



Utilization of Essential Oils to Control Sprout Growth of Potato Tubers

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Abstract

Finding supplementary treatments with high sprout suppression efficacy is necessary for maintaining optimum potato (*Solanum tuberosum* L.) tuber quality in storage. The objective of this research was to determine the efficacy of sweet orange (*Citrus sinensis*), spearmint (*Mentha viridis*), and oregano (*Origanum vulgare*) essential oils (EOs) as sprout suppressor treatments and optimize their application methods. EOs were applied either thermally, using cv. Russet Burbank and cv. Ranger Russet tubers at different stages of dormancy, or applied via air-wicking method using mini tubers of cv. Russet Burbank. After the treatments, sprout growth of tubers was monitored and different tuber tissues were collected for biochemical analysis in the air-wicking study. Overall, thermal application of EOs was an effective method, and oregano EO exhibited higher efficacy for sprout control. When applied using an air-wick method, temporary sprout suppression until 6-weeks and lower reducing sugar content in bud tissues were observed with spearmint EO. Increase in chlorogenic acid content and activity of antioxidant enzyme was observed in primary bud tissues with oregano EO treatment, indicating a stress induction response. Overall, EO treatments impacted sugar metabolism, antioxidant enzymes, and secondary metabolites, which significantly influence the sprouting of potato tubers.

Resumen

Es necesario encontrar tratamientos complementarios con una alta eficacia de supresión de brotes para mantener una calidad óptima del tubérculo de papa (*Solanum tuberosum* L.) en el almacenamiento. El objetivo de esta investigación fue determinar la eficacia de los aceites esenciales (AE) de naranja dulce (*Citrus sinensis*), menta verde (*Mentha viridis*) y orégano (*Origanum vulgare*) como tratamientos supresores de brotes y optimizar sus métodos de aplicación. Los Eos se aplicaron térmicamente, utilizando tubérculos de las variedades Russet Burbank y Ranger Russet en diferentes etapas de latencia, o se aplicaron mediante el método de absorción de aire utilizando mini tubérculos de la variedad Russet Burbank. Después de los tratamientos, se monitoreó el crecimiento de los brotes de tubérculos y se recolectaron diferentes tejidos de tubérculos para su análisis bioquímico en el estudio de absorción de aire. En general, la aplicación térmica de AE fue un método efectivo, y el AE de orégano mostró una mayor eficacia para el control de brotes. Cuando se aplicó utilizando un método de suministro en el aire, se observó una supresión temporal de los brotes hasta las 6 semanas y un menor contenido de azúcar reductor en los tejidos de las yemas con EO de menta verde. Se observó un aumento en el contenido de ácido clorogénico y la actividad de la enzima antioxidante en los tejidos primarios de las yemas con el tratamiento con AE de orégano, lo que indica una respuesta de inducción de estrés. En general, los tratamientos con AE afectaron el metabolismo del azúcar, las enzimas antioxidantes y los metabolitos secundarios, que influyen significativamente en el brote de los tubérculos de papa.

Keywords Antioxidants · Enzymes · Orange essential oil · Oregano essential oil · Phenolics · Reducing sugars · Spearmint essential oil · Tuber dormancy · Tuber sprouting

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Introduction

Potato (*Solanum tuberosum* L.) is the third most important food crop with an annual production of 440 million hundredweight in the United States (USDA 2024). Over 90% of fall-harvested tubers are placed into medium to long-term

storage for year-round use (Suttle et al. 2016). Persistent postharvest storage management is essential to maintain high tuber qualities as premature sprouting of potato tubers can affect shelf-life, processing, and nutritional qualities (Dogramaci et al. 2024a). The duration of dormancy varies considerably among different potato varieties and can be impacted significantly by storage environment. Cultivated potato tubers are usually physiologically dormant at harvest, and will not sprout under growth conducive conditions, therefore they are considered endodormant (Suttle 2007; Suttle et al. 2016). After endodormancy is released, tubers eventually begin to sprout with the primary bud becoming dominant and other buds remaining paradormant due to apical dominance. As tubers age, apical dominance dissipates and all or majority of tuber buds sprout (Eshel and Teper-Bamnolker 2012; Eshel 2015). However, if potato tubers are stored under cold temperature ($<3^{\circ}\text{C}$), they will remain ecodormant for a longer period, but they will eventually sprout after certain duration in the storage (Suttle 2007; Suttle et al. 2016).

Storing tubers under cold temperature is an effective approach to suppress sprout growth, however it can cause cold-induced sweetening, which impacts the color of potato chips and fries (Rosen et al. 2018; Tai et al. 2020). Therefore, supplementary management approaches such as application of sprout-suppressing chemicals are needed for tubers stored above 3°C . Among sprout suppressors, chlorpropham (CIPC) is the most widely used postharvest treatment in the United States and in major potato producing countries (e.g., China, India, Russia). However, CIPC is no longer registered for use in potato storage facilities in the European Union, and there is an accelerated search for alternative management practices (Visse-Mansiaux et al. 2021a; 2024). There are alternative sprout-suppressing chemicals, but they are not as effective as CIPC (reviewed in Dogramaci et al. 2024a). Therefore, finding effective alternative sprout suppressing management strategies is a major focus of the potato industries around the world (Dogramaci et al. 2024a; Paul et al. 2016).

In this context, essential oils (EOs) have emerged as a potential sprout control method for potatoes (Gómez-Castillo et al. 2013; Teper-Bamnolker et al. 2010). EOs have unique chemical compositions, and major constituents are divided into two distinct groups, terpenes and non-terpenes/phenylpropanoids (Chen et al. 2024). These active chemical constituents of EOs have diverse biological properties such as anti-bacterial, anti-viral, anti-inflammatory, and antioxidant activities (Dhifi et al. 2016). Several EOs of medicinal herbs or spices (e.g., spearmint, peppermint, orange, caraway, clove, coriander, dill, oregano, lavender, sweet marjoram, rosemary, salvia, lemon balm, garlic) and their major constituents have been previously investigated to control

sprout growth in potato storage (Finger et al. 2018; Frazier et al. 2004; Goodarzi et al. 2016; Li et al. 2022; Mukhlid et al. 2024; Owolabi et al. 2010; 2013; Şanlı and Karadoğan 2019; Saunders and Harper 2019; Shukla et al. 2019; Song et al. 2008; Teper-Bamnolker et al. 2010; Vokou et al. 1993). Organic potato production utilizes many of these EOs, and several commercial products containing EOs or their main chemical constituent are already registered for use in potato storage across different countries (Mukhlid et al. 2024).

For example, an orange peel EO based commercial product (ARGOS®) is registered for use in potato storage in several European countries (Visse-Mansiaux et al. 2021a). The active ingredient of orange EO is D-limonene, a colorless monoterpene, which is considered safe due to low toxicity to animals (Kim et al. 2013). Orange EO has exhibited sprout suppression and pesticidal properties relevant for utilization in potato postharvest storage (Saunders and Harper 2019). Likewise, there is a spearmint (*Mentha spicata* L.) EO based commercial product (Biox-M) available for utilization in potato storage. The active ingredients of spearmint EO are carvone, limonene, and 1,8-cineole, which are classified as monoterpenes and mostly colorless compounds (Wu et al. 2019). Previous research (Alzarqaa et al. 2024; Coleman et al. 2001; Song 2009) reported sprout suppression of potato tuber in postharvest storage with application of spearmint EO or its active ingredient (carvone). Oregano (*Origanum spp.*) is another mediterranean herb, containing volatile compounds and has been widely used in postharvest quality preservation and disease prevention of fruits and vegetables (El-Abbasy et al. 2023; Pirozzi et al. 2020; Montero et al. 2015). Previously, Vokou et al. (1993) wick applied oregano EO to suppress sprout growth in potato tubers, but the result was not effective as other EOs. The main active ingredient of oregano EO is carvacrol, which has various biological properties including high antioxidant and antimicrobial activities (Fonseca et al. 2021; Rúa et al. 2019). Beneficial role of oregano EO to control potato pathogens, such as *Rhizoctonia solani* (Wu et al. 2023), *Alternaria alternata*, *Fusarium culmorum*, *Erwinia carotovora*, *Pythium debaryanum* (Kosakowska et al. 2024), and *Pectobacterium carotovorum* subsp. *carotovorum* (Jílková et al. 2024) have been reported.

The biological functions of EOs largely depend on the profile of phenylpropanoid compounds in EOs and are based on either additive, synergistic, or antagonistic effects of those compounds on specific plant tissues. In addition to causing necrosis of tuber meristem tissues, EOs exhibit diverse biological activities based on chemistry and mode of action. The antioxidant and redox properties of EOs are related to the specific chemical structure of monoterpene phenols (i.e. thymol, carvacrol, carvone, limonene), which has a benzene ring with an attached hydroxyl group, and their overall ability to

decompose or quench peroxides and free radicals in plant tissues (Dhifi et al. 2016). Release of tuber dormancy and sprouting is associated with accumulation of reactive oxygen species in bud tissues (Liu et al. 2023), and antioxidant function of EOs might be relevant to influence redox regulation and dormancy progression in potato tubers. The mode of action of EOs is not only limited to their direct role in free radical scavenging, but EOs also alter signaling pathways related to oxidative stress regulation (Jugreet et al. 2020). Beyond modulating oxidative stress signaling, EOs potentially modulate primary and secondary metabolisms in plant tissues. Changes in reducing sugar and ethylene content in tuber bud tissues and subsequent sprout control of cv. Chipsona by palmarosa (*Cymbopogon martini*) and ajwain (*Trachyspermum ammi*) EOs were reported by Shukla et al. (2019). Lower reducing sugar content and alteration in sugar metabolisms along with sprout inhibition in menthol and peppermint EO treated tubers were previously observed by Santos et al. (2019). Therefore, the mode of action of EOs related to tuber sprout control might involve alteration in redox regulation, sugar metabolisms, and phytohormone regulations. Along with mode of action, it is important to note that stability or viability of active constituents of EOs also determines their overall biological functions related to tuber sprout control.

