consistent with previous findings in sugarbeet (Moraghan, 1987). In rapeseed (*Brassica napus*), higher concentrations of Cl accumulation were measured in leaves than in flowers and siliques (Podleśna, 2009). Other research on potato documented a correlation between petiole and tuber Cl concentrations and found that petiole Cl concentrations were always higher (generally greater than 10 times) tuber Cl concentrations for samples collected on the same day (McBride, 1985). McBride also found that tuber Cl concentrations decreased from the first measurement date (end of June) to the time of harvest. Peak nutrient uptake occurs during times of significant above ground growth (Horneck and Rosen, 2008). Photosynthates are translocated into tubers during tuber bulking, which subsequently increases water uptake into tubers (Lang et al., 1999). Chloride concentration as a proportion of tuber mass decreases during this tuber bulking stage as a result. Standard grower practice is to leave desiccated vines in the field after harvest. The majority of plant Cl is in the tops at the end of the season and this nutrient is added back into the system. Although Cl leaches out of sandy soil, frequent KCl application paired with incorporation of high Cl crop residue can result in elevated soil Cl over time.

Previous research has documented a mutual antagonism between nitrate and Cl in potato (James et al., 1970b; Saffigna and Keeney, 1977), tomato (Kafkafi et al., 1982), tobacco

(Fuqua et al., 1987), soybean (*Glycine max*) (Weigel et al., 1973), barley (*Hordeum vulgare*) (Glass and Siddiqi, 1985; Goos et al., 1989), and sugarbeet (James et al., 1970a) but it is not clear that this competition results in N deficiency in potato plants when soil Cl is high. Murarka et al. (1973) conducted greenhouse experiments in similar soil (sandy loam with pH of 6.0) but with half as much initial soil K. They applied different sources of all three nutrients (Cl was applied as KCl and $CaCl_2$) and measured K, N, and Cl concentrations in plants. The consistency in their initial soil allowed them to measure nutrient uptake accurately. They documented an antagonism between uptake of N and Cl. At elevated Cl application, both nitrate-N and total N concentrations were depressed but the protein fraction was not affected. This would indicate that while Cl does impede nitrate uptake, plant N concentrations are functionally adequate and the conversion of available N to protein is not impacted. Additionally, they observed that a greater percentage of total N was converted to protein at lower rates of N application. It appears that in the absence of N deficiency, potato plants regulate total available N to meet physiological needs so the antagonism with Cl does not affect growth. In our study the experimental design minimized the interaction between N and Cl. Total N concentration in tops and tubers, as well as nitrate-N in petioles, were generally unaffected by K source or time of K application in any of the three factorials. This result may indicate that replenishing N through weekly applications can minimize the antagonism between Cl and N during peak aboveground growth ensuring that optimum N is available to meet crop need.

A positive interaction in uptake between N and K has been documented in potato (Singh and Lal, 2012). That interaction was not observed in this research in which the highest nitrate-N in petioles measured at the lowest K rate. This difference in observation is likely because our experimental design was intended to minimize differences in K availability due to high initial soil K. Additionally, N was applied consistently to all plots and was replenished throughout the growing season.

Petiole Analyses:

Petioles are used as a diagnostic tool in potato production systems. Extension publications with criteria for optimum preplant soil test values, as well as in-season petiole nutrient concentrations, are available to guide fertility management decisions. Optimum nutrient concentrations vary by potato variety and growing region. Russet Burbank potatoes

were planted in this research and recommendations for that variety will be discussed herein. Some scientists have suggested that petiole diagnostic criteria should be adjusted to take petiole Cl concentration into account given the antagonism between nitrate-N and Cl (Saffigna and Keeney, 1977; James et al., 1994). As this has not been implemented, current petiole diagnostic recommendations will be discussed (Lang et al., 1999; Stark et al., 2004; Pavek, 2013). In this research, control plots with no treatment applied had soil measurements of 0.79 cmol K kg^{-1} and 24 mg S kg^{-1} (Table 3.3). These are adequate for the growing season according to regional recommendations, which suggest that with preplant soil measurements of 0.62 cmol K kg^{-1} and 10 mg S kg^{-1}, no fertilization is required (Lang et al., 1999).

Petiole nutrient recommendations are available by plant growth stage for Russet Burbank potatoes grown in the Columbia Basin of Oregon and Washington (Lang et al., 1999; Stark et al., 2004). In 2014, petioles were collected 70 DAP (June 20) and 97 DAP (July 17) which correspond to potato plant developmental Stage II and the early part of developmental Stage III, respectively (Lang et al., 1999). One extension guide for the region suggests that sufficient petiole K concentrations should be between 80.0-110.0 g kg^{-1} during Stage II and 60.0-90.0 g kg^{-1} during Stage III (Lang et al., 1999). Another indicates that petiole K concentrations above 80.0 g kg^{-1} during State III are sufficient (Stark et al., 2004). Petiole K concentrations in this research ranged from 102.8-109.3 g kg^{-1} at the first collection date in Stage II (Table 3.4, Table 3.7, and Table 3.10) and 87.3-97.4 g kg^{-1} in Stage III (Table 3.5, Table 3.8, and Table 3.11). These measurements are within the recommended range for the first collection date and both within the recommended range and in excess of the recommended range depending on treatment for the second collection date. Other research conducted in Idaho suggests that K deficiency in Russet Burbank potatoes will not occur if petiole K concentrations stay above 70.0 g kg^{-1} during the growing season (Westermann and Tindall, 2000) and specifically during the time of tuber initiation (McDole et al., 1978). Petiole K concentrations in this study far exceeded this recommended flat rate. Initial soil K was adequate and the additional K added from treatment application contributed to the elevated petiole K concentrations.

One regional extension publication advises that petiole S concentration should not fall below 2.0 g kg^{-1} throughout the growing season (Stark et al., 2004) while another makes more specific recommendations that petiole S stay between 2.2-2.5 g kg^{-1} during Stage II and 2.0-2.2 g kg^{-1} during Stage III (Lang et al., 1999). In this study petiole S concentrations were 1.7-1.9 g kg^{-1}

during Stage II (Table 3.4, Table 3.7, and Table 3.10) and 1.4-1.6 g kg^{-1} during Stage III (Table 3.5, Table 3.8, and Table 3.11). These concentrations are lower than extension recommendations for both collection dates despite adequate soil S in control plots. There is a discrepancy between soil S and petiole S recommendations.

Consistent with previous research (Gardner and Jones, 1975; Rykbost et al, 1993), petiole nitrate-N concentrations in this study decreased throughout the growing season. Extension guidelines for Washington recommend that petiole nitrate-N concentrations should be between 15.0-26.0 g kg^{-1} during Stage II and between 12.0-20.0 g kg^{-1} during Stage III (Lang et al., 1999). Idaho guidelines are similar and suggest that petiole nitrate-N concentrations of 20.0-25.0 g kg^{-1} during Stage II and 15.0-20.0 g kg^{-1} during Stage III are adequate for optimum tuber yield (Stark et al., 2004). In this research petiole nitrate-N concentrations were 19.9-22.3 g kg^{-1} during the first collection date in Stage II (Table 3.4, Table 3.7, and Table 3.10) and 14.6-16.7 g kg^{-1} during the second in Stage III (Table 3.5, Table 3.8, and Table 3.11). Petiole nitrate-N ranges are adequate according to the Washington guide and slightly lower than Idaho extension recommendations. In addition to recommendations by plant growth stage, diagnostic petiole nitrate-N concentrations are also available by date (Pavek, 2013). These recommendations advise that Russet Burbank potatoes petiole concentrations should be 24.0-27.0 g kg^{-1} on June 15th and 18.0-21.0 g kg^{-1} on July 15th (Pavek, 2013). Petiole nitrate-N concentrations in this research are lower than the recommended range for both collection dates. Although the recommendations by date do not list optimum potato planting dates, this trial was planted at an appropriate date according to standard regional practice. The highest recommended rate of N application for the region is between 358 kg ha^{-1} (Stark et al., 2004) and 395 kg ha^{-1} (Lang et al., 1999). In this research, N was applied at 395 kg ha^{-1} to all plots. This high rate of total N application should be adequate to meet potato crop N requirements although petiole nitrate-N concentrations were not always optimal.

In this research, petiole Cl concentrations were highly affected by K source, rate, and time of application. Concentrationss increased when KCl was the K source, as application rate increased, and as KCl was applied closer to petiole sampling date. Elevated petiole Cl concentrations with increased KCl application have also been documented in sugarbeet (James et al., 1970a) and potato (McBride, 1985). Although not compared statistically between collection dates, in this research Cl concentrations were always higher in petioles collected later

in the season, which is indicates that potatoes continue to accumulate Cl throughout the growing season. Although Cl is an essential micronutrient, it is not metabolized into plant compounds and high concentrations of Cl are maintained in above ground plant tissue, including petioles, throughout the growing season.

Despite significant differences in petiole Cl concentrations by treatment, the antagonism between N and Cl in petioles that has been documented by other researchers was not strongly measured in this study. Previous researchers have documented an inverse relationship between potato petiole Cl and petiole nitrate-N. As KCl is applied at higher rates, and thus more Cl is available to potato plants, petiole Cl concentrations have increased while petiole nitrate-N concentrations were depressed (Jackson et al., 1982; Jackson and McBride, 1984; McBride, 1985; James et al., 1994). Although there was a slight depression in petiole nitrate-N with elevated Cl concentrations in some cases, this antagonism was not consistent throughout all petiole collections and factorials. With few exceptions, petiole nitrate-N concentrations were insignificant by treatment. In contrast to previous studies, in this research N was applied weekly at a uniform rate to all treatments during periods of peak uptake throughout the growing season and was thus replenished and available for plant uptake. This application method likely minimized the interaction and allowed the Cl uptake and movement in the system to be unhindered by N availability.

