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Review

The epidemiology of *Pectobacterium* and *Dickeya* species and the role of calcium in postharvest soft rot infection of potato (*Solanum tuberosum*) caused by the pathogens: A review

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Contamination of potato with soft rotting enterobacteria belonging to the *Pectobacterium* and *Dickeya* genera is one of the biggest problems in potato production. Calcium plays an important role in minimising the severity and incidence of potato tuber soft rot in storage. This review gives a detailed assessment of the epidemiology of the pathogens and how calcium affects potato tuber soft rot in storage.

Key words: Potato, soft rot, calcium, *Pectobacterium*, *Dickeya*.

INTRODUCTION

Potato (*Solanum tuberosum* L.) is grown worldwide and is the fourth most important crop in the world (Krauss, 2008; Kandil et al., 2011). To meet the food and nutritional needs of an ever-increasing population, predicted to reach 6.3 billion in 2020, there is need to manage and control pests and diseases (Krauss, 2001). Bacterial soft rot causes losses of up to 60%, in the field, in transit and during storage (Abo-Elyousr et al., 2010; Toth et al., 2011; Ngadze et al., 2012). Potato tuber soft rot is caused by pectinolytic *Pectobacterium* and *Dickeya* bacterium species (Czajkowski et al., 2011). Postharvest soft rots can occur as a result of injuries during harvesting and handling (Conway, 1989; Bhat et al., 2010) and the prevailing weather conditions during the growing season can also affect disease occurrence on stored tubers (Cwalina-Ambroziak et al., 2009).

Calcium is an important nutrient for plant growth and is normally present in adequate amounts in calcareous alkaline soils and in irrigation water (Stark et al., 2004). Tuber internal defects can be reduced by improving tuber calcium, and an increase in tuber calcium improves storability (Conway, 1989; Ozgen and Palta, 2005) whilst localized tissue calcium deficiency initiates cell death and tissue necrosis (Kleinhenz et al., 1999). Calcium is a determining factor in the resistance and susceptibility of potato tubers to bacterial soft rot (Miles et al., 2009) and thus, effective postharvest control of bacterial soft rot in potato can be achieved by increasing tuber calcium through fertilization and postharvest vacuum infiltration with calcium sulphate or calcium nitrate (Conway et al., 1992). Other cultural practices that work hand-in-hand with nutrient management include tillage, irrigation management, crop sequence and soil pH adjustment (Huber and Haneklaus, 2007). There is no existing practical or effective chemical control for bacterial tuber soft rot. However, yield losses can be

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reduced by good crop husbandry, use of non-contaminated planting material and cultivation of resistant or tolerant varieties (Conway et al., 1992; Toth et al., 2003; Abo-Elyousr et al., 2010).

SOFT ROT BACTERIA

The main enterobacteria that cause tuber soft rot are *Pectobacterium carotovora* subspecies *carotovora* (*Pcc*), *Pectobacterium atrosepticum* (*Pa*), *Pectobacterium carotovora* subspecies *brasiliense* (*Pcb*) and *Dickeya* species (Lojkowska and Kelman, 1994; Ngadze et al., 2012).Tubers can be contaminated by more than one bacterial pathogen and contamination is unavoidable (Perombelon, 2000). The soft rot bacteria are rod shaped, gram negative, non-sporing, facultative anaerobes. They are mobile and have peritrichous flagella (Samson et al., 2005; Czajkowski et al., 2011). *Pectobacterium* species occur singly, in pairs and at times in small chains.

On nutrient agar, bacterial colonies incubated for 48 h at 28°C are round convex shaped and cream coloured (Mahmoudi et al., 2007). Soft rot bacteria are opportunistic pathogens which produce cell wall degrading enzymes in large amounts thereby out-competing other pathogens. They are pectinolytic and produce a wide range of enzymes which include proteases, cellulases, pectinases and xylanases (Perombelon, 2002). The susceptibility of tubers to rotting differs with varieties and also with the rate of wound healing (Murant and Wood, 1957) as well as tuber calcium content (Locascio et al., 1992; Czajkowski et al., 2011)

