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Ethylene production and ethylene effects on respiration rate of postharvest sugarbeet roots

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ABSTRACT

Ethylene elevates respiration, is induced by wounding, and contributes to wound-induced respiration in most postharvest plant products. Ethylene production and its effects on respiration rate, however, have not been determined during storage of sugarbeet (*Beta vulgaris* L.) root, even though any elevation in respiration due to ethylene would increase storage losses and reduce postharvest quality. To determine the effect of ethylene on sugarbeet root storage respiration rate, sugarbeet root ethylene production was quantified, and the effects of exogenous ethylene, an ethylene biosynthesis inhibitor, and ethylene response inhibitors on root respiration rate were determined using uninjured, severely injured, and conventionally harvested roots. Ethylene production was low (0.045–0.047 pmol kg^{-1} s^{-1}) in uninjured and conventionally harvested and piled roots. Consequently, ethylene concentrations in commercial piles 0–67 d after piling were low, ranging from <0.001 to 0.054 $\mu L L^{-1}$. Exogenous ethylene at concentrations of 0.020–14 $\mu L L^{-1}$ increased root respiration. The increase in respiration rate, however, was transient at ethylene concentrations $\leq$0.11 $\mu L L^{-1}$ suggesting that any ethylene effects on respiration rate in commercial piles would be short term. Severe injury induced ethylene production an average of 3.7-fold and increased respiration rate 3–4 d after injury. Wound-induced ethylene production, however, was not directly responsible for wound-induced respiration since elimination of wound-induced ethylene production by the ethylene synthesis inhibitor aminoethoxyvinylglycine had no effect on wound-induced respiration. The ethylene response inhibitors 1-methylcyclopropene (1-MCP) and silver thiosulfate reduced wound-induced respiration 3–4 d after injury when applied after wounding. A portion of the increase in respiration due to wounding, therefore, required ethylene perception. However, when applied prior to wounding, 1-MCP elevated wound-induced respiration 3–4 d after injury, suggesting that blockage of ethylene receptors prior to injury was ineffective at eliminating ethylene perception after wounding, possibly due to the synthesis of new receptors after the injury. Moreover, 1-MCP effects on root respiration rate occurred only when roots were severely injured; 1-MCP had no effect on respiration rate of uninjured or conventionally harvested roots. Postharvest sugarbeet roots, therefore, produce ethylene, increase ethylene production in response to wounding, and respond to exogenous ethylene with an increase in respiration rate, but ethylene production and ethylene effects on root respiration rate are likely to be small under commercial storage conditions and of limited economic significance.

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1. Introduction

Ethylene has significant effects on the quality and storage life of many harvested plant products. Ethylene accelerates ripening, chlorophyll degradation, and softening in many fruits and vegetables, causes petal abscission, senescence and color changes in flowers, alters aroma, taste and texture in many edible plant products, and induces respiration in nearly all postharvest plant organs (Kays and Paull, 2004). While most postharvest ethylene effects are not important for a crop such as sugarbeet (*Beta vulgaris* L.) that is non-climacteric and not marketed for direct consumption, any increase in respiration rate would negatively affect the quality, storage losses, and value of postharvest sugarbeet roots.

Respiration is typically the principal cause for the decline in sugarbeet root quality during storage (Campbell and Klotz, 2006). Respiration in sugarbeet root is fueled by catabolism of sucrose (Barbour and Wang, 1961) and is estimated to cause 50–80% of the sucrose loss that occurs during storage (Wyse and Dexter, 1971; Tungland et al., 1998). Respiration also produces heat, which significantly contributes to the warming of the large outdoor piles in which sugarbeet roots are stored. With increasing temperature,

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increases in respiration rate, sucrose loss, the incidence and severity of storage diseases, and the accumulation of the carbohydrate impurities, glucose and fructose, which are responsible for sucrose loss during processing, occur (Campbell and Klotz, 2006).

Ethylene production and ethylene effects on respiration rate are largely unknown for sugarbeet roots. To our knowledge, ethylene production has not been quantified in sugarbeet roots. Ethylene induction by wounding in sugarbeet roots has also not been studied, even though ethylene production is typically induced in plants in response to injury (Yang and Hoffman, 1984) and sugarbeet roots sustain substantial injury during harvest and piling (Steensen, 1996). One study has demonstrated that sugarbeet roots respond to exogenous ethylene with an increase in respiration rate (Dilley et al., 1970). The physiological and commercial significance of this finding, however, remains to be determined since roots were exposed to 1000 $\mu L L^{-1}$ ethylene at 20 °C—an unusually high concentration of ethylene and a temperature well above typical sugarbeet root storage temperatures.