In general, active constituents of most EOs biodegrade over time, which leads to having minimum residues in potato tubers during long-term storage (Teper-Bamnolker et al. 2010). However, the efficacy of EOs for sprout control, improving postharvest storage qualities, and disease prevention largely depends on various factors, including concentration and composition of the active ingredients in the EOs, method and time of application, dormancy stages of the potato tubers at the time of application, storage environment (temperature, humidity, air circulation), and potato varieties. Therefore, optimizing the method and time of application of EOs to potato tubers is warranted to determine the viability of their utilization in commercial storage. There is also a significant knowledge gap in understanding the biochemical mechanisms of EOs related to tuber sprout control. Based on these needs and the existing knowledge gap, the main objective of this research is to investigate the efficacy of three organic EOs (sweet orange, spearmint, and oregano) and optimize the application method and timing of these treatments to suppress sprout growth of potato tubers during long-term storage. The research was divided in two sets of experiments: i) thermal application of three EOs at different phases of bud dormancy (dormant, peeping, sprouting) using Russet Burbank (long dormancy) and Ranger Russet (short dormancy) tubers; ii) air-wick application of three EOs using mini tubers of cv. Russet Burbank after 20-weeks of postharvest storage (peeping phase). Due to their higher genetic stability, micro-propagated mini tubers are a good

model system to investigate changes in molecular and biochemical mechanisms of potatoes under different postharvest treatments and storage environments. For the first set of experiments, sprout growth of tubers following thermal EO treatments were determined, while for the second set, the impact of EO wick treatments on sugar metabolisms, antioxidant enzymes, and phenolic metabolites in different tuber tissues (primary bud, secondary bud, and tuber flesh) was investigated. The first set of experiments with thermal application of EOs will be referred to as the “thermal application” study, while the second set of experiments with air-wick application of EOs will be referred as “wicking” study. The main goal of the biochemical analysis of the wicking study is to elucidate the potential role of stress-induced secondary metabolites and antioxidants in EO related to sprout control of potato tubers.

Materials and Methods

Tuber Materials and Essential Oils

In year one, Russet Burbank certified seed was planted at the University of Idaho Kimberly Research and Extension Center (Kimberly, ID, USA; UIKREC) in April 2021 and grown following conventional production practices. In year two, an additional cultivar, Ranger Russet was added to the experiment and certified seed was planted in April 2022. Cultivars were harvested in September of 2021 (Russet Burbank) and 2022 (Russet Burbank and Ranger Russet) and placed under different storage conditions to induce/suppress sprout growth (described below) prior to thermal applications of EOs. Certified mini tubers of Russet Burbank were obtained from Valley Tissue Culture (Halstad, MN, USA) in September 2021.

Three organic EOs: sweet orange (*Citrus sinensis*), spearmint (*Mentha viridis*), and oregano (*Origanum vulgare*) were obtained from a commercial source (Plant Therapy, Twin Falls, ID, USA) and used in both experiments. Gas chromatography analysis (Table 1 and Supplementary File) of the EOs was provided by the commercial vendor and the main active ingredient content of three EOs were 93.2% limonene in sweet orange EO, 61.2% carvone in spearmint EO, and 76% carvacrol in oregano EO. All other reagents and chemicals for biochemical analysis were purchased from Sigma-Aldrich (St. Louis, MO, USA).

Experimental Design to Determine Sprout Control with Thermal Application of EOs

A split plot experimental design included four treatments (untreated control, sweet orange, oregano, and spearmint

Table 1 Top 5 compounds detected from consolidated content analysis of Organic spearmint (*Mentha viridis*): Density: 0.925, Flashpoint: 67.2°C; Organic Oregano (*Origanum vulgare*): Density: 0.948, Flashpoint: 63°C; Organic Sweet Orange (*Citrus sinensis*): Density: not provided, Flashpoint: 46°C. Compound analysis was obtained from the certificate of analysis- GC profiling by Laboratoire Phytochimie (Plant Therapy, Twin Falls, ID)

	Compound	%	Class
Organic Spearmint (<i>Mentha viridis</i>)			
1	Carvone	61.18	Monoterpenic ketone
2	Limonene	17.45	Monoterpene
3	Myrcene	1.71	Monoterpene
4	<i>cis</i> -Dihydrocarvone	1.59	Monoterpenic ketone
5	β -Bourbonene	1.15	Sesquiterpene
Organic Oregano (<i>Origanum vulgare</i>)			
1	Carvacrol	76.04	Monoterpenic alcohol
2	para-Cymene	6.66	Monoterpene
3	Thymol	3.66	Monoterpenic alcohol
4	γ -Terpinene	2.43	Monoterpene
5	β -Caryophyllene	1.06	Sesquiterpene
Organic Sweet Orange (<i>Citrus sinensis</i>)			
1	Limonene	93.2	Monoterpene
2	Myrcene	1.92	Monoterpene
3	1,8-Cineole	0.77	Monoterpenic ether
4	α -Pinene	0.54	Monoterpene
5	Linalool	0.34	Monoterpenic alcohol

EOs) on two levels of sprouted tubers (peeping and sprouting). In year two, dormant (non-sprouted) tubers were included for each cultivar. The experiment was conducted at UIKREC. After harvest, Russet Burbank and Ranger Russet tubers were placed in varying temperatures directly after harvest to induce/suppress sprout growth (n=15 tubers per replicate, four replicates per treatment).

In year one, Russet Burbank tubers were stored either at 5.6°C or 8.9°C to induce the ‘peeping’ stage or ‘sprouted’ stage, respectively, prior to thermal EO applications. Thermal applications were conducted on March 2, 2022 (27-weeks in storage).

In year two, to induce the ‘peeping’ stage, Russet Burbank and Ranger Russet tubers were placed directly into 12.8°C (95% relative humidity; RH), and to induce the ‘sprouted’ stage, tubers were placed directly into 18.3°C (95% RH). An additional sprouting stage was included: using ‘dormant’ tubers that were placed directly into 4.4°C (95% RH) after harvest. On November 29, 2022, tubers stored in 18.3°C (‘sprouted’ stage) were transferred to 12.8°C temperature until the experiment was conducted. Ranger Russet tubers were treated with thermal EO applications on December 8, 2022 (12-weeks in storage). Thermal EO applications for Russet Burbank were conducted on February 16, 2023 (21-weeks in storage).

EO treatments were applied using a thermal aerosol applicator. Measured oil product was injected into a hot-plate type volatilization chamber and dispersed under heat,

which forms a fog of minute droplets of EO. Each EO was thermally applied at 100 ppm. Preliminary studies were performed to identify the optimal application temperature for each EO (data not shown). Spearmint EO was applied at 120°C, sweet orange EO at 132°C, and oregano EO at 150°C. Product was applied at approximately a rate of 2.6 mL/min at respective temperatures. The heated EO vaporized and circulated through the chamber for 30 min before the volatilization chamber was disconnected and air circulation re-established in the treatment container and plenum. Air within the treatment box was re-circulated for 24 h (ambient temperature; approximately 18.3°C) and then vented. After recirculation, tubers were placed at 8.9°C (95% RH) for sprouting evaluations. Tubers were evaluated for sprout development (described below) one day prior to application of treatments to confirm the dormancy stage. In year two, a CIPC standard treatment was included as comparison to industry standard practices (n=15 tubers, four replicates per treatment). The CIPC treatment was a thermal application of the commercial sprout inhibitor (Aceto Agricultural Chemicals Corporation, New Hyde Park, NY, USA) at 22 ppm and applied on November 17, 2022, following industry standards for both cultivars.

Sprout Development Measurements

Tubers were evaluated for sprout development one day prior to application of treatments and approximately one week and one month after EO thermal applications. In year two, an additional evaluation occurred 6-weeks after treatment for both cultivars and 8-weeks after treatment for Ranger Russet. Sprout development ratings and visual damage to sprouts were determined. Sprout development was rated on a 1 to 4 scale (1=no sprout development, 2=“peeping” where at least one potato eye is showing initial sprout development, 3=sprout appears pointed and is elongating but sprout length is less than 5mm, 4=sprout length>5mm). Visual sprout damage, assessed by the presence of blackening or necrosis, to meristematic tissue of bud or sprout development (called sprout damage), was calculated on a percent incidence basis.

Sprouts were removed from tubers (n=15) and weighed for each sample at the final evaluation. Sprout weight per tuber was calculated dividing the total sprout weight by the number of tubers in each sample.

Experimental Design to Determine Sprout Control of Mini Tubers with Air-Wick Application Method of EOs

The second set of experiments with mini tubers of Russet Burbank was conducted at Edward T. Schafer Agricultural

Research Centre (USDA-ARS, Fargo, ND, USA) year one (2021–2022). After harvest, mini tubers of Russet Burbank were cured at ~21°C (95% RH) for 2-weeks and then temperature was ramped down to 8°C for storage. The air-wick applications and CIPC treatment occurred 20 weeks after harvest (February 24, 2022). For each treatment, 112 mini tubers with an average 12.4 g weight were used (~1,400 g total weight); each treatment included three replicates. For the CIPC treatment (Tokyo Chemical Industry, Portland, OR, USA), tubers were immersed in a liquid solution (10 ppm) for 1 min, and drained and placed in a fume hood for 15 min before placing in 8.3 L Nalgene container for storage. Wick-ing treatment of EOs was performed using a standardized method based on application container's volume and surface area (Edwards 1999), weight of tubers treated in containers, and relative density of EOs. For each EO treatment (at 100 ppm rate), 112 mini tubers were placed in a 8.3 L Nalgene container with a glass beaker containing a tissue paper (Kim Wipes, KimTech Science, Roswell, GE, USA) placed at the center of the container. Based on the relative density of EOs, 623 µl sweet orange EO, 559 µl oregano EO, and 573 µl spearmint EO treatments were pipetted onto the tissue paper, and the containers were immediately sealed to allow evaporation of EOs in the container system. The containers for each treatment were stored separately at 8°C (95% RH) in different environmental chambers. Lids of the containers were removed after 48 h of treatment. A set of tubers were used as controls without the chemical treatments and stored under the same environmental conditions for tuber tissue sampling at 0 d, and 1-, 3-, 5-, and 8- weeks after the treatments.

