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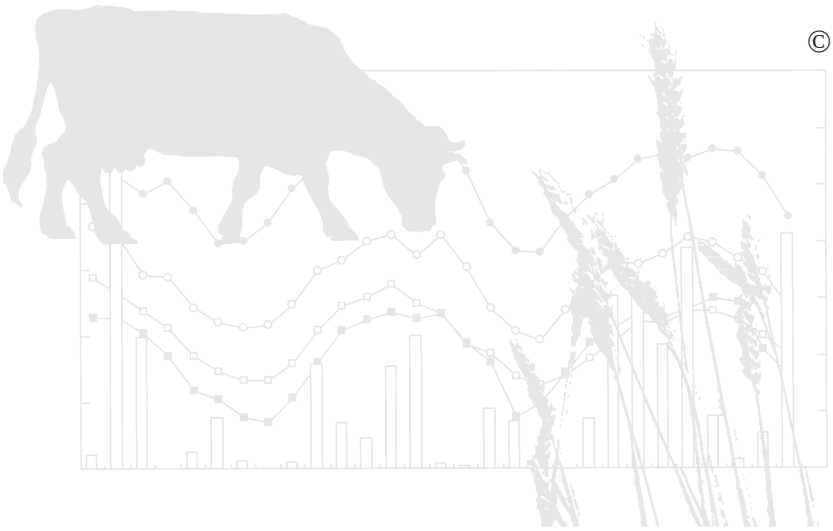
Australian Journal of Experimental Agriculture

Volume 40, 2000



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Australian Journal of Experimental Agriculture, 2000, **40**, 471–481

1-Methylcyclopropene treatment efficacy in preventing ethylene perception in banana fruit and grevillea and waxflower flowers

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Abstract. Premature ripening and/or senescence and abscission induced by exposure to ethylene are significant postharvest problems. Banana fruit and grevillea and Geraldton waxflower flowers are among affected commodities. Treatment with 1-methylcyclopropene gas or silver thiosulfate liquid can be used to prevent ethylene perception and response. Treatment of banana fruit with 10 nL 1-methylcyclopropene/L for 12 h at 20°C afforded protection against subsequent serial treatments over 13 days of subsets with 100 μL ethylene/L for 24 h at 20°C. Protection of *Grevillea* 'Sylvia' inflorescences was effective only for 2 days. Thereafter, fruit and inflorescences regained sensitivity to ethylene. In contrast, neither banana fruit nor grevillea inflorescences treated with 10 nL 1-methylcyclopropene/L for 12 h at 2°C were protected against ethylene. 1-Methylcyclopropene binding to ethylene receptors was apparently not achieved at the lower temperature. Increasing the 1-methylcyclopropene concentration to 100 nL/L, applied at 2.5°C to banana fruit, achieved protection against ethylene. Waxflower sprigs treated with 10 nL 1-methylcyclopropene/L for 12 h at 2 or 20°C regained full sensitivity to ethylene after about 2 and 4 days, respectively. In contrast, pulsing waxflower with 0.5 mmol Ag^+/L as silver thiosulfate for 12 h at 2 or 20°C afforded protection against ethylene for the 10 days duration of the experiment.

Introduction

Ethylene regulates a number of plant processes that have commercial significance in postharvest horticulture (Abeles *et al.* 1992). Unintentional exposure to ethylene can reduce the postharvest life of both cut flowers and fruit by eliciting abscission and/or accelerating ripening and senescence (Reid 1985). Such effects can be prevented by treating sensitive produce with chemical inhibitors of ethylene biosynthesis or perception (Sherman 1985).

Silver thiosulfate (STS) liquid is used widely as a commercial anti-ethylene treatment for cut flowers and potted flowering plants (Veen 1983; Nowak and Rudnicki 1990). STS applied as a pulse moves readily in the transpiration stream of cut flowers and accumulates in their receptacles (Veen and van de Geijn 1978). Ag^+ in the STS complex binds to and blocks ethylene receptors (Sisler 1982). The commercial use of STS is being reconsidered in some countries due to possible environmental hazards (Serek *et al.* 1994*a*). Adoption of silver retrieval methods used in film processing (Cooley 1988) may alleviate some current concerns. Alternatively, the novel gaseous inhibitor of ethylene perception, 1-methylcyclopropene (1-MCP), may have commercial potential (Serek *et al.* 1994*b*). 1-MCP has been shown to prevent ethylene responses in a range of cut flowers (Serek *et al.* 1995*a*, 1995*b*; Sisler *et al.* 1996*a*), potted flowering plants (Serek *et al.* 1994*b*), climacteric fruit (Sisler *et al.* 1996*b*; Golding *et al.* 1998; Jiang *et al.* 1999*a*, 1999*b*) and non-climacteric fruit (Ku *et al.* 1999; Porat *et al.* 1999).

In contrast to STS, the efficacy of 1-MCP has been reported to be poor when it is applied at low temperature. For example, 1-MCP treatment at 20°C was effective in protecting cut *Penstemon* flowers against ethylene, but no protection was afforded when it was applied at 2°C (Serek *et al.* 1995*a*). Increasing the concentration of 1-MCP applied during low temperature

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treatment improved efficacy to levels similar to treatment at 20°C (Reid *et al*. 1996). Reasons for this variable response at different temperatures are not known.

1-MCP molecules bind permanently to ethylene receptors and irreversibly prevent ethylene action (Sisler *et al*. 1996*a*). Nonetheless, 1-MCP-treated cut carnation flowers, banana and tomato fruit regain sensitivity to ethylene at between 10 and 15 days after treatment with 1-MCP (Sisler *et al*. 1996*b*; Sisler and Serek 1997). Recovery of competence to respond to ethylene was suggested by Sisler and Serek (1997) to be due to the synthesis of new ethylene receptors.

Some fruit, including bananas, are highly sensitive to ethylene. Exposure to just 0.1 L ethylene/L can initiate ripening (Burg and Burg 1962). Unintentional exposure of such fruit to ethylene during postharvest handling induces premature ripening and reduces shelf life (Reid 1985). Similarly, exposure of some native Australian cut flowers, including Geraldton waxflower and grevillea, to ethylene elicits rapid flower abscission and thereby reduces vase life (Joyce 1988, 1989; Joyce *et al*. 1993).

