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1-MCP blocks ethylene-induced petal abscission of *Pelargonium peltatum* but the effect is transient

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Abstract

Continual exposure to 1.5 μl l^{-1} ethylene caused 100% petal abscission within 2 h from detached flowers of *Pelargonium peltatum* (L.) 'Pink Blizzard' (ivy geranium) harvested just after the stigmatic lobes had separated. When flowering plants were first pretreated for 2 h with 1 μl l^{-1} 1-MCP, ethylene-induced petal abscission was completely inhibited. However, the effect was transient, since percent abscission increased with time after 1-MCP treatment. Based on percent abscission from detached flowers after a 2-h ethylene exposure, the half-life of 1-MCP activity was about 2, 3 and 6 days after 1-MCP treatment at 25, 20.7, and 12°C, respectively, and there was no evidence for a residual effect after 4 or 5 days at 25 and 20.7°C, respectively. A second application of 1-MCP renewed the inhibitory effect. Following 1-MCP treatment, the force required to separate petals from the flower declined linearly with time. The time until complete loss of the inhibitory effect was strongly temperature dependent, e.g. ≈ 1 day at 25°C versus 3–4 days at 12°C. The usefulness of 1-MCP as a commercial treatment to prevent petal abscission from Pelargoniums will depend on shipping and storage temperature and application frequency.

Keywords: Ethylene; 1-methylcyclopropene; 1-MCP, postharvest; Petal abscission; Flower senescence; Ivy geranium

1. Introduction

Continuous exposure to ≤ 1 μl l^{-1} exogenous ethylene has been reported to cause petal abscission within 1 h from flowers of *Pelargonium xhortorum*, zonal geranium, (Evensen et al., 1991) and *P. domesticum*, Martha Washington pelargoniums, (Deneke et al., 1990; Evensen, 1991; Evensen and Olson, 1992), one of the most rapid responses to ethylene known. During commercial shipping and handling of flowering *Pelargonium* species and many other members of the Geraniaceae (Van Doorn and Stead, 1997), ethylene-induced petal abscission can be a significant problem. Abscised flowers reduce visual impact of the potted plant and can increase the incidence of botrytis and other saprophytic pathogens. Pelargonium flower petals eventually abscise even without ex-

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posure to exogenous ethylene, especially when the flowers are pollinated (Phillippi, 1961; Clark et al., 1997), but this occurs over a longer period depending on the species and cultivar.

Silver thiosufate (STS) applied as a spray is very effective against petal shatter of seed geraniums (Cameron and Reid, 1982) and has become widely used commercially. However, silver is a heavy metal pollutant, and there has been rising concerns about ground water pollution. In addition, STS has recently been classified as a plant growth regulator by the United States Environmental Protection Agency (EPA) but has not yet been registered for use. Thus, it cannot be legally marketed and used in the USA.

The compound 1-methylcyclopropene (1-MCP) was originally patented by Sisler and Blankenship (1996) and in several systems has been an effective antagonist of ethylene action (Serek et al., 1995; Sisler et al., 1996; Sisler and Serek, 1997). 1-MCP effectively blocked ethylene action in a range of plant systems, including abscission of phlox flowers (Porat et al., 1995), abscission of buds and flowers from potted flowering tuberous begonia and kalanchoe plants (Serek et al., 1994), senescence of *Cybidium* orchid flowers (Heyes and Johnston, 1998), and ripening of bananas (Golding et al., 1999) and apples (Fan and Mattheis, 1999).

Since it is well established that ethylene promotes pelargonium and geranium petal abscission and that 1-MCP antagonizes ethylene action, we proposed that 1-MCP should be an effective, environmentally friendly alternative to STS for use on different species of pelargonium. As expected, we found in preliminary experiments that an overnight exposure to 1-MCP completely inhibited ethylene-induced petal abscission of *P. xhortorum* and *P. peltatum* flowers. However, in a subsequent greenhouse trial, we observed significant petal abscission on controls and 1-MCP-treated plants after 14 days Thus, without treatment with exogenous ethylene, there was no apparent beneficial effect of 1-MCP. It is interesting to note that while 1-MCP increased the display life of ethylene-treated potted flowering begonias, roses, and kalanchoes, it had no influence on the overall display life of any of these species in the absence of exogenous ethylene (Serek et al., 1994, Table 1). Thus, it appeared that the 1-MCP effect could be transitory in some systems. To our knowledge, the nature of the transitory changes in sensitivity has not been characterized.