Sprout Growth Score

Changes in color of tuber eye (brown to white) and bud/eye movements (peeping of tuber bud) were monitored weekly, and length (mm) of the sprouts were measured once the bud started to emerge. A different sprout growth score scale was used in the “air-wicking” study to differentiate distinct sprouting stages and to identify the effect of EO treatments on potential sprout control of mini tubers. The sprout length was then converted to a sprout score using an established protocol (dormant=0; <1 mm=1; 1–2 mm=2; 2–3 mm=3; >3 mm=4). A subsample (n=6 tubers; three replicates) was used for each replication and tubers were marked to monitor sprout growth from same tubers in weekly interval.

Sampling and Extraction of Tuber Tissues for Biochemical Analysis

Tissues of primary bud, secondary bud, and tuber flesh tissues were collected separately from a subset of tubers (n=12

per replicate and total 3 replications) at 0 d, 1-, 3-, 5-, and 8- weeks after the treatments, and all tissues were frozen in liquid nitrogen and stored at -80°C freezer until processing for biochemical analysis. Primary and secondary bud tissues were excised precisely (without flesh tissues) from the meristem region using a sharp scalpel, while for tuber flesh, a block of tissues was taken out using a cork borer and tissue discs from the center of the cylinder were cut and collected. Tuber tissues were freeze-dried and ground to powder using mortar and pestle in liquid nitrogen. For reducing sugar, sucrose, starch, protein, and phenolic metabolite analysis, tuber tissues (~15 mg dry weight-DW) were extracted in methanol using a protocol described by Silva et al. (2021). For analysis of enzymes related to carbohydrate metabolism and antioxidant activity, 100 mg (DW) of tuber tissues were extracted using 0.1 M potassium phosphate buffer (containing 0.5% polyvinylpyrrolidone and 3 mM ethylenediaminetetraacetic acid) following a modified protocol for potato (Dogramaci et al. 2024b).

Analysis of Reducing Sugar, Sucrose, Starch, and Protein

Reducing sugar, sucrose, starch, and protein content of all three tuber tissues (primary buds, secondary buds, and tuber flesh) collected at 1-, 3-, and 8- weeks after treatment were determined. Glucose, fructose, and sucrose content of the tuber tissues were analyzed using a protocol originally described by Baxter et al. (2003). Tuber tissue extracts (10 µL) were added in 96-well microplate along with 160 µL reagent mixture containing 15.5 mL 4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid (HEPES) buffer (1 M, pH 7.0), 480 µL adenosine tri-phosphate (ATP 109 mM), 480 µL nicotinamide adenine dinucleotide phosphate (NADP⁺ 48.4 mM), and 80 µL glucose-6-phosphate dehydrogenase (G6PDH 0.77 U). After taking the baseline absorbance readings, 5 µL hexokinase (1500 U/mL), 5 µL phosphoglucose isomerase (350 U/mg protein), and 5 µL invertase (300 U/mg solid) were added in 1-h intervals and changes in absorbance at 340 nm were recorded using a SpectraMax microplate reader (Molecular Device, San Jose, CA, USA).

For determination of starch and protein, insoluble pellet fraction from the methanol extract was used. In the pellet, 400 µL of sodium hydroxide (0.1 M NaOH) was added and homogenized to carry hydrolysis. The mixture was then incubated at 95°C for 1 h in a shaker (500 rpm). For the protein assay, 5 µL of sample was added to the well of the microplate and mixed with 250 µL of Bio-Rad protein dye (Bradford 1976). The reaction was carried out in the dark for 10 min and the absorbance was recorded at 595 nm using a microplate reader. Total protein content was expressed as mg/g DW based on a standard curve prepared with different concentrations of bovine serum albumin (BSA). Starch

of the tuber tissue extracts was determined based on the method described by Baxter et al. (2003), where hydrolysis of the sample was stopped by adding 70 μL of 1M glacial acetic acid. Then 40 μL of the sample was added in the well of the microplate and mixed with 80 μL of reagent mixture containing 0.5 M sodium acetate (pH 4.9), 1.2 μL of amyloglucosidase (14U/mg), and 12 μL of α -amylase (0.004U/mg). The microplate was then incubated at 55°C for 1 h in a shaker (300 rpm) and absorbance was recorded at 340 nm in a microplate reader.

Analysis of Glucose-6-Phosphate Dehydrogenase (G6PDH) and Succinate Dehydrogenase (SDH) Enzyme Activities

Activity of G6PDH enzyme was determined for all three tuber tissues at 0 d, 1-, and 3-weeks after treatment using a protocol described by Deutsch (1978) with modifications (Dogramaci et al. 2024b). Potato tissue extract (100 μL) was mixed with an enzyme reaction mixture containing β -NADP (0.0058 mM nicotinamide adenine dinucleotide phosphate), MgCl_2 (0.088 mM magnesium chloride), glucose-6-phosphate (0.053 mM), and maleimide (0.77 mM). Absorbance reading of the sample mixed with the reaction mixture was recorded at 0 min and after 5 min of incubation at 340 nm using a UV–VIS spectrophotometer. Shift (Δ) in absorbance after 5 min was used to quantify G6PDH activity based on the extinction coefficient of NADPH (reduced nicotinamide adenine dinucleotide phosphate; 0.0622 $\text{mM}^{-1}\text{m}^{-1}$).

For determining SDH activity, a protocol described by Bregman (1987) was used. At first, a reaction mixture containing 0.5 mL potassium phosphate buffer (0.4 M; pH 7.2), 0.2 mL sodium succinate (0.15 M; pH 7.0), 0.2 mL sodium azide (0.2 M), and 0.1 mL 2,6-dichlorophenolindophenol (DCPIP; 6.0 g L^{-1}) was prepared and 1 mL of mixture was added to 200 μL potato tissue extracts. The rate of change of absorbance per min was measured at 600 nm and SDH activity was determined using extinction coefficient of DCPIP (0.0191 $\text{mM}^{-1}\text{m}^{-1}$).

Analysis of Antioxidant Enzymes

The activity of Guaiacol Peroxidase (GPX) was determined using an assay protocol described by Laloue et al. (1997). Potato tissue extracts (10 μL) were mixed with 990 μL enzyme reaction mixture containing 1 M potassium phosphate buffer (pH 6.8), 56 mM guaiacol solution, and 50 mmol hydrogen peroxide (H_2O_2). Shift in absorbance after 3 min was recorded at 470 nm and GPX activity was measured based on the extinction co-efficient of the oxidized product tetraguaiacol (0.266 $\text{mM}^{-1}\text{m}^{-1}$).

To determine activity of Catalase (CAT), a spectrophotometric protocol described by Beers and Sizer (1952) was

used. A reaction mixture, containing 0.059 M H_2O_2 (Merck Co. & Inc., Whitehouse Station, NJ) and 0.05 M potassium phosphate buffer solution (pH 7.0), was prepared and 1450 μL of mixture was added to 50 μL of potato tissue extracts. Disappearance of peroxide due to activity of CAT was monitored over 5 min and the shift in absorbance per min was recorded at 240 nm. One unit of CAT activity was defined as the amount that decomposes one micromole of H_2O_2 .

Characterization of Phenolic Compounds

Phenolic compounds of potato tuber tissues were characterized using a reverse phase high performance liquid chromatography (HPLC; Agilent 1260 Infinity series, Agilent Technologies, CA, USA) based analytical technique optimized for potato tissues (Dogramaci et al. 2024b). Two solvents, 0.01 M phosphoric acid (pH 2.5; Solvent A) and 100% methanol (Solvent B) were eluted at a 1 mL/min flow rate and a step gradient method was used. A C-18 analytical column (ZORBAX SB-C18 250 $\times$ 0.046 m internal diameter) was used, and standard curves were prepared using pure phenolic standards. Absorbances were recorded at 214, 230, 258, 260, and 306 nm wavelength using DAD 1100 diode array detector. Chromatograms were analyzed using OpenLab CDS software and concentration of phenolics were calculated and expressed as $\mu\text{g/g}$ DW.

Data Analysis

Sprout development variables (sprout rating at each evaluation time, sprout weight, and sprout damage) from “thermal application” study were analyzed using the analysis of variance (ANOVA) via the ‘car’ package in R (RStudio, v3.1–2; Fox et al. 2023). For Russet Burbank, a linear model for each sprout development variable was fitted where EO application, year, and EO application by year interaction was considered the fixed effects. For Ranger Russet, a linear model for each sprout development variable was fitted where EO application was considered the fixed effect. All significant differences between means for treatments, cultivars, and interactions were compared at alpha of 0.05 by estimated marginal means procedures (RStudio, v. 1.10.0, 2024; Lenth 2024). For the “air wicking” study, statistical analysis of sprout growth score and biochemical analysis data was performed using R version 4.4.2 using the packages ‘car’ and ‘multcomp’, and the plots were generated using ‘tidyverse’ and ‘ggplot2’. A one-way analysis of variance (ANOVA) was conducted to assess the effects of treatments and among tuber tissue types on sprouting and biochemical parameters at each time point followed by Tukey’s test ($P < 0.05$, and $P < 0.01$) for multiple comparisons using the ‘emmeans’ package (Lenth 2024).