Here, we characterize ethylene production and ethylene effects on respiration rate in stored sugarbeet roots and examine the role of ethylene in promoting wound-induced respiration. Experiments were conducted with both greenhouse-grown and field-grown roots to allow ethylene production and ethylene effects on respiration to be evaluated under both controlled and actual production conditions. Roots from greenhouse-grown plants were used to separately determine postharvest and wound-induced effects on ethylene production and respiration rate. The injury delivered to roots in these experiments was more severe than the injuries typically caused by conventional harvest and piling operations, but generated sufficient differences in ethylene production and respiration rates to allow relationships between the hormone and wound-induced respiration to be determined. Conventionally harvested, field-grown roots were also used to quantify postharvest ethylene production rate and ethylene effects on storage respiration for roots which sustained injuries typical in type and severity to those encountered during commercial production and to determine the feasibility of using an ethylene inhibitor in commercial sugarbeet storage.

2. Materials and methods

2.1. Plant material and postharvest storage conditions

Roots of sugarbeet hybrid Beta 6225 (Betaseed, Inc., Shakopee, MN, USA) were used for determining ethylene production rate, exogenous ethylene effects, and effects of the ethylene inhibitors, aminoethoxyvinylglycine (AVG), 1-methylcyclopropene (1-MCP), and silver thiosulfate (STS) on wound-induced respiration. The hybrid was greenhouse grown in Sunshine Mix #1 (Sun Gro Horticultural Products, Seba Beach, Alberta, Canada) in 15 L pots with supplemental light under a 16 h/8 h day/night regime. Taproots were hand harvested 16–18 weeks after planting and only healthy roots of relatively similar size were used in each experiment. Roots were washed to remove potting media which may contain microorganisms to ensure that respiration and ethylene determinations were due only to root tissue. Care was taken to minimize root injury during washing, and roots were gently dried prior to use. Roots were wounded by tumbling 30 min in a pilot scale beet washer (Great Western batch washer; Hallbeck, 1982) which caused extensive abrasion of the root surface and severe bruising. Roots were stored for 4 d at 10 °C and 90% relative humidity to mimic the storage conditions that typically occur after harvest. Individual roots were the experimental unit with 3 replicates per treatment used in all experiments except for the determination of root respiration in wounded and unwounded roots where 6 replicates per treatment were used. All experiments were repeated at least once with similar results.

Field-grown, mechanically harvested roots were used for determining the effect of 1-MCP on storage properties during prolonged storage. Roots were produced using standard production practices (Khan, 2005) and exhibited no symptoms of disease. Roots for 1-MCP fumigation, submergence, and foliar application experiments were obtained from a commercial field planted with the hybrid VDH-66626 (SESVanderHave, Rilland, Netherlands) after delivery to a centralized storage location, were harvested from field plots planted with the commercial hybrid Resist (Syngenta, Longmont, CO), or were harvested from field plots of the hybrid, ACH-999 (Crystal Beet Seed, Moorhead, MN, USA), respectively. Prior to postharvest treatment or storage, roots were washed, randomized and divided into 10–12 root samples which served as the experimental unit, with 3 replications per treatment for the fumigation experiment and 5 replications per treatment for submergence and foliar application experiments. Roots were stored for up to 120 d at 4 °C and 95% relative humidity to mimic long-term storage conditions.

Roots were also obtained from a commercial sugarbeet pile in Moorhead, MN, USA, immediately after piling. Regularly shaped roots that exhibited no symptoms of disease were selected, stored at 10 °C and 90% relative humidity for 24 h, and used for determining ethylene production rate by commercially produced and piled roots. Replicates were comprised of 2 randomly selected roots with six replicates.