The primary purpose of this research was to study the transitory nature of the 1-MCP effect on ethylene-induced petal abscission of *P. peltatum*. In particular, we studied the apparent decline in effectiveness in prevention of ethylene-induced petal abscission and associated changes in pull force as a function of time and temperature after treatment. We also described some of the phenotypical changes that accompany flower development and ethylene sensitivity in *P. peltatum*.

2. Materials and methods

2.1. Plant material

Flowering plants of *P. peltatum* 'Pink Blizzard' plants were obtained from a commercial nursery (Monterey Bay Nursery, Watsonville, CA) in October 1999. Plants were transferred to Davis, transplanted into 4 l containers with UC mix (containing peat, sand and composted redwood) and grown in glass greenhouses at 23/17°C day/night temperature. Supplemental lighting with an irradiance of about 200 μmol s^{-1} m^{-2} was provided from 06:00 to 22:00 h each day. Plants were watered and fertilized (0.1 kg g^{-1} N from a modified Hoagland solution) as necessary. Plants flowered freely under these conditions with no other floral initiation treatments. Unless otherwise noted, all inflorescence with open flowers were removed from each plant about 2 weeks before the beginning of each experiment. Thus, only relatively young inflorescences were present when experiments were started.

2.2. Flower development in P. peltatum

Development of individual flowers was observed daily in the greenhouse (average daily temperature (ADT) = 20–21°C) to determine specific stages of floral development and rates of change.

Table 1
Stages of development for *Pelargonium peltalum* 'Pink Blizzard' defined for the current study[a]

Stage of flower development	Petals	Anthers	Stigma	Duration (days)
−1	Not fully reflexed	Visible but not fully extended	Not visible	1
0	Fully open, vibrant colors	Anthesis	Not visible	2.5
1	Fully open, vibrant colors	Starting to curl down, some pollen sac abscission	Just visible- stigmata lobes just separating	1
2	Fully open, colors fading	Curling down, most pollen sacs abscised	Stigmatic lobes fully separated	1–2
3	Lower angle of attachment, reflexing, colors fading	Pollen sacs abscised	Stigmatic lobes curling down	8–12

[a] The approximate duration of each stage was measured in a ≈ 21°C (average daily temperature) greenhouse. Photos of stages 0–3 are given in Fig. 1.

Five stages were defined (Table 1) based on visual clues that could be easily identified during harvest. Stages 0–3 are shown in Fig. 1. Stage-1 occurred essentially one day before stage 0 and was identified by the lack of fully reflexed petals (Table 1).

2.3. Application of 1-MCP

1-MCP (as EthylBloc) was obtained from Biotechnologies for Horticulture, Burr Ridge, IL. Plants were sealed in $75 \times 31 \times 46$ cm (≈ 107–l volume) glass aquariums that served as treatment chambers (four plants per chamber). Fifty mg of EthylBloc powder (formulated as a gas embedded in a cyclodextran polymer) was weighed and placed in a test tube taped to the inside wall of the chamber. Since a significant percentage of 1-MCP is released immediately after addition of liquid, the chamber lid was first sealed, and then ≈ 1 ml hot water was injected into the test tube (just enough to cover the powder) by using a hypodermic needle through a septum in the lid. We have found that hot water is as effective for releasing the 1-MCP as the mixing solution supplied by the manufacturer (data not shown). Within 10 min, there was ≈ 1 μl l^{-1} 1-MCP in the treatment chamber. In all experiments, 1-MCP treatment was conducted at 22°C. Plants were removed from the chambers, and thus 1-MCP exposure, after 2 h. In all cases, time 'zero' was defined as the moment when the plants were removed from the treatment chambers.

2.4. Ethylene sensitivity and stage of flower development

Twelve plants were treated with 1-MCP as described above. Immediately after 1-MCP treatment, 16 individual flowers were harvested at five stages of development as defined in Table 1. Flowers of each stage were also harvested from plants that had not been treated with 1-MCP. Flowers were exposed to 1.5 μl l^{-1} ethylene and petal abscission was measured after 1, 2 and 3 h of ethylene exposure, as described below.