Table 2 Effect of essential oil (EO) application on sprout development (rating, sprout weight, and peeping eye damage) prior and after EO applications for Russet Burbank tubers that were *peeping at time of application*

EO application	Sprout rating after application (1 to 4) ¹		Sprout weight per tuber (g/tuber)	Sprout damage (%)
	1 week	4-weeks		
Control	2.7 c	3.8 b	Approximately 4-weeks	1-week after application
Sweet Orange	2.0 b	3.8 b	0.50 c	18 a
Oregano	1.3 a	3.5 a	0.35 b	66 b
Spearmint	2.2 b	3.8 b	0.18 a	100 c
P-value	2.2 b	3.8 b	0.44 bc	69 b
	<0.001	<0.001	<0.001	<0.001

Means averaged between two years. Tubers had a mean sprout rating of 2.2 prior to application

¹Values in each column followed by the same letter are not significantly different at $\alpha=0.05$

Results

Effect of Thermal Application of EOs

In general, oregano EO was very effective at causing sprout damage to peeping eyes when evaluated 1-week after application regardless of the sprout growth stage (Tables 2–6). Spearmint and sweet orange EOs were not as effective as oregano EO but showed some ability to affect sprout tissue and development when applied at the dormant or sprouted growth stages for Ranger Russet and all growth stages for Russet Burbank. Oregano EO exhibited promise as a “rescue treatment” to potatoes that had already broken dormancy with substantially elongated sprouts. The cultivars appeared to respond differently to the EO treatments and were dependent upon the sprout growth stage. Below are specific results for each cultivar.

Russet Burbank (combined two years)

For Russet Burbank tubers, if the EO was applied when tubers were peeping, all EO treatments had significantly lower sprout ratings compared to the control 1-week after treatment (Table 2). Sustained sprout suppression was observed for 4-weeks after oregano EO treatment, which resulted in significantly lower sprout rating and sprout weight per tuber. Sweet orange had a lower sprout weight per tuber compared to the control. Visual ratings of sprout damage (blackening of meristematic tissue) were significantly highest with oregano EO (100%) and spearmint and orange EO had 66% to 69% damage, respectively. EO applications produced significantly higher sprout damage compared to the control (18%). If tubers were sprouting

Table 3 Effect of essential oil (EO) application on sprout development (rating, sprout weight, and peeping eye damage) after EO applications for Russet Burbank tubers that were *sprouted at time of application* and sprout weight per tuber approximately 4-weeks after application

EO Application	Sprout rating after application (1 to 4) ¹		Sprout weight per tuber (g/tuber)	Sprout damage (%)
	1-week	4-weeks		
Control	4.0 d	4.0 b	Approximately 4-weeks	1-week after application
Sweet Orange	3.3 c	4.0 b	0.93 b	9 a
Oregano	1.3 a	3.8 a	0.90 b	49 b
Spearmint	3.1 b	3.9 b	0.51 a	100 d
P-value	<0.001	0.01	1.01 b	58 c
	<0.001	<0.001	<0.001	<0.001

Means averaged between two years. Tubers had a mean sprout rating of 4.0 prior to application

¹Values in each column followed by the same letter are not significantly different at $\alpha=0.05$

when the EO applications occurred, all EO treatments significantly impacted sprout ratings compared to the control (Table 3). The impact of spearmint and sweet orange EOs were transient and were not observed after 1 month nor in sprout weight per tuber.

Ranger Russet (year two only)

The applications of the oregano EO treatment to dormant Ranger Russet tubers had lower sprout ratings than the control at 1-week, 4-weeks and 6-weeks after treatment (Table 4). A significant effect of spearmint EO on sprout rating was observed after 4-weeks compared to the control. There were no significant differences in sprout weight per tuber after 8-weeks after treatments. Oregano EO treatment showed 100% sprout damage whereas only 18% of the control and 53% and 65% of the orange and spearmint EO treatments, respectively, showed damage. If Ranger Russet tubers were peeping at the time of application, a difference in sprout rating was only observed after 1-week post-treatment and showed the oregano EO treatment with a significantly lower sprout rating (Table 5). To mimic an application of an EO as a rescue treatment when tubers are already sprouting, sprouted Ranger Russet tubers had a lower sprout rating with an application of oregano EO after 1 week, 4-weeks and 6-weeks compared to the control (Table 6). Spearmint EO only showed a significant impact 1-week after treatment. A reduced sprout weight per tuber was seen in the oregano EO-treated tubers compared to the sweet orange and control. No EO treatment was as effective at maintaining a minimal sprout rating and development as the thermal application of CIPC at inhibiting sprout growth.

Table 4 Effect of essential oil (EO) application on sprout development (rating, sprout weight, and peeping eye damage) after EO applications for Ranger Russet tubers that were *dormant at time of application* and sprout weight per tuber 8-weeks after application in 2023

EO application	Sprout development rating after application (1 to 4) ¹				Sprout weight per tuber (g/tuber)	Sprout damage (%)
	1-week	4-weeks	6-weeks	8-weeks	8-weeks	1-week after application
Control	1.8 b	2.9 c	4.0 b	4.0 a	1.18 a	18 a
Sweet Orange	1.8 b	2.5 b	3.9 b	4.0 a	0.89 a	53 b
Oregano	1.1 a	2.1 a	3.7 a	4.0 a	0.87 a	100 c
Spearmint	1.7 b	2.9 c	4.0 b	4.0 a	1.20 a	65 b
P-value	<0.001	<0.001	0.004	0.43	0.11	<0.001

Tubers had a mean sprout rating of 1.6 prior to application. CIPC standard tubers had a mean sprout rating of 2.0 at 8-weeks; it was not included in the statistical analysis

¹Values in each column followed by the same letter are not significantly different at $\alpha=0.05$

Table 5 Effect of essential oil (EO) application on sprout development rating after EO applications for Ranger Russet tubers that were *peeping at time of application* and sprout weight per tuber 8-weeks after application in 2023

EO application	Sprout development rating after application (1 to 4) ¹				Sprout weight per tuber (g/tuber)	Sprout damage (%)
	1-week	4-weeks	6-weeks	8-weeks	8-weeks	1-week after application
Control	2.2 b	3.0 a	3.8 a	3.9 a	0.68 a	20 a
Sweet Orange	2.0 b	2.9 a	3.8 a	3.9 a	0.57 a	36 a
Oregano	1.1 a	2.5 a	3.7 a	4.0 a	0.72 a	100 b
Spearmint	1.8 b	2.8 a	3.7 a	3.9 a	0.54 a	45 a
P-value	<0.001	0.29	0.54	0.74	0.60	0.006

Tubers had a mean sprout rating of 2.1 prior to application. CIPC standard tubers had a mean sprout rating of 2.0 at 8-weeks; it was not included in the statistical analysis

¹Values in each column followed by the same letter are not significantly different at $\alpha=0.05$

Table 6 Effect of essential oil (EO) application on sprout development rating prior and after EO applications for Ranger Russet tubers that were *sprouted at time of application* and sprout weight per tuber 8-weeks after application in 2023

EO application	Sprout development rating after application (1 to 4) ¹				Sprout weight per tuber (g/tuber)	Sprout damage (%)
	1-week	4-weeks	6-weeks	8-weeks	8-weeks	1-week after application
Control	2.8 c	3.5 b	3.8 b	3.9 a	1.09 bc	5 a
Sweet Orange	3.0 c	3.6 b	3.9 b	4.0 a	1.47 c	54 b
Oregano	1.0 a	1.8 a	3.3 a	3.9 a	0.51 a	100 c
Spearmint	2.3 b	3.4 b	3.9 b	4.0 a	0.91 ab	52 b
P-value	<0.001	<0.001	<0.004	0.28	0.004	<0.001

Tubers had a mean sprout rating of 2.8 prior to application. CIPC standard tubers had a mean sprout rating of 2.0 at 8-weeks; it was not included in the statistical analysis

¹Values in each column followed by the same letter are not significantly different at $\alpha=0.05$

Effect of Air-wick Application of EOs on Mini Tuber Sprout Development

Results of the air-wicking study with mini tubers of Russet Burbank revealed limited impact of EO treatments on sprout control immediately after application. Lowest sprout growth scores were observed with CIPC treatment (used as treated control) for both primary and secondary buds of the mini tubers (Fig. 1). Among EO treatments, spearmint EO exhibited sprout suppression until 6-weeks after treatment, and was significantly different ($P<0.05$) for primary bud than the untreated control. However, 7-weeks after treatment, sprout growth of primary bud resumed in spearmint EO treated tubers. Sweet orange EO also suppressed sprout

growth until 3-weeks after treatment but was ineffective afterwards. Similar to the observation of the thermal application studies, EO treatments damaged the majority of bud tissue tips and paused the growth of the sprout for a short period of time. Unlike the result of the thermal application studies, the application of oregano EO as air-wick method was not effective in sprout suppression of Russet Burbank mini tubers.

Reducing Sugar, Sucrose, Starch, and Protein Content in Tuber Tissues Following EO Treatments

Reducing sugars, starch, sucrose, and protein content changed significantly in bud and flesh tissues of Russet

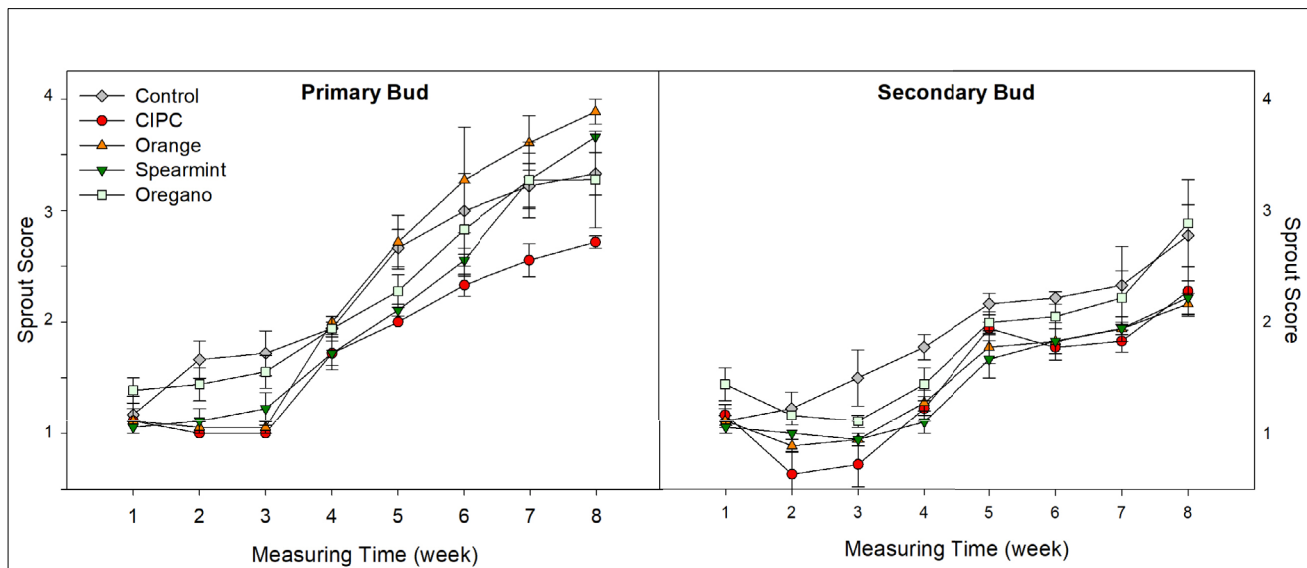


Fig. 1 The changes in sprout growth score of primary bud and secondary bud of mini tubers of Russet Burbank with CIPC and essential oil (EO) treatments during 1 to 8-weeks after treatment application. The vertical bars represent standard error