In line with published information, it was proposed that the postharvest longevity of banana fruit and native Australian cut flowers would be extended by treatment with 1-MCP. Moreover, it was hypothesised that protection of banana fruit and cut flowers against ethylene would not be achieved when low concentrations of 1-MCP are applied at low temperature. The present study examines the influence of temperature on 1-MCP treatment efficacy in terms of preventing ethylene-induced ripening of banana fruit and flower abscission from waxflower and grevillea. The duration of protection afforded by treatment with 1-MCP was determined for each commodity. Also, 1-MCP treatment was compared with STS treatment for waxflower.

Materials and methods

Plant material

Mature green banana (*Musa* sp. 'Williams'; Cavendish subgroup AAA) fruit were obtained from a commercial plantation near Murwillumbah (northern New South Wales; 28°20'S, 153°24'E). Fruit were harvested in May (autumn), June, July and August (winter) and October (spring). Harvested fruit were held overnight in a cool room at 16°C. They were then transported to a retail market about 70 km away. Fruit free of visual defects were selected and taken within 1 h to the laboratory. Fruit were removed from hands and assigned to treatment lots. Hands were used as replicates. Fruit were labelled and dipped in fungicide [0.55 mL/L of Sportak (a.i. prochloraz)] for 2 min.

Grevillea 'Sylvia' (*G. banksii* x *G. whiteana*) inflorescences were harvested from plants growing at a commercial nursery near Redland Bay (south-east Queensland; 27°37'S, 153°18'E). Leaves were trimmed from stems using secateurs. Inflorescences were then placed into styrofoam boxes lined with moist newsprint and ice to minimise moisture loss and heating, respectively. They were transported to the laboratory within 2 h of harvest. Stem ends were recut under deionised water, removing at least 2 cm from the base to avoid air embolisms. Individual stems were randomly assigned to vases containing 10 mg/L available chlorine as dichloroisocyanurate (DICA, sodium salt) in deionised water. The 375-mL capacity plastic vases were covered with a piece of low density polyethylene film to minimise evaporation and prevent contamination by falling flowers.

Flowering waxflower (*Chamelaucium uncinatum*) stems were harvested from plants at a farm near Gatton (south-east Queensland; 27°34'S, 152°17'E). Stems were immediately stood into buckets containing deionised water and transported within 30 min to the laboratory. Sprigs about 20 cm long were cut from the stems with secateurs. They were prepared as described for *G*. 'Sylvia' inflorescences. Leaves which would otherwise be submerged in vase solution were removed from the lower section of the sprigs.

Chemicals

1-MCP was synthesised according to Sisler and Serek (1997). However, lithium diisopropylamide was substituted for phenyllithium (E. Sisler pers. comm.). 1-MCP was quantified by gas chromatography using the method described by Jiang *et al*. (1999*a*). STS at 40 mmol Ag^+/L was prepared as described by Reid *et al*. (1980). Ethylene gas was obtained from a pressurised cylinder of pure ethylene. An ethylene stock was quantified by gas chromatography using the method described by Taylor *et al*. (1997).

Treatment of banana fruit

In experiment 1, fruit were placed individually into open 2.2-L glass jars and held in controlled environment rooms at 2.5, 5, 7.5, 10, 12.5, 15 or 20°C. Pulp temperature was monitored on additional fruit until they had reached the prescribed temperature. At this time, a 100-mL beaker containing 10 mL of 1 mol KOH/L was placed into each jar to absorb carbon dioxide from respiration. Filter paper wicks were stood vertically into each beaker to maximise the surface area of KOH. Plastic screw-on lids were fastened onto each jar. Half of the fruit at each temperature were treated on day 0 with 15 L1-MCP/L for 12 h. An aliquot of 1-MCP gas was injected through a rubber septum in each lid. The other fruit were enclosed in air without 1-MCP.

Following 1-MCP treatment, the lids were removed from each jar and the rooms were ventilated using exhaust fans. All fruit were then transferred to 20°C. Once the pulp temperature of all fruit had reached 20°C, half of the fruit from each of the 0 or 15 L 1-MCP/L treatments were treated on day 1 with 100 L/L ethylene for 24 h at 20°C inside 60-L glass chambers. Ethylene gas was injected through a rubber septum in the lid of each chamber. A small fan in each chamber stirred the ethylene gas. The remaining half of the fruit were sealed into identical chambers but were not treated with ethylene.

In experiment 2, fruit were placed at 2.5, 15 or 20°C and treated on day 0 with 0, 1, 2, 4, 8 or 15 L 1-MCP/L for 12 h. Fruit were then transferred to 20°C. Half of the fruit from each concentration by temperature treatment were treated on day 1 with ethylene as described for the first experiment.

In experiment 3, fruit were placed at 2.5, 15 or 20°C and treated on day 0 with 0, 10, 100 or 1000 nL 1-MCP/L for 12 h. Fruit were then transferred to 20°C. Half of the fruit from each concentration by temperature treatment were exposed to ethylene as described for the previous experiments.

In experiment 4, fruit were enclosed in glass chambers and treated on day 0 with 15 L 1-MCP/L for 12 h at 20°C. Control fruit were enclosed in other chambers without 1-MCP. Different subsamples of the fruit treated with 15 L 1-MCP/L were exposed on days 1, 5, 10, 20 or 30 to 100 L ethylene/L for 24 h at 20°C.

In experiment 5, fruit were enclosed in chambers and treated on day 0 with 10 nL 1-MCP/L for 12 h at 2 or 20°C. Control fruit at each temperature were enclosed in chambers without 1-MCP. Different subsamples of fruit treated with 10 nL 1-MCP/L were then exposed on days 1, 4, 7, 10, 13, 16, 19, 22, 25, 28 or 31 to 100 L ethylene/L for 24 h at 20°C.

Whenever fruit from all 5 experiments described above were not receiving 1-MCP or ethylene treatment, they were held in a controlled environment room operating at 20°C and at 90% relative humidity (RH).

Treatment of Grevillea *'Sylvia' inflorescences*

G. 'Sylvia' inflorescences standing in individual vases were enclosed in glass chambers each containing 6 beakers of 1 mol KOH/L . Inflorescences were treated on day 0 with 10 nL 1-MCP/L for 12 h at 2 or 20°C. Control inflorescences were kept in other chambers without 1-MCP. Different subsamples of 1-MCP-treated inflorescences were then exposed to 10 L ethylene/L for 12 h at 20°C daily from day 1 until the end of vase life on day 5. When not receiving 1-MCP or ethylene treatments, inflorescences were held in a vase life room at 20 ± 2°C and 50–70% RH. Overhead cool white fluorescent lights provided 13 mol/m^2. s at inflorescence height and were run on a 12-h on/off cycle.

