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Potato Dormancy Regulation: Use of Essential Oils for Sprout Suppression in Potato Storage

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ABSTRACT

Sprout suppression is essential in assuring potato quality. Release of natural tuber dormancy is affected by production as well as storage environmental factors, cultivars and tuber metabolic activities. Plant growth regulators are also shown to play important roles in regulating tuber dormancy. In commercial storage, sprouting is primarily controlled by low temperature combined with chemical inhibitors, such as Chlorpropham (CIPC). However, increasing concerns regarding the safety and environmental impact of chemical residues have increased interest in investigating the potential of alternate sprout inhibitors as well as disease suppressors, including essential oils. Literature has shown carvone, a major component of caraway, dill and spearmint oils, can temporarily inhibit sprouting and long-term sprout inhibition can be achieved by repeated treatments. Carvone plays a role in enhancing degradation of 3-hydroxy-3-methylglutaryl coenzyme A reductase (HMG-CoA reductase), a key enzyme that catalyzes the rate limiting reaction in the mevalonate pathway. Carvone and many essential oils exhibit great potential to be used for sprout suppression under commercial storage conditions for both consumption and seed potatoes.

Keywords: HMG-CoA reductase, meristem, plant growth regulators, R-(-)-carvone, S-(+)-carvone
Abbreviations: ABA, abscisic acid; **CIPC**, Chlorpropham or isopropy N-(3-chlorophenyl) carbamate; **GA**, gibberellins; **HMG-CoA reductase**, 3-hydroxy-3-methylglutaryl coenzyme A reductase; **IAA**, indole-3-acetic acid; **IPC**, isopropyl *N*-chlorophenyl carbamate; **MH**, maleic hydrazide

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INTRODUCTION

Grown in more than 100 countries, potato (*Solanum tuberosum* L.) is a key part of the global sustainable food system. It is also the most significant vegetable crop in Canada, which is grown through out all 10 provinces on close to 400,000 acres of land (Statistics Canada 2008). Potato produces more food energy on less land than corn, wheat or rice (International Potato Center 2008). It is the world's number one non-grain food commodity with production now at a record of 320 million tonnes in 2007. More than half of total production is generated from developing countries, rendering it as an important source of income to millions of farmers. Thus, the potato crop is a significant economic mechanism for the production of food to address intensifying health needs and the delivery of new bioproducts.

Demand for potato is increasing and is year-round. However, producing potato throughout the year is not feasible in most parts of the world, therefore, long-term storage is essential. Since potato tubers are metabolically active even during storage, sprout growth occurs after a period of natural dormancy (Viola *et al.* 2007). During storage, effective sprout control is essential to successfully store the potatoes and minimize losses. Sprouting can result in tuber weight loss due to water loss through the lenticels, reducing tuber sugar levels, increasing bruising susceptibility and production of toxic glycoalkaloids (Vaughn and Spencer 1993; Hartmans *et al.* 1995). To achieve effective sprout suppression, numerous studies have been conducted to gain a better understanding of the mechanisms regulating tuber dormancy, dormancy release and sprout development.

This review first briefly describes the mechanisms involved in regulating potato tuber dormancy and sprout development in order to gain insights on the internal factors regulating postharvest sprouting during storage. Then the advantages and disadvantages of currently used sprout control methods are discussed. A final section will be on the use of essential oil components, particularly carvone, in inhibiting sprouting and fungal growth during potato storage.

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Invited Review

TUBER DORMANCY IN POTATOES

Potato tuber dormancy can be defined as "the physiological state of the tuber in which autonomous sprout growth will not occur, even when placed under favourable conditions for sprouting (darkness, temperatures between 15 and 20°C, relative humidity about 90%)" (European Association for Potato Research 1985 cited by Wiltshire and Cobb 1996). Tuber dormancy is generally considered to begin at tuber initiation and terminate when buds are capable of sprouting (Wiltshire and Cobb 1996). At harvest, all tuber buds are in a state of endodormancy (Suttle 2000). At this state, tubers will not sprout even when placed under favorable conditions. This true stage of dormancy is also referred to as innate dormancy (Jefferies and Lawson 1991). After innate dormancy is released, bud growth is normally suppressed by unfavorable external conditions, such as low storage temperature, and the tubers enter an enforced dormancy (Wiltshire and Cobb 1996).