Burbank mini tubers following EO and CIPC treatments. Overall, reducing sugar (glucose and fructose) content increased gradually in both primary and secondary bud tissues from 1- to 8-weeks, which coincided with sprout emergence and growth (Fig. 2A & 2B). The opposite trend was observed in tuber flesh tissues, where reducing sugar content decreased between 1- to 8-weeks after treatment. Significantly lower reducing sugar content in secondary bud tissues were observed with CIPC treatment after 8-weeks. Among EO treatments, spearmint EO, which suppressed sprout growth until 6-weeks, also exhibited lower reducing sugar (glucose and fructose) content in secondary bud when compared to the control after 8-weeks. After 8-weeks of treatment, lower fructose content in secondary bud tissues were also observed with oregano EO treatment (Fig. 2B).

For the spearmint EO treatment, lower sucrose content was observed in the primary bud after 1-week (Fig. 3A), and it enhanced starch content of primary buds after 1 and 3-weeks (Fig. 3B). Lower starch content in secondary bud tissues was observed with spearmint and oregano EO after 8-weeks of treatment application (Fig. 3B). Interestingly, sucrose content decreased considerably between 3- to 8-weeks after application in primary bud tissues regardless of EO treatments, while it increased in secondary bud tissues from 3- to 8-weeks (Fig. 3A). The increase in sucrose content in secondary bud tissues coincided with the time of active sprout growth of secondary buds. Sprout suppressing treatment of CIPC resulted in lower sucrose content in primary bud tissues after 1-week of treatment when compared to untreated control. At the same time-point of 1-week, significantly lower sucrose content was determined in tuber flesh tissues with all EO treatments.

However, in 3- and 8-weeks after treatment, no significant effect of sprout suppressing treatments on sucrose content was detected for the tuber tissues. Similarly, CIPC and EO treatments had no significant impact on the protein content of the tuber tissues (Fig. 3C). Interestingly, significantly higher protein content was observed in secondary bud tissues compared to primary bud and tuber flesh at 1- and 8-weeks' time points.

Impact of EO Treatments on G6PDH and SDH Enzyme Activities of Tuber Tissues

Significantly higher G6PDH activity was observed in tuber flesh tissues, when compared to primary and secondary bud tissues at all time points (0 d, 1-week, 3-weeks; Fig. 4A). Among treatments, higher G6PDH activity was observed in primary bud tissues of CIPC-treated tubers at 1-week. At the same time, CIPC and all three EO treatments also resulted in higher G6PDH activity in tuber flesh tissues compared to untreated control. However, at 3-week time-point, only EO treatments enhanced G6PDH activity in tuber flesh tissues.

Similar to the results of G6PDH activity, higher average SDH activity was also observed in tuber flesh tissues when compared to bud tissues at 0 d and 1-week after treatment (Fig. 4B). At 3-weeks after treatment, higher SDH activity in primary bud tissues was observed with sweet orange and oregano EO treatments when compared to the untreated control, CIPC, and spearmint EO treatments. Same EO treatments (sweet orange and oregano) also had higher sprout growth scores at 5- and 6-weeks after treatment application than the other treatments.

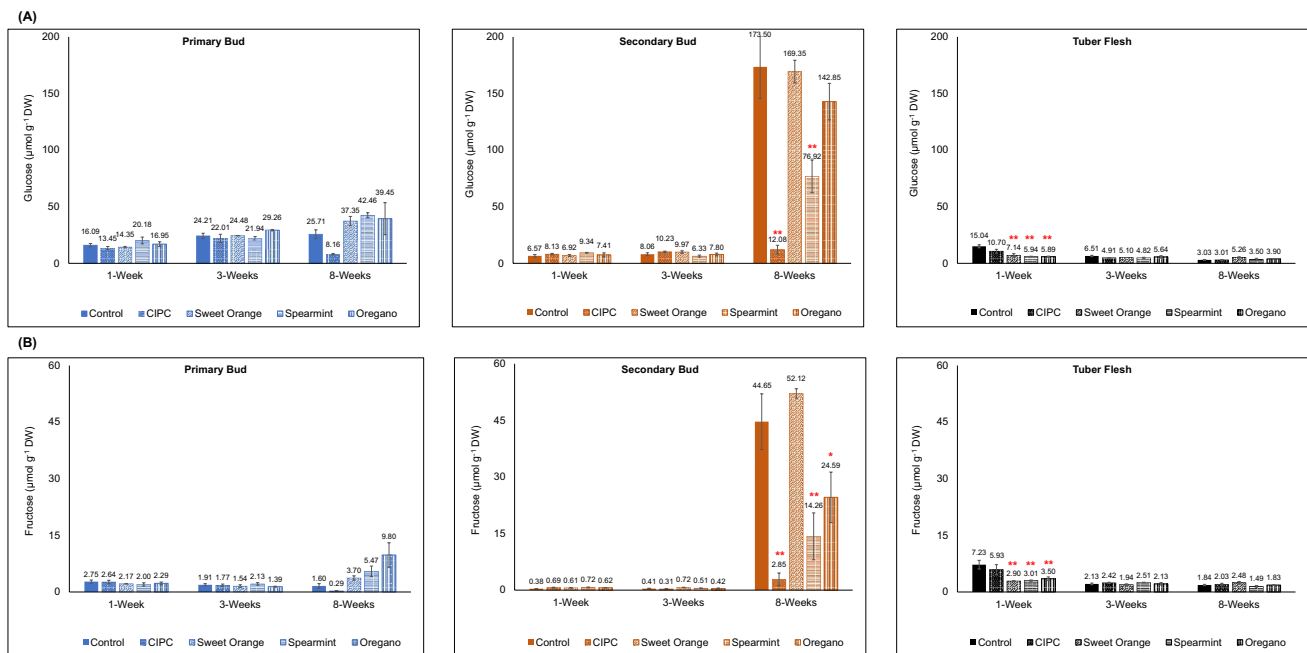


Fig. 2 Glucose (A) and fructose (B) content ($\mu\text{mol g}^{-1}$ dry weight) in primary bud, secondary bud, and tuber flesh of mini tubers of cv. Russet Burbank with CIPC and essential oil (EO) treatments at 1-, 3-, and 8-weeks after treatment. The vertical bars show standard error and * and ** represent the least significant differences between control and sprout suppressing treatments separately for tuber tissue types and each time point and at $P < 0.05$ and $P < 0.001$ respectively

Antioxidant Enzymes (CAT & GPX) and Phenolic Profile in Tuber Tissues

Overall, significantly higher GPX activity was observed in bud tissues when compared to the tuber flesh at 1-, 3-, and 8-weeks after treatment application (Fig. 5A). Effect of sprout suppressing treatments on GPX activity of tuber bud tissues were also significant at 1- and 8-weeks after treatments. After 1-week of treatment, higher GPX activity was observed in primary bud tissues of sweet orange and oregano EO treated tubers when compared to the control. Interestingly, lower GPX activity was observed in primary bud tissues of CIPC and spearmint EO treated tubers and secondary bud tissues of spearmint EO treated tubers at 8-weeks, which also had a lower sprout score at 6-weeks. Overall, sprout suppressing treatments did not significantly affect the GPX activity of tuber flesh tissues at any time points.

Results of this study indicated no significant differences in CAT activity between three different tuber tissue types; however, significant effect of sprout suppressor treatments on CAT activity was observed at 3-, 5-, and 8-weeks (Fig. 5B). Specifically, at 5-weeks, lower CAT activity was determined in primary and secondary bud tissues of tubers treated with CIPC and spearmint EO when compared to control, sweet orange, and oregano EO treatments. Interestingly, tuber flesh tissues of CIPC and spearmint EO treated tubers also had lower CAT activity; these treatments also

resulted in lower sprout growth scores. However, 8-weeks after the treatment, higher CAT activity was observed in bud tissues of EO treated tubers, particularly with sweet orange and oregano EO treatments, which resumed sprout growth after temporary pause.