2.2. Ethylene concentration and production determinations

Ethylene concentration was determined by gas chromatography using a 45 cm long alumina (60–80 mesh) column operating at 80 °C with a nitrogen carrier gas flow rate of 0.5 mL s^{-1} and injector/detector temperatures of 150/250 °C, respectively. Ethylene production rates were calculated from the ethylene concentration in 1 mL samples drawn from the headspace of air-tight, septum-equipped chambers 6 h after insertion of roots. For determining ethylene production of wounded and unwounded roots, and conventionally harvested and piled roots, 9.5 L chambers containing 2 roots per chamber were used. For determining ethylene production after AVG treatment, 4.5 L chambers were used with 1 root per chamber. Ethylene concentrations in commercial sugarbeet piles were determined using 50 mL air samples collected 1.5 m below the upper surface of ventilated and unventilated piles located in Moorhead, MN, USA. Ventilated and unventilated piles were 9.8 and 5.5 m high, respectively. Air samples were collected with air-tight syringes attached to 1.5 m lengths of Tygon tubing (Norton Performance Plastics Corp., Akron, OH, USA) inserted into holes that had been drilled into the piles. Prior to analysis, the ethylene concentration in each sample was concentrated 10-fold by absorption into a 1 mL 0.25 mol L^{-1} mercury perchlorate solution and subsequent release into a 5 mL volume following injection of 4 mol L^{-1} NaCl. Three replicate air samples were collected from different locations in the piles at each sampling time.

2.3. Respiration rate determination

Respiration rate was determined using infrared carbon dioxide gas analyzers and an open system with continuous airflow over roots. Respiration rates of individual roots were determined at 10 °C with a LI-COR LI-6400 Photosynthesis System (Lincoln, NE, USA) attached to a 7 L sample chamber with an air flow of 1000 $\mu mol\ s^{-1}$ (Haagenson et al., 2006). Respiration rate of 10-root samples was determined at 4 °C with a LI-COR LI-6252 carbon dioxide analyzer using 23 L sample chambers and an air flow of 350 $\mu mol\ s^{-1}$ (Campbell and Klotz, 2007).

2.4. Exogenous ethylene treatment

Roots were exposed to 0, 0.020, 0.11, 1.4 or 14 μL L^{-1} ethylene for 4 d at 10 °C. Ethylene treatments were administered to roots contained in 22.7 L air-tight chambers equipped with a septum, with 3 roots per chamber. Each chamber contained 40 mL of 5 mol L^{-1} sodium hydroxide soaked onto filter paper to prevent carbon dioxide accumulation in the chambers. Approximately 50 mL of potassium permanganate ($KMnO_4$)-soaked vermiculite was also added to the 0 μL L^{-1} control chamber to scavenge for root-produced ethylene. Chambers were opened and roots were removed daily for respiration rate determinations, after which roots were returned to chambers, chambers were resealed, and ethylene reinjected. Ethylene concentrations were determined by gas chromatography after each injection of ethylene to the chamber with the mean concentration for each chamber used to describe the treatment.

2.5. Ethylene inhibitor treatments

AVG (Valent BioSciences, Libertyville, IL, USA) was applied by submerging wounded and unwounded roots in an aerated 50 μmol L^{-1} aqueous solution for 1 h at room temperature with controls similarly submerged in aerated water. Silver thiosulfate (STS) was prepared by adding an equal volume of 8 mmol L^{-1} silver nitrate to a rapidly stirring solution of 24 mmol L^{-1} sodium thiosulfate and was applied by immersing roots in an aerated solution for 1 h at room temperature. 1-MCP was applied to greenhouse-grown roots by enclosing single roots in 9.5 L air-tight, septum-equipped chambers with 180 mg of the MCP-releasing agent EthylBloc™ (AgroFresh Inc., Spring House, PA, USA) for 24 h at 20 °C. After sealing, MCP was released by injecting 3 mL distilled water into the beaker containing the EthylBloc. 1-MCP concentrations for each chamber were verified by GC analysis using a Porapak Q column and 1-butene as a standard (Sisler and Serek, 1997) with the mean concentration used to describe the treatment. 1-MCP concentrations were 0.84 and 0.46 μL L^{-1} for prewound and postwound treatments, respectively. 1-MCP was applied to field-grown roots by fumigation, submergence, or as a preharvest foliar spray. Roots were enclosed in 2.7 m^3 polyethylene tents and fumigated with 0, 1, or 5 μL L^{-1} 1-MCP (SmartFresh™; AgroFresh, Inc.) for 24 h at 13.5–17.5 °C. For submergence treatments, roots were immersed in aqueous solutions containing 0, 15 or 25 μL L^{-1} 1-MCP (AFxRD-020; Rohm and Haas, Philadelphia, PA, USA) and 1% (v/v) surfactant (AF-400; Rohm and Haas) for 10 s at room temperature. Foliar 1-MCP treatment was applied as an aqueous 50 μL L^{-1} solution with 1% (v/v) AF-400 which was sprayed to run off on field plots 5 d prior to harvest, with untreated plots used as controls.