SOFT ROT BACTERIA HOST RANGE

Bacteria belonging to the *Dickeya* and *Pectobacterium* genera have a wide range of plant hosts and the host range overlaps but not completely (Ma et al., 2007). The *Dickeya* species are dominant worldwide and infect maize, *Chrysanthemum* species, banana, potato, *Dianthus* species and tomato (Samson et al., 2005) among other hosts. *Pectobacterium carotovora* subspecies *carotovora* (*Pcc*) has a wide host range which includes onions, carrots, potatoes, lettuce, tomatoes, cucumbers, ornamentals and others (Rashid et al., 2012). *Pectobacterium atroseptica* (*Pa*) is almost exclusive to potato (Ma et al., 2007). *Pectobacterium carotovora* subspecies *brasiliense* and *Pcc* are more aggressive than *Pa* in causing potato tuber and stem rot (Marquez-villavicencio et al., 2011). However, *Pa* has a wider host range compared to *Pcc* and *Pcb* (Czajkowski et al., 2011). *Pectobacterium carotovora* subspecies *carotovora* and *Pa* are virulent at 28 to 32°C but *Pcc* is more pathogenic at higher temperatures than *Pa* (Schober and Zadoks, 1999; Rashid et al., 2012). Studies by Ngadze et al. (2012) showed that *Dickeya dadantii* is more virulent than *Pa* and *Pcb* under Zimbabwean climatic conditions.

THE GEOGRAPHICAL DISTRIBUTION OF SOFT ROT BACTERIA

Potato tuber losses during storage and in transit due to bacterial soft rot caused by *Pa* and *Pcc* are of worldwide occurrence and importance (McGuire and Kelman, 1983; Bain and Pérombelon, 1988; Snijder and van Tuyl, 2003) and the species of *Pectobacterium* that cause soft rots vary with climatic conditions and geographical location (Peltzer and Sivasithamparam, 1985). The *Pectobacterium carotovora* subspecies *carotovora* occurs both in temperate and warm climates (Abo-Elyousr et al., 2010) while *P. atroseptica* is restricted to temperate climates (Perombelon, 2000). The *P. carotovora* subspecies *brasiliense* was first reported in Brazil in 2004 and later in South Africa, United States, Israel (Marquez-Villavicencio et al., 2011) and Zimbabwe (Ngadze et al., 2012). The first *Dickeya* species report on potato was in the Netherlands in the 1970s (Toth et al., 2011). *Dickeya* species occur in temperate, subtropical and tropical regions (Czajkowski et al., 2011). In storage, the extent of potato decay depends on the cultivar, storage conditions, inoculum concentration (Bain and Perombelon, 1988) and tuber characteristics like calcium content.

EPIDEMIOLOGY AND AETIOLOGY

Host-pathogen relationships determine the ability of a host plant or plant organ to avoid infection or invasion by the pathogen. Avoidance or resistance/tolerance is achieved through inherent tolerance/resistance mechanisms of the host plant or plant organ related to its ability to reduce or limit pathogen penetration, development and its ability to reproduce (Graham and Webb, 1991; Toth et al., 2003). The major source of field inoculum is the mother tuber. Bacteria can contaminate progeny tubers when they are transmitted by soil water through the roots and via the vascular system. When contaminated progeny tubers in storage are exposed to conditions favourable for bacterial growth, tissue maceration occurs (Perombelon, 2002; Abo-Elyousr et al., 2010; Czajkowski et al., 2011). Tissue maceration is the separation of cells from each other in a tissue system (Bateman, 1968). Soft rot bacteria can survive for several months, from season to season (Perombelon, 2002) and tubers can be contaminated through wounds created during harvesting and handling. Survival of soft rot bacteria in the soil depends on soil pH, temperature and moisture. Bacteria can survive for up to 6 months in the soil even in the absence of plant debris (Czajkowski et al., 2011). Airborne insects can carry soft rot bacteria from one plant to another. Bacteria can also be present in aerosols especially on rainy days and are viable for up to

10 min. Contaminants of bacteria can also be found in surface and irrigation water (Czajkowski et al., 2011).