Treatment of waxflower sprigs

In 3 separate experiments, flowering waxflower 'Lollypop', 'Alba' and 'Mid Pink' sprigs were treated on day 0 with 10 nL 1-MCP/L in chambers or were pulsed with STS at 0.5 mmol Ag^+/L for 12 h. Both chemicals were applied at 2 or 20°C. Untreated sprigs (i.e. 0 nL 1-MCP/L or 0 mmol Ag^+/L) were also maintained at 2 or 20°C. Following these treatments, different subsamples of flowering sprigs treated with 1-MCP or Ag^+ were exposed daily to 10 L ethylene/L for 12 h at 20°C from day 1 until the end of vase life on about day 10. When not receiving 1-MCP, STS or ethylene treatments, sprigs were kept in the same vase life room used for *G*. 'Sylvia' inflorescences.

Assessment of banana fruit

Fruit were weighed every second day for calculation of weight loss. Skin colour was assessed daily using the CSIRO (1972) 8-point rating scale, where a score of 1 is 'green' and 8 is 'yellow with increasing brown areas'. Firmness was also assessed daily on a 5-point scale, where 1 is 'hard' and 5 is 'oversoft' (Wills and Tirmazi 1982). Objective determinations of skin colour and fruit firmness were also made every second day in all experiments except experiment 5. Skin colour was measured using a Minolta CR-200 Chroma Meter. Fruit firmness was assessed using a digital firmness meter (Macnish *et al*. 1997). Shelf life (SL) was judged as the time in days, from day 0 of the experiment, for fruit to reach eating ripe condition of a firmness score of 4, 'eating soft'. Shelf life following ethylene (SLFE) treatment was also recorded for experiments 4 and 5, and was the time in days after exposure to ethylene for fruit to reach the eating ripe condition.

Assessment of cut flowers

Grevillea 'Sylvia' inflorescences were assessed daily for flower abscission after gently brushing them 3 times by hand and using the rating scale: 1, <10%; 2, 10–30%; 3, 30–50%; 4, 50–80%; 5, >80% flower abscission relative to the initial number on a stem. Flower wilting and discolouration were rated daily using the scale: 1, none/slight; 2, moderate; 3, advanced. Opening of flowers on inflorescences was recorded daily using the scale: 1, <5%; 2, 5–25%; 3, >25%. Vase life (VL) of *G*. 'Sylvia' inflorescences was subjectively determined as the time in days to loss of visual appeal at >10% flower abscission and/or moderate flower discolouration and/or wilting. Vase life following ethylene (VLFE) treatment was also calculated.

Grevillea 'Sylvia' inflorescences and flowering waxflower sprigs were weighed daily for calculation of fresh weight change. Vase solution usage was determined daily by weighing the vases. Flower abscission from waxflower sprigs was assessed daily after gently brushing them 3 times by hand. Flower abscission was expressed as the percentage of flowers abscised out of the initial day 0 number on a sprig. Vase life of sprigs was judged as the time in days to loss of visual appeal at >10% flower abscission and/or ≥50% of flowers on a sprig having lost turgor as evidenced by a decreased angle between the petals and central style. As for *G*. 'Sylvia', VLFE was also estimated.

Experiment design and data analysis

Fruit and flowers were arranged in controlled environment rooms in completely randomised designs (CRD). In experiments with bananas, 3–10 replicate fruit were used for each treatment, depending upon the particular experiment. There were 5 replicate inflorescences or sprigs in all experiments with flowers. Data are presented as treatment means ± standard errors. Treatment means ± standard errors presented in figures were calculated and plotted using SigmaPlot Version 2.0 (Jandel Corporation) software. All data were analysed by the balanced ANOVA function of Minitab Release 11.12 (Minitab Inc.) software. Following ANOVA, the least significant difference (l.s.d.) test at $P = 0.05$ was used to separate treatment means. In experiments with bananas, colour meter, colour score, firmness meter and firmness score data were compared on a temporal basis as the time to reach a hue angle of ≤90°, a score of 6, 'full yellow'; a displacement of ≥0.5 mm, and a score of 4, 'eating soft', respectively. Flower abscission data from *G*. 'Sylvia' and waxflower experiments were analysed as the percentage change in abscission recorded immediately following ethylene treatment. A logistic transformation of percentage data was performed prior to statistical analysis (McCullagh and Nelder 1989).

Results

1-MCP treatment temperature for banana

Treatment of fruit with 15 L 1-MCP/L at 2.5, 5, 7.5, 10, 12.5, 15 or 20°C followed by subsequent exposure to either 0 or 100 L ethylene/L at 20°C were equally effective in significantly (P<0.05) extending shelf life (Fig. 1) and delaying skin degreening and fruit softening (data not presented) compared with fruit not treated with 1-MCP. Similar protection against endogenous

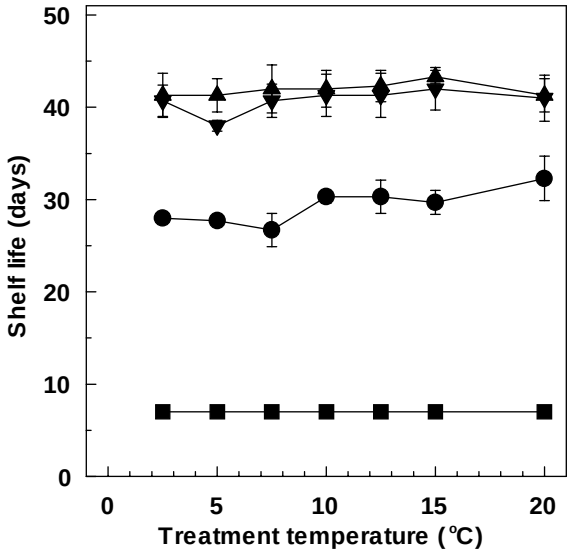

Figure 1. Shelf life of banana fruit treated with 0 L 1-MCP/L and 0 L ethylene/L (●), 0 L 1-MCP/L and 100 L ethylene/L (■), 15 L 1-MCP/L and 0 L ethylene/L (▲) or 15 L 1-MCP/L and 100 L ethylene/L (▼). 1-MCP treatment was conducted on day 0 for 12 h at 2.5, 5, 7.5, 10, 12.5, 15 and 20°C. Ethylene treatment was conducted on day 1 for 24 h at 20°C. Vertical bars show the standard errors of means. Where no vertical bars appear, the standard errors were smaller than the size of the symbols; l.s.d. (P = 0.05) = 7.3.