2.6. Sucrose and extractable sucrose determinations

Sucrose concentration and juice purity were determined with an Autopol 880 saccharimeter and J57 refractometer (Rudolf Research Analytical, Hackettstown, NJ, USA) using aluminum sulfate-clarified brei extracts (McGinnis, 1982). Extractable sucrose yield was calculated from sucrose concentration and juice purity using the equations of Dexter et al. (1967).

2.7. Statistical analysis

Analysis of variance was used to determine significant differences between treatments ($P \leq 0.05$). LSDs were determined for storage properties in 120 d 1-MCP experiments when the corresponding *F*-test indicated significant differences at the 0.05 probability level.

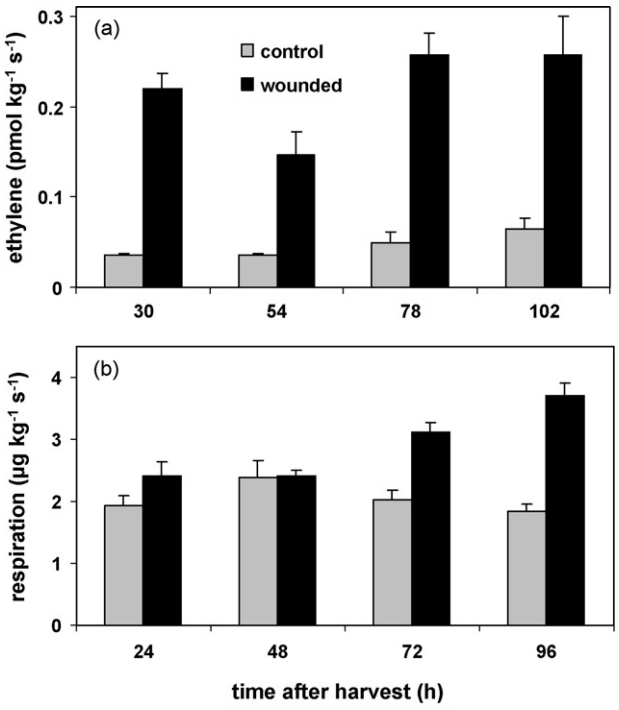

Fig. 1. Ethylene production (a) and respiration rate (b) of unwounded (control) and wounded sugarbeet roots during 4 d storage at 10 °C. Respiration rate was measured as the rate of CO_2 produced. Error bars are the standard error of the mean. Respiration rate, $n = 6$; ethylene production, $n = 3$.

3. Results

3.1. Ethylene production in wounded, unwounded, and commercially harvested roots

Sugarbeet roots that were hand harvested and sustained minimal injury produced low, but detectable, levels of ethylene during the first 4 d after harvest (Fig. 1a, control). Ethylene production was similar throughout the 4 d storage period and averaged 0.047 pmol kg^{-1} s^{-1}. Severe injury to roots increased ethylene production an average of 3.7-fold. The elevation in ethylene production in response to wounding was apparent after 1 d in storage and persisted through the 4 d duration of the experiment. Wounding also caused an increase in root respiration rate after 3 and 4 d in storage (Fig. 1b). The respiration rate of wounded roots was 54 and 102% greater than that of unwounded control roots 3 and 4 d after injury, respectively. The increase in respiration due to wounding occurred 2 d after the wound-induced increase in ethylene production.

Ethylene production by commercially harvested and piled roots was similar to that of unwounded sugarbeet roots. Mechanically harvested and piled roots produced ethylene at a rate of 0.045 ± 0.008 pmol kg^{-1} s^{-1} 24 h after harvest (data not shown). Air samples collected from commercial piles confirmed a low ethylene production rate for conventionally harvested and piled roots (Table 1). Ethylene concentrations in ventilated and nonventilated piles were ≤0.002 μL L^{-1} during the first 21 d after piling. After 67 d, ethylene concentrations in piles increased, but remained below 0.060 μL L^{-1}.

3.2. Exogenous ethylene effects on root respiration rate

Exogenous ethylene at concentrations of 0.020–14 μL L^{-1} increased root respiration rate within 24 h after exposure (Fig. 2). However, the increase in respiration rate in roots exposed to 0.020 and 0.11 μL L^{-1} ethylene was transient. Respiration rate increased

Table 1
Ethylene concentration in air samples collected from ventilated and nonventilated commercial sugarbeet piles in Moorhead, MN, USA.