In this research, petiole Na, Mg, and Ca concentrations were generally lower with elevated petiole K concentrations, which is consistent with previous findings (Table 3.7, Table 3.8, Table 3.10, and Table 3.11). A reduction in uptake of other cations with elevated K application has been documented in various plant species (Kretschmer et al., 1953; Heenan and Campbell, 1981) and other researchers have measured petiole cation antagonism to varying degrees. Generally a strong antagonism between Mg and K and a weak antagonism between Ca and K are observed (Jackson et al., 1982; Chapman et al., 1992; James et al., 1994). In this research, the antagonism between Mg and K was measured in potato tops with the highest concentrations of Mg recorded with the lowest rates of K application.

Finally, although not compared statistically, petiole Na concentrations (0.55-0.93 g kg^{-1}) were considerably lower than petiole K concentrations (87.26-108.93 g kg^{-1}) for both petiole collection dates. Although soil K was always higher than soil Na, the difference between the two was not as great as the difference in nutrient concentrations measured in petioles. Soil Na

ranged from 0.41-0.48 cmol kg^{-1}, and soil K from 0.79-1.19 cmol kg^{-1}. The low concentrations of petiole Na as compared to petiole K may indicate that the plant is taking up K while filtering out Na. The ability of certain plant species to preferentially exclude Na has been documented (Munns, 2002; Tester and Davenport, 2003).

Plants synthesize organic acid anions in the cytosol if cations have been taken up in excess of anion uptake (Hiatt and Leggett, 1971; Blevins et al., 1974; Marschner, 2012). This process occurs in the cytosol where elevated cation concentrations result in hydrogen ions being pumped out of the cell, which in turn elevates pH. Organic acid anions are formed as a result, for the stabilization of cytosol pH and charge compensation (Marschner, 2012). Although total cations are generally greater than total anions in plant tissue, the difference between the two (Σcation - Σanion) can be affected by fertilizer application. In this research, petiole total cation concentrations were unaffected by treatment even when individual cation concentrations varied. Petiole total anion concentrations, and subsequently ion balance (Σcation - Σanion) were affected by treatment (Table 3.4, Table 3.5, Table 3.7, Table 3.8, Table 3.10, and Table 3.11). Anion concentrations were consistently elevated with higher petiole Cl concentrations indicating that Cl was a driver of changes in total anions. With some exception (Jackson et al., 1982), this is consistent with previous research which found that potato petiole cation concentrations were unaffected by treatment even when there were significant differences in individual petiole cation concentrations, while anion differences were highly significant by treatment and were elevated at higher KCl application (James et al., 1994). Other researchers have documented the influence of Cl concentrations on total plant anions and a subsequent reduction in ion balance (Σcation - Σanion) with elevated plant Cl concentrations in various species (Noggle, 1966) including forage crops (Tremblay et al., 2013), and tomato (Kafkafi et al., 1982). It can be inferred that there is a negative relationship between plant Cl concentration and organic anion acid synthesis.

Yield and Specific Gravity:

The yields reported here are on the low end for the region where yields are generally above 51 Mg ha^{-1} but can be as high as 78 Mg ha^{-1} (Lang et al., 1999; Dung et al., 2015). In 2014, the field was infected with white mold and above ground biomass died in mid-August reducing tuber bulking time. This research was conducted in a field with adequate pre-plant K (Lang et al.,

1999; Stark et al., 2004) to minimize tuber yield differences between treatments. There were no differences in tuber yields in either year, which is consistent with previous research conducted in high K soil (Dubetz and Bole, 1975; Krentos and Orphanos, 1979; Panique et al., 1997). Some researchers have observed a clear increase in yield following K application (Jackson and McBride, 1984; Westermann et al., 1994; Bansal and Umar, 1998; Singh and Lal, 2012; Grzebisz et al., 2015). However other studies, including one conducted in the same growing region (Davenport and Bentley, 2001), reported inconsistent yield responses despite initial soil test K being lower than regional extension recommendations (Rhue et al., 1986; Allison et al., 2001; Mohr and Tomasiewicz, 2012). These mixed results suggest that K management based on pre-plant soil test recommendations alone can be inadequate in some regions.

In this research, increased K application rate and K application closer to time of harvest reduced specific gravity, but no differences in specific gravity by K source were measured. These trends reflect the influence of soil salt on specific gravity. High rate and/or late season fertilizer application increases uptake of both salt and water by tubers and results in reduced specific gravity. Although it is generally established (Timm and Merkle, 1963; McDole et al., 1978; Laboski and Kelling, 2007) that K source impacts specific gravity, this has not been found in all studies (Davenport and Bentley, 2001). Other researchers have also measured a reduction in specific gravity with higher rates of K application (Timm and Merkle, 1963). Westermann et al. (1994) also observed that specific gravity was not affected by K source. They concluded that N depressed specific gravity more than K, and that K uptake influenced specific gravity more than the accompanying anion (Cl vs. sulfate). They also found that petiole K and petiole nitrate-N concentrations were both negatively correlated with specific gravity. In some instances, a negative correlation between specific gravity and petiole K, petiole Cl, and petiole anion concentrations was observed in this research. These negative correlations suggest that elevated plant Cl concentrations can reduce specific gravity but that it is not the only factor to consider. The relationship between K application and specific gravity is more complicated than simply modifying K source. Adequate K and N are necessary for high yields and growers have many factors to consider when making fertility decisions in potato production systems. As this and other research indicates that Cl leaches out of the system when applied earlier (September), whereas K remains available, modifications of time of K application, rather than K source, may help growers achieve optimum specific gravity.

Specific gravity can be affected by multiple factors including percent tuber water and sugar to starch ratio. The cause of lower specific gravity, while not obvious from the weight in water weight in air measurement method, can affect tuber processing quality. One study found that although KCl did affect specific gravity, the application of KCl did not have an effect on the uniformity of fry color or tuber "sugar ends" (Jackson and McBride, 1984). The authors suggest that while an increase in tuber nutrient concentrations (Cl, K, Ca, Mg) will reduce tuber osmotic potential and consequently increase concentration of water in tubers, the ratio of starch to sugar is unaffected. Consistent with this conclusion, another study found that although N and phosphorus application did affect tuber starch, sugar, and protein concentrations, K application did not (Sharma and Arora, 1988). The ratio of starch to sugar can lead to darker fry color and reduced end product quality. Despite the fact that the end product may be unaffected by higher tuber water concentrations, growers are likely to continue to manage K applications in an effort to ensure higher specific gravity in order to meet contract agreements.

CONCLUSIONS

In this research, Cl levels in potato plant tissue were measured for different K sources at varying rates and times of application in an attempt to track the fate of Cl in a potato production system where nutrients are not limited. These data support the conclusion that Cl is taken up unhindered by potato plants in large quantities when it is available and that Cl accumulates in plant tissue (particularly above ground biomass) until harvest. As there was no penalty, it appears that high levels of Cl are not detrimental to plant physiology, yield, or tuber quality if managed correctly, although maintaining low soil Cl levels can be challenging with regular application of high Cl fertilizer and crop residue inputs. If elevated plant Cl concentrations are of concern, applying KCl further in advance of plant uptake will minimize Cl availability. Potassium rate and time of application may have more of an effect on specific gravity than K source.

Although other researchers have documented an antagonism in uptake between Cl and N, that competition was not measured in this research. This suggests that that competition between nitrate and Cl decreases that when nitrogen is applied throughout the growing season to meet crop demand during peak aboveground growth. The competition between Cl and nitrate may be inconsequential if initial soil K is high, and K is applied at the recommended rate to meet potato crop need.

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Table 3.1. Treatments applied in field trials with Russet Burbank potatoes in 2013 and 2014 listing K source[†], K rate in K_2O (kg ha^{-1}), and application timing.[‡]

2013§				
		Planting	*In-Season*	
	KCl	112; 224	112; 224	
	SOP	112; 224	112; 224	
2014¶				
Factorial:	**Source x Timing**	Constant Rate		
		September	*Preplant*	*In-Season*
	KCl	224	224	224
	SOP	224	224	224
	Kmag	224	224	224
Factorial:	**Rate x Timing**	Constant Source		
		September	*Preplant*	*In-Season*
	KCl	112; 224; 448	112; 224; 448	112; 224; 448
	SOP	n/a	n/a	n/a
	Kmag	n/a	n/a	n/a
Factorial:	**Rate x Source**	Constant Timing		
		September	*Preplant*	*In-Season*
	KCl	n/a	n/a	112; 224; 448
	SOP	n/a	n/a	112; 224; 448
	Kmag	n/a	n/a	112; 224; 448

† K sources: KCl (0-0-60-0 S-45 Cl), SOP is K_2SO_4 (0-0-52-18 S), and Kmag is $K_2SO4*2MgSO_4$ (0-0-22-22 S-11 Mg).

‡ Control plots were planted both years.

§ Field was planted on April 24 and at-planting treatments were applied the same day while in-season treatments were applied 49 days after planting (DAP).

¶ Field was planted on April 11. September treatments were applied 206 days prior to planting, preplant treatments were applied 14 days prior to planting, and in-season treatments were applied 35 DAP.