Potato tubers are developed from the underground lateral shoots called stolons (Western Potato Council 2003), and a potato tuber is, in fact, a highly modified stem. Tuber initiation begins when the longitudinal cell division in the apical meristem arrests and apical dominance is released. Initially, the lateral portion of the stolon enlarges due to cell elongation, followed by longitudinal cell division in the pith and the cortex of the apical region. When the enlarged stolons reach the size of two to four millimeters in diameter, longitudinal cell division is replaced by random cell divisions and cell enlargement until the tubers reach the final size (Xu *et al.* 1998). Since each tuber is a highly modified stem, the so-called buds or eyes on the tuber are actually apical and lateral meristems. For the purposes of growth and development, these buds are the most important structures of a potato tuber. Studies have shown that excised buds or isolated apical meristems are capable of regenerating a complete shoot apex when sufficient nutrients and plant growth regulators are supplied (van der Schoot 1996). During the process of tuberization, the lateral buds on a tuber become dormant sequentially, and the apical bud is the last one to become dormant (Fernie and Willmitzer 2001).

The duration of innate dormancy is largely dependent on the cultivar, the environmental growing conditions, including day length, temperature and water supply, and the postharvest storage conditions, such as temperature, humidity, air circulation and concentration of oxygen and carbon dioxide (Turnbull and Hanke 1985; Claassens and Vreugdenhil 2000). For instance, long photoperiod (18-h light) during tuberization could shorten dormancy by about one week (van Ittersum 1992). Studies have also shown cool and wet growing conditions during tuber formation extend dormancy, whereas hot (30-32°C) and dry conditions shorten dormancy (van Ittersum and Scholte 1992; Suttle 2000). Moreover, when developing tubers are exposed to low temperature (< 3°C) in the field, the stressful conditions could result in premature sprouting due to premature breaking of dormancy (Suttle 2000). Thus, growing conditions appear to be one of the most critical factors influencing the duration of innate tuber dormancy in potatoes.

Mechanisms of dormancy induction and release: metabolic activities

Tuber dormancy in potatoes is triggered by environmental conditions and achieved via regulations of physiological activities. During dormancy the metabolic processes including respiration, transpiration and translocation are greatly suppressed to reserve energy and resources under stressful conditions, nevertheless, potato tubers are still metabolically active. Tuber respiration rate drops quickly soon after harvest and is maintained at a low level throughout the dormancy period. When sprouting begins, the rate of respiration increases again (Schippers 1977). Changes in respiration rate are relatively small in relation to temperature changes when below 10°C. When the storage temperature rises above 10°C, there is generally a positive relationship between temperature increase and respiration rate rise (Schippers 1977; Wiltshire and Cobb 1996). Therefore, potato storage is commonly maintained at constant low temperatures between 4 to 15°C. Sudden fluctuations in storage temperature can lead to a rapid increase in respiration (Wiltshire and Cobb 1996). Reconditioning of potato tubers is a process which uses this phenomenon to lower the reducing sugar level. When the temperature is increased between 10 to 20°C, reducing sugars, such as glucose and fructose accumulated during low temperature, are metabolized by glycolysis and respiration. The lowered level of reducing sugars can enhance the potato process quality and prevent dark fry color and bitter taste caused by high levels of reducing sugars (Wiltshire and Cobb 1996).

The outgrowth of tuber buds is most likely restricted by a lack of resources needed for morphogenesis since excised buds are capable of growing into a complete shoot apex when supplied with sufficient nutrients and plant growth regulators. van der Schoot (1996) indicated tuber buds could communicate with other cells via signaling through plasma membranes or through symplasmic connections. The converse is also true. Tuber buds can also be isolated when signaling pathways are blocked. The isolation of meristems from the rest of the tuber could limit the supply of substrates and other materials required for the outgrowth of the buds. At the dormant stage, cells in the bud are shown to arrest primarily in the G1 state, as DNA synthesis is nearly absent and the biosynthesis of RNA and protein is highly reduced (MacDonald and Osborne 1988; Campbell *et al.* 1996). Most of the resources needed for morphogenesis are reserved in parenchyma cells and are unable to be transported to the buds.