The susceptibility of tubers to bacterial soft rot is influenced by tuber water potential, membrane permeability, intercellular concentration of reducing sugars, polyphenol oxidase, oxygen level and other factors. Low oxygen concentration increases susceptibility to tuber soft rot resulting in extensive tissue degradation (McGuire and Kelman, 1983). Studies by Schober and Zadoks (1999) on chicory heads showed that the highest growth rate of *Pcc* occurred at 10°C while that of *Pa* was at 15°C and at water potential ranging from -0.12 to -0.8 MPa. The lag phase of the growth curve increased with decreasing water potential (Schober and Zadoks, 1999). Depletion of oxygen in tubers due to tissue respiration impairs host resistance. It negatively affects cell wall lignification and suberization, thereby resulting in tuber degradation by pectinolytic enzymes (Perombelon, 2002). Growth of *Pa* is inhibited by the antibacterial phytoalexin rishitin. Lyon et al. (1992) found no correlation between cultivars and their resistance to soft rot due to rishitin accumulation. *Pectobacterium* lack enzymes capable of degrading both lignin and suberin. The external suberized periderm provides the first line of defence against pathogen invasion and moderates the exchange of oxygen, carbon dioxide and water (McGuire and Kelman, 1983; Lyon et al., 1992). Low oxygen concentrations and high carbon dioxide concentrations inhibit suberin and periderm formation (Lyon et al., 1992). Contrarily, studies by Murant and Wood (1957) showed that the rate of suberization differed among varieties but was not directly related to disease resistance or susceptibility to rotting.

The availability of water results in the proliferation of lenticels and swelling of cortical cells, making it easy for bacteria to penetrate due to cell membrane permeability and leakage of cell contents (Perombelon, 2002). Increasing tuber water content affects susceptibility to attack by bacteria and storage in humid atmosphere increases rotting (Murant and Wood, 1957).

Pectobacterium species produce pectolytic enzymes (polygalacturonase and pectin lyase) which macerate tuber tissue and induce electrolyte leakage and cell death (McGuire and Kelman, 1986). The ability of *Pectobacterium* species to macerate the plant tissue depends on the amounts of plant cell wall degrading enzymes secreted (Flego et al., 1997). Pectins are made up of chains of polygalacturonic acid residues with rhaminose insertions. The chain allows spaces for insertion of cations (Conway et al., 1992). In the potato medullary tissue, galacturonic acid precipitates calcium to form calcium pectate (McGuire and Kelman, 1986).

Studies by Marquez-Villavicencio et al. (2011) showed that potato soft rot was affected by physiological characteristics such as tuber size and maturity. Smaller tubers were more resistant to soft rot than larger ones.Mature tubers were more resistant due to a better developed periderm and presence of antibacterial substances as well as less water content. Early harvested tubers had higher water content and less toxic substances (e.g. phytoalexins and phenolic compounds) and thus exhibited a higher incidence of tuber soft rot than mature ones (Abo-Elyousr et al., 2010). Abo-Elyousr et al. (2010) concluded that increasing the storage period to up to 4 months increased susceptibility of potato tubers to soft rot.

SYMPTOMS OF TUBER DISEASE

Symptoms of potato tuber diseases may be influenced by conditions such as soil and tuber mineral content, soil moisture, temperature, physical factors, chemical factors and genetics (Miles et al., 2009). When seed tubers are infected by *Pectobacterium* and *Dickeya* species, field symptoms will include reduced emergence, wilting, chlorosis, tuber and stem rot, blackleg, haulm desiccation and plant death (de Haan et al., 2008). Tuber soft rot begins at the stolon end and lenticels. It also infects tuber wounds under moist conditions, causing lesions (Czajkowski et al., 2011). Symptoms of tuber soft rot range from a slight vascular discolouration to complete tuber decay. Infected tuber tissues have a cream to tan colour and a brown to black colour at the margins. At higher temperatures (27°C), rots caused by *Dickeya* species produce a creamier, cheesy rot than that by *P. atrosepticum* (Toth et al., 2011). Bacterial ooze from infected tubers onto healthy tubers results in the rotting of healthy tubers (Czajkowski et al., 2011).

PLANT NUTRITION AND DISEASES

The resistance and susceptibility of a plant to diseases can be determined by the plant's nutrition. The plant's nutrition determines the morphological structure of the host and the ability of pathogens to survive. It is a defence mechanism and an important potential cultural control practice. Inorganic fertilizers such as calcium, magnesium, nitrogen and potassium alter pathogenicity and improve plant resistance to diseases (Huber and Haneklaus, 2007; Huber and Jones, 2012). The mineral nutrition, such as calcium, nitrogen, magnesium, potassium and phosphorus, during the growth period of a potato plant can influence the occurrence of tuber soft rot in storage (Mcguire and Kelman, 1983). It is believed that there is increased susceptibility of plants to diseases due to the lack or deficiency of essential elements such as calcium and magnesium (Czajkowski et al., 2011). The use of plant nutrients to control diseases is an environmentally friendly practice and there is need to provide a balanced nutrition so as to effectively control diseases (Dordas, 2008). Increasing nitrogen results in increased disease severity, potassium increases host plant resistance and silicon creates a physical barrier against fungal hyphae.

