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Comparison of hydrogen sulphide with 1-methylcyclopropene (1-MCP) to inhibit senescence of the leafy vegetable, pak choy

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ABSTRACT

Postharvest fumigation with hydrogen sulphide (H_2S) can inhibit senescence of a range of fruit and vegetables. It has been suggested that the mode of action of hydrogen sulphide is through inhibiting either the endogenous production and/or the action of ethylene. This study compared the effect of fumigation with 250 $\mu L\,L^{-1}$ hydrogen sulphide and 10 $\mu L\,L^{-1}$ 1-methylcyclopropene (1-MCP) on a range of factors associated with senesence of the leafy vegetable, pak choy stored at 10 °C and ventilated with ethylene-free air or air containing 0.1 $\mu L\,L^{-1}$ ethylene. When pak choy was stored in an ethylene-free atmosphere, hydrogen sulphide and 1-MCP were equally effective in inhibiting the loss of green colour, respiration, ion leakage and endogenous ethylene production. However, for containers ventilated with ethylene, 1-MCP was more effective in inhibiting loss of green colour, respiration and ethylene production than hydrogen sulphide. Sequential fumigation with 1-MCP followed by hydrogen sulphide showed no difference in any quality factor to produce fumigated with 1-MCP. The study concluded that (i) the mode of action of hydrogen sulphide included inhibiting the action of ethylene and (ii) for pak choy, 1-MCP was a more effective fumigation treatment than hydrogen sulphide.

1. Introduction

Hydrogen sulphide (H_2S) has been identified as a gaseous plant growth regulator that affects diverse plant physiological functions such as germination, stomatal movement, root development and flower senescence (Hancock and Whiteman, 2016). A role for hydrogen sulphide in regulation of postharvest senescence was first reported by Zhang et al. (2011) who found delayed senescence in cut flowers and shoot explants. Beneficial effects of postharvest fumigation with hydrogen sulphide have now been extended to a wide range of fruit and vegetables with an increase in postharvest life achieved through the inhibition of various senescence characteristics (Fotopoulos et al., 2015). However, the mode of action of hydrogen sulphide in inhibiting senescence remains unclear but some interaction with ethylene would seem likely given the central role of ethylene in promoting ripening and senescence (Abeles et al., 1992). The only reported study on hydrogen sulphide and ethylene production was by Al Ubeed et al. (2017) who found that hydrogen sulphide inhibited ethylene production by the green leafy vegetable, pak choy. They suggested that the mode of action of hydrogen sulphide in delaying senescence could be by inhibiting endogenous production of ethylene and/or by inhibiting the action of ethylene.

The discovery of 1-methylcyclopropene (1-MCP) as a competitive inhibitor of the action of ethylene (Sisler and Blankenship, 1996) was a landmark development in postharvest technology. 1-MCP is a competitive inhibitor of ethylene perception and acts by strongly binding to ethylene receptor sites thus preventing binding and the subsequent signalling that triggers ripening and senescence. Numerous subsequent studies have since shown that 1-MCP can extend the postharvest life of a wide range of commodities (Watkins, 2015). Included in such studies, Able et al. (2005) found that 1-MCP extended the shelf life of pak choy by inhibiting loss of green colour when 1 $\mu L\,L^{-1}$ ethylene was present in the atmosphere around produce.

Since both hydrogen sulphide and 1-MCP have been shown to inhibit senescence of pak choy, this study compared the effect of fumigating pak choy (*Brassica rapa* subsp. *Chinensis* − also known as bok or pok choy, choi or tsoi) in both the presence and absence of exogenous ethylene. The study was undertaken by fumigating pak choy leaves with hydrogen sulphide, 1-MCP and sequential fumigation of 1-MCP followed by hydrogen sulphide. Treated produce was then stored at 10 °C and ventilated with ethylene-free air (< 0.001 $\mu L\,L^{-1}$ ethylene) or air containing 0.1 $\mu L\,L^{-1}$ ethylene. Quality measures determined were loss