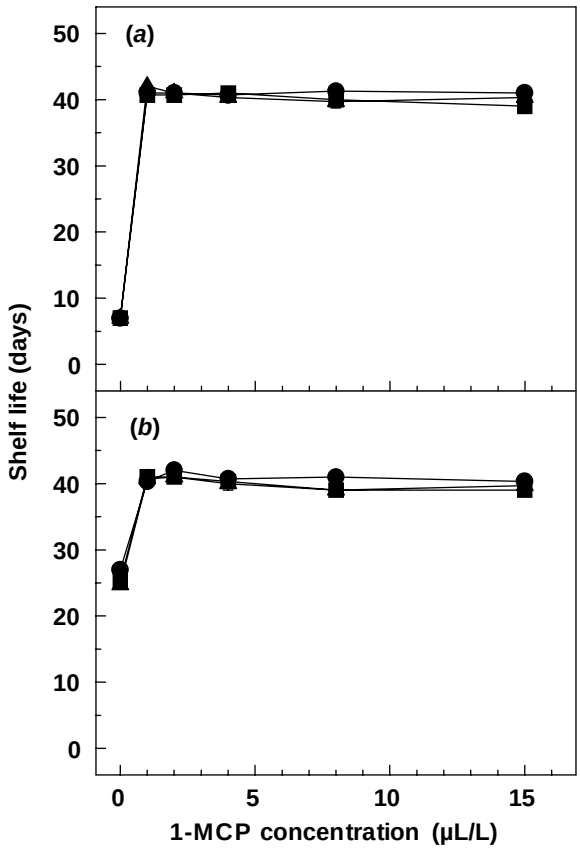

Figure 2. Shelf life of banana fruit treated on day 0 with 0, 1, 2, 4, 8 or 15 L 1-MCP/L for 12 h at 2.5 (●), 15 (■) or 20°C (▲). (*a*) Half of the fruit from each of these treatments were then exposed on day 1 to 100 L ethylene/L for 24 h at 20°C. (*b*) The other half of the fruit were not exposed to exogenous ethylene. Standard errors of means were smaller than the size of symbols; l.s.d. (P = 0.05) = 6.6.

(–ethylene treatment) or exogenous (+ethylene treatment) ethylene was afforded for fruit treated with 1, 2, 4, 8 or 15 L 1-MCP/L . Thus, treatment with 1-MCP at 2.5, 15 or 20°C did not differentially affect efficacy at any of these 5 1-MCP concentrations (Fig. 2). The minimum 1-MCP treatment concentration necessary across all 3 temperatures of 2.5, 15 or 20°C to afford fruit with full protection against ethylene-induced ripening was generally 100 nL/L (Fig. 3). In the case of 2 treatments, viz. 1-MCP at 2.5°C not subsequently exposed to ethylene and 1-MCP at 20°C followed by exposure to ethylene, treatment with 1000 nL 1-MCP/L was significantly (P<0.05) more effective than 100 nL 1-MCP/L in extending the shelf life of fruit. Treatment of fruit with 10 or 100 nL 1-MCP/L for 12 h at 2.5°C afforded only partial protection against subsequent ethylene treatment. Ripening of fruit treated with 10 nL 1-MCP/L for 12 h at 2.5°C was delayed further when the treatment temperature was increased to 15 or 20°C.

Timing of ethylene treatment for banana

Fruit treated with 15 L 1-MCP/L on day 0 did not respond to ethylene treatment until day 20, as evidenced by a significant (P<0.05) reduction in shelf life compared with 1-MCP-treated fruit exposed to ethylene on days 1, 5 or 10 (Table 1). Ripening of 1-MCP-treated fruit was hastened following ethylene treatment on days 20 and 30, as demonstrated by reduced shelf lives following ethylene (SLFE) treatment (Table 1) and rapid skin colouration and fruit softening (data not presented). Treatment of fruit with 10 nL 1-MCP/L at 2°C did not prevent rapid ripening induced by subsequent ethylene treatment, as evidenced by reduced shelf lives and similar SLFE for fruit treated with ethylene at different times during the experiment (Table 2). 1-MCP treatment at 20°C afforded protection to fruit against ethylene treatment for up to 13 days after 1-MCP treatment (Table 2). Thereafter, the SLFE of fruit were not significantly different (P>0.05) from fruit treated only with ethylene. The SLFE for fruit treated with 1-MCP on day 0 at 2 or 20°C, and subsequently exposed to ethylene on day 31, was reduced compared with other

Table 1. Shelf life (SL) and shelf life following ethylene (SLFE) treatment of banana fruit treated on day 0 with – or + 1-MCP for 12 h at 20°C, following which individual subsamples were exposed sequentially to ethylene for 12 h at 20°C on five different days

Values in parentheses show shelf life relative to the longest recorded (%)
Data followed by the same letters are not significantly different (l.s.d. = 2.6 for shelf life data and 2.4 for shelf life following ethylene data) at $P = 0.05$ ($n = 10$)

Day of exposure to ethylene	SL (days) 0 L 1-MCP/L	SL (days) 15 L 1-MCP/L	SLFE (days) 0 L 1-MCP/L	SLFE (days) 15 L 1-MCP/L
		Control treatments		
0	31.8[A] (74)	42.7c (100)	—	—
1	7.0[A] (16)	—	6.0a	—
		Sequential ethylene treatments		
1	—	41.7c (98)	—	40.7f
5	—	41.0bc (96)	—	36.0e
10	—	40.2bc (94)	—	30.2d
20	—	35.1a (82)	—	15.1c
30	—	38.6b (90)	—	8.6b

[A]Control fruit were excluded from the statistical analysis of SL.

fruit because natural ripening had already commenced. Fruit treated with 10 nL 1-MCP/L at 20°C were afforded only partial protection against ethylene, as evidenced by reduced shelf life compared with fruit not treated with 1-MCP or ethylene (Table 2).