Table 3.2. USDA #1s and specific gravity for Russet Burbank potatoes in 2013 and 2014 as affected by K source, rate of application, or time of application.†

2013 ‡			2014 § Source x Timing			Rate x Timing			Rate x Source		
Factor	Specific Gravity¶	USDA # 1s Mg ha^{-1}	Factor	Specific Gravity¶	USDA # 1s Mg ha^{-1}	Factor	Specific Gravity¶	USDA # 1s Mg ha^{-1}	Factor	Specific Gravity¶	USDA # 1s Mg ha^{-1}
Source#			*Source*#			*Rate*††			*Rate*††		
KCl	1.077	57	KCl	1.067	49	112	1.070 a	44	112	1.068 a	43
SOP	1.079	60	Kmag	1.066	45	224	1.067 b	48	224	1.066 ab	44
Timing			SOP	1.068	45	448	1.065 c	48	448	1.064 b	49
Planting	1.078	60	*Timing*			*Timing*			*Source*#		
In-Season	1.078	57	September	1.067	48	September	1.070 a	49	KCl	1.066	45
Rate††			Preplant	1.067	46	Preplant	1.066 b	46	Kmag	1.066	47
112	1.079	60	In-Season	1.066	44	In-Season	1.066 b	45	SOP	1.068	44
224	1.077	58	Control‡‡	1.071	48	Control‡‡	1.071	47	Control‡‡	1.071	48
Control‡‡	1.083	58									
Significance§§	**p-value**	**p-value**	***Significance***	**p-value**	**p-value**	***Significance***	**p-value**	**p-value**	***Significance***	**p-value**	**p-value**
Block	0.556	0.881	Block	0.050	0.323	Block	<0.0001	0.004	Block	0.078	0.581
Rate	0.367	0.684	Source	0.403	0.376	Rate	<0.0001	0.404	Rate	0.005	0.122
Source	0.083	0.516	Timing	0.656	0.461	Timing	<0.0001	0.427	Source	0.185	0.571
Timing	0.543	0.359	Source x Timing	0.002	0.179	Rate x Timing	0.172	0.268	Rate x Source	0.357	0.745
Rate x Source	0.651	0.409									
Rate x Timing	0.517	0.252									
Source x Timing	0.697	0.457									

† DAP = days after planting. Full harvest data, including tuber size categories and internal quality, is included in the appendix.

‡ Treatments were applied at planting (Planting) and 49 DAP (In-Season). A 3.0 m length of the center row of each plot was harvested 135 DAP.

§ Treatments were applied 206 days prior to planting (September), 14 days prior to planting (Preplant), 35 DAP (In-Season). A 4.6 m length of a center row of each plot was harvested 137 DAP.

¶ A subsample of tubers in the 170-283 g category was used to measure specific gravity.

SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

†† All rates are in K_2O (kg ha^{-1}).

‡‡ Values are treatment means for control plots. Control plots are not included in statistical analysis.

§§ Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

Table 3.3. Source x Timing Factorial: Soil analysis and plant material nutrient concentration as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

		Soil †			Tubers ‡			Tops §		
Factor		**Cl**	**S**	**K**	**Cl**	**N**	**K**	**Cl**	**N**	**K**
		(mg kg^{-1})		(cmol kg^{-1})	(g kg^{-1})					
Source ¶										
KCl		42 a	23 b	0.90	1.7 a	15	21 a	19 a	27	46
Kmag		134 b	76 a	0.97	1.2 b	16	21 a	14 b	28	47
SOP		14 b	39 b	0.86	1.1 b	16	20 b	14 b	28	45
Timing #										
September		14 b	22 b	0.91	1.0 c	16	21	14 b	28	46
Preplant		27 a	60 a	0.89	1.6 a	15	21	16 ab	27	46
In-Season		29 a	56 a	0.94	1.3 b	16	21	18 a	27	46
Control ††		16	24	0.79	1.3	15	20	15	28	45
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.724	0.542	0.414	0.098	0.026	0.004	0.949	0.055	0.249
Source	2	<0.0001	<0.0001	0.250	<0.0001	0.617	0.008	<0.0001	0.738	0.663
Timing	2	0.002	0.001	0.717	<0.0001	0.315	0.427	0.007	0.543	0.994
Source x Timing	4	0.000	0.016	0.142	0.001	0.506	0.529	0.000	0.647	0.266
Residuals	32									

* DAP = days after planting. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Soil samples were collected June 18-20, 2014 (68-70 DAP). Four soil cores (0-20 cm depth) were collected from the two middle rows of each plot and mixed well prior to analysis.

‡ Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis.

§ Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP).

¶ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

September treatments were applied 206 days prior to planting, preplant treatments 14 days prior to planting, and in-season treatments 35 DAP.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.4. Source x Timing Factorial: Nutrient analysis for petioles collected on 70 DAP as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference§**
		(g kg^{-1})								(mol_c kg^{-1})		
Source ¶												
KCl		107	3.5	7.1 a	0.72	4.9	1.7 b	22	16 a	0.34	0.23 a	0.12
Kmag		109	3.2	5.7 b	0.59	5.2	1.8 ab	22	10 b	0.34	0.22 b	0.12
SOP		105	3.5	6.3 b	0.65	5.3	1.9 a	22	9.6 b	0.33	0.21 b	0.12
Timing #												
September		105	3.3 b	6.3	0.64	5.3	1.9	22	9.5 b	0.33	0.21	0.12
Preplant		109	3.2 b	6.2	0.64	5.2	1.8	22	13 a	0.34	0.22	0.12
In-Season		107	3.7 a	6.5	0.67	5.0	1.8	22	14 a	0.34	0.22	0.12
Control ††		106	3.7	6.8	0.93	4.9	1.8	20	11	0.32	0.20	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.000	0.607	0.007	0.003	0.016	<0.0001	<0.0001	0.818	<0.0001	<0.0001	0.015
Source	2	0.366	0.168	0.002	0.141	0.169	0.031	0.661	<0.0001	0.402	0.007	0.441
Timing	2	0.301	0.032	0.645	0.887	0.242	0.278	0.935	<0.0001	0.358	0.056	0.902
Source x Timing	4	0.699	0.071	0.147	0.738	0.116	0.779	0.129	<0.0001	0.435	0.643	0.592
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on June 20, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

September treatments were applied 206 days prior to planting, preplant treatments 14 days prior to planting, and in-season treatments 35 DAP.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.5. Source x Timing Factorial: Nutrient analysis for petioles collected 97 DAP as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference§**
		(g kg^{-1})								(mol_c kg^{-1})		
Source ¶												
KCl		91	5.9	11 a	0.61	2.3	1.5	16 b	36 a	0.34	0.23 a	0.11 b
Kmag		94	5.2	10 b	0.61	2.2	1.5	15 b	27 b	0.34	0.20 b	0.14 a
SOP		91	5.9	11 a	0.70	2.3	1.5	17 a	26 b	0.34	0.21 b	0.13 a
Timing #												
September		92	5.7	11	0.63	2.4	1.6	16	27 b	0.34	0.21	0.13
Preplant		92	5.8	11	0.65	2.2	1.5	16	31 a	0.34	0.22	0.12
In-Season		92	6.0	10	0.65	2.1	1.5	16	31 a	0.34	0.22	0.12
Control ††		88	6.1	12	0.78	2.4	1.5	17	28	0.33	0.22	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.058	0.248	0.343	0.003	0.003	0.183	<0.0001	0.076	0.063	<0.0001	0.003
Source	2	0.549	0.903	0.021	0.294	0.559	0.243	0.031	<0.0001	0.943	<0.0001	<0.0001
Timing	2	0.948	0.782	0.205	0.963	0.059	0.099	0.412	0.034	0.825	0.291	0.209
Source x Timing	4	0.391	0.742	0.897	0.760	0.290	0.973	0.012	0.010	0.275	0.001	0.237
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on July 17, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

September treatments were applied 206 days prior to planting, preplant treatments 14 days prior to planting, and in-season treatments 35 DAP.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.6. Rate x Timing Factorial: Soil analysis and plant material nutrient concentration as affected by K rate and time of application when K source is KCl.*

		Soil †			Tubers ‡			Tops §		
Factor		**Cl**	**S**	**K**	**Cl**	**N**	**K**	**Cl**	**N**	**K**
Rate ¶		(mg kg^{-1})		(cmol kg^{-1})	(g kg^{-1})					
112		24 b	23	0.83 b	1.5 b	16	20 b	20 ab	27	45 b
224		42 a	23	0.90 b	1.7 b	15	21 b	19 b	27	46 b
448		49 a	22	1.1 a	2.0 a	15	22 a	23 a	25	51 a
Timing #										
September		15 b	25	0.95	1.1 b	15 b	21 b	15 b	27	47
Preplant		53 a	23	0.91	2.2 a	15 b	21 ab	22 a	26	47
In-Season		47 a	21	0.97	1.9 a	17 a	22 a	24 a	26	47
Control ††		16	24	0.79	1.3	15	20	15	28	45
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.603	0.042	<0.0001	0.615	0.674	0.003	0.879	0.004	0.444
Rate	2	0.007	0.742	<0.0001	<0.0001	0.411	0.002	0.043	0.067	0.010
Timing	2	<0.0001	0.186	0.539	<0.0001	0.008	0.022	<0.0001	0.274	0.981
Rate x Timing	4	0.241	0.018	0.172	0.033	0.420	0.635	0.471	0.605	0.125
Residuals	32									