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of green colour (as the primary measure of consumer acceptance), respiration (as a measure of general metabolism), ion leakage (as a measure of cellular integrity), and endogenous ethylene production as the primary driver of senescence,

2. Materials and methods

2.1. Produce

Pak choy plants (cv. 'Shanghai') were harvested from a local commercial farm at Mangrove Mountain, NSW, Australia, and transported to the laboratory within two hours. Pak choy heads selected for the study were of uniform size (10 cm length) and colour and without damage to leaves or stem. The four outside leaves from each head were selected and gently cleaned under running tap water. The leaves from all heads were randomly distributed into 12 treatment units with each containing a total of 25 leaves that weighed between 250 and 350 g. Experiments were replicated with pak choy obtained from the same farm on three occasions over a one month period.

2.1.1. Treatments and experiment design

The pak choy leaves in each treatment unit were placed into separate 4 L containers that were fitted with inlet and outlet ports and held at 20 °C. After two hours at 20 °C, groups of three units were sealed and treated with one of the following:

- Fumigation with hydrogen sulphide vapour at a concentration of 250 $\mu L\ L^{-1}$: Hydrogen sulphide gas was generated *in situ* by adding solid $NaHS.H_2O$ (Sigma Aldrich, Australia) (2.4 mg) into a dry beaker that was placed into a container. The container was then sealed and water (2 mL) was injected into the beaker through a septum in the container lid to instantaneously and quantitatively liberate hydrogen sulphide gas (Zhao et al., 2014). Containers remained sealed for four hours at 20 °C then exposed to ambient air for five hours.
- Fumigation with 1-MCP at a concentration of 10 $\mu L\ L^{-1}$: 1-MCP gas at the desired concentration was generated *in situ* by placing SmartFresh™ powder (0.14% of active ingredient) (supplied by AgroFresh, Australia) (66.4 mg) into a dry beaker in a container which was then sealed. Water (2 mL) was injected into the beaker through a septum in the container lid to liberate 1-MCP gas. Containers remained sealed for four hours at 20 °C then exposed to ambient air for five hours.
- Fumigation with 1-MCP at 10 $\mu L\ L^{-1}$ followed by fumigation with hydrogen sulphide at 250 $\mu L\ L^{-1}$: Using the above methods, containers of produce were fumigated with 1-MCP for four hours, followed by one hour in ambient air then fumigated with hydrogen sulphide for four hours.

The concentrations of hydrogen sulphide and 1-MCP were selected used as the respective optimum concentrations reported by Al Ubeed et al. (2017) and Sonnthida Sambath, University of Newcastle, unpublished data) for pak choy. The control treatment was left untreated in unsealed containers held in ambient air at 20 °C for nine hours.

After nine hours, all the containers were sealed, placed at 10 °C and ventilated with ethylene-free air or air containing 0.1 $\mu L\ L^{-1}$ ethylene at a flow rate of 45 $mL\ min^{-1}$. Ethylene-free air was generated by passing compressed ambient air through a tube filled with potassium permanganate adsorbed onto alumina pellets. The ethylene concentration of the air was analysed as < 0.001 $\mu L\ L^{-1}$ which was the analytical limit of detection. The 0.1 $\mu L\ L^{-1}$ ethylene gas stream was achieved by mixing the ethylene-free air with a regulated flow of ethylene from a cylinder (1 $mL\ L^{-1}$ ethylene in air, BOC Gases, Sydney). Both gas streams were humidified by bubbling through water held in a 2 L glass jar (height 2.25 m) to ensure a high humidity of 97–99% RH was maintained in the gas stream to minimise water loss.

2.2. Quality assessment

Leaves in each treatment unit were visually assessed daily for green colour and analysed after two, four and six days at 10 °C for respiration rate (as evolved carbon dioxide) and endogenous ethylene production. Ion leakage was destructively assessed after three and six days storage.