In this study, HPLC analysis of tuber tissues detected chlorogenic acid and caffeic acid as major phenolics in primary and secondary bud tissues of Russet Burbank tubers (Table 7). Additionally, syringic and vanillic acids were determined in some bud tissues, but not in all samples or time points (Table 7). Overall, negligible amounts of gallic acid, catechin, and ferulic acid were detected in some tuber flesh tissue samples (data not shown). Chlorogenic acid content gradually increased from 0 d to 3-weeks in primary bud tissues. Higher content of this phenolic acid was observed in primary bud tissues at 1- and 3-weeks, when primary bud started to grow at faster rate. Among all treatments, significantly higher chlorogenic acid content was observed in bud tissues at 1- and 3-weeks with oregano EO treatment. However, chlorogenic acid was significantly low in bud tissues of spearmint EO treated tubers at 3-weeks and in secondary bud tissues of CIPC treated tubers at 8-week. Caffeic acid content was higher in secondary bud tissues at 0 d and remained at higher levels than primary bud tissues at 3-, 5-, and 8-weeks after treatment. At 1-week, bud tissues of CIPC treated tubers had lower caffeic acid content. Higher caffeic acid content was observed in primary bud tissues of tubers treated with EOs at 5-weeks (Table 7). Following the trend

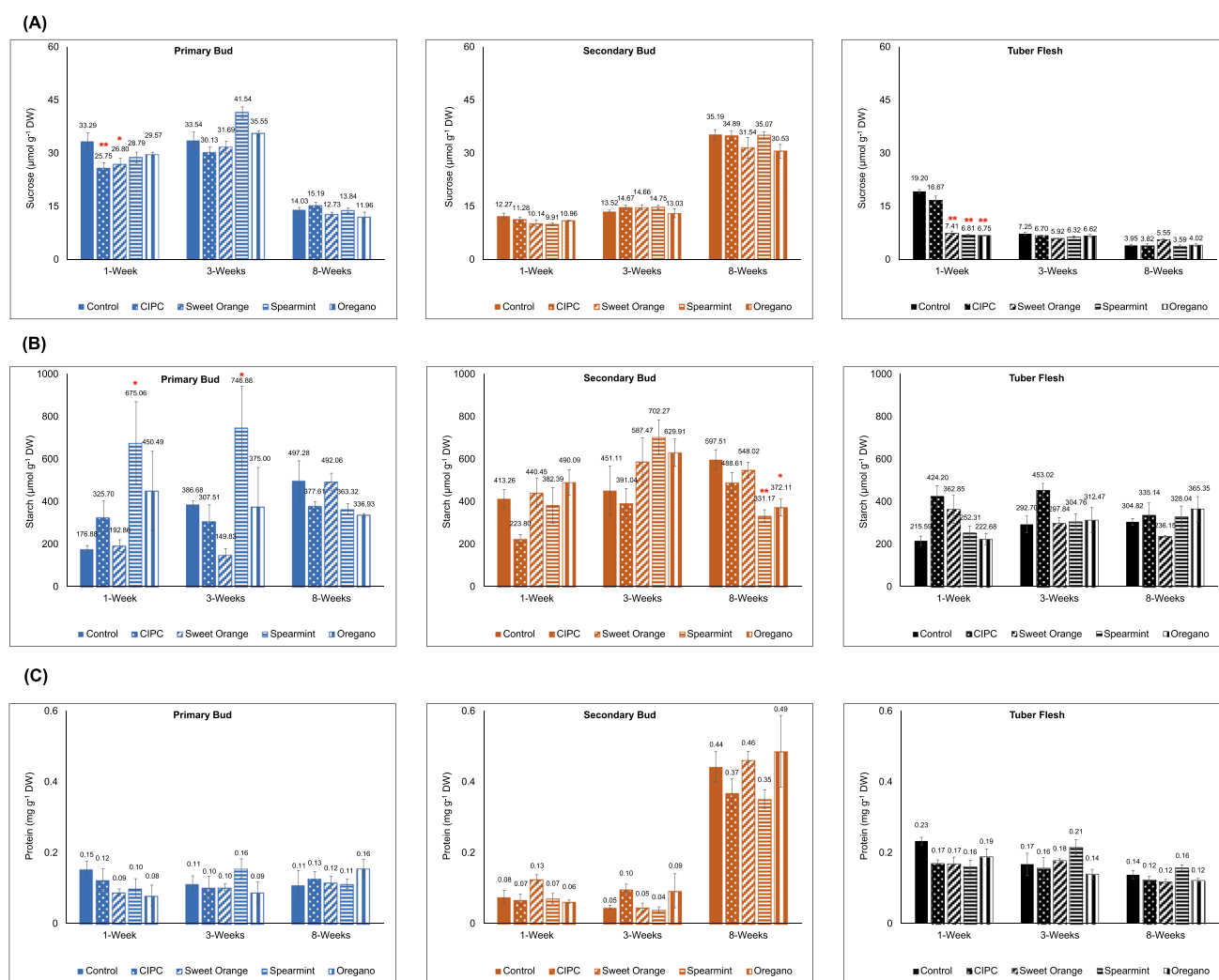


Fig. 3 Sucrose (A), starch (B) ($\mu\text{mol g}^{-1}$ dry weight), and protein (C) (mg g^{-1} dry weight) contents in primary bud, secondary bud, and tuber flesh of mini tubers of cv. Russet Burbank with CIPC and essential oil (EO) treatments at 1-, 3-, and 8-weeks after treatment. The vertical

bars show standard error and * and ** represent the least significant differences between control and sprout suppressing treatments separately for tissue types and each time point and at $P < 0.05$ and $P < 0.001$ respectively

of the above two phenolic acids, higher syringic acid content was observed in secondary bud tissues of sweet orange EO treated tubers at 3-weeks and oregano EO treated tubers at 5-weeks (Table 7). Besides the 8-week control, vanillic acid was not detected in primary bud tissues. While vanillic acid was determined in secondary bud tissues at 5- and 8-weeks, considerably higher content of this phenolic acid was observed in oregano EO treated tubers.

Discussion

The results of this study indicated efficacy of EO treatments for controlling tuber sprout growth significantly varies due to the method of application, dormancy stages of tubers, and dormancy duration of different potato cultivars.

Intriguingly, thermal application of oregano EO was more effective than the other EOs for controlling sprout growth of Russet Burbank and Ranger Russet tubers. Sweet orange and spearmint EOs are currently used commercially in Europe for controlling potato tuber sprouting, while oregano EO is underutilized and needs further optimization for commercial storage application. Our results suggest thermal application of oregano EO has potential for commercial potato storage treatments, particularly as a rescue treatment or as a complementary treatment with other sprout suppressing chemicals corroborating with previous reports (Visse-Mansiaux et al. 2021b). Oregano and sweet orange EOs were effective when applied thermally at the dormant stage of the tubers, while spearmint EO was not effective at the dormant stage, particularly for Ranger Russet tubers. The stability of active ingredient of the EOs vary

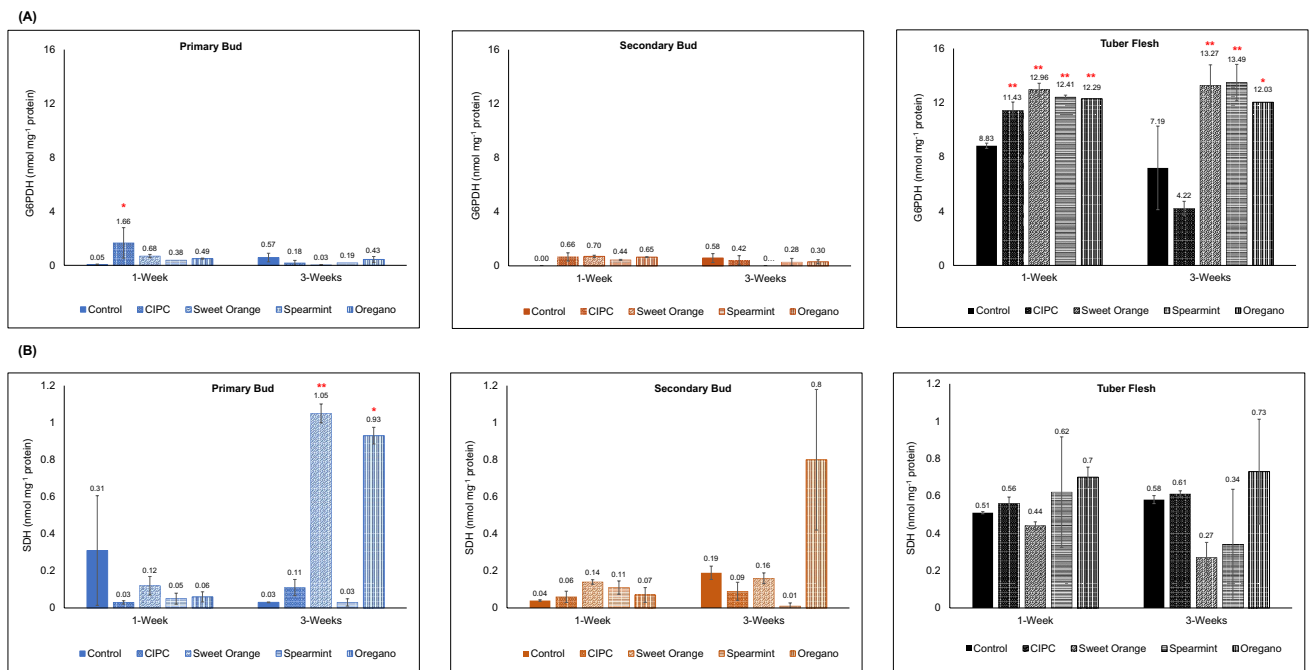


Fig. 4 Activities of glucose-6-phosphate dehydrogenase (A) and succinate dehydrogenase (B) (nmol mg⁻¹ protein) enzymes in primary bud, secondary bud, and tuber flesh of mini tubers of cv. Russet Burbank with CIPC and essential oil (EO) treatments at 1-, and 3-weeks after

treatment. The vertical bars show standard error and * and ** represent the least significant differences between control and sprout suppressing treatments separately for tissue types and each time point and at $P < 0.05$ and $P < 0.001$ respectively