During tuberization, storage metabolism aids the developing tuber to accumulate carbohydrates, which is stored as starch. Soon after the tuber is detached from the mother plant, reserve mobilization starts to occur and the tuber shifts from a sink to a source for the tuber buds (Viola *et al.* 2007). In a dormant tuber, over 70% of carbohydrate is stored as starch and sucrose (Viola *et al.* 2007). When sprouts start to develop, in order to continuously supply the building materials for cell division and cell expansion, storage carbohydrate must be converted to soluble sugars such as glucose and fructose (Claassens and Vreugdenhil 2000). Indeed, an overall decrease in starch content in non-dormant tubers was found and a sharp decrease occurred during sprouting (Davies and Viola 1988). Additionally, reducing sugars increased during dormancy release and prior to sprout development (Dimalla and van Staden 1977; Bailey *et al.* 1978). The rates of conversion and mobilization are also reflected on enzyme activities. During dormancy, starch is mainly degraded by starch phosphorylase and by amylase to a certain extent (Bailey *et al.* 1978). Bailey *et al.* (1978) reported that the activities of starch phosphorylase and α-amylase, increased prior to sprouting, followed by a decrease. Davies and Viola (1988) later found that amylase activities decreased initially but α-amylase activity gradually increased during sprouting. In addition to the breakdown of carbohydrates, prior to the outgrowth of sprouts, storage proteins, such as patatin and the 22 kDa storage proteins, break down to free amino acids (Davies and Ross 1984; Suh *et al.* 1990; Brierley *et al.* 1996). This process is likely to be associated with the demand for nitrogen by sprout growth (Davies and Ross 1984; Davies and Ross 1987). Protein, RNA and DNA synthesis occurs throughout the dormancy period in tuber buds. However, the levels of synthesis were shown to increase during dormancy release (MacDonald and Osborne 1988). Alam *et al.* (1994) stated that dormancy release is likely associated with the regulation of protein synthesis, but is not controlled by nucleic acid synthesis.

These evidences suggest that, during dormancy release, the isolation of tuber buds gradually declines as all the metabolites including reducing sugars, amino acids and other dissolved molecules with small molecular mass, move

toward the tuber buds via diffusion due to chemical gradients. Therefore, the release of dormancy is based on the establishment of a sink-source relationship within the tuber as cells develop functional competence to mobilize and transport carbohydrates as well as other nutrients from parenchyma cells (source) to dividing cells in tuber buds (sink) (Sonnewald 2001; Viola *et al.* 2007). Once the sink-source relationships have been established, the tuber is completely released from dormancy and rapid metabolic transitions consistently occur with bud development (Viola *et al.* 2007).

Changes in the levels of plant growth regulators during dormancy and dormancy release

Plant hormones, a major group of plant growth regulators, are substances naturally produced by plants to control plant growth and development functions, such as root and shoot growth, flowering and fruit setting and ripening, among others. The impact of plant growth regulators on regulating potato tuber dormancy has been extensively studied as they are generally considered to be the most important internal factors regulating tuber dormancy (Sorce *et al.* 2005). Endogenous plant hormones regulate tuber dormancy by varying the level of specific hormones or by adjusting the relative concentrations of these hormones. The sensitivity of tuber tissues to specific hormones also differs over the time of the physiological aging process, which is another approach the plant have developed to regulate dormancy (Wiltshire and Cobb 1996; Viola *et al.* 2007).

Auxins are the first plant hormones that were studied as potential regulators of potato tuber dormancy (Suttle 2000). Indole-3-acetic acid (IAA), the most important member of the auxin family, is known to stimulate cell expansion and cell division (Goldsmith 1993; Cleland 1995). In potato tubers, auxins are necessary for sprout growth but they do not exert any influence on dormancy (Wiltshire and Cobb 1996). The levels of endogenous auxins were found to only increase in tubers that had broken dormancy and sprouted (Sukhova *et al.* 1993; Sorce *et al.* 2000). Faivre-Rampant *et al.* (2004) reported a strong up-regulation of potato *ARF6*, a gene encoding a member of auxin response factor family, in early stage of sprouting, particularly in the peripheral zones of the tunica and corpus of the apical meristem. Sorce *et al.* (2005) reported auxins probably regulate bud development by transporting substantial amounts of IAA from the pith to the tuber buds during the dormancy period.

Gibberellins (GA) are involved in promoting and maintaining seed germination. Studies have shown GA-deficient mutants of tomato and *Arabidopsis* could not germinate without exogenous GA (Koornneef and Vanderveen 1980; Groot and Karssen 1987). The effect of GA on tuber dormancy was first studied by applying exogenous GA on dormant tubers. It was shown that exogenous GA was capable of breaking tuber dormancy (Brian *et al.* 1955; Hemberg 1985). Suttle (2004) later demonstrated that endogenous GA levels were equivalent between tubers releasing dormancy and tubers in deep dormancy. Endogenous GA only increased after sprouts started to grow. Thus GA, appears to play a role only in controlling subsequent sprout growth rather than breaking dormancy.