2.2.1. Visual leaf colour (market life)

Visual assessment of the change in leaf colour from green to yellow of individual leaves used a scoring scale of 0–5 where 0 = green, 1 = 10%, 2 = 20%, 3 = 30%, 4 = 50% and 5 = > 70% loss of original green colour (Li et al., 2017). The mean colour score of all leaves in a treatment unit was calculated daily. An average colour score of 3.0 was considered to be the limit of consumer acceptability and the time for leaves to reach a mean score of 3.0 was designated as the market life. Assessment of a unit was terminated when the mean score of 3.0 was attained.

2.2.2. Respiration rate

A container of produce was sealed to allow the accumulation of a measurable concentration of carbon dioxide. A gas sample (1 mL) was collected in a syringe from the atmosphere of a sealed container after four hours. The concentration of carbon dioxide in the gas sample was determined by injecting into a thermal conductivity gas chromatograph as described by Huque et al. (2013) and the respiration rate calculated.

2.2.3. Ethylene production

The ethylene concentration in the ventilating gas stream was monitored at regular intervals at the inlet port with a gas sample (1 mL) that was analysed by flame ionization gas chromatography as described by Huque et al. (2013). Endogenous ethylene production of pak choy during storage was determined by sealing a container and immediately collecting a gas sample (1 mL) that was analysed for the exogenous background ethylene concentration. After three hours, another gas sample was collected and analysed for ethylene concentration. The difference in the two readings was used to calculate the rate of endogenous ethylene production.

2.2.4. Ion leakage

At each assessment, five leaves were chosen at random from the 25 leaves in a unit and used to determine the ion leakage using the method described by Lu (2007).which involved collecting two disks (5 mm diameter) from each leaf and immersing the disks in distilled water (40 mL) for two hours at 25 °C when the conductivity of the solution was measured with a conductivity meter (Model 4071, Jenway, Staffordshire, UK). The solution was then boiled for 15 min and after cooling to room temperature (20 °C), the total conductivity was remeasured. Ion leakage was calculated as the percentage change in conductivity from the initial to final value.

2.3. Statistical analysis

Data from each experiment were analysed by two-way analysis of variance (ANOVA) and where a significant difference between treatments was found the least significant difference (LSD) at $P = 0.05$ was calculated. Statistical procedures were performed using SPSS for Windows version 22.0 software package (SPSS Chicago, IL).

3. Results

3.1. Market life

The market life, as designated by the time for pak choy leaves to lose 30% of green colour intensity (score 3), was found to be significantly affected ($P < 0.001$) by hydrogen sulphide and 1-MCP when stored in air or in ethylene at 10 °C. Table 1 shows that the market life

Table 1
Market life of pak choy fumigated with hydrogen sulphide and 1-MCP then ventilated with ethylene-free air or 0.1 μL L^{-1} ethylene during storage at 10 °C.

Treatment	Market life (days)	
	Stored in air	Stored in ethylene
Control	9.3^{a}	8.0^{a}
H_2S	11.8^{b}	10.3^{b}
1-MCP	11.6^{b}	11.4^{c}
1-MCP + H_2S	12.2^{b}	12.1^{c}
LSD	0.72	0.77

Different batches of pak choy were stored in air and in ethylene. Each value is the mean of nine treatment units (3 replicates × 3 batches of produce). Treatments in each column not sharing the same superscript letter are significantly different at $P = 0.05$.

of pak choy stored in air was increased by the fumigation treatments but there was no significant difference between hydrogen sulphide, 1-MCP and hydrogen sulphide + 1-MCP. As expected, the market life of pak choy of control leaves was reduced by the addition of ethylene into the storage atmosphere but there was a differential effect between the applied treatments; fumigation with hydrogen sulphide + 1-MCP and 1-MCP were not significantly different but were both greater than the market life of leaves fumigated with hydrogen sulphide.