Days after harvest	Ethylene concentration ($\mu L\,L^{-1}$)	
	Ventilated pile	Nonventilated pile
0	0.0015 ± 0.0005	nd
4	0.0007 ± 0.0003	0.001
7	0.0017 ± 0.0017	0.0007 ± 0.0007
9	0.0007 ± 0.0007	nd
21	0.002 ± 0.0006	0.0013 ± 0.0003
30	0.0 ± 0.0	0.0057 ± 0.0009
67	0.054 ± 0.004	0.028 ± 0.007

Values are mean ± SE of the mean. $n = 3$ for all data points except for 7 d, nonventilated pile sample where $n = 1$. nd, not determined.

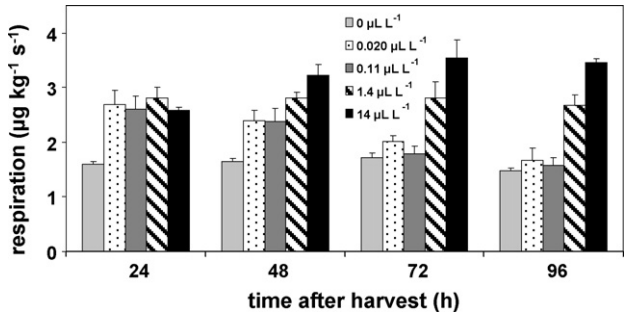

Fig. 2. Respiration rate of roots exposed to 0, 0.020, 0.11, 1.4 and 14 $\mu L\,L^{-1}$ ethylene for 4 d at 10 °C. Respiration rate was measured as the rate of CO_2 produced. Error bars are the standard error of the mean ($n = 3$).

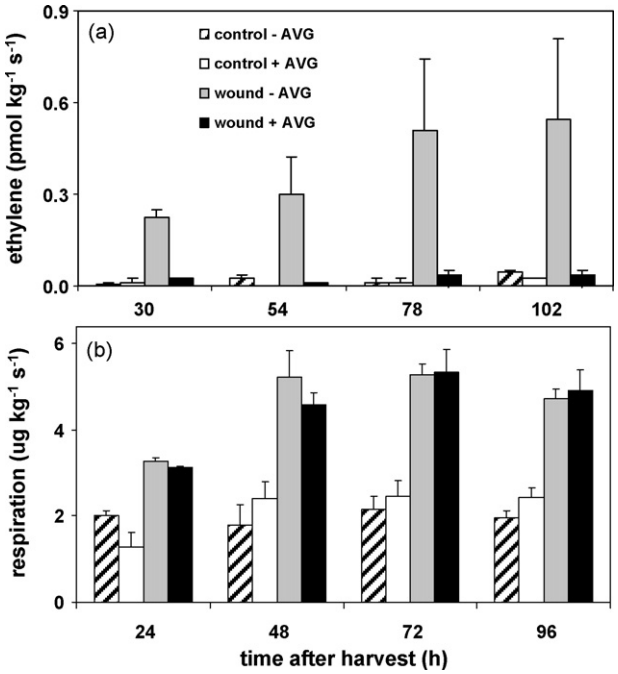

Fig. 3. Effect of aminoethoxyvinylglycine (AVG) on ethylene production (a) and respiration rate (b) of unwounded (control) and wounded sugarbeet roots during 4 d storage at 10 °C. AVG (50 $\mu mol\,L^{-1}$) was applied after wounding. Respiration rate was measured as the rate of CO_2 produced. Error bars are the standard error of the mean.

an average of 55% during the first 48 h of exposure to 0.020 and 0.11 $\mu L\,L^{-1}$ ethylene, but was unaffected by either ethylene concentration at 72 or 96 h. At ethylene concentrations of 1.4 and 14 $\mu L\,L^{-1}$, root respiration rate was elevated above that of controls for the 4 d duration of the experiment, with respiration rates increased an average of 73 and 100%, respectively.

3.3. Ethylene biosynthesis inhibitor effects on root ethylene production and respiration rate

The ethylene biosynthesis inhibitor, aminoethoxyvinylglycine, effectively eliminated wound-induced ethylene biosynthesis (Fig. 3a). AVG reduced ethylene production in wounded roots from a 4 d average of 0.39 pmol kg^{-1} s^{-1} to 0.028 pmol kg^{-1} s^{-1}. This rate was statistically similar to that of unwounded roots with or without AVG treatment. AVG had no significant effect on the ethylene production rate of unwounded roots.