* DAP = days after planting. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.
† Soil samples were collected June 18-20, 2014 (68-70 DAP). Four soil cores (0-20 cm depth) were collected from the two middle rows of each plot and mixed well prior to analysis.
‡ Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283g size category were cut longitudinally and used for analysis.
§ Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP).
¶ K rate in K_2O (kg ha^{-1}).
# September treatments were applied 206 days prior to planting, preplant treatments 14 days prior to planting, and in-season treatments 35 DAP.
†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.7. Rate x Timing Factorial: Nutrient analysis for petioles collected 70 DAP as affected by K rate and time of application when K source is KCl.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference§**
		(g kg^{-1})								(mol_c kg^{-1})		
Rate ¶												
112		103 b	3.7 a	6.8 ab	0.69	5.4 a	1.9 a	21	13 b	0.33	0.22	0.11
224		107 a	3.5 a	7.1 a	0.72	4.9 b	1.3 b	22	16 a	0.34	0.23	0.12
448		109 a	3.0 b	6.2 b	0.56	5.4 a	1.9 a	21	16 a	0.34	0.22	0.12
Timing #												
September		105	3.3 b	6.4	0.60	5.3	1.9	21	9.7 b	0.33	0.21 b	0.12
Preplant		107	3.3 b	6.7	0.65	5.2	1.8	21	18 a	0.34	0.23 a	0.11
In-Season		107	3.7 a	6.8	0.72	5.2	1.8	21	18 a	0.34	0.23 a	0.11
Control ††		106	3.7	6.8	0.93	4.9	1.8	20	11	0.32	0.20	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	<0.0001	0.784	0.008	0.019	<0.0001	<0.0001	<0.0001	0.081	<0.0001	<0.0001	<0.0001
Rate	2	0.012	0.003	0.054	0.080	0.019	0.005	0.323	<0.0001	0.071	0.126	0.811
Timing	2	0.459	0.054	0.493	0.281	0.997	0.267	0.592	<0.0001	0.082	<0.0001	0.058
Rate x Timing	4	0.081	0.122	0.060	0.855	0.052	0.168	0.001	0.010	0.009	0.033	0.750
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on June 20, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

September treatments were applied 206 days prior to planting, preplant treatments 14 days prior to planting, and in-season treatments 35 DAP.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.8. Rate x Timing Factorial: Nutrient analysis for petioles collected 97 DAP as affected by K rate and time of application when K source is KCl.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference §**
		(g kg^{-1})								(mol_c kg^{-1})		
Rate ¶												
112		89 b	6.2 a	11	0.66	2.3	1.5	16	32 b	0.34	0.22	0.12
224		91 b	5.9 a	11	0.61	2.3	1.5	16	36 a	0.34	0.23	0.11
448		97 a	4.9 b	11	0.59	2.3	1.4	15	38 a	0.34	0.22	0.11
Timing #												
September		93	5.6	11	0.67	2.4	1.6 a	16	27 b	0.34	0.21 b	0.13 a
Preplant		90	5.9	11	0.65	2.2	1.4 b	15	39 a	0.34	0.23 a	0.10 b
In-Season		94	5.5	11	0.55	2.3	1.4 b	15	40 a	0.34	0.24 a	0.10 b
Control ††		87	6.1	12	0.78	2.4	1.5	17	28	0.33	0.22	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.025	0.292	0.031	0.006	<0.0001	0.003	0.001	0.112	0.013	0.018	0.045
Rate	2	0.009	0.003	0.086	0.657	0.768	0.586	0.067	0.013	0.482	0.471	0.712
Timing	2	0.301	0.523	0.122	0.225	0.409	<0.0001	0.085	<0.0001	0.847	<0.0001	0.001
Rate x Timing	4	0.132	0.191	0.512	0.826	0.043	0.587	0.421	0.929	0.431	0.951	0.928
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on July 17, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

September treatments were applied 206 days prior to planting, preplant treatments 14 days prior to planting, and in-season treatments 35 DAP.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.9. Rate x Source Factorial: Soil analysis and plant material nutrient concentration as affected by K source and rate of application when K is applied in-season.*

		Soil †			Tubers ‡			Tops §		
Factor		**Cl**	**S**	**K**	**Cl**	**N**	**K**	**Cl**	**N**	**K**
		(mg kg^{-1})		(cmol kg^{-1})	(g kg^{-1})					
Rate ¶										
112		18 b	41 c	0.81 b	1.2 b	16	21 b	17	28	44 b
224		29 a	56 b	0.94 b	1.3 b	16	21 b	18	27	46 b
448		27 ab	85 a	1.2 a	1.6 a	16	22 a	18	26	50 a
Source #										
KCl		47 a	21 c	0.97	1.9 a	17	22 a	24 a	26	47
Kmag		14 b	105 a	1.0	1.2 b	15	22 a	15 b	27	48
SOP		12 b	56 b	0.93	1.0 c	16	21 b	13 b	27	46
Control ††		16	24	0.79	1.3	15	20	15	28	45
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.836	0.408	0.110	0.801	0.183	0.003	0.347	0.031	0.648
Rate	2	0.051	<0.0001	<0.0001	<0.0001	0.130	0.024	0.582	0.119	0.003
Source	2	<0.0001	<0.0001	0.504	<0.0001	0.061	0.015	<0.0001	0.376	0.511
Rate x Source	4	0.063	<0.0001	0.798	<0.0001	0.489	0.164	0.644	0.618	0.327
Residuals	32									

* DAP = days after planting. Treatments were applied 35 DAP. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Soil samples were collected June 18-20, 2014 (68-70 DAP). Four soil cores (0-20 cm depth) were collected from the two middle rows of each plot and mixed well prior to analysis.

‡ Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283g size category were cut longitudinally and used for analysis.

§ Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP).

¶ K rate in K_2O (kg ha^{-1}).

SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.10. Rate x Source Factorial: Nutrient analysis for petioles collected 70 DAP as affected by K source and rate of application when K is applied in-season.*

		----------Cations----------				----------Anions----------						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference §**
		----------(g kg^{-1})----------								----------(mol_c kg^{-1})----------		
Rate ¶												
112		105	3.9 a	6.8 a	0.72 a	5.0	1.9	22 a	11 b	0.34	0.22 a	0.12
224		107	3.7 a	6.5 a	0.67 a	5.0	1.8	21 a	13 a	0.34	0.22 a	0.12
448		107	3.1 b	5.3 b	0.54 b	5.3	1.9	20 b	14 a	0.33	0.21 b	0.12
Source #												
KCl		107	3.7 a	6.8 a	0.72 a	5.2	1.8	21	18 a	0.34	0.23 a	0.11 b
Kmag		107	3.2 b	5.4 b	0.55 b	5.1	1.9	22	11 b	0.33	0.21 b	0.12 ab
SOP		105	3.7 a	6.4 a	0.65 ab	4.9	1.9	21	10 b	0.33	0.21 b	0.13 a
Control ††		106	3.7	6.8	0.93	4.9	1.8	20	11	0.32	0.20	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	<0.0001	0.353	0.001	<0.0001	<0.0001	<0.0001	<0.0001	0.483	<0.0001	<0.0001	0.001
Rate	2	0.748	0.001	0.001	0.021	0.325	0.079	0.004	<0.0001	0.161	0.010	0.987
Source	2	0.743	0.038	0.002	0.042	0.309	0.190	0.745	<0.0001	0.220	<0.0001	0.022
Rate x Source	4	0.651	0.856	0.674	0.798	0.342	0.728	0.404	0.012	0.680	0.883	0.517
Residuals	32											

* DAP = days after planting. Treatments were applied 35 DAP. Thirty petioles were collected on June 20, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 3.11. Rate x Source Factorial: Nutrient analysis for petioles collected 97 DAP as affected by K source and rate of application when K is applied in-season.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference §**
		(g kg^{-1})								(mol_c kg^{-1})		
Rate ¶												
112		92 b	5.8 a	11 a	0.65	2.2	1.5	17 a	29	0.34	0.22	0.12
224		92 b	6.0 a	10 a	0.65	2.1	1.5	16 ab	31	0.34	0.22	0.12
448		97 a	4.9 b	9.9 b	0.61	2.3	1.5	15 b	32	0.34	0.21	0.13
Source #												
KCl		94	5.5	11 a	0.55 b	2.3	1.4 b	15	40 a	0.34	0.24 a	0.10 b
Kmag		95	5.4	10 b	0.66 a	2.1	1.5 a	16	28 b	0.34	0.21 b	0.13 a
SOP		91	5.7	11 a	0.69 a	2.2	1.5 a	16	26 b	0.34	0.20 b	0.13 a
Control ††		87	6.1	12	0.78	2.4	1.5	17	28	0.33	0.22	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.049	0.735	0.979	<0.0001	0.002	0.597	0.004	0.014	0.001	<0.0001	0.046
Rate	2	0.025	0.005	0.013	0.683	0.226	0.791	0.005	0.218	0.640	0.477	0.166
Source	2	0.207	0.703	0.001	0.028	0.336	0.003	0.738	<0.0001	0.401	<0.0001	<0.0001
Rate x Source	4	0.706	0.409	0.956	0.422	0.265	0.955	0.519	0.080	0.558	0.149	0.782
Residuals	32											

* DAP = days after planting. Treatments were applied 35 DAP. Thirty petioles were collected on July 17, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

GENERAL CONCLUSIONS

Sarah Elizabeth Light

Although the results of this research are not sufficient to modify best management practices in potato production, general findings may provide impetus for additional research that could. Despite the inconsistencies of the results, essential oils may prove useful as a component of an integrated disease management plan targeted toward *V. dahliae*. There were essential oils that were very effective in inhibiting *V. dahliae* growth *in vitro,* and there were no phytotoxic consequences from essential oil application to the potato seed. More work is needed to determine how essential oils impact *V. dahliae* growth in order to assess the best method of application, optimum rates of application, or if a combination of products would be more efficacious. Isolation of the specific component compounds could be more effective in inhibiting fungal growth. Any one of these and/or a combination of multiple compounds may provide opportunities to help manage *V. dahliae* by facilitating the production of a product that can be easily applied in the field, and/or that is not cost prohibitive to growers.