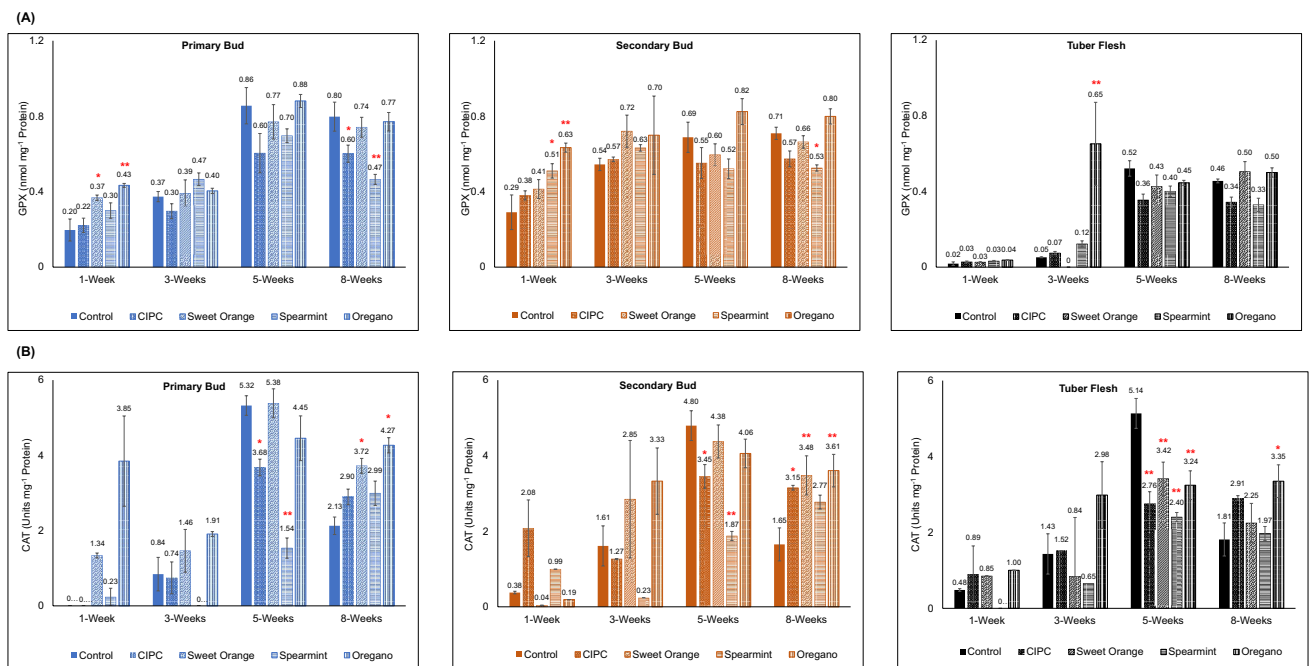


Fig. 5 Activities of guaiacol peroxidase (A) (nmol mg⁻¹ protein) and catalase (B) (Unit mg⁻¹ protein) in primary bud, secondary bud, and tuber flesh of mini tubers of cv. Russet Burbank with CIPC and essential oil (EO) treatments at 1-, 3-, 5- and 8-weeks after treatment. The

vertical bars show standard error and * and ** represent the least significant differences between control and sprout suppressing treatments separately for tissue types and each time point and at $P < 0.05$ and $P < 0.001$ respectively

Table 7 Phenolic compounds ($\mu\text{g g}^{-1}$ dry weight) detected (reverse phase HPLC analysis) in primary and secondary bud tissues of Russet Burbank tubers at 0 d, and 1-week, 3-weeks, 5-weeks, 8-weeks after dip application of CIPC and wick application of three essential oil (EO) treatments (sweet orange, spearmint, oregano)

Treatments	Tissue Types	0 d	1-week	3-weeks	5-weeks	8-weeks
Chlorogenic Acid						
Control	Primary Bud	4.59	10.46	16.36	16.49	14.52
	Secondary Bud	10.83	5.53	10.85	15.90	17.81
CIPC	Primary Bud		7.85	16.77	15.03	12.25
	Secondary Bud		5.54	14.41	16.18	8.39*
Sweet orange EO	Primary Bud		10.70	14.08	20.38	15.34
	Secondary Bud		7.26	5.07*	19.72	16.76
Spearmint EO	Primary Bud		10.80	7.19**	20.56	15.35
	Secondary Bud		7.36	4.65*	15.64	12.79
Oregano EO	Primary Bud		15.61**	11.28*	17.95	16.22
	Secondary Bud		10.25**	8.16	20.12	15.25
Caffeic Acid						
Control	Primary Bud	4.50	5.72	5.9	5.82	5.71
	Secondary Bud	7.48	7.25	6.38	7.81	5.98
CIPC	Primary Bud		5.30	6.35	5.82	6.76
	Secondary Bud		5.03*	8.25	9.02	7.93
Sweet orange EO	Primary Bud		5.93	5.55	7.72*	5.00
	Secondary Bud		6.01	6.68	8.77	7.14
Spearmint EO	Primary Bud		5.48	6.00	7.79*	4.68
	Secondary Bud		6.19	6.85	8.82	6.79
Oregano EO	Primary Bud		6.70	6.03	7.82*	4.87
	Secondary Bud		6.60	7.49	9.1	6.07
Syringic Acid						
Control	Primary Bud	1.47	1.81	2.42	n.d	1.80
	Secondary Bud	2.66	2.43	2.21	3.05	2.83
CIPC	Primary Bud		1.53	2.34	1.9	2.15
	Secondary Bud		1.82	2.76	2.93	3.42
Sweet orange EO	Primary Bud		1.70	1.74	2.59	1.54
	Secondary Bud		1.78	3.02	2.85	2.62
Spearmint EO	Primary Bud		1.58	2.24	2.52	1.64
	Secondary Bud		2.09	2.61	2.93	2.60
Oregano EO	Primary Bud		2.26	n.d	n.d	1.66
	Secondary Bud		2.24	2.70	3.82	2.19
Vanillic Acid						
Control	Primary Bud	n.d	n.d	n.d	n.d	0.51
	Secondary Bud	2.76	2.20	0.41	0.63	1.36
CIPC	Primary Bud		n.d	n.d	n.d	n.d
	Secondary Bud		n.d	n.d	0.84	0.78
Sweet orange EO	Primary Bud		n.d	n.d	n.d	n.d
	Secondary Bud		n.d	n.d	0.78	3.67
Spearmint EO	Primary Bud		n.d	n.d	n.d	n.d
	Secondary Bud		n.d	1.47	0.82	0.45
Oregano EO	Primary Bud		n.d	n.d	n.d	n.d
	Secondary Bud		n.d	2.32	4.97	3.00

*($P < 0.05$) and **($P < 0.001$) represent the least significant differences between control and sprout suppressing treatments separately for primary and secondary bud and for each time point

under different temperatures, which can impact their overall efficiency and function (Pavela and Sedlák 2018). As the oregano EO treatment was effective for temporary sprout control at all three dormancy stages (dormant, peeping, and sprouting) for both potato cultivars, it might provide greater

flexibility in timing of application based on the need of the sprout control during storage. Other studies indicated the effect of such EO treatment may be transient and can be lessened with washing (Teper-Bamnolker et al. 2010). Previously, Vokou et al. (1993) did not find sprout suppressing

effect with a wick application of oregano EO; however, the same treatment exhibited antibacterial efficacy against *Erwinia carotovora* subsp. *astroseptica* (a.k.a. *Pectobacterium atrosepticum*) which causes soft rot disease in potato and in other vegetables. Therefore, oregano EO not only has potential benefits against temporary sprout control but can also be beneficial for managing potato diseases in postharvest storage. Baydar and Karadoğan (2003) reported sprout suppressing effect of volatile oil extracted from *Origanum onites* (Cretan oregano). Similarly, Şanlı et al. (2019) also observed some sprout suppressing effect of Cretan oregano EO on tuber sprout growth. Though literature on the application of oregano EO to potato tubers is limited, there are other indications for Cretan oregano based EO inhibiting germination and sprouting of bread wheat (Atak et al. 2016).

Comparing our thermal application results to previous research utilizing a cold-wicking application reinforces the need to test EO treatments under both thermal and cold-wicking methods. No EO thermal application was as effective for long-term sprout control as thermal applications of CIPC, which is the standard commercial method of application. These results emphasize the inability of EO applications to replace CIPC for long-term, consistent sprout control of stored potatoes. Thermal application can be an effective short-term sprout control method for some EOs like oregano EO, but there are chances of rapid evaporation and degradation of active ingredients, which can lead to a decrease in the efficacy of EOs (Owolabi et al. 2013). Multiple thermal applications of EOs, such as oregano EO, need further investigation as an effective and economical choice for commercial use.

Our results confirmed previous findings, when EOs were applied using air-wick method to mini tubers of Russet Burbank, spearmint EO exhibited higher efficacy up to 5–6 weeks after treatment. On the contrary, oregano EO, which provided better sprout control with thermal application, was not effective with air-wick method. Previous study by Şanlı and Karadoğan (2019) observed reduction in efficacy of peppermint EO and S-(+)-carvone, the active ingredient of caraway and dill seed oils, with increase in storage temperature. Therefore, to achieve higher efficacy of spearmint EO, thermal application might not be suitable, as it could reduce the efficacy of carvone and other active ingredients. This response of spearmint EO providing greater control with wick applications compared to thermal or cold aerosol applications was previously reported in Frazier et al. (2004).

Significant reduction in sprout growth of cv. Austrian Crescent fingerling potato tubers for up to 90 days with treatments of spearmint EO was recently reported by Alzarqaa et al. (2024). However, in our results, the sprout suppressing effect of spearmint EO on Russet Burbank mini tubers was observed for up to 6 weeks after treatment,

which is not sufficient for long term sprout control. Previously, Teper-Bamnlker et al. (2010) observed degradation of R-carvone to its derivatives in buds of treated tubers after 5 days of application. Kleinkopf et al. (2003) also reported that for long-term tuber sprout control in storage, repeated application of S-(+)-carvone or spearmint EO is necessary and at a higher threshold (concentration) level. Therefore, further research is needed to test multiple applications of spearmint EO in different concentrations (higher threshold) to optimize its utilization for commercial potato storage.