AVG, however, had no effect on sugarbeet root respiration rate (Fig. 3b). Similar respiration rates were observed for wounded roots with or without AVG treatment during all 4 d of the experiment, indicating wound-induced respiration was not affected by the roots ability to synthesize ethylene. AVG also had no significant effect on the respiration rate of unwounded roots.

3.4. Ethylene response inhibitor effects on root respiration rate

The effect of the ethylene response inhibitor, 1-methylcyclopropene, on wound-induced respiration was dependent on application time relative to wounding (Fig. 4). 1-MCP applied prior to wounding had no effect on the respiration rate of wounded roots after 1 and 2 d storage, but caused it to increase by 42 and 29% after 3 and 4 d storage, respectively (Fig. 4a). Applied after wounding, 1-MCP increased respiration rate of wounded roots 37% after 1 d in storage, but decreased respiration of wounded roots by 35 and 33% after 3 and 4 d storage, respectively (Fig. 4b). Silver thiosulfate, another ethylene response inhibitor, caused a similar reduction in respiration rate 3 and 4 d after harvest when applied after wounding (Fig. 5). The respiration rate of unwounded roots was not significantly affected by 1-MCP (Fig. 4a and b).

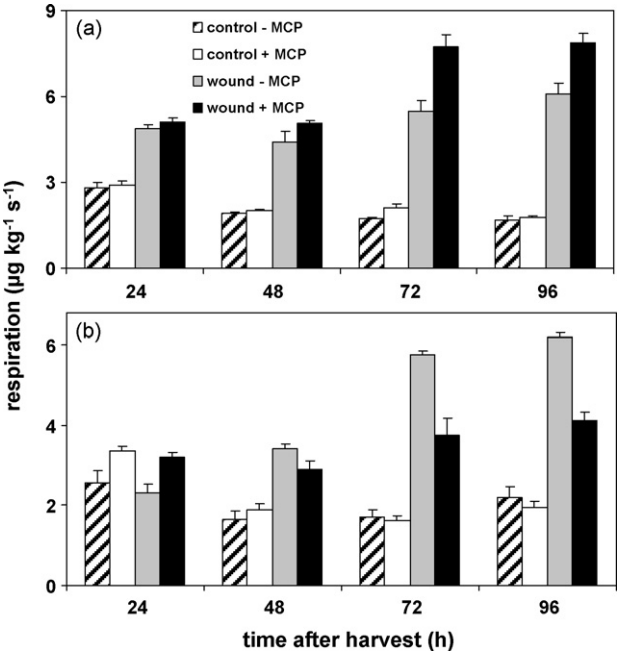

Fig. 4. Effect of 1-methylcyclopropene (1-MCP) on respiration rate of unwounded (control) and wounded sugarbeet roots during 4 d storage at 10 °C when applied (a) before wounding and (b) after wounding. 1-MCP was applied at concentrations of 0.84 and 0.46 $\mu L\,L^{-1}$ for (a) prewound and (b) postwound treatments, respectively. Respiration rate was measured as the rate of CO_2 produced. Error bars are the standard error of the mean ($n = 3$).

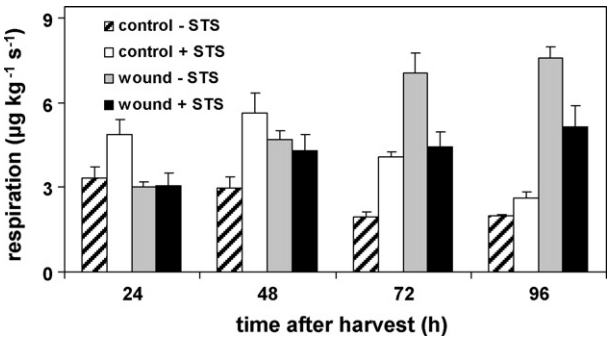

Fig. 5. Effect of silver thiosulfate (STS) on respiration rate of unwounded (control) and wounded sugarbeet roots during 4 d storage at 10 °C. STS (4 mmol L^{-1}) was applied after wounding. Respiration rate was measured as the rate of CO_2 produced. Error bars are the standard error of the mean ($n = 3$).