Despite increased regulation, metam sodium remains the most used active ingredient in commercial potato production. The concerns with heavy reliance on chemical application include adverse effects on soil ecology and human health. The impacts of any essential oil product should be evaluated to ensure that it is not also detrimental to these metrics. More comprehensive research is needed on the use of essential oils or other alternative products before growers will modify practices that would reduce or eliminate the use of metam sodium soil fumigation. Ultimately only an integrated alternative management plan that is reasonable to implement, does not decrease yield or tuber quality, comparable to or lower in cost than metam sodium, and effective at reducing disease will be widely adapted by growers.

In this research, Cl levels in potato plant tissue were measured for different K sources at varying rates and times of application in an attempt to track the fate of Cl in a potato production system where nutrients are not limited. These data support the conclusion that Cl is taken up unhindered by potato plants in large quantities when it is available and that Cl accumulates in plant tissue (particularly above ground biomass) until harvest. As there was no penalty, it appears that high levels of Cl are not detrimental to plant physiology, yield, or tuber quality if managed correctly, although maintaining low soil Cl levels can be challenging with regular application of high Cl fertilizer and crop residue inputs. If elevated plant Cl concentrations are of concern, applying KCl further in advance of plant uptake will minimize Cl availability. Potassium rate and time of application may have more of an effect on specific gravity than K source.

Although other researchers have documented an antagonism in uptake between Cl and N, that competition was not measured in this research. This suggests that that competition between nitrate and Cl decreases that when nitrogen is applied throughout the growing season to meet crop demand during peak aboveground growth. The competition between Cl and nitrate may be inconsequential if initial soil K is high, and K is applied at the recommended rate to meet potato crop need.

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APPENDICES

Table 4.1. Tuber yield, size category, specific gravity, and internal damage for Russet Burbank in 2013 as affected by K source, rate of application, or time of application.*

					USDA #1s				
Factor		**Specific Gravity**	**0-113 g**	**cull**	**113-170 g**	**170-283 g**	**> 283 g**	**USDA # 1s**	**total † internals**
			Mg ha^{-1}						
Source ‡									
KCl		1.077	12	8.4	20 b	22	16	57	2.3
SOP		1.079	12	8.4	25 a	21	14	60	2.2
Timing §									
Planting		1.078	12	10 a	22	22	17	61	2.1
In-Season		1.078	13	6.4 b	23	21	13	57	2.4
Rate (kg K_2O ha$^{-1)}$									
112		1.079	13	8.2	24	21	14	60	2.0
224		1.077	12	8.6	21	21	16	58	2.5
Control ¶		1.083	16	8.0	27	22	9.4	58	2.4
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.556	0.168	0.000	0.006	0.873	0.160	0.881	0.059
Rate	1	0.367	0.221	0.789	0.057	1	0.459	0.684	0.282
Source	1	0.083	0.974	0.942	0.007	0.833	0.447	0.516	0.904
Timing	1	0.543	0.289	0.003	0.366	0.567	0.079	0.359	0.400
Rate x Source	1	0.651	0.730	0.606	0.056	0.751	0.675	0.409	0.547
Rate x Timing	1	0.517	0.949	0.146	0.620	0.12	0.447	0.252	0.547
Source x Timing	1	0.697	0.452	0.151	0.601	0.559	0.017	0.457	0.904
Rate x Source x Timing	1	0.898	0.981	0.586	0.109	0.581	0.796	0.391	0.904
Residuals	28								

* Tubers were harvested 135 days after planting (DAP) from a 3.0 m length of the middle row of each plot and a subsample of tubers in the 170-283 g category was used to measure specific gravity and internal quality. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Mean number of tubers (out of 10 sampled) with hollow heart, vascular discoloration, brown center, or internal brown spot.

‡ SOP is K_2SO_4.

§ Field was planted on April 24. Treatments were applied at planting (Planting) and 49 DAP (In-Season)

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.2. Source x Timing Factorial: Tuber yield, size category, specific gravity, and internal damage for Russet Burbank in 2014 as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

				----------USDA #1s----------				
Factor	**Specific Gravity**	**cull**	**0-113 g**	**113-170 g**	**170-283 g**	**> 283 g**	**USDA # 1s**	**Total† Internals**
		----------Mg ha^{-1}----------						
Source ‡								
KCl	1.067	3.0	13. b	26	16	6.3	49	2.1
Kmag	1.066	2.1	15 ab	25.	16	3.9	45	1.9
SOP	1.068	3.0	16 a	24	17	3.5	45	2.1
Timing §								
September	1.067	3.0	16	29 a	14	4.2	48	2.1
Preplant	1.067	1.8	14	24 b	17	4.9	46	1.7
In-Season	1.066	3.2	14	22 b	18	4.5	44	2.3
Control ¶	1.071	3.5	15	28	14	5.1	48	2.2

Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.050	0.017	0.000	0.030	0.031	0.081	0.323	0.310
Source	2	0.403	0.309	0.026	0.773	0.955	0.173	0.376	0.788
Timing	2	0.656	0.067	0.134	0.003	0.278	0.899	0.461	0.082
Source x Timing	4	0.002	0.155	0.762	0.015	0.497	0.711	0.179	0.205
Residuals	32								

*Tubers were harvested 137 days after planting (DAP) from a 4.6m length of one of the center rows of each plot. A subsample of tubers in the 170-283 g category was used to measure specific gravity and internal quality. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Mean number of tubers (out of 10 sampled) with hollow heart, vascular discoloration, brown center, or internal brown spot.

‡ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

§ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.3. Source x Timing Factorial: Nutrient analysis for petioles collected 70 DAP as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference§**
		(g kg^{-1})								(mol_c kg^{-1})		
Source ¶												
KCl		107	3.5	7.1 a	0.72	4.9	1.7 b	22	16 a	0.34	0.23 a	0.12
Kmag		109	3.2	5.7 b	0.59	5.2	1.8 ab	22	10 b	0.34	0.22 b	0.12
SOP		105	3.5	6.3 b	0.65	5.3	1.9 a	22	9.6 b	0.33	0.21 b	0.12
Timing #												
September		105	3.3 b	6.3	0.64	5.3	1.9	22	9.5 b	0.33	0.21	0.12
Preplant		109	3.2 b	6.2	0.64	5.1	1.8	22	13 a	0.34	0.22	0.12
In-Season		107	3.7 a	6.5	0.67	5.0	1.8	22	13 a	0.34	0.22	0.12
Control ††		106	3.7	6.8	0.93	4.9	1.8	20	11	0.32	0.20	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.000	0.607	0.007	0.003	0.016	<0.0001	<0.0001	0.818	<0.0001	<0.0001	0.015
Source	2	0.366	0.168	0.002	0.141	0.169	0.031	0.661	<0.0001	0.402	0.007	0.441
Timing	2	0.301	0.032	0.645	0.887	0.242	0.278	0.935	<0.0001	0.358	0.056	0.902
Source x Timing	4	0.699	0.071	0.147	0.738	0.116	0.779	0.129	<0.0001	0.435	0.643	0.592
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on June 20, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.4. Source x Timing Factorial: Nutrient analysis for petioles collected 97 DAP as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference§**
		(g kg^{-1})								(mol_c kg^{-1})		
Source ¶												
KCl		91	5.9	11 a	0.61	2.3	1.5	16 b	36 a	0.34	0.23 a	0.11 b
Kmag		94	5.7	10 b	0.61	2.2	1.5	15 b	27 b	0.34	0.20 b	0.14 a
SOP		91	5.9	11 a	0.70	2.3	1.5	17 a	26 b	0.34	0.21 b	0.13 a
Timing #												
September		92	5.7	11	0.63	2.4	1.6	16	27 b	0.34	0.21	0.13
Preplant		92	5.8	11	0.65	2.2	1.5	16	31 a	0.34	0.22	0.12
In-Season		92	6.0	10	0.65	2.1	1.5	16	31 a	0.34	0.22	0.12
Control ††		87	6.1	12	0.78	2.4	1.5	17	28	0.33	0.22	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.058	0.248	0.343	0.003	0.003	0.183	<0.0001	0.076	0.063	<0.0001	0.003
Source	2	0.549	0.903	0.021	0.294	0.559	0.243	0.031	<0.0001	0.943	<0.0001	<0.0001
Timing	2	0.948	0.782	0.205	0.963	0.059	0.099	0.412	0.034	0.825	0.291	0.209
Source x Timing	4	0.391	0.742	0.897	0.760	0.290	0.973	0.012	0.010	0.275	0.001	0.237
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on July 17, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.5. Source x Timing Factorial: Soil analysis for samples collected 68-70 DAP as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

Factor		pH	Cl	Mehlich III P	S	Ca	Mg	K	Na
			----------(mg kg^{-1})----------			----------(cmol kg^{-1})----------			
Source †									
KCl		6.0	42 a	83	23 b	6.4 a	2.1 b	0.90	0.46
Kmag		5.8	14 b	77	76 a	5.8 b	2.4 a	0.97	0.47
SOP		5.9	14 b	97	39 b	6.2 ab	2.1 b	0.86	0.45
Timing ‡									
September		6.0 a	14 b	88	22 b	6.0	2.1	0.91	0.44
Preplant		5.8 b	27 a	86	60 a	6.2	2.2	0.89	0.46
In-Season		5.9 b	29 a	82	56 a	6.1	2.3	0.94	0.48
Control §		6.0	16	103	24	6.2	2.1	0.79	0.42
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.139	0.724	0.123	0.542	0.006	0.207	0.414	0.043
Source	2	0.087	<0.0001	0.170	<0.0001	0.019	<0.0001	0.250	0.805
Timing	2	<0.0001	0.002	0.860	0.001	0.398	0.077	0.717	0.059
Source x Timing	4	0.030	0.000	0.745	0.016	0.507	0.962	0.142	0.228
Residuals	32								

* DAP = days after planting. Four soil cores (0-20 cm depth) were collected June 18-20, 2014 from the two middle rows of each plot and mixed well prior to analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

‡ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

§ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.6. Source x Timing Factorial: Nutrient concentration of above ground plant material (tops) as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.