Cytokinins stimulate cell division by releasing a G1 cell cycle block (Francis and Sorrell 2001). As cells in dormant tuber buds are primarily resting in the G1 state, cytokinins can be identified as the true dormancy breaking hormones. Studies have shown exogenous cytokinins play a role in potato tuber dormancy release. Hemberg (1970) first demonstrated that exogenous cytokinins were capable of breaking dormancy and inducing sprouting in dormant potato tubers. Within tubers, endogenous cytokinin levels increased at the end of dormancy (Sukhova *et al.* 1993) to stimulate cell division needed for sprout development. Zubko *et al.* (2005) developed a line of transgenic potato tubers with an elevated cytokinin level by over-expressing the *Sho* gene, which encodes an enzyme for cytokinin synthesis. Their transgenic tubers were shown to have significantly reduced dormancy levels. In addition to increasing cytokinin contents over the dormancy period, dormant tubers also appeared to develop an increasing sensitivity to cytokinins over time (Turnbull and Hanke 1985; Suttle 2001). Newly harvested tubers were often found insensitive to exogenous cytokinins.

Abscisic acid (ABA) plays an important role in seed dormancy induction (Morris *et al.* 1991). There is evidence indicating that ABA inhibits seed germination by interfering with cell wall loosening, and thus inhibits cell expansion (Schopfer and Plachy 1985). ABA is often considered to be a sprout inhibitor in potato by many researchers (Sonnewald 2001). In tubers, the highest concentrations of endogenous ABA were found in dormant tubers and its content decreased during storage, which correlated with the gradual loss of dormancy (Suttle 1995). Previous and recent studies have shown that ABA is required for inducing and maintaining dormancy in potato tubers (Suttle and Hultstrand 1994; Ludford 1995; Destefano-Beltran *et al.* 2006). Recently, Sorce *et al.* (2005) studied the levels of ABA in bud tissues and found that the ABA content increased throughout the dormancy period. However, the critical threshold ABA concentration required for breaking dormancy in both buds and tubers is yet to be identified. It has been suggested that ABA is not the only factor that controls tuber dormancy (Sorce *et al.* 2005).

The effects of ethylene, another naturally occurring plant hormone, on the regulation of dormancy in seeds and other tubers have been extensively studied (Suttle 2000, 2004). Several studies have shown that exogenous ethylene exposure can alter tuber sprout responses, but the tubers response to ethylene treatments appeared to depend on concentration, duration and tuber cultivars (Suttle 2004). Continuous ethylene treatment has been shown to suppress sprouting (Rylski *et al.* 1974; Cvikrova *et al.* 1994; Prange *et al.* 1998). In contrast, Rylski *et al.* (1974) showed that short-term ethylene treatment promoted dormancy release. Potato tubers produce only limited amounts of ethylene and its functions in tuber dormancy regulation still remains unclear (Suttle 2004).

Several other groups of endogenous compounds have also been studied in their relation to potato tuber dormancy regulation, including phenolic compounds, methyl jasmonates and volatile compounds produced by potato tubers. Potato periderm contains a considerable amount of phenolic compounds. Cvikrova *et al.* (1994) demonstrated that phenolic acids likely participated in the endogenous regulation of tuber dormancy, maintenance and release. Their study also showed that the content of free phenolic acids gradually increased during tuber dormancy and reached a peak at the end of dormancy. The loss of tuber dormancy is paired with a reduction in free phenolic acid content and an increase of phenolic conjugate content in tubers. Furthermore, tuber buds with the highest level of free phenolic acids resulted in delayed dormancy break (Cvikrova *et al.* 1994). The role of jasmonic acid derivatives such as jasmonates in tuber dormancy was also studied but not clearly defined (Suttle 2004). However, studies have shown that a derivative of jasmonic acid, tuberonic acid, was closely associated with tuberization (van den Berg and Ewing 1991). As tuber dormancy is initiated from tuberization, jasmonates were suspected to play a part in dormancy induction. Furthermore, potato tubers naturally produce a variety of volatile compounds. Meigh *et al.* (1973) extracted tuber peel samples and identified a group of methylated naphthalenes with sprout-growth inhibiting activity. Individual isomers of dimethylnaphthalene and their mixtures were later shown to be effective in suppressing sprout growth when applied externally (Filmer and Rhodes 1985; Lewis *et al.* 1997). The roles of these volatile compounds, extracted from potato tubers, were mainly studied as sprout suppressants.

van der Schoot (1996) indicated that cell-to-cell communication through plasma membranes is controlled by means of growth regulator production, signal receptor den-

sities alteration and adjustment of the cells sensitivity to growth regulators. Some researchers suggested that, rather than being the regulator of dormancy, growth regulators in fact mediate nutrient fluxes (Trewavas 1981; Turnbull and Hanke 1985). Thus, the effects of growth regulators are dependent on other factors, such as the propagation of secondary messengers and binding receptors. Since the system is constantly changing, the plants' responses to growth regulators are likely to be different each time signalling receptor-binding occurs. This may partially explain why the attempts of using growth regulators in sprouting suppressant often produce inconsistent or unsatisfactory results.