1-MCP treatment for Grevillea *'Sylvia'*

Grevillea 'Sylvia' inflorescences treated with 10 nL 1-MCP/L at 2°C were not protected from subsequent exposure to ethylene, as evidenced by rapid flower abscission (data not presented) and rapid loss of fresh

Table 2. Shelf life (SL) and shelf life following ethylene (SLFE) treatment (days) of banana fruit treated on day 0 with – or + 1-MCP for 12 h at 2 or 20°C, following which individual subsamples were exposed sequentially to ethylene for 24 h at 20°C on different days

Values in parentheses show SL relative to the longest recorded for fruit treated at 2°C (%) or 20°C (%)
Data followed by the same letters are not significantly different (l.s.d. = 1.7 for SL data and 1.4 for SLFE data) at $P = 0.05$ ($n = 5$)

Day of exposure to ethylene	1-MCP treatment at 2°C 0 nL/L SL	0 nL/L SLFE	10 nL/L SL	10 nL/L SLFE	1-MCP treatment at 20°C 0 nL/L SL	0 nL/L SLFE	10 nL/L SL	10 nL/L SLFE
				Control treatments				
0	34.4[A] (96)	—	—	—	31.2[A] (86)	—	—	—
1	8.0[A] (22)	7.0y	—	—	8.0[A] (22)	7.0y	—	—
				Sequential ethylene treatments				
1	—	—	8.6a (24)	7.6y	—	—	20.0e (55)	19.0t
4	—	—	12.0b (33)	8.0yx	—	—	20.0e (55)	16.0u
7	—	—	14.0c (39)	7.0y	—	—	21.6ef (60)	14.6u
10	—	—	17.0d (47)	7.0y	—	-	21.2ef (59)	11.2w
13	—	—	22.0f (61)	9.0x	—	—	23.2fg (64)	10.2xw
16	—	—	24.2g (67)	8.2yx	—	—	24.0g (66)	8.0yx
19	—	—	28.0h (78)	9.0x	—	—	27.0h (75)	8.0yx
22	—	—	30.0i (83)	8.0yx	—	—	30.0i (83)	8.0yx
25	—	—	33.0j (92)	8.0yx	—	—	32.8j (91)	7.8yx
28	—	—	35.0k (97)	7.0y	—	—	36.2k (100)	8.2yx
31	—	—	36.0k (100)	5.0z	—	—	35.4k (98)	5.8z

[A] Control fruit were excluded from the statistical analysis of SL.

Table 3. Vase life (VL) and vase life following ethylene (VLFE) treatment (days) of *G.* 'Sylvia' inflorescences treated on day 0 with – or + 1-MCP for 12 h at 20°C, following which individual subsamples were exposed sequentially to ethylene for 12 h at 20°C on five different days

Values in parentheses show VL relative to the longest recorded for inflorescences treated at 2°C (%) or 20°C (%)
Data followed by the same letters are not significantly different (l.s.d. = 1.0 for VL data and 0.8 for VLFE data) at $P = 0.05$ ($n = 5$)

Day of exposure to ethylene	1-MCP treatment at 2°C				1-MCP treatment at 20°C			
	0 nL/L		10 nL/L		0 nL/L		10 nL/L	
	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE
			Control treatments					
0	4.0[A] (87)	—	4.6[A] (100)	—	3.6[A] (78)	—	4.6[A] (100)	—
1	2.0[A] (43)	1.0[A]	—	—	2.0[A] (43)	1.0[A]	—	—
			Sequential ethylene treatments					
1	—	—	2.0a (43)	1.0y	—	—	4.6c (100)	3.6w
2	—	—	3.0bc (65)	1.0y	—	—	4.2c (91)	2.2x
3	—	—	3.8c (83)	0.8y	—	—	3.8c (83)	0.8y
4	—	—	4.2c (91)	0.4zy	—	—	4.4c (96)	0.6zy
5	—	—	4.4c (96)	0.0z	—	—	4.6c (100)	0.2zy

[A]Control inflorescences were excluded from the statistical analysis of VL and VLFE.

weight (data not presented), which contributed to reduced vase life (Table 3). In contrast, inflorescences treated with 1-MCP at 20°C were afforded protection against ethylene treatment for 2 days after 1-MCP treatment (Table 3). Thereafter, ethylene-induced flower abscission terminated vase life. However, it was observed that flower abscission from inflorescences treated with 1-MCP at 20°C was not as rapid in response to ethylene treatment. Moreover, abscission was not as complete as in inflorescences treated with 1-MCP at 2°C. Flower wilting, opening and discolouration were not affected by 1-MCP treatment (data not presented). Vase solution usage decreased

Table 4. Vase life (VL) and vase life following ethylene (VLFE) treatment (days) of flowering Geraldton waxflower (*Chamelaucium uncinatum* 'Lollypop') sprigs treated on day 0 with – or + 1-MCP or – or + STS (Ag^+) for 12 h at 20°C, following which individual subsamples were exposed sequentially to ethylene for 12 h at 20°C on nine different days

Values in parentheses show VL relative to the longest recorded for sprigs treated at 2°C (%) or 20°C (%)
Data followed by the same letters are not significantly different (l.s.d. = 1.9 for VL data and 1.4 for VLFE data) at $P = 0.05$ ($n = 5$)

Day of exposure to ethylene	Treatment at 2°C						Treatment at 20°C					
	0 nL 1-MCP/L or 0 mmol Ag^+/L		10 nL 1-MCP/L		0.5 mmol Ag^+/L		0 nL 1-MCP/L or 0 mmol Ag^+/L		10 nL 1-MCP/L		0.5 mmol Ag^+/L	
	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE
					Control treatments							
0	8.6[A] (88)	–	—	—	—	—	6.4[A] (73)	—	—	—	—	—
1	2.0[A] (20)	1.0[A]	—	—	—	—	2.0[A] (23)	1.0[A]	—	—	—	—
					Sequential ethylene treatments							
1	—	—	7.4cd (76)	6.4v	7.4cd (76)	6.4v	—	—	7.2cd (82)	6.2v	3.2ab (36)	2.2yx
2	—	—	3.0ab (31)	1.0zy	6.6bc (67)	4.6w	—	—	7.6cd (86)	5.6wv	2.6a (30)	0.6zy
3	—	—	4.4ab (45)	2.4yx	7.6cd (78)	4.6w	—	—	6.8c (77)	3.8xw	3.8ab (43)	1.0zy
4	—	—	5.0bc (51)	1.0zy	9.0d (92)	5.0wv	—	—	7.8cd (89)	3.8xw	3.8ab (43)	0.2zy
5	—	—	5.6bc (57)	0.8zy	6.0bc (61)	1.4y	—	—	8.0cd (91)	3.2x	5.2bc (59)	1.2zy
6	—	—	5.4bc (55)	0.6zy	7.4cd (76)	1.6yx	—	—	8.8d (100)	2.8x	4.2ab (48)	0.0z
7	—	—	7.2cd (73)	0.8zy	4.8b (49)	0.0z	—	—	5.4bc (61)	0.2zy	3.2ab (36)	0.0z
8	—	—	8.0cd (82)	0.8zy	4.8b (49)	0.0z	—	—	7.6cd (86)	0.2zy	3.6ab (41)	0.0z
9	—	—	9.8d (100)	0.8zy	8.2cd (84)	0.2zy	—	—	7.0cd (80)	0.0z	3.6ab (41)	0.0z

[A]Control sprigs were excluded from the statistical analysis of VL and VLFE.