3.2. Respiration rate

The respiration rate was also measured on the same leaves that were used to determine market life. There was a significant interaction between the treatment and storage time for pak choy stored in air ($P < 0.01$) and in ethylene ($P < 0.05$). The results presented in Table 2 firstly show that the respiration rate of untreated pak choy leaves held in air increased during storage. There was no significant difference between control and fumigated leaves after two days storage in air but all fumigation treatments had a significantly lower respiration rates than control leaves after four and six days. The only significant difference between the three fumigation treatments was at six days where leaves fumigated with hydrogen sulphide has a higher respiration rate than leaves fumigated with 1-MCP or 1-MCP + hydrogen sulphide which were not signficantly different.

Table 2 also shows that the addition of ethylene into the storage atmosphere increased the respiration rate of all treatments. Untreated control leaves showed an increase in respiration during storage but the fumigation treatments showed a different response. All fumigation treatments had a significantly lower respiration rate than control leaves

Table 2
Respiration rate of pak choy fumigated with hydrogen sulphide and 1-MCP then ventilated with ethylene-free air or 0.1 μL L^{-1} ethylene during storage at 10 °C.

Treatment	Respiration rate (ng kg^{-1} s^{-1})		
	2 d	4 d	6 d
Stored in air			
Control	4.3^{c}	5.4b	6.2^{a}
H_2S	3.4^{cde}	3.0^{de}	4.3^{c}
1-MCP	3.8^{cd}	2.5^{e}	3.0^{de}
1-MCP + H_2S	3.6^{cd}	2.2^{e}	3.0^{de}
LSD		1.2	
Stored in ethylene			
Control	6.8^{c}	8.0^{b}	9.1^{a}
H_2S	5.3^{d}	3.8^{ef}	4.9^{de}
1-MCP	4.2^{ef}	3.7^{f}	3.8^{f}
1-MCP + H_2S	4.0^{ef}	3.3^{f}	3.7^{f}
LSD		1.1	

Each value is the mean of nine treatment units (3 replicates × 3 batches of produce). Values in each storage atmosphere not sharing the same superscript letter are significantly different at $P = 0.05$.

Table 3
Ion leakage of pak choy fumigated with hydrogen sulphide and 1-MCP then ventilated with ethylene-free air or 0.1 μL L^{-1} ethylene during storage at 10 °C.

Ventilating gas	Treatment	Ion leakage (%)		
		3 d	6 d	Mean^{a}
Air	Control	26.2	35.0	30.6^{b}
Air	H_2S	16.4	21.0	18.7^{a}
Air	1-MCP	16.0	20.9	18.5^{a}
Air	1-MCP + H_2S	14.6	21.9	18.2^{a}
	LSD			4.8
Air	Control (air)	20.8	42.2	31.5^{a}
C_2H_4	Control (C_2H_4)	32.8	68.8	50.8^{b}
C_2H_4	H_2S	24.2	40.7	32.4^{a}
C_2H_4	1-MCP	25.6	40.9	33.2^{a}
C_2H_4	1-MCP + H_2S	19.5	42.9	31.2^{a}
	LSD			11.2

Different batches of pak choy were stored in air and in ethylene. [a] Mean values for treatments are from 18 assessments readings (3 containers × 2 storage times × 3 batches of produce). LSD values are at $P = 0.05$ and mean values in each experiment not sharing the same superscript are significantly different.

at the three storage times but leaves fumigated with hydrogen sulphide had a higher respiration at two and six days than leaves fumigated with 1-MCP and 1-MCP + hydrogen sulphide which were not signficantly different.

3.3. Ion leakage

For leaves exposed to ethylene-free air, the level of ion leakage in pak choy leaves was significantly affected by treatment and storage time ($P < 0.001$) but there was no significant interaction between treatment and storage time. The data in Table 3 show that, as expected, ion leakage increased with increasing time and that it was significantly lower in the three fumigation treatments compared to control leaves with no significant difference between the different fumigation treatments.