FACTORS AFFECTING CALCIUM UPTAKE

The above-ground vegetative part of the potato plant is higher in calcium than in the tubers due to the tubers' low rate of transpiration as calcium moves passively throughout the plant in the xylem as a result of the transpiration pull (Ozgen et al., 2002; McGuire and Kelman, 1983). Foliage calcium is increased by low humidity and high air temperature both of which result in increased transpiration.

Sandy soils normally have a low cation exchange capacity and potato tubers harvested from them are low in calcium and therefore susceptible to soft rot compared to those high in calcium (McGuire and Kelman, 1983, 1986). Calcium application in general potato production is recommended when soil exchangeable calcium is below 300 mg/kg but this amount is generally considered sufficient. Testing soil for exchangeable calcium, however, does not predict the calcium required by tubers (Gunter and Palta, 2008). Studies by Gunter and Palta (2008) showed that tuber calcium varies with variety and season but had no relationship to soil calcium. Increasing tuber calcium can be achieved by improving calcium uptake by placing calcium in the tuber and stolon area. Calcium fertilizer should be placed on the hill where tubers develop (Kratzke and Palta, 1986; Conway et al., 1992; Palta, 1996; Stark et al., 2004). Application of calcium to the main root system does not increase tuber calcium since water and nutrients will be transported to the leaves (Ozgen et al., 2006). Tubers have less transpiration rates than the leaves and hence cannot compete effectively for calcium applied to the main root system. Gunter and Palta (1998) showed that the accumulation of calcium in tubers varied among cultivars and seasons, and concluded that different cultivars have different calcium uptake thresholds due to their genetic makeup implying that improvement of tuber calcium can be done through plant breeding.

Uptake also depends on the general health of the plant, availability of nutrients, such as nitrogen, calcium, potassium, phosphorus and magnesium in the soil, time of application, the stage of growth and the source of calcium (Westermann, 1993; Palta, 1996). Calcium can be absorbed by tubers directly from the soil solution though the deposition and diffusion of calcium in the tubers is affected by cultivar, maturity, soil type, fertilizer practices and weather. This is confirmed partly by the observation that early harvested tubers have less calcium content than late harvested tubers (Conway et al., 1992). Further, cations such as magnesium compete with calcium thereby impeding calcium uptake by plants (Conway et al., 1992; McGuire and Kelman, 1983), while increasing potassium reduces calcium uptake (Bangerth, 1979; White et al., 2009). Calcium fertilizers increase potassium, sulphur and phosphorus concentrations in the soil but reduce magnesium concentration (White et al., 2009). A pH of 5 and below resulted in calcium deficiency and the maximum availability of soil calcium was at pH 6.5 to 8.5 (Westermann, 1993). Therefore, there is need to balance soil nutrients and soil pH.Calcium is transported together with water in the xylem. Therefore to effectively increase tuber calcium supplemental calcium should be added during the tuber bulking stage because the tubers develop later in the season. Tubers have their own roots which take up water and calcium (Palta, 2010) and applications must be within reach of these tuber roots. An effective way of applying calcium is through fertigation (Westermann, 1993; Palta, 1996) while less soluble fertilizers can be applied by side dressing before the last hilling (Ozgen et al., 2006). Injection of fertilizer into irrigation water requires careful irrigation management so as to achieve uniformity of fertilizer application while avoiding leaching and runoff (Westermann, 1993).

Calcium can be applied as calcium chloride, calcium nitrate, gypsum (calcium sulphate), lime and calcium-ammonium-nitrate and normally, application is effective when split (Ozgen et al., 2002; 2006). Lime and gypsum have low water solubility whereas calcium nitrate is highly soluble (Palta, 1996; Kleinhenz et al., 1999). Studies by McGuire and Kelman (1983) showed that calcium nitrate was more effective in increasing calcium concentration of peel and medullary tissue than calcium chloride and calcium sulphate. However, liming and fertilization does not guarantee an increase in calcium content in storage organs by the required amounts due to inefficient distribution of calcium in the storage organs. Research by Ozgen et al., (2006) showed that the application of gypsum was not effective in increasing the calcium concentration in tuber tissue, even when gypsum was applied in combination with other soluble calcium fertilizers due to low amounts of gypsum fertilizer they applied during their study. In some cases (in stored tubers for instance), calcium can be added directly on storage organs or by dipping in calcium chloride solutions for longer periods as a direct calcium treatment to increase calcium. Other methods include vacuum or pressure infiltration, which have been used to increase calcium levels in apples so as to improve storage quality (Conway, 1989). Tuber tissue maceration is reduced by calcium chloride and calcium propionate salts but their effectiveness depends on the method of application, organism and concentration (Hajhamed et al., 2007).