Table 5. Vase life (VL) and vase life following ethylene (VLFE) treatment (days) of flowering Geraldton waxflower (*Chamelaucium uncinatum* 'Alba') sprigs treated on day 0 with — or + 1-MCP or – or + STS (Ag^+) for 12 h at 20°C, following which individual subsamples were exposed sequentially to ethylene for 12 h at 20°C on 10 different days

Values in parentheses show VL relative to the longest recorded for sprigs treated at 2°C (%) or 20°C (%)
Data followed by the same letters are not significantly different (l.s.d. = 2.6 for VL data and 2.0 for VLFE data) at $P = 0.05$ ($n = 5$)

Day of exposure to ethylene	Treatment at 2°C						Treatment at 20°C					
	0 nL 1-MCP/L or 0 mmol Ag^+/L		10 nL 1-MCP/L		0.5 mmol Ag^+/L		0 nL 1-MCP/L or 0 mmol Ag^+/L		10 nL 1-MCP/L		0.5 mmol Ag^+/L	
	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE
						Control treatments						
0	6.2[A] (62)	—	—	—	—	—	4.4[A] (45)	—	—	—	—	—
1	2.0[A] (20)	1.0[A]	—	—	—	—	2.0[A] (20)	1.0[A]	—	—	—	—
						Sequential ethylene treatments						
1	—	—	8.8bc (88)	7.8w	8.6bc (86)	7.6w	—		8.4bc (86)	7.4w	7.0b (71)	6.0xw
2	—	—	4.4a (44)	2.4y	8.0bc (80)	6.0xw	—		7.2bc (73)	5.2xw	6.6a (67)	4.6x
3	—	—	4.6a (46)	2.4y	10.0c (100)	7.0w	—		6.2a (63)	3.2yx	5.8a (59)	3.2yx
4	—	—	5.4a (54)	1.4zy	8.6bc (86)	4.8x	—		8.0bc (82)	4.0yx	8.0bc (82)	4.0yx
5	—	—	5.6a (56)	0.8zy	9.0bc (90)	4.0yx	—		6.0a (61)	1.0zy	9.6c (98)	4.6x
6	—	—	7.0b (70)	1.0zy	9.8c (98)	3.8yx	—		7.2bc (73)	1.2zy	8.2bc (84)	2.4y
7	—	—	7.8bc (78)	0.8zy	9.2bc (92)	2.2zy	—		8.6bc (88)	1.6zy	7.0b (71)	1.2zy
8	—	—	7.2bc (72)	0.4zy	8.8bc (88)	1.6zy	—		7.4bc (76)	0.4zy	7.2bc (73)	0.4zy
9	—	—	6.6a (66)	0.4zy	10.0c (100)	1.0zy	—		8.4bc (86)	0.2z	7.2bc (73)	0.2z
10	—	—	7.6bc (76)	0.2z	9.6c (96)	0.2z	—		8.2bc (84)	0.6zy	9.8c (100)	0.4zy

[A]Control sprigs were excluded from the statistical analysis of VL and VLFE.

rapidly in association with flower abscission induced by ethylene treatment (data not presented).

1-MCP and STS treatment for waxflower

Treatment of waxflower 'Lollypop', 'Alba' and 'Mid Pink' sprigs with 10 nL 1-MCP /L at 2°C provided some protection against ethylene treatment for 1, 3 and 2 days, respectively (Tables 4–6). Thereafter, flower abscission (data not presented) and loss of fresh weight (data not presented) in response to ethylene were rapid and resulted in reduced vase life. In contrast, virtually no flower abscission was observed throughout the 10-day duration of these experiments from parallel sets of sprigs treated with STS at 2°C and then exposed to ethylene (data not shown). Thus, vase life was effectively extended by STS relative to sprigs treated with 1-MCP at 2°C. Sprigs of 'Lollypop', 'Alba' and 'Mid Pink' treated with 1-MCP at 20°C were largely protected from ethylene for 6, 4 and 3 days, respectively (Tables 4–6, respectively). Thereafter, flower abscission (data not presented) and loss of fresh weight (data not presented) were rapid.

As for parallel sets of sprigs treated with STS at 2°C, those treated with STS at 20°C remained insensitive to ethylene for the duration of these experiments (Tables 4–6). In fact, there was virtually no flower abscission at all (data not presented), except for 'Lollypop' sprigs. Accumulation of Ag^+ by 'Lollypop', 'Alba' and 'Mid Pink' sprigs, based on solution uptake measured during STS pulsing, at 2°C was 0.067 ± 0.009, 0.031 ± 0.005 and 0.054 ± 0.002 mol Ag^+/g FW, respectively. For parallel sets of sprigs pulsed at 20°C, 0.353 ± 0.010, 0.213 ± 0.006 and 0.160 ± 0.005 mol Ag^+/g FW were taken up, respectively.