Factor		N	P	Mg	K	Ca	S	Cl
		----------(g kg^{-1})----------						
Source †								
KCl		27	1.6	5.2	46	14	1.6 b	19 a
Kmag		28	1.7	5.3	47	14	1.7 a	14 b
SOP		28	1.6	5.6	45	14	1.6 b	14 b
Timing ‡								
September		28	1.7	5.5	46	15	1.7	14 b
Preplant		27	1.6	5.1	46	14	1.6	16 ab
In-Season		27	1.7	5.5	46	14	1.7	18 a
Control §		28	1.6	5.6	45	15	1.6	15
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.055	0.549	0.862	0.249	0.229	0.734	0.949
Source	2	0.738	0.263	0.574	0.663	0.960	0.052	<0.0001
Timing	2	0.543	0.853	0.346	0.994	0.239	0.086	0.007
Source x Timing	4	0.647	0.761	0.372	0.266	0.761	0.380	0.000
Residuals	32							

* DAP = days after planting. Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP). Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

‡ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

§ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.7. Source x Timing Factorial: Nutrient concentration of harvested tubers as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

Factor		N	P	Mg	K	Ca	S	Cl
		----------(g kg^{-1})----------						
Source †								
KCl		15	3.0 ab	0.80 b	21 a	0.37	1.16 b	1.7 a
Kmag		16	3.1 a	0.86 a	21 a	0.37	1.27 a	1.2 b
SOP		16	2.9 b	0.82 b	20 b	0.37	1.21 ab	1.1 b
Timing ‡								
September		16	3.1	0.84	21	0.35	1.2	1.0 c
Preplant		15	2.9	0.81	21	0.37	1.2	1.6 a
In-Season		16	3.0	0.82	21	0.38	1.2	1.3 b
Control §		15	2.8	0.81	20	0.34	1.1	1.27
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.026	0.004	0.262	0.004	0.717	0.184	0.098
Source	2	0.617	0.053	0.004	0.008	1.000	0.020	<0.0001
Timing	2	0.315	0.111	0.324	0.427	0.126	0.486	<0.0001
Source x Timing	4	0.506	0.602	0.477	0.529	0.090	0.949	0.001
Residuals	32							

* DAP = days after planting. Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

‡ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

§ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.8. Source x Timing Factorial: Tuber, tops, and total uptake as affected by K source and time of application when K is applied at 224 kg K_2O ha^{-1}.*

		Tuber				Tops				Total †			
Factor		**N**	**S**	**Cl**	**K**	**N**	**S**	**Cl**	**K**	**N**	**S**	**Cl**	**K**
		(kg ha^{-1})											
Source ‡													
KCl		175	13	19 a	243	69	4.2	48	115	245	18	67 a	358
Kmag		172	14	13 b	234	85	5.4	44	144	257	19	57 ab	378
SOP		181	14	12 b	231	78	4.5	40	127	259	18	53 b	358
Timing §													
September		190	14	12 b	245	78	4.8	40	128	268	19	52	373
Preplant		170	13	18 a	232	79	4.6	44	130	249	18	62	362
In-Season		168	14	14 b	229	76	4.7	49	128	244	18	63	357
Control ¶		187	14	16	251	80	4.6	45	134	267	18	61	384
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.150	0.598	0.094	0.515	0.338	0.556	0.733	0.827	0.057	0.564	0.442	0.455
Source	2	0.662	0.811	<0.0001	0.632	0.130	0.102	0.392	0.088	0.529	0.270	0.036	0.480
Timing	2	0.085	0.456	0.002	0.422	0.902	0.946	0.233	0.985	0.203	0.488	0.088	0.691
Source x Timing	4	0.594	0.134	0.029	0.098	0.044	0.054	0.016	0.127	0.249	0.028	0.057	0.145
Residuals	32												

* DAP = days after planting. Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP). Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Total uptake the uptake in tops plus tubers.

‡ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

§ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.9. Rate x Timing Factorial: Tuber yield, size category, specific gravity, and internal damage for Russet Burbank in 2014 as affected by K rate and time of application when K source is KCl.*

Factor		Specific Gravity	cull	0-113 g	113-170 g	170-283 g	> 283 g	USDA # 1s	Total† Internals
					----------USDA #1s----------				
			----------(Mg ha^{-1})----------						
Rate ‡									
112		1.070 a	2.4	15	24	15 b	2.2	44	2.5
224		1.067 b	3.0	13	26	16 ab	2.8	48	2.1
448		1.065 c	3.6	14	23	19 a	2.6	48	2.2
Timing §									
September		1.0701 a	2.9	16	29 a	16	2.0	49	2.2
Preplant		1.066 b	3.4	13	22 b	17	3.1	46	1.9
In-Season		1.066 b	2.7	13	22 b	18	2.5	45	2.7
Control ¶		1.071	3.5	15	28	14	2.3	47	2.2
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	<0.0001	0.095	<0.0001	0.016	<0.0001	<0.0001	0.004	0.644
Rate	2	<0.0001	0.363	0.302	0.418	0.038	0.711	0.404	0.699
Timing	2	<0.0001	0.707	0.064	0.013	0.544	0.240	0.427	0.216
Rate x Timing	4	0.172	0.563	0.777	0.393	0.612	0.729	0.268	0.404
Residuals	32								

* DAP = days after planting. Tubers were harvested 137 DAP from a 4.6m length of one of the center rows of each plot. A subsample of tubers in the 170-283 g category was used to measure specific gravity and internal quality. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Mean number of tubers (out of 10 sampled) with hollow heart, vascular discoloration, brown center, or internal brown spot.

‡ K rate in K_2O (kg ha^{-1}).

§ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.10. Rate x Timing Factorial: Nutrient analysis for petioles collected 70 DAP as affected by K rate and time of application when K source is KCl.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference§**
		(g kg^{-1})								(mol_c kg^{-1})		
Rate ¶												
112		103 b	3.7 a	6.8 ab	0.69	5.4 a	1.9 a	21	13 b	0.33	0.22	0.11
224		107 a	3.5 a	7.1 a	0.72	4.9 b	1.7 b	22	16 a	0.34	0.23	0.12
448		109 a	3.0 b	6.2 b	0.56	5.4 a	1.9 a	21	16 a	0.34	0.22	0.12
Timing #												
September		105	3.3 b	6.4	0.60	5.3	1.9	21	9.7 b	0.33	0.21 b	0.12
Preplant		107	3.3 b	6.7	0.65	5.2	1.8	21	18 a	0.34	0.23 a	0.11
In-Season		107	3.7 a	6.8	0.72	5.2	1.8	21	18 a	0.34	0.23 a	0.11
Control ††		106	3.7	6.8	0.93	4.9	1.8	20	11	0.32	0.20	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	<0.0001	0.784	0.008	0.019	<0.0001	<0.0001	<0.0001	0.081	<0.0001	<0.0001	<0.0001
Rate	2	0.012	0.003	0.054	0.080	0.019	0.005	0.323	<0.0001	0.071	0.126	0.811
Timing	2	0.459	0.054	0.493	0.281	0.997	0.267	0.592	<0.0001	0.082	<0.0001	0.058
Rate x Timing	4	0.081	0.122	0.060	0.855	0.052	0.168	0.001	0.010	0.009	0.033	0.750
Residuals	32											

* DAP= days after planting. Thirty petioles were collected on June 20, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.11. Rate x Timing Factorial: Nutrient analysis for petioles collected 97 DAP as affected by K rate and time of application when K source is KCl.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference §**
		(g kg^{-1})								(mol_c kg^{-1})		
Rate ¶												
112		89 b	6.2 a	11	0.66	2.3	1.5	16	32 b	0.34	0.22	0.12
224		91 b	5.9 a	11	0.61	2.3	1.5	16	36 a	0.34	0.23	0.11
448		97 a	4.9 b	11	0.59	2.3	1.4	15	38 a	0.34	0.23	0.11
Timing #												
September		93	5.6	11	0.67	2.4	1.6 a	16	27 b	0.34	0.21 b	0.13 a
Preplant		90	5.9	11	0.65	2.2	1.4 b	15	39 a	0.34	0.23 a	0.10 b
In-Season		94	5.5	11	0.55	2.3	1.4 b	15	40 a	0.34	0.24 a	0.10 b
Control ††		87	6.1	12	0.78	2.4	1.5	17	28	0.33	0.22	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.025	0.292	0.031	0.006	<0.0001	0.003	0.001	0.112	0.013	0.018	0.045
Rate	2	0.009	0.003	0.086	0.657	0.768	0.586	0.067	0.013	0.482	0.471	0.712
Timing	2	0.301	0.523	0.122	0.225	0.409	<0.0001	0.085	<0.0001	0.847	<0.0001	0.001
Rate x Timing	4	0.132	0.191	0.512	0.826	0.043	0.587	0.421	0.929	0.431	0.951	0.928
Residuals	32											