SPROUT CONTROL IN STORAGE

Premature sprouting in storage can result in substantial economic losses due to weight loss and reduced tuber quality. Therefore, it is crucial to effectively inhibit sprouting in storage. Prevention of premature sprouting can be achieved mainly by interfering with dormancy breaking or by restricting the development of meristems (Wiltshire and Cobb 1996; Kleinkopf *et al.* 2003).

Low temperature storage is commonly used to extend the storage period by prolonging the natural dormancy through an enforced dormancy (Wiltshire and Cobb 1996). In most commercial storage in North America, after the curing period (a process that stimulates suberization, wound healing and reduces respiration), the tubers are stored at 4 to 5°C for seed tubers, at 7 to 10°C for fresh market and at 10 to 15°C for processing potatoes (Western Potato Council 2003). The respiration rate of potato tubers is the lowest at 2-3°C. However, low temperatures can cause undesirable cold-induced sweetening by degradation of starch to reducing sugars (Hartmans *et al.* 1995). This process starts with low storage temperatures causing an imbalance in the rate of starch turnover and glycolysis, and as a consequence, sucrose is formed in the tuber. Sucrose is subsequently hydrolysed to hexoses, including glucose and fructose by invertases and results in an accumulation of reducing sugars (Sonnewald 2001). Accumulation of reducing sugars is a particular concern for potatoes produced for fresh market and for the processing industry as it causes a browning and a bitter taste (Hartmans *et al.* 1995). Consequently, most tubers are stored at relatively higher temperatures combined with applications of sprout suppressants to avoid sweetening and to achieve good sprout inhibition.

Since the growth of the tuber bud (shoot apex) is achieved through cell division and cell expansion, the prevention of sprout growth can be accomplished through interference with cell division and cell expansion. Chlorpropham [isopropy N-(3-chlorophenyl) carbamate or CIPC], the most commonly used sprout suppressant in the market to date, inhibits sprouting by interfering with mitotic cell division. CIPC interrupts spindle formation and permanently damages the tuber buds (Nurit *et al.* 1989; Kleinkopf *et al.* 2003). CIPC was first introduced to the market in 1951 and has been one of the most widely used sprout suppressant in commercial storage ever since. It is often applied in storages as an aerosol fog. Other formulas such as spray, dust and delayed-released granules are also available on the market. CIPC is sometimes used as a mixture with propham (isopropyl N-phenylcarbamate or IPC). IPC has the same mode of action as CIPC, but it acts faster than CIPC (Meredith 1995a); it is, therefore, mixed with CIPC to achieve better initial sprout control.

Other chemical suppressants used presently are maleic hydrazide (MH) and tecnazene (1,2,4,5-tetrachloro-3-nitrobenzene). MH is an isomer of uracil, a pyrimidine base in RNA (Wiltshire and Cobb 1996). Cremlyn (1978) suggested that MH interferes with mitosis by incorporating into RNA. MH is applied to the crop as a foliar spray approximately 2 to 3 weeks before harvest or vine kill. Timing of MH application is essential for successful sprout inhibition (Wiltshire and Cobb 1996). It must be applied after cell division in tuber is completed as MH inhibits cell division but not enlargement. Since it is translocated from the vine to the tubers, there must be a sufficient amount of time to allow for adequate translocation. Tecnazene has been used as a sprout suppressant in UK for more than half a decade. Tecnazene is volatile, and is applied as a powder or as granules while loading tubers into the storage. Its sprout suppression effect can be compromised if it is applied after the tubers have broken dormancy. Tecnazene appears to prevent cell division and elongation, but it has no effect on wound healing (Meredith 1995b). The mode of action is not yet well understood.

In recent years, there are growing concerns on the levels of chemical residues in potato tubers, particularly for CIPC, and on their potential negative impacts on human health and the environment. CIPC was reported to be one of the three pesticides found in highest concentrations in the diet of the average American (Gartrell *et al.* 1986). In addition, a study done in the early 1980s showed that CIPC comprised over 90% of the total synthetic chemical residues found in U.S. potatoes (Gunderson 1988). In 2002, the allowable residue tolerance on fresh potatoes in the U.S. was reduced from 50 to 30 ppm, and in Europe the residue limit is 5 to 10 ppm (Kleinkopf *et al.* 2003). Along with rising input costs, there is more pressure to develop alternative sprout suppressants that are sustainable, economical, with improved environmental and health benefits, resulting in increased consumer acceptance and confidence in food safety.