The experiment was repeated on leaves that were ventilated with 0.1 μL L^{-1} ethylene during storage but with the inclusion of an additional control treatment that was ventilated with air. There was a significant effect of treatment and storage time ($P < 0.001$) and the data in Table 3 show that the three fumigation treatments exhibited a similar reduction in ion leakage compared to the ethylene-ventilated control. Ion leakage of the air-ventilated control was significantly higher than that of the ethylene-ventilated control but was not significantly different to the three fumigation treatments that were ventilated with ethylene. Thus hydrogen sulphide and 1-MCP were equally effective in negating the deleterious effect of ethylene in increasing ion leakage.

3.4. Ethylene production

The rate of endogenous ethylene production of leaves stored in air and in ethylene showed a significant effect of treatment and storage time for pak choy stored in air and in ethylene ($P < 0.001$) but there was no significant interaction between treatment and storage time. The data in Table 4 show that for pak choy stored in air, the three fumigation treatments had a significantly lower rate of endogenous ethylene production than control leaves but with no significant difference between the fumigation treatments.

The addition of ethylene into the storage atmosphere markedly decreased the rate of endogenous ethylene production in all treatments. However, control leaves still had a significantly higher endogenous ethylene production than the fumigation treatments but fumigation with hydrogen sulphide was not as effective as fumigation with 1-MCP and 1-MCP + hydrogen sulphide in reducing ethylene production.

Thus, fumigation with hydrogen sulphide was not as effective in

Table 4
Ethylene production of pak choy fumigated with hydrogen sulphide and 1-MCP then ventilated with ethylene-free air or 0.1 μL L^{-1} ethylene during storage at 10 °C.

Treatment	C_2H_4 production (ng kg^{-1} s^{-1})			
	2 d	4 d	6 d	Mean[a]
Stored in air				
Control	0.24	0.17	0.09	0.17[b]
H_2S	0.13	0.09	0.07	0.09[a]
1-MCP	0.15	0.10	0.07	0.10[a]
1-MCP + H_2S	0.10	0.08	0.06	0.08[a]
LSD				*0.024*
Stored in ethylene				
Control	0.096	0.062	0.048	0.065[c]
H_2S	0.068	0.045	0.034	0.049[b]
1-MCP	0.044	0.029	0.024	0.032[a]
1-MCP + H_2S	0.042	0.030	0.028	0.033[a]
LSD				0.015

Different batches of pak choy were stored in air and in ethylene. [a] Mean values for treatments are from 27 assessments (3 replicates × 3 storage times × 3 batches of produce). LSD values are at $P = 0.05$ and mean values in each storage atmosphere not sharing the same superscript are significantly different.

reducing ethylene production as fumigation with 1-MCP while for pak choy stored in air all three fumigation treatments were equally effective in decreasing ethylene production.

4. Discussion

For pak choy stored in an ethylene-free air stream, fumigation with hydrogen sulphide or 1-MCP was found to be equally effective in inhibiting senescence as exhibited by extending the market life (i.e. inhibiting loss of green colour) and reducing the respiration rate and ion leakage. Sequential fumigation with 1-MCP followed by hydrogen sulphide did not generate any added benefit over a single fumigation of either compound.

When pak choy was stored in an exogenous ethylene stream, untreated produce showed a decrease in market life and an increase in respiration rate and ion leakage as would be expected from ethylene enhancing the rate of senescence. While all three fumigation treatments showed a beneficial response compared to untreated produce, fumigation with hydrogen sulphide was less effective than with 1-MCP in extending market life and reducing respiration while for ion leakage, hydrogen sulphide and 1-MCP were equally effective in inhibiting the increase during storage. For all three quality characteristics there was no added benefit from the combined fumigation of 1-MCP followed by hydrogen over that achieved by 1-MCP alone.