Discussion

Exposure of banana fruit and grevillea and waxflower flowers to ethylene reduces their postharvest life by inducing ripening (Burg and Burg 1962) and abscission (Joyce *et al*. 1993), respectively. Treatment of plant tissue with 1-MCP inhibits ethylene responses by binding irreversibly to ethylene receptors (Sisler and Serek 1997). Sisler *et al*. (1996*b*) found that treatment of banana fruit with just 0.7 nL 1-MCP/L for 24 h at 24°C effectively delayed ripening compared with control fruit that were treated only with ethylene. However, the relative degrees to which ripening was delayed in comparison with any other 1-MCP concentrations were not presented. Jiang *et al*. (1999*b*) reported that treatment of banana fruit with 50 nL 1-MCP/L for 12 h at 20°C essentially eliminated ethylene-induced ripening. In the present study, complete protection of

Table 6. Vase life (VL) and vase life following ethylene (VLFE) treatment (days) of flowering Geraldton waxflower (*Chamelaucium uncinatum* 'Mid Pink') sprigs treated on day 0 with – or + 1-MCP or – or + STS (Ag^+) for 12 h at 20°C, following which individual subsamples were exposed sequentially to ethylene for 12 h at 20°C on eight different days

Values in parentheses show VL relative to the longest recorded for sprigs treated at 2°C (%) or 20°C (%)
Data followed by the same letters are not significantly different (l.s.d. =1.6 data and 1.3 for VLFE data) at $P = 0.05$ ($n = 5$)

Day of exposure to ethylene	Treatment at 2°C						Treatment at 20°C					
	0 nL 1-MCP/L or 0 mmol Ag^+/L		10 nL 1-MCP/L		0.5 mmol Ag^+/L		0 nL 1-MCP/L or 0 mmol Ag^+/L		10 nL 1-MCP/L		0.5 mmol Ag^+/L	
	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE	VL	VLFE
					Control treatments							
0	5.8[A] (78)	—	—	—	—	—	4.4[A] (67)	—	—	—	—	—
1	2.0[A] (27)	1.0[A]	—	—	—	—	2.0[A] (30)	1.0[A]	—	—	—	—
					Sequential ethylene treatments							
1	—	—	5.4ab (73)	4.4xw	5.8bc (78)	4.8w	—	—	5.6b (85)	4.6xw	4.4ab (67)	3.4x
2	—	—	3.8a (51)	1.8y	6.4bc (86)	4.4xw	—	—	4.8ab (73)	2.8yx	6.4bc (97)	4.4xw
3	—	—	4.0ab (54)	1.0zy	6.8bc (92)	3.8xw	—	—	5.0ab (76)	2.0y	5.8bc (88)	2.8yx
4	—	—	4.6ab (62)	0.6zy	6.6bc (89)	2.6yx	—	—	4.4ab (67)	0.4zy	5.6b (85)	1.6y
5	—	—	5.4ab (73)	0.4zy	5.0ab (68)	0.4zy	—	—	4.4ab (67)	0.0z	5.0ab (76)	0.4zy
6	—	—	4.8ab (65)	0.0z	4.6ab (62)	0.0z	—	—	5.4ab (82)	0.2z	4.6ab (70)	0.0z
7	—	—	5.0ab (68)	0.0z	6.8bc (92)	0.8zy	—	—	6.6bc (100)	0.0z	4.4ab (67)	0.0z
8	—	—	7.4c (100)	0.2z	5.4ab (73)	0.0z	—	—	6.4bc (97)	0.0z	6.2bc (94)	0.0z

[A]Control sprigs were excluded from the statistical analysis of VL and VLFE.

banana fruit against ethylene was achieved when 1-MCP was applied at 100 nL/L for 12 h at 20°C. Banana fruit ripening has also been reported to be delayed following treatment with the high 1-MCP concentrations of 45–450 L 1-MCP/L for 1–6 h at 20°C (Golding *et al.* 1998). These concentrations were apparently above the 1-MCP-binding saturation point for banana fruit because 1-MCP diffusion out from fruit was measured for several days following treatment (Golding *et al.* 1998).

The present study also showed that treatment of *G.* 'Sylvia' inflorescences and waxflower flowers with 10 nL 1-MCP/L for 12 h at 20°C on day 0 was highly effective in preventing flower abscission induced by exposure to ethylene on day 1. This result is in general agreement with the results of Serek *et al.* (1995*a*), where treatment of carnation and *Penstemon* flowers with 10–20 nL 1-MCP/L for 6 h at 20°C prevented ethylene-induced senescence and abscission.

1-MCP treatment efficacy was reported to be poor when it was applied to cut *Penstemon* and *Kalanchoe* flowers at the low temperature of 2°C and at low concentrations of 5–20 nL/L (Serek *et al.* 1995*a*; Reid *et al.* 1996). This assertion was supported in the present study. Treatment of banana fruit and *G.* 'Sylvia' inflorescences with 10 nL 1-MCP/L for 12 h at 2°C did not prevent ethylene-induced ripening (Table 2) or flower abscission (data not presented), respectively. Treatment of banana fruit with 10 nL 1-MCP/L for 12 h at 2.5°C provided only partial protection against ethylene compared with fruit treated at 15 or 20°C (Fig. 3). Increasing the concentration of 1-MCP applied for 12 h at 2.5, 15 or 20°C to 100 nL/L further delayed banana fruit ripening compared with fruit treated with 10 nL 1-MCP/L. This effect was more pronounced at 2.5°C. This positive high-concentration effect is in agreement with the findings of Reid *et al.* (1996) and suggests that binding of 1-MCP to ethylene receptors was incomplete when applied at low temperature and at the low concentration. Nevertheless, bananas and cut flowers should be protected against ethylene if treated with low 1-MCP concentrations at 20°C before cooling.

1-MCP binding is apparently incomplete at low temperature. Poor binding at low temperature could be due to conformational changes in a membrane-located protein that is the ethylene receptor. Conformational changes to membranes are believed to occur at low temperature, notably in chilling-sensitive plant species (Lyons 1973). Treatment with high 1-MCP concentrations at low temperature may result in a relatively greater accumulation and/or non-specific binding of 1-MCP molecules in plant tissues. When such tissue is transferred