Similar to unwounded roots in the above experiment, 1-MCP had no effect on the respiration rate of conventionally produced and harvested roots during storage (Table 2). 1-MCP, applied at rates of 1 or 5 µL L^{-1} as a postharvest fumigant, had no effect on root respiration rate during the first 10 d of storage, or after 30, 60, 90 or 120 d storage. Similarly, 1-MCP did not significantly alter respiration rate relative to controls when applied as a 15 or 25 µL L^{-1} postharvest dip or as a 50 µL L^{-1} preharvest foliar spray (Table 2). Sucrose content and extractable sucrose yield, a measure of the sugar produced after processing as affected by both sucrose and nonsucrose impurity concentrations, were also unaltered by 1-MCP treatments.

4. Discussion

Sugarbeet roots produce low concentrations of ethylene, which are increased by severe injury. In this study, uninjured sugarbeet roots produced ethylene at a rate of 0.047 pmol kg^{-1} s^{-1}. A low rate of ethylene production (<1 pmol kg^{-1} s^{-1}) is common for root crops including carrot (*Daucus carata* L.), parsnip (*Pastinaca sativa* L.), radish (*Raphanus sativus* L.), rutabaga (*Brassica napus* L.), and turnip (*Brassica campestris* L.) and contrasts with ethylene production rates of 0.5–5000 pmol kg^{-1} s^{-1} for fruits and rates as high as 42,000 pmol kg^{-1} s^{-1} in fading flowers (Gross et al., 2004; Kays and Paull, 2004). Ethylene production in this study was stimulated 3 to 5-fold by severe root injury. Induction of ethylene by mechanical injury is common in plants and plant products, although not universally observed in all plant products (Yang and Hoffman, 1984; Gross et al., 2004).

Ethylene, when applied at concentrations of 0.020–14 µL L^{-1}, increased respiration in sugarbeet roots. Ethylene, therefore, may have a role in regulating sugarbeet storage respiration rate, if present in sufficient quantities. Ethylene in storage piles can originate from sugarbeet roots or from pathogens on the roots. Dehydration, cold temperature stress, and frost injury are common in sugarbeet piles and induce ethylene production in other plant species (Yang and Hoffman, 1984). Storage diseases due to bacterial and fungal pathogens also occur in sugarbeet storage piles and can be a source for ethylene since many bacterial and fungal plant pathogens produce ethylene (Fukuda et al., 1993; Qadir et al., 1997). That exogenous ethylene increased sugarbeet root respiration is perhaps not surprising since ethylene stimulates respiration in most plant products (Kays and Paull, 2004). Ethylene-induced respiration, however, was transient at ethylene concentrations less than 1 µL L^{-1}, and ethylene effects on respiration rate dissipated after 48–72 h of exposure to the hormone at these concentrations. Since ethylene concentrations measured in storage piles 0–67 d after piling were less than 0.1 µL L^{-1}, it is likely that any ethylene effects on respiration rate in commercial sugarbeet piles is short-lived.

Although exogenous ethylene induced sugarbeet root respiration, wound-induced ethylene production was not directly responsible for the elevated respiration of wounded roots. AVG effectively eliminated wound-induced ethylene such that ethylene

Table 2
Effect of 1-MCP applied as a postharvest fumigant, postharvest dip, or preharvest foliar treatment on respiration rate, sucrose content and extractable sucrose yield of conventionally produced and harvested sugarbeet roots during 120 d storage at 4 °C.