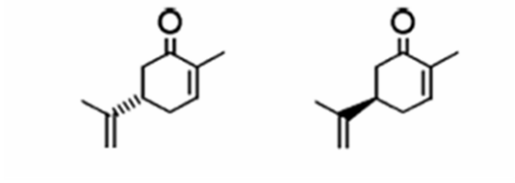
THE POTENTIAL OF USING ESSENTIAL OILS AND THEIR MAJOR COMPONENTS AS POTATO SPROUT SUPPRESSANTS

Since commonly used cold storage techniques or treatments with chemical sprout inhibitors are often problematic, naturally occurring compounds have drawn considerable attention as new alternative sprout suppressants, such as naturally occurring essential oils obtained from a wide range of plants. The essential oils can be obtained from all parts of plants, including the flowers, leaves, stems, roots and seeds, by distillation and/or extraction (Oosterhaven *et al.* 1995b). These oils are water-insoluble and commonly contain a mixture of branched five carbon (isoprene) units referred as terpenes. Monoterpenes which consist of two isoprene units (C_{10}), represent the major components of essential oils (Buchanan *et al.* 2000). The presence of monoterpenes in plants often serves as a defense mechanism against insects and microorganisms (Vaughn and Spencer 1991).

The history of using essential oil components in the inhibition of sprouting goes back for many centuries. For generations, the Incas of South America have buried their potatoes in pits covered with soil and the leaves of Muña plants. Muña plants belong to the genera *Minthostachys* and *Satureja* (Aliaga and Feldheim 1984), members of the mint family (Lamiaceae). These plants naturally grow in the Andes region, from southern Peru to Argentina. The Muña plants contain rich amounts of essential oils that are comprised of over 98% monoterpenes (Vaughn and Spencer 1993). Oil from Muña plants was shown to be more effective than CIPC in reducing sprouting, fresh weight loss, and tuber rot over a period of 225 days (Aliaga and Feldheim 1984). In addition, certain volatile monoterpenes obtained from various plants have been shown to be potent growth inhibitors of plants and microorganisms, and appear to be involved in allelopathic interactions (Vaughn and Spencer 1991). Studies conducted as early as 1969 have suggested that volatile monoterpenes, such as 1,8-cineole, carvone and pulegone, could be used for application as volatile sprout suppressants for potatoes (Meigh 1969; Beveridge *et al.* 1981; Beveridge *et al.* 1983; Aliaga and Feldheim 1984; Vaughn and Spencer 1991; Vokou *et al.* 1993). Most of these compounds have low toxicities to humans and are widely used in flavorings, medicines and perfumes (Vaughn and Spencer 1991).

Carvone, 2-methyl-5-(1-methylethenyl)-2-cyclohexene-1-one, is a member of monoterpenes and it is one of the

most studied monoterpenes to date for its effect on sprout growth suppression (de Carvalho and Fonseca 2006). It has the composition $C_{10}H_{14}O$, with a molecular weight of 150 and a specific gravity of 0.996 kg/L at 20°C. It is a colorless volatile liquid, slightly soluble in water (Capelle *et al.* 1996). It can be found in many natural plant extracts, such as caraway, dill and mint oils. Carvone contains two enantiomers: S-(+)-carvone and R-(-)-carvone (**Fig. 1**). S-(+)-carvone is the major compound in caraway seed oil (50-70%), dill seed oil (40-60%) and dill weed oil (40%) (Hartmans *et al.* 1995; de Carvalho and Fonseca 2006). R-(-)-carvone, which smells like spearmint, is present in spearmint at a level greater than 51% (de Carvalho and Fonseca 2006).



S-(+)-Carvone R-(-)-Carvone

Fig. 1 Enantiomers of carvone [S-(+)-carvone and R-(-)-carvone]. Molecular formula: $C_{10}H_{14}O$ (Schlyter *et al.* 2004).