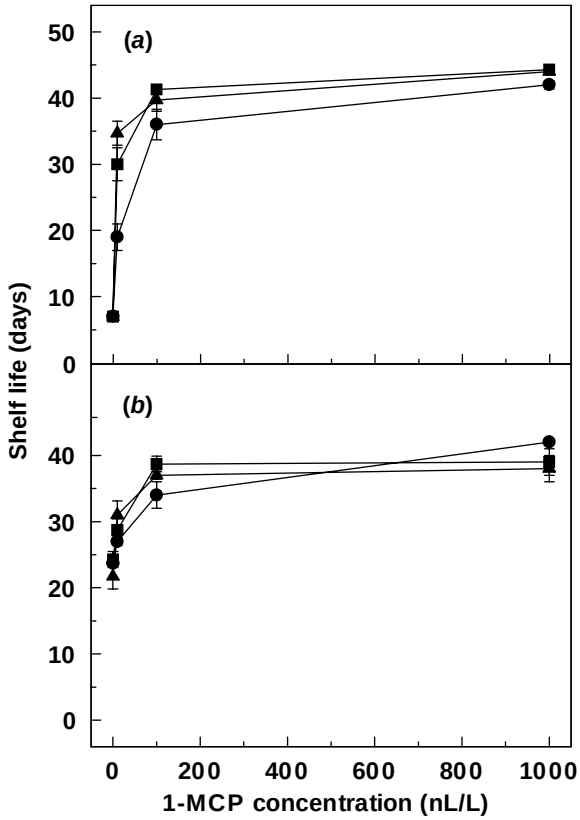

Figure 3. Shelf life of banana fruit treated on day 0 with 0, 10, 100 or 1000 nL 1-MCP/L for 12 h at 2.5 (●), 15 (■) or 20°C (▲). (*a*) Half of the fruit from each of these treatments were then exposed on day 1 to 100 μL ethylene/L for 24 h at 20°C. (*b*) The other half of the fruit were not exposed to exogenous ethylene. Vertical bars show the standard errors of means. Where no vertical bars appear, the standard errors were smaller than the size of the symbols; l.s.d. (P = 0.05) = 4.0.

to higher temperature, the residual 1-MCP molecules could bind to specific ethylene receptors.

The duration of protection afforded by treatment with 1-MCP varied depending on the treatment temperature (2 *v*. 20°C) and the plant tissue type (banana fruit *v*. grevillea or waxflower flowers). Banana fruit treated with 10 nL 1-MCP/L at 20°C regained sensitivity to ethylene treatment 16 days after treatment and then ripened rapidly (Table 2). This result is consistent with the findings of Sisler *et al*. (1996*b*) and Sisler and Serek (1997). Regaining competence of 1-MCP-treated plant tissue to respond to ethylene is thought to be due to the synthesis of new ethylene receptors (Sisler and Serek 1997). Treatment of fruit with a higher 1-MCP concentration of 15 L/L did not alter the time at which fruit began to regain sensitivity to ethylene; viz. 10–20 days. Due to fixed time intervals between successive ethylene treatments, it was not determined precisely when banana fruit regained sensitivity to ethylene. However, fruit did not fully regain competence to ripen rapidly in response to ethylene until day 30, which was considerably later than for fruit treated with 10 nL 1-MCP/L (Table 1). This difference suggests that 10 nL 1-MCP/L did not block ethylene receptors to the same extent as treatment with 15 L 1-MCP/L. It is possible that a threshold number of receptors required to elicit a response was reached more rapidly in fruit treated with 10 nL 1-MCP/L. Jiang *et al*. (1999*b*) found that banana fruit treated with 1000 nL 1-MCP/L for 12 h at 20°C did not fully regain the capacity to respond to ethylene for 20–25 days after 1-MCP treatment. From a commercial perspective, 1-MCP treatments may be useful in preventing premature ripening during extended periods of banana handling and transport. At the completion of handling and transport, fruit could be ripened with ethylene.

Treatment of *G*. 'Sylvia' inflorescences with 10 nL 1-MCP/L at 20°C afforded protection against ethylene for only 2 days after 1-MCP treatment (Table 3). This observation suggests that the synthesis of new ethylene receptors in the abscission zones of *G*. 'Sylvia' inflorescences is rapid compared with banana fruit (cf. Tables 1–3). Alternatively, it is possible, although not likely (Sisler *et al*. 1996*a*), that 1-MCP did not bind permanently to ethylene receptors in *G*. 'Sylvia' inflorescences.

Waxflower sprigs treated with 10 nL 1-MCP/L for 12 h at 2°C were afforded only short-term protection of about 2 days against ethylene (Tables 4–6). Treatment of sprigs with 10 nL 1-MCP/L for 12 h at 20°C provided comparatively longer-term protection of about 4 days against ethylene (Tables 4, 5 and 6). As suggested for *G*. 'Sylvia', these data indicate that receptor synthesis in abscission zones of waxflower flowers is rapid. 1-MCP evidently blocked ethylene receptors during treatment at 2°C, since the waxflower sprigs were fully protected against ethylene applied immediately after the 1-MCP treatment.

In contrast to 1-MCP treatment, pulsing waxflower sprigs with 0.5 mmol Ag^+/L as STS at 2 or 20°C provided complete protection against ethylene for the about 10-day durations of experiments (Tables 4–6). Minor flower abscission from 'Lollypop' sprigs pulsed with STS at 20°C was associated with this cultivar accumulating the most Ag^+ (0.353 mol/g FW) during STS pulsing. 'Lollypop' may have suffered STS phytotoxicity. Uptake of Ag^+ by waxflower above

0.6 mol/g sprig FW was reported by Joyce (1988) to be toxic and to cause flower abscission. The critical level of Ag^+ accumulation may vary with genotype. Cameron and Reid (1981) suggested that effective STS treatment concentrations are usually close to their phytotoxic level. Nevertheless, earlier workers have shown that effective Ag^+ treatments provide long-term protection against ethylene. For example, new growth of pea seedlings following spray treatment with silver nitrate showed no sensitivity to ethylene, indicating that Ag^+ acted systemically (Beyer 1976). Additionally, STS treatment prevented ethylene-induced flower abscission from *Zygocactus* for at least 4 weeks (Cameron and Reid 1981). Recently, Newman *et al*. (1998) reported that STS treatment was more effective than 1-MCP treatment in affording developing buds on cut *Gypsophila paniculata* inflorescences with long-term protection against ethylene. They proposed that the STS complex remained available in the inflorescence and capable of binding to receptors formed as the buds opened into flowers. Likewise, in the present study, it is probable that Ag^+ was retained as a pool in or around waxflower flower abscission zones and remained available to bind to new ethylene receptors as they formed.

STS treatment was more effective in providing waxflower with long-term protection against ethylene than 1-MCP treatment. Further applied research is needed to devise optimum 1-MCP treatment protocols that provide cut flowers with long-term protection against ethylene. Retreating with 1-MCP or developing sustained 1-MCP release devices may afford such protection. Nonetheless, effective short-term protection for brief but critical periods of unrefrigerated export by airplane can be achieved with a single treatment.

Acknowledgments

The authors thank Mrs N. Harris, Mr E. Bunker and Mr K. Young for providing banana fruit and grevillea and waxflower cut flowers, respectively. Advice on statistics from Mr A. Lisle and financial support from the Rural Industries Research and Development Corporation and The University of Queensland are also gratefully acknowledged.

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Received 29 August 1999, accepted 13 January 2000