Comparison of the effects of the fumigation treatments when stored in air and ethylene showed that the market life and ion leakage of leaves fumigated with 1-MCP were not significantly different in the two ventilating atmospheres. This indicates that 1-MCP was fully able to negate the effect of exogenous ethylene on loss of chlorophyll and loss of cellular integrity. The increase in respiration rate due to the presence of ethylene, however, was not fully negated by 1-MCP. In contrast, hydrogen sulphide only fully negated the effects of exogenous ethylene for ion leakage.

Endogenous ethylene production of pak choy stored in air was decreased by all three fumigation treatments with no significant difference between treatments. When pak choy was stored in exogenous ethylene, endogenous ethylene production of leaves in control and all fumigation treatments was greatly reduced compared to leaves stored in air. Such an effect has been shown for a range of postharvest produce (Saltveit, 1999) including for pak choy (Al Ubeed et al., 2017). However, in addition, there was a greater reduction in loss of pak choy quality attributes of all fumigated leaves relative to control but the reduction in ethylene production achieved by hydrogen was not as great as with 1-MCP alone or in combination with hydrogen sulphide. This additional reduction in endogenous ethylene production by the fumigation treatments relative to control is consistent with an added negative feedback mechanism in operation for hydrogen sulphide and for 1-MCP. While the primary action of 1-MCP is considered to be through blocking the action of ethylene, the literature is ambivalent on the effect of 1-MCP on ethylene production. For leafy vegetables, Sun et al. (2012) reported that ethylene production of Chinese kale (*Brassica. alboglabra*) was strongly inhibited by 1-MCP whereas Kenigsbuch et al. (2007) reported mint leaves had increased ethylene production.

Thus for pak choy, hydrogen sulphide and 1-MCP appear to inhibit both the production of endogenous ethylene and the action of ethylene. In a low ethylene environment, inhibition of ethylene production could lead to inhibition of senescence. Indeed, Li et al. (2014) and Zheng et al. (2016) have shown that fumigation with hydrogen sulphide down regulated the expression of genes associated with ethylene biosynthesis of broccoli florets and apple slices, respectively. However, the inhibition of senescence by hydrogen sulphide in the presence of exogenous ethylene indicates that the primary mode of action of hydrogen sulphide could be by inhibiting the action of ethylene. One possibility is that hydrogen sulphide binds to the same ethylene receptor genes as 1-MCP. However, 1-MCP is reputed to bind through a copper I cofactor that requires a cysteine residue (Cys_{65}) to be present to successfully coordinate in the ETR1 binding domain (Lacey and Binder, 2014). While hydrogen sulphide could theoretically bind to the copper ion in the receptor, as it is of similar size to ethylene, it would likely need to deprotonate to bind strongly. In addition, the allosteric (shape change) effect on the receptor would almost certainly differ from coordination of hydrogen sulphide and 1-MCP (Pirrung et al., 2008). However, it is well documented that a range of ethylene receptors can be present in horticultural produce with five such receptors having been identified (Lacey and Binder, 2014) and hydrogen sulphide may bind to one or more of these systems. In a recent study on banana ripening, Ge et al. (2017) found that co-fumigation of hydrogen sulphide with ethylene up-regulated expression of ethylene receptor genes MaETR, MaERS1 and MaERS2, while suppressing expression of genes associated with ACC synthase (MaACS1, MaACS2) and ACC oxidase (MaACO1, MaACO2) compared to ethylene alone. In the presence of hydrogen sulphide, these factors were collectively proposed to reduce the ethylene response in bananas.

Whatever the bonding site of hydrogen sulphide, it must be less tightly bound than 1-MCP and can be partially displaced by exogenous ethylene to cater for the greater inhibition by 1-MCP of various aspects of senesence in the presence of ethylene. The lack of any cumulative effect of 1-MCP and hydrogen sulphide could be due to the stronger binding of 1-MCP to a receptor gene or that 1-MCP binds to a receptor that is more central to the action of ethylene. Regardless of the mode of action of hydrogen sulphide and 1-MCP, for pak choy, fumigation with 1-MCP would appear be a more effective commercial option to inhibit senescence than fumigation with hydrogen sulphide.

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