Inhibition of sprouting by carvone

Carvone, particularly S-(+)-carvone, has been shown to be effective in suppressing sprouting both on small and large-scale studies with different apparatus (Vaughn and Spencer 1991; Hartmans *et al.* 1995; Oosterhaven *et al.* 1995b). Meigh (1969) first showed that carvone could effectively suppress sprouting when applied at a constant vapor concentration. Later studies supported their findings and further stated that the effect of carvone was concentration-dependent and that the treatments should ensure a low, stable headspace concentration around the tubers (Hartmans *et al.* 1995; Sorce *et al.* 1997; Cizkova *et al.* 2000). As a vapor, carvone eventually disappears from storage mainly due to leakage, ventilation, absorption by the tubers and building materials, or metabolism by tubers and microorganisms in storage (Hartmans *et al.* 1998). Therefore, repeat applications are necessary to maintain the storage headspace concentration above a threshold level for a certain period of time (Kleinkopf *et al.* 2003). Osterhaven *et al.* (1995a), using systems consisting of sprouts growing from potato eyepieces, showed that applications of 250 μL of carvone to 30 eyepieces in a sealed 20-L container (12.5 μL/L), reduced sprout growth at varying rates following a 2 to 4 day exposure, but did not completely eliminate growth. Seven days of treatment completely inhibited sprout growth throughout the experiment. In a semi-large scale study, Hartmans *et al.* (1995) found a 100 mg/kg S-(+)-carvone treatment followed by a 42-hr ventilation free period applied every 6 weeks to 15 tonnes of tubers in a semi-large storage facility was able to successfully suppress sprouting for 6 months. Beveridge *et al.* (1981, 1983) applied carvone as liquid mixed with an alumina solid carries. They found that carvone at a concentration of 100 mg/kg did not prevent sprouting but at 500 mg/kg sprouting was successfully suppressed. Cizkova *et al.* (2000) further noted that directly spraying carvone treatments onto the tubers could cause necroses and rotting on the tuber surface. It was recommended to apply carvone treatments after curing. A study conducted on wounded tuber tissues showed the presence of S-(+)-carvone prevented the activity of suberization and cambium layer formation (Oosterhaven *et al.* 1995c). However, after the S-(+)-carvone and its bioconversion products were completely depleted from the tissue and the atmosphere, both processes were restored. As the inhibition effect caused by carvone is not permanent, the potential of using it in seed tuber storage was also studied by Sorce *et al.* (1997). They concluded that headspace concentrations within the range of 0.34 to 1.06 μmol/mol were most effective in inhibiting sprouting in seed tubers. In 1994, a biological sprout inhibitor Talent® was commercially marketed as a sprout inhibitor in the Netherlands (Wiltshire and Cobb 1996). Talent® contains 95% of the S-(+)-carvone isomer in a liquid formulation; and the recommended application rate is 600 mL/ton for effective sprout inhibition (Kerstholt *et al.* 1997).

Studies conducted on spearmint (*Mentha spicata*) showed that the major component of spearmint, R-(-)-carvone, can also effectively prevent potato sprouting during storage (Frazier *et al.* 1998, 2000, 2004). Oosterhaven *et al.* (1995a) compared the efficacy of the two isomers and found that S-(+)-carvone is a more potent inhibitor than R-(-)-carvone as S-(+)-carvone inhibited sprout growth after treating the non-dormant tubers for two days and it took R-(-)-carvone four days to suppress the elongation of the sprouts. The difference was likely caused by the differential uptake rates between S-(+)-carvone and R-(-)-carvone since the endogenous concentration of S-(+)-carvone and its derivatives were twice as high as R-(-)-carvone-treated sprouts after four days exposure. The same stereospecific effects were also found in apple seed germination (Reynolds 1987). Apple seed germination was reduced by 50% when treated with 0.058 mM S-(+)-carvone and the equivalent inhibitory effect was achieved by using 0.38 mM of R-(-)-carvone. Pathirana *et al.* (1992) investigated the chiral recognition of carvone isomers by phospholipid monolayers and found that when compressed at 30°C, monolayers with S-(+)-carvone absorbed twice as much heat and underwent a larger entropy change than monolayers with R-(-)-carvone.

Thus far, all studies have confirmed that with repeated applications at certain concentrations, both isomers of carvone can effectively inhibit sprouting for a considerable period of time. S-(+)-carvone appears to act upon sprout inhibition faster than its isomer. It also presents high potential to be used in seed potato storage.

Mode of action of S-(+)-carvone

The mode of action of many monoterpene compounds remains unclear. Vaughn and Spencer (1991) identified several monoterpenes, including 1,4-cineole, 1,8-cineole, fenchone, limonene oxide, linalool and terpinen, with phytotoxicity effects on potato sprouts. However, they did not find any single structural functional group or chemical factor specifically associated with phytotoxicity. The authors suggested that volatility of the compound might play a role in the level of phytotoxicity. In general, the more volatile compounds, such as 1,4-cineole, 1,8-cineole and fenchone, are more phytotoxic than compounds (citral, citronellol, geraniol, pulegone and α-terpineol) that are less volatile. In their experiment, a short-term exposure (24 hr) caused no visible injury on emerged tuber sprouts when treated with less volatile monoterpenes, but mild necrosis occurred on the tissue when exposed for 7 days. This response also indicated that certain monoterpenes may disrupt cell membranes by acting as a solvent (Vaughn and Spencer 1991). In addition, the presence of an oxygen function may be crucial for the activity. Reynolds (1987), in a lettuce seed germination study, showed that the strongest germination inhibitors were oxygenated terpenes and that hydrocarbon monoterpenes produced the least inhibition. It was also proposed that the presence of an unsaturated ketone group in carvone could also play a role in inhibiting sprout growth (Capelle *et al.* 1996).