	Days after harvest	1-MCP postharvest treatments								1-MCP preharvest treatment		
		Fumigation treatments				Submergence treatments				Foliar spray treatment		
		0 µL L^{-1}	1 µL L^{-1}	5 µL L^{-1}	LSD	0 µL L^{-1}	15 µL L^{-1}	25 µL L^{-1}	LSD	0 µL L^{-1}	50 µL L^{-1}	LSD
Respiration rate (µg kg^{-1} s^{-1})	1	1.48	1.58	1.60	ns	–	–	–		–	–	
	2	1.51	1.58	1.53	ns	–	–	–		–	–	
	3	1.37	1.44	1.33	ns	–	–	–		–	–	
	4	1.37	1.45	1.30	ns	–	–	–		–	–	
	5	1.20	1.19	1.18	ns	–	–	–		1.81	1.79	ns
	6	1.04	1.00	1.08	ns	–	–	–		–	–	
	7	1.06	1.11	0.97	ns	–	–	–		–	–	
	8	1.08	1.15	1.13	ns	–	–	–		–	–	
	9	1.11	1.15	1.02	ns	–	–	–		–	–	
	10	1.05	1.01	1.04	ns	–	–	–		–	–	
	30	1.01	0.91	0.91	ns	1.75	1.99	1.56	0.29	1.22	1.11	ns
	60	1.16	1.14	1.11	ns	1.63	1.65	1.59	ns	1.11	1.03	ns
	90	1.59	1.29	1.51	ns	–	–	–		1.24	1.12	ns
	120	1.84	1.66	1.76	ns	1.60	1.50	1.58	ns	1.30	1.15	ns
Sucrose (kg t^{-1})	10	169	169	167	ns	–	–	–		–	–	
	30	–	–	–		125	121	125	ns	–	–	
	60	164	165	169	ns	–	–	–		–	–	
	120	160	165	161	ns	113	118	113	ns	161	156	ns
Extractable sugar (kg t^{-1})	10	156	155	155	ns	–	–	–		–	–	
	30	–	–	–		101	95	100	ns	–	–	
	60	150	151	154	ns	–	–	–		–	–	
	120	142	141	141	ns	83	84	80	ns	132	125	ns

ns, not significant at $P \leq 0.05$; –, not determined.

production by wounded roots was similar to that of unwounded roots. Eliminating wound-induced ethylene production, however, did not eliminate or reduce wound-induced respiration, indicating that wound-induced respiration did not require an increase in ethylene synthesis.

Wounding, however, may have altered the sensitivity of sugarbeet roots to ethylene, and this change in sensitivity may have had a role in wound-induced respiration. Inhibition of ethylene perception with 1-MCP or STS after wounding reduced wound-induced respiration 3 and 4 d after injury. Ethylene perception, therefore, was required for at least a portion of the increase in respiration due to wounding. Blockage of ethylene perception prior to wounding, however, was ineffective at reducing wound-induced respiration, suggesting that new ethylene receptors were generated post-wounding. Interestingly, blockage of ethylene perception with 1-MCP prior to injury increased respiration in wounded roots 3 and 4 d after injury. This increase is consistent with an increase in ethylene sensitivity, as suggested by the results discussed above, and an increase in ethylene production. Increased ethylene production after 1-MCP treatment has been documented in several plant organs and occurs when autoinhibition of ethylene biosynthesis is disrupted by blockage of ethylene perception (Mullins et al., 2000; Rapaka et al., 2008). The response of sugarbeet root respiration to ethylene response inhibitors is consistent with an increase in ethylene sensitivity after injury; additional research, however, is needed to establish whether ethylene sensitivity is actually enhanced by wounding.

Experiments conducted with greenhouse-grown plants established that sugarbeet roots produce and respond to ethylene; experiments with field-grown roots suggest that ethylene production and ethylene effects on respiration rate are likely to be of limited economic significance in commercial practice. Although conventional harvest and piling operations injure sugarbeet roots (Steensen, 1996; Wiltshire and Cobb, 2000), the mechanical injuries sustained by conventionally harvested and piled roots were not sufficiently severe to increase ethylene production above that observed for uninjured roots. As a result, only very low ethylene concentrations (<0.002 $\mu L\,L^{-1}$) were detected in sugarbeet piles in the week following harvest when wound-induced ethylene production would be expected to be at its highest. Ethylene concentrations in commercial piles did increase with time in storage, possibly due to the development of fungal or bacterial infections on the stored roots. However, ethylene concentrations remained below 0.055 $\mu L\,L^{-1}$ during 67 d in storage. That 1-MCP applied before or after harvest had no effect on the respiration rate, sucrose yield, or extractable sucrose yield of conventionally harvested roots during 1–120 d in storage also indicates that any ethylene effects on commercially harvested roots during storage were nonexistent or sufficiently small as to be undetectable.

In conclusion, postharvest sugarbeet roots produce ethylene, respond to wounding with an increase in ethylene production, and respond to exogenous ethylene with an increase in respiration rate. Ethylene production rates and their effect on root respiration, however, were small under commercial storage conditions and were unlikely to have any commercial significance. In light of this, it is not surprising that the ethylene response inhibitor, 1-MCP, which has been used successfully to improve storage of a wide range of postharvest products (Blankenship and Dole, 2003), had no beneficial effects on stored sugarbeet roots.

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