The differences in the efficacy of EOs between the two experiments in our study may not be solely due to the method of applications (thermal vs. air-wick) but also based on the dormancy stages of the tubers when EOs were applied. It is also important to note that in mini tuber experiment, EOs were applied after 20-weeks of storage, when Russet Burbank tubers were applied as early as the peeping stage. Our first experiment with the thermal application of EOs to tubers also confirmed that spearmint EO was more effective at the peeping and sprouting stages of the tubers. Similar to the findings of the previous research with EOs or their active constituents (Suttle et al. 2016; Teper-Bamnlker et al. 2010), both thermal and air-wick applications of EOs physically damaged the tip of the sprout (tip necrosis) mostly, which caused temporary cessation in sprout growth. Over time, with or without washing of tubers, the damaged eye or bud tissues generally resumed growth (Teper-Bamnlker et al. 2010), which was also observed in our investigation. However, to understand the positive or negative impact of EOs towards tuber sprout control, it is important to investigate the potential changes in biochemical regulation of tuber tissues following application of EOs.

In general, transportation and mobilization of assimilates such as nutrients or carbohydrates from parenchyma tissues to bud tissues generally coincide with sprouting of potato tubers. Sprout-suppressing chemicals potentially alter this transportation and accumulation of sugars from source (storage tissues of parenchyma) to sink (bud tissues) and thus control sprout growth of potato tubers. Our results with the air-wick method of application of EOs also suggested that suppression of growth of secondary buds by CIPC and spearmint EO treatments might be due to their ability to suppress reducing sugar accumulation in these bud tissues. Previously, Abbasi et al. (2015) reported lower total sugar content in CIPC and spearmint EO-treated tubers at the end of the storage when compared to the control treatment. Similarly, Shukla et al. (2019) observed higher reducing sugar content in lemon grass and clove oil EO treated tuber tissues, which induced sprouting, while palmarosa and ajwain EOs suppressed sprout growth and reduced sugar content. The inability of sweet orange and oregano EOs to alter sugar content of bud tissues of Russet Burbank mini tubers, might

be the reason for their inefficacy in sprout suppression, yet the thermal application may suggest heating of these oils may shift effectiveness on sprout suppression. The gradual reduction of glucose, fructose, and sucrose content in tuber flesh tissues and increase of these sugars in bud tissues from 1- to 8-weeks irrespective of the treatments suggest potential translocation of the reducing sugars from parenchyma tissues (flesh) to bud tissues during sprouting. Interestingly, the changes in reducing sugars and sucrose were more prominent in secondary bud tissues after 8 weeks, when they were at an active sprouting stage. Overall, determining reducing sugars, sucrose, starch, and protein as well as other biochemical parameters separately for different tissue types (primary, secondary, tuber flesh) allowed us to understand the translocation of these metabolites between tuber tissues during sprouting and how sprout suppressing treatments potentially altered the flow of nutrients. In addition to determining the sugars, starch, and protein, it is also important to know the flow or partitioning of the carbon between major metabolic pathways to improve our understanding on the metabolic regulation associated with dormancy and sprouting of potato tubers. In this context, the tricarboxylic acid cycle (TCA) plays a critical role in the generation of energy molecules (adenosine triphosphate) by oxidizing carbohydrate or respiratory substrate for the growing tissues such as bud tissues during germination or sprouting (Cavalcanti et al. 2014). This important metabolic cycle not only indicates respiratory flow but also provides insights on oxidation–reduction state of the plant tissues (Zhang and Fernie 2023).

Succinate dehydrogenase (SDH) is a key enzyme of TCA cycle and catalyzes the oxidation of succinate to fumarate and modulate cellular signaling, chelation, photorespiration and redox regulation in plant cells (Zhang et al. 2023). Overall, in our results, higher SDH activity was observed in tuber flesh tissues compared to primary and secondary bud tissues at 0 day and 1-week after treatment, indicating higher respiration and energy metabolism in parenchyma tissues of potato tubers. Interestingly, the SDH activity increased in primary bud tissues of sweet orange EO-treated tubers and both primary and secondary bud tissues of oregano EO treated tubers after 3-weeks. Increase in SDH activity in bud tissues with these two EOs along with higher sprout growth suggest that these treatments might have induced respiration and oxidative stress regulation during active sprouting and such changes reflected on their failure to suppress sprout growth of Russet Burbank mini tubers. On the contrary, CIPC treatment resulted in lower SDH activity in primary bud tissues after 1-week, while secondary bud tissues of spearmint EO treated tubers had lower SDH activity after 3-weeks, and both treatments exhibited sprout suppression. In a previous research, Lyu et al. (2023) reported that application of grape seed oil as sprout suppressing treatment

altered γ -aminobutyric acid (GABA) metabolism or GABA shunt, which is a diversion or bypass of TCA cycle. Overall, our results suggest that SDH activity might be a good indicator of dormancy and sprouting of potato tubers and TCA cycle plays a critical metabolic role in this physiological process of potato tubers. In addition to the TCA cycle, the pentose phosphate pathway (PPP) also plays an important role in carbon homeostasis and is involved in both catabolic and anabolic regulations of plant cells (Stincone et al. 2015). The role of PPP in potato tuber dormancy and sprouting has not been investigated thoroughly. Previous research with winter wheat revealed that activity of G6PDH, the first rate-limiting enzyme of the PPP was significantly high in cultivars that are susceptible to pre-harvest or early sprouting when compared to a sprouting resistant cultivar (Barnard and Pretorius 2005). Dogramaci et al. (2024b) observed an increase in G6PDH activity in tuber flesh tissues with methyl jasmonate treatment, while the activity of this enzyme was lower in bud tissues with this sprout inhibitory treatment. In our current investigation, G6PDH activity reduced in tuber flesh with CIPC treatment, while it increased with all EO treatments after 3-weeks, suggesting higher metabolic activity through PPP in tuber flesh following EO treatments. On the contrary, activity of this enzyme was lower in bud tissues of EO-treated tubers after 3-weeks, indicating an inverse trend in this enzyme activity between tuber flesh and bud tissues and confirming previous findings by Dogramaci et al. (2024b). This might be due to different anabolic needs between tuber tissue types during sprouting and how shift in carbon flow occurs between metabolic pathways such as PPP and TCA cycle. Regulation of PPP and TCA cycle is also directly related to oxidative stress or redox regulation, which plays a pivotal role in dormancy release and sprouting of potato tubers (Haider et al. 2021; Liu et al. 2023).

Our results indicate higher activity of an antioxidant enzyme, GPX, in primary and secondary bud tissues compared to tuber flesh, and average GPX activity slowly increased in bud tissues between 1–8 weeks after sprout suppressing treatments. CIPC and spearmint EO treatments resulted in lower GPX activity in bud tissues, while sweet orange and oregano EOs enhanced activity of this enzyme. Higher GPX activity in primary and secondary bud tissue samples, particularly with sweet orange and oregano EO treated tubers, reveals higher role of this stress-associated antioxidant enzyme in bud tissues during sprouting. Higher activity of peroxidase enzyme was previously observed in potato tubers following application of caraway and clove EOs (Afify et al. 2012). Peroxidase or GPX are generally associated with the polymerization of secondary metabolites and support tissue structural adjustments, which might be important during active growth of sprouts of potato tuber.

Similar to the results of GPX activity, higher activity of CAT, another antioxidant enzyme, was also observed with sweet orange and oregano EO treatments, indicating higher oxidative stress pressure in these EO-treated tubers during sprouting. Higher sprout growth score with these EO treatments may be associated with higher oxidative pressure and antioxidant activity in bud tissues during sprouting. In plant cells, CAT is responsible for converting hydrogen peroxide to water molecules and helping to reach redox homeostasis (Weydert and Cullen 2010). Therefore, higher activity of this enzyme is a sign of active growth, specifically to counter oxidative pressure of growing tuber tissues.

In addition to antioxidant enzymes, secondary metabolites like phenolics and flavonoids also help to stabilize oxidative stress pressure in plant cells and mostly induce it as part of the overall stress response. Previous research by Cvikrova et al. (1995) suggested that free phenolic acids generally decrease during sprouting, but phenolic conjugates increase in tuber tissues. In this research, a higher concentration of chlorogenic acid was found in tuber bud tissues, a phenolic conjugate. Furthermore, an increase in chlorogenic acid content with oregano EO treatment in Russet Burbank mini tubers indicates that potential induction of this phenolic is associated with sprout growth of potato tubers. Similar to the result of chlorogenic acid, higher content of another hydroxycinnamic acid, caffeic acid was also observed in bud tissues with EO treatments. Phenolics are stress protective compounds, and oregano and other EOs might have induced stress responses in bud tissues, which has relevance in developmental transition of tubers from dormancy to sprouting. On the contrary, a lower content of these phenolics was observed with CIPC treatment, which suppressed sprout growth. Therefore, our results suggest that higher content of phenolic acid quantified in bud tissues is likely due to sprouting of potato tubers and stress response induced by EO treatments. Whether the role of phenolics in active growing tissues of potato tubers is for stress protection or for tissue structural adjustments need further examinations.

Conclusions

Collectively, results of biochemical analysis suggest that higher sugar content, metabolic activity related to respiration, higher antioxidant enzyme, and hydroxycinnamic acid content are related to active sprout growth and potential induction of stress response. Specifically, higher chlorogenic acid content and increase activity of GPX, which has roles in phenolic polymerization, was observed with oregano EO treatment. Furthermore, effective sprout suppressing treatments must alter these metabolic regulations such as

reduction in sugar content, respiratory rate, antioxidants and phenolics in bud tissues. Future studies with different potato cultivars, application methods, and treatments at various dormancy and sprouting stages are required to further refine the role of these metabolic regulations in tuber dormancy and sprouting. Overall, oregano EO exhibited promise as a thermal treatment and specifically can be utilized as a rescue treatment, while the air-wick method is a suitable application method for spearmint EO treatment. Current commercial applications to potatoes for sprout control are predominantly applied as a thermal application while potatoes are in storage. Evaluating potential sprout inhibitors and EOs for commercial use should include thermal application treatments to properly assess potential utilization in the industry.

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Data Availability Data will be made available upon request.

Declarations

Ethical Approval USDA is an equal opportunity provider and employer. Mention of trade names in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA.

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