EFFECT OF CALCIUM ON PLANT RESISTANCE TO SOFT ROT

Increasing calcium concentration in the potato tubers helps reduce the incidence of tuber soft rot during storage, thereby increasing shelf life (Kratze and Palta, 1986; Palta, 2010). Abo-Elyousr et al. (2010) reported a correlation between tuber cell wall, calcium content and the level of resistance to soft rot while McGuire and Kelman (1983) found tuber calcium concentration to be high in the cortex and periderm. Calcium, which is a secondary messenger in plant cells, contributes to maintenance of cell membrane stability and cell wall structure (Ozgen et al., 2002). McGuire and Kelman (1983) showed that soft rot severity caused by *Pa* was inversely related to tuber calcium concentration just as application of calcium effectively reduced decay caused by *P. carotovora.* The surface area decay of potato tubers by *Pa* reduced from 93 to 15% and medullary calcium concentration increased from 0.022 to 0.063% after being held in a mist chamber for 60 h (Conway et al., 1992). Studies conducted by Locascio et al. (1992) showed that the in-season application of calcium fertilizer reduced bacterial soft rot incidence from 43 to 4% in 3 years. As calcium increased, disease severity decreased because an increase in tuber calcium most likely led to an increase in the cross-linkages of pectate chains, thereby reduced susceptibility to tuber soft rot. Calcium phosphite is used as a nutritional compound and it has an antimicrobial action against pathogens. When tubers were artificially infected with *P. carotovora*, it reduced the lesion area (Lobato et al., 2008, 2010).

MECHANISMS OF CALCIUM INDUCED RESISTANCE TO SOFT ROT

Calcium in the middle lamella is responsible for promoting gelling in a pectin solution (Conway, 1989) and provides stable reversible inter-molecular linkages between pectin molecules by making the cell wall rigid (Gunter and Palta, 1998). McGuire and Kelman (1983) showed that, at the highest levels of calcium fertilization, tuber surface area decay was reduced by almost half and Abo-Elyousr et al. (2010) reported that varieties with the highest amount of pectin substances and calcium content recorded the lowest weight of rotting tissue. Presumably, calcium bridging of the plasma membrane components reduced electrolyte leakage and maceration by pectolytic enzymes (McGuire and Kelman, 1986) since extracellular calcium is thought to help in maintaining the selective permeability of plasma membranes because of the bridging of calcium ions on phosphate and carboxylate groups of phospholipid head groups at the membrane surface (Gunter and Palta, 2008; Geary et al., 2010).

Tubers with high calcium have an improved structural integrity of both the plasmalemma and cell wall materials as compared to tubers with low calcium content. This is thought to inhibit the multiplication and spread of the bacterial pathogen throughout the tissue (McGuire and Kelman, 1986). The activity of Polygalacturonase (PG), a cell-wall-degrading enzyme produced by bacterial and fungal pathogens, is inhibited by calcium and hence cannot breakdown the pectin in the plant tissue cell walls.

Calcium prevents PGs from interacting with the pectin polymer and blocks the diffusion of PGs through the cell wall (Goodwin et al., 1997; Huber and Jones, 2012). Goodwin et al. (1997) reported that the level of calcium in canola leaf extracts was significantly correlated to disease resistance and to inhibition of PG activity by *Leptosphaeria maculans*. Increasing calcium content of beans decreased the activity of PG and pectate transeliminase thereby increasing resistance to Pcc (Krauss, 1999) while Benson et al. (2009) showed that pink soft rot disease infection and severity decreased with an increase in the available calcium between 3 and 343 mg/L.

CONCLUSION AND PERSPECTIVES

Although host plant resistance and cultural methods have been shown fairly conclusively that they play an important role in the control of soft rots, their deliberate and coordinated use has not been widespread and loss caused by soft rots remain high. These losses will continue to haunt farmers until resistant varieties become ubiquitous on farms. In the meantime, avoidance of infection through use of certified seed remains a cornerstone in safeguarding losses in potato production caused by soft rot pathogens. The occurrence of even more virulent subspecies of soft rots makes host plant resistance in this area very important.

Conflict of Interests

The author(s) have not declared any conflict of interests.

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