According to Oosterhaven *et al.* (1993, 1995c), S-(+)-carvone plays a role in enhancing the degradation of 3-hydroxy-3-methylglutaryl coenzyme A reductase (HMG-CoA reductase), which is crucial for the biosynthesis of cytokinins, gibberellic acids, abscisic acid, membrane components and photosynthetic components. The possible mode of action of S-(+)-carvone at a molecular level was first elucidated from animal studies. A study done on rats showed that cyclic monoterpenes, like cineole or menthol, reduced

the activity of HMG-CoA reductase (Clegg *et al.* 1982). The enzyme catalyzes the rate limiting reaction in the mevalonate pathway (Goldstein and Brown 1990). The mevalonate pathway is important for the production of a large number of isoprenoids and their derivatives, vital components for diverse cellular functions ranging from cholesterol biosynthesis to growth control. The blockage of the pathway in animal cell lines resulted in a loss of protein synthesis and an arrest in cell cycling (Siperstein 1984; Sinensky and Logel 1985). In plants, mevalonate pathway or HMG-CoA reductase pathway is important for the production of many important secondary metabolites including plant hormones like ABA, GA, cytokinins, membrane components and components required for photosynthesis (Bach 1987; Bach *et al.* 1991; Weissenborn *et al.* 1995; Bach *et al.* 1999). Therefore, HMG-CoA reductase plays a vital role in plant growth and development. When radish seedlings were treated with an HMG-CoA reductase inhibitor, mevinolin, mevalonate starvation resulted in a complete inhibition in root elongation (Bach and Lichtenthaler 1983). In potato, S-(+)-carvone was proposed to act as an intermediate leading to enhanced degradation of HMG-CoA reductase and the impairment of HMG-CoA reductase activity was correlated with the disappearance of the enzyme (Oosterhaven *et al.* 1993; Oosterhaven *et al.* 1995c). The reduction in HMG-CoA reductase activity was unlikely caused by a direct effect of S-(+)-carvone on the enzyme itself, as the addition of S-(+)-carvone at concentrations ranging from 1 to 0.01 μM in the HMG-CoA reductase assay system did not reduce the enzyme activity. The reduction in enzyme activity also appeared to increase with time. When potato sprouts were treated with S-(+)-carvone for one day, the HMG-CoA reductase activity was partially inhibited. After a 4-day exposure, the activity was inhibited completely while the HMG-CoA reductase mRNA-level was not affected. Based on the lipophylic characteristics of S-(+)-carvone, Oosterhaven *et al.* (1993) proposed that S-(+)-carvone interacted with the membrane system of the plant cell, possibly by changing the membrane fluidity, thus the lipid microenvironment of HMG-CoA reductase was altered resulting in an enhanced degradation and/or a disturbed insertion of the protein in the microsomal membrane. However, if this hypothesis was true, it is unlikely that enzyme HMG-CoA reductase would be the only enzyme affected by the disruption of membrane fluidity.

CONCLUSION

In conclusion, many essential oils and their major components, particularly carvone, have shown promising sprout suppression effects. Besides sprout suppression effects, carvone was also shown to be effective in inhibiting the growth of certain fungi and bacteria including *Fusarium solani*, *Fusarium sulphureum*, *Streptococcus thermophilus*, *Lactococcus lactis* and *Escherichia coli* (Farag *et al.* 1989; Gorris *et al.* 1994; Oosterhaven *et al.* 1995b). Carvone has a Generally Recognized As Safe (GRAS) status (Hall and Oser 1965) and it is considered to have low human toxicity level (Kerstholt *et al.* 1997). Carvone residue was mainly found in the peel in treated tubers, but it dissipated quickly when the commodity is ventilated and is not in contact with carvone (Hartmans *et al.* 1995; Osterhaven *et al.* 1995b). Hartmans *et al.* (1995) demonstrated that the average residue levels in IPC and CIPC treated tubers were over two times higher than carvone treated tubers.

Although carvone containing essential oils and purified carvone appear to have great potentials, CIPC is still the most economical option for sprout suppression. Future studies are necessary to determine the optimal concentrations, treatment intervals and application methods to generate a more reliable and economical option for potato growers and processors.

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