* DAP = days after planting. Thirty petioles were collected on July 17, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.12. Rate x Timing Factorial: Soil analysis for samples collected 68-70 DAP as affected by K rate and time of application when K source is KCl.*

Factor		pH	Cl	Mehlich III P	S	Ca	Mg	K	Na
			----------(mg kg^{-1})----------			----------(cmol kg^{-1})----------			
Rate †									
112		6.0	24 b	79	23	6.2 a	2.06 ab	0.83 b	0.45 a
224		6.0	42 a	83	23	6.4 a	2.10 a	0.90 b	0.46 a
448		6.0	49 a	89	22	5.8 b	1.98 b	1.1 a	0.41 b
Timing ‡									
September		6.0	15 b	87	25	6.1	2.01	0.95	0.43
Preplant		5.9	53 a	87	23	6.2	2.09	0.91	0.43
In-Season		6.0	47 a	77	21	6.1	2.03	0.97	0.45
Control §		6.0	16	103	24	6.2	2.10	0.79	0.42
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.006	0.603	0.349	0.042	0.001	0.018	<0.0001	<0.0001
Rate	2	0.937	0.007	0.333	0.742	0.021	0.051	<0.0001	0.004
Timing	2	0.110	<0.0001	0.269	0.186	0.831	0.210	0.539	0.134
Rate x Timing	4	0.018	0.241	0.757	0.018	0.706	0.102	0.172	0.009
Residuals	32								

* DAP = days after planting. Four soil cores (0-20 cm depth) were collected June 18-20, 2014 from the two middle rows of each plot and mixed well prior to analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† K rate in K_2O (kg ha^{-1}).

‡ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

§ Values are treatment means for control plots. Control plots are not included in statistical analysis

Table 4.13. Rate x Timing Factorial: Nutrient concentration of above ground plant material (tops) as affected by K rate and time of application when K source is KCl.*

Factor		N	P	Mg	K	Ca	S	Cl
		----------(g kg^{-1})----------						
Rate †								
112		27	1.8	5.8 a	45 b	15	1.64	20 ab
224		27	1.6	5.2 ab	46 b	14	1.60	19 b
448		25	1.7	4.9 b	51 a	13	1.57	23 a
Timing ‡								
September		27	1.7	5.2	47	14	1.68 a	14 b
Preplant		26	1.7	5.2	47	14	1.55 b	22 a
In-Season		26	1.6	5.6	47	14	1.58 ab	24 a
Control §		28	1.6	5.6	45	15	1.58	15
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.004	0.010	0.510	0.444	0.029	0.176	0.879
Rate	2	0.067	0.401	0.033	0.010	0.193	0.364	0.043
Timing	2	0.274	0.628	0.350	0.981	0.824	0.039	<0.0001
Rate x Timing	4	0.605	0.622	0.013	0.125	0.003	0.215	0.471
Residuals	32							

* DAP = days after planting. Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP). Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† K rate in K_2O (kg ha^{-1}).

‡ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

§ Values are treatment means for control plots. Control plots are not included in statistical analysis

Table 4.14. Rate x Timing Factorial: Nutrient concentration of harvested tubers as affected by K rate and time of application when K source is KCl.*

Factor		N	P	Mg	K	Ca	S	Cl
		----------(g kg^{-1})----------						
Rate †								
112		16	2.9	0.80	20 b	0.36	1.2	1.5 b
224		15	3.0	0.80	21 b	0.37	1.2	1.7 b
448		15	3.0	0.82	22 a	0.38	1.2	2.0 a
Timing ‡								
September		15 b	2.9	0.81	20.5 b	0.34 b	1.2	1.1 b
Preplant		15 b	3.0	0.80	21.4 ab	0.37 ab	1.1	2.2 a
In-Season		17 a	3.1	0.81	21.8 a	0.40 a	1.2	2.0 a
Control §		15	2.8	0.81	20	0.34	1.1	1.3
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.674	0.175	0.037	0.003	0.628	0.252	0.615
Rate	2	0.411	0.871	0.741	0.002	0.589	0.758	<0.0001
Timing	2	0.008	0.123	0.732	0.022	0.016	0.395	<0.0001
Rate x Timing	4	0.420	0.653	0.662	0.635	0.709	0.529	0.033
Residuals	32							

* DAP = days after planting. Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† K rate in K_2O (kg ha^{-1}).

‡ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

§ Values are treatment means for control plots. Control plots are not included in statistical analysis

Table 4.15. Rate x Timing Factorial: Tuber, tops, and total uptake as affected by K rate and time of application when K source is KCl.*

		Tuber				Tops				Total†			
Factor		**N**	**S**	**Cl**	**K**	**N**	**S**	**Cl**	**K**	**N**	**S**	**Cl**	**K**
		(kg ha^{-1})											
Rate ‡													
112		178	13	17 b	232	97 a	5.9 a	72 a	160 a	275 a	19	88 a	392
224		175	13	19 ab	243	69 b	4.2 b	48 b	115 b	245 b	18	67 b	357
448		168	13	23 a	249	71 b	4.4 b	65 a	140 a	239 b	17	88 a	389
Timing §													
September		181	15 a	14 b	257	78	4.9	42 b	135	260	19	56 b	391
Preplant		166	13 ab	24 a	238	73	4.3	63 a	127	239	17	87 a	365
In-Season		173	12 b	21 a	229	87	5.3	80 a	153	260	18	112 a	382
Control ¶		187	14	16	251	80	4.6	45	134	267	18	61	384
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.497	0.525	0.720	0.667	0.019	0.079	0.332	0.021	0.075	0.128	0.255	0.066
Rate	2	0.586	0.832	0.010	0.543	0.001	0.003	0.023	0.005	0.017	0.142	0.025	0.217
Timing	2	0.340	0.054	<0.0001	0.179	0.169	0.190	<0.0001	0.137	0.184	0.095	<0.0001	0.471
Rate x Timing	4	0.169	0.556	0.094	0.449	0.023	0.023	0.150	0.183	0.016	0.088	0.228	0.214
Residuals	32												

* DAP = days after planting. Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP). Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Total uptake the uptake in tops plus tubers.

‡ K rate in K_2O (kg ha^{-1}).

§ Treatments were applied 206 days prior to planting (September), 14 DAP (Preplant) and 35 DAP (In-Season).

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.16. Rate x Source Factorial: Tuber yield, size category, specific gravity, and internal damage for Russet Burbank in 2014 as affected by K source and rate of application when K is applied in-season.*

					----------USDA #1s----------				
Factor		**Specific Gravity**	**cull**	**0-113 g**	**113-170 g**	**170-283 g**	**> 283 g**	**USDA # 1s**	**Total† Internals**
			----------(Mg ha^{-1})----------						
Rate ‡									
112		1.068 a	1.9	15	24	16	2.9	43	2.2
224		1.066 ab	3.2	14	22	18	4.5	44	2.3
448		1.064 b	2.3	14	25	19	5.6	49	2.5
Source §									
KCl		1.066	2.7	13 b	22	18	5.5	45	2.7
Kmag		1.066	1.8	15 a	26	18	3.4	47	2.1
SOP		1.068	2.8	15 a	23	17	4.1	44	2.3
Control ¶		1.071	3.5	15	28	14	5.1	48	2.2
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.078	0.128	0.011	0.206	0.197	0.153	0.581	0.589
Rate	2	0.005	0.119	0.406	0.288	0.313	0.058	0.122	0.836
Source	2	0.185	0.188	0.047	0.128	0.780	0.164	0.571	0.399
Rate x Source	4	0.357	0.433	0.655	0.721	0.396	0.603	0.745	0.947
Residuals	32								

* DAP = days after planting. In-season treatments were applied 35 DAP. Tubers were harvested 137 DAP from a 4.6m length of one of the center rows of each plot. A subsample of tubers in the 170-283 g category was used to measure specific gravity and internal quality. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Mean number of tubers (out of 10 sampled) with hollow heart, vascular discoloration, brown center, or internal brown spot.

‡ K rate in K_2O (kg ha^{-1}).

§ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.17. Rate x Source Factorial: Nutrient analysis for petioles collected 70 DAP as affected by K source and rate of application when K is applied in-season.*

		----------Cations----------				----------Anions----------						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference §**
		----------(g kg^{-1})----------								----------(mol_c kg^{-1})----------		
Rate ¶												
112		105	3.9 a	6.8 a	0.72 a	5.0	1.9	22 a	11 b	0.34	0.22 a	0.12
224		107	3.7 a	6.5 a	0.67 a	5.0	1.8	22 a	13 a	0.34	0.22 a	0.12
448		107	3.1 b	5.3 b	0.54 b	5.2	1.9	20 b	14 a	0.33	0.21 b	0.12
Source #												
KCl		107	3.7 a	6.8 a	0.72 a	5.2	1.8	21	18 a	0.34	0.23 a	0.11 b
Kmag		107	3.2 b	5.4 b	0.55 b	5.1	1.9	22	11 b	0.33	0.21 b	0.12 ab
SOP		105	3.7 a	6.4 a	0.65 ab	4.9	1.9	21	10 b	0.33	0.21 b	0.13 a
Control ††		106	3.7	6.8	0.93	4.9	1.8	20	11	0.32	0.20	0.122
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	<0.0001	0.353	0.001	<0.0001	<0.0001	<0.0001	<0.0001	0.483	<0.0001	<0.0001	0.001
Rate	2	0.748	0.001	0.001	0.021	0.325	0.079	0.004	<0.0001	0.161	0.010	0.987
Source	2	0.743	0.038	0.002	0.042	0.309	0.190	0.745	<0.0001	0.220	<0.0001	0.022
Rate x Source	4	0.651	0.856	0.674	0.798	0.342	0.728	0.404	0.012	0.680	0.883	0.517
Residuals	32											

* DAP = days after planting. In-season treatments were applied 35 DAP. Thirty petioles were collected on June 20, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.18. Rate x Source Factorial: Nutrient analysis for petioles collected 97 DAP as affected by K source and rate of application when K is applied in-season.*

		Cations				Anions						
Factor		**K**	**Mg**	**Ca**	**Na**	**P**	**S**	**NO_3-N**	**Cl**	**Cations†**	**Anions ‡**	**Difference §**
		(g kg^{-1})								(mol_c kg^{-1})		
Rate ¶												
112		92 b	5.8 a	10.7 a	0.65	2.2	1.5	17 a	29	0.34	0.22	0.12
224		92 b	6.0 a	10.4 a	0.65	2.1	1.5	16 ab	31	0.34	0.22	0.12
448		97 a	4.9 b	9.86 b	0.61	2.3	1.5	15 b	32	0.34	0.21	0.13
Source #												
KCl		94	5.5	11 a	0.55 b	2.3	1.4 b	15	40 a	0.34	0.24 a	0.10 b
Kmag		95	5.4	10 b	0.66 a	2.1	1.5 a	16	28 b	0.34	0.21 b	0.13 a
SOP		91	5.7	11 a	0.69 a	2.2	1.5 a	16	26 b	0.34	0.20 b	0.13 a
Control ††		87	6.1	12	0.78	2.4	1.5	17	28	0.33	0.22	0.12
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.049	0.735	0.979	<0.0001	0.002	0.597	0.004	0.014	0.001	<0.0001	0.046
Rate	2	0.025	0.005	0.013	0.683	0.226	0.791	0.005	0.218	0.640	0.477	0.166
Source	2	0.207	0.703	0.001	0.028	0.336	0.003	0.738	<0.0001	0.401	<0.0001	<0.0001
Rate x Source	4	0.706	0.409	0.956	0.422	0.265	0.955	0.519	0.080	0.558	0.149	0.782
Residuals	32											

* DAP = days after planting. In-season treatments were applied 35 DAP. Thirty petioles were collected on July 17, 2014 from plants in the center rows of each plot. The fourth fully developed petiole was sampled and leaflets removed immediately after collection. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Sum of cations is the sum of K, Mg, Ca, and Na on a molar charge basis.

‡ Sum of anions is the sum of Cl, NO_3-N, SO_4-S, and H_2PO_4-P on a molar charge basis.

§ Net charge difference is calculated as ΣCations – ΣAnions.

¶ K rate in K_2O (kg ha^{-1}).

SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

†† Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.19. Rate x Source Factorial: Soil analysis for samples collected 68-70 DAP as affected by K source and rate of application when K is applied in-season.*

Factor		pH	Cl	Mehlich III P	S	Ca	Mg	K	Na
			----------(mg kg^{-1})----------			----------(cmol kg^{-1})----------			
Rate †									
112		5.9	18 b	80	41 c	6.2	2.2 b	0.81 b	0.47
224		5.9	29 a	82	56 b	6.1	2.3 a	0.94 b	0.48
448		5.8	27 ab	79	85 a	6.1	2.3 a	1.19 a	0.45
Source ‡									
KCl		6.0 a	47 a	77	21 c	6.1	2.0 b	0.97	0.45
Kmag		5.7 b	14 b	79	105 a	6.1	2.5 a	1.0	0.47
SOP		5.8 b	12 b	85	56 b	6.2	2.1 b	0.93	0.48
Control §		6.0	16	103	24	6.3	2.1	0.79	0.42
Significance	**Df**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.601	0.836	0.283	0.408	0.006	0.051	0.110	0.036
Rate	2	0.791	0.051	0.921	<0.0001	0.655	0.040	<0.0001	0.162
Source	2	<0.0001	<0.0001	0.675	<0.0001	0.690	<0.0001	0.504	0.393
Rate x Source	4	0.475	0.063	0.759	<0.0001	0.009	<0.0001	0.798	0.022
Residuals	32								

* DAP = days after planting. In-season treatments were applied 35 DAP. Four soil cores (0-20 cm depth) were collected June 18-20, 2014 from the two middle rows of each plot and mixed well prior to analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† K rate in K_2O (kg ha^{-1}).

‡ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

§ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.20. Rate x Source Factorial: Nutrient concentration of above ground plant material (tops) as affected by K source and rate of application when K is applied in-season.*

Factor		N	P	Mg	K	Ca	S	Cl
		----------	----------	----------	(g kg^{-1})	----------	----------	----------
Rate †								
112		28	1.7	5.8 a	44 b	14.3 a	1.6	17
224		27	1.7	5.5 a	46 b	13.6 ab	1.7	18
448		26	1.6	4.9 b	50 a	12.3 b	1.6	18
Source ‡								
KCl		26	1.6	5.5	47	14	1.6	24 a
Kmag		27	1.6	5.3	48	13	1.7	15 b
SOP		27	1.7	5.3	46	13	1.6	13 b
Control §		28	1.6	5.6	45	15	1.6	15
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.031	0.249	0.651	0.648	0.009	0.362	0.347
Rate	2	0.119	0.660	0.024	0.003	0.017	0.166	0.582
Source	2	0.376	0.894	0.702	0.511	0.592	0.325	<0.0001
Rate x Source	4	0.618	0.412	0.118	0.327	0.175	0.135	0.644
Residuals	32							

* DAP = days after planting. In-season treatments were applied 35 DAP. Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP). Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.
† K rate in K_2O (kg ha^{-1}).
‡ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.
§ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.21. Rate x Source Factorial: Nutrient concentration of harvested tubers as affected by K source and rate of application when K is applied in-season.*

Factor		N	P	Mg	K	Ca	S	Cl
		----------	----------	----------	(g kg^{-1})	----------	----------	----------
Rate †								
112		16	3.1	0.84	21 b	0.41	1.2	1.2 b
224		16	3.0	0.82	21 b	0.38	1.2	1.3 b
448		16	3.1	0.85	22 a	0.39	1.2	1.6 a
Source ‡								
KCl		17	3.1	0.81 b	22 a	0.40	1.2 b	1.9 a
Kmag		15	3.1	0.89 a	22 a	0.40	1.3 a	1.2 b
SOP		16	3.0	0.81 b	21 b	0.38	1.2 b	1.0 c
Control §		15	2.8	0.81	20	0.34	1.1	1.3
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.183	0.607	0.147	0.003	0.706	0.253	0.801
Rate	2	0.130	0.623	0.392	0.024	0.212	0.851	<0.0001
Source	2	0.061	0.333	<0.0001	0.015	0.308	0.018	<0.0001
Rate x Source	4	0.489	0.953	0.433	0.164	0.802	0.779	<0.0001
Residuals	32							

* DAP = days after planting. In-season treatments were applied 35 DAP. Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† K rate in K_2O (kg ha^{-1}).

‡ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

§ Values are treatment means for control plots. Control plots are not included in statistical analysis.

Table 4.22. Rate x Source Factorial: Tuber, tops, and total uptake as affected by K source and rate of application when K is applied in-season.*

		Tuber				Tops				Total †			
Factor		**N**	**S**	**Cl**	**K**	**N**	**S**	**Cl**	**K**	**N**	**S**	**Cl**	**K**
		(kg ha^{-1})											
Rate ‡													
112		177	13	13 b	229	94 a	5.5	60	147	271 a	19	73	376
224		168	14	14 b	229	76 b	4.7	49	128	244 b	18	63	357
448		172	14	18 a	247	71 b	4.3	51	139	243 b	18	69	386
Source §													
KCl		173	12 b	21 a	229	87	5.3	80 a	153	260	18	100 a	382
Kmag		171	15 a	13 b	246	79	4.9	44 b	139	250	20	57 b	385
SOP		172	13 ab	12 b	230	75	4.4	36 b	122	247	18	47 b	352
Control ¶		187	14	16	251	80	4.6	45	134	267	18	61	384
Significance	**DF**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Block	4	0.457	0.799	0.950	0.917	0.122	0.447	0.830	0.236	0.249	0.739	0.870	0.460
Rate	2	0.648	0.970	0.002	0.231	0.013	0.079	0.283	0.366	0.031	0.603	0.413	0.293
Source	2	0.972	0.044	<0.0001	0.311	0.319	0.240	<0.0001	0.088	0.478	0.157	<0.0001	0.156
Rate x Source	4	0.219	0.553	0.010	0.606	0.071	0.036	0.224	0.248	0.012	0.106	0.211	0.158
Residuals	32												

* DAP = days after planting. In-season treatments were applied 35 DAP. Tops were collected from a 0.9m length of an outside row of each plot on August 5, 2014 (116 DAP). Tubers were harvested on August 26, 2014 (137 DAP). A subsample of 3 tubers in the 170-283 g size category were cut longitudinally and used for analysis. Values followed by different letters are significantly different at the 0.05 probability level using a Least Significant Difference test.

† Total uptake the uptake in tops plus tubers.

‡ K rate in K_2O (kg ha^{-1}).

§ SOP is K_2SO_4 and Kmag is $K_2SO4*2MgSO_4$.

¶ Values are treatment means for control plots. Control plots are not included in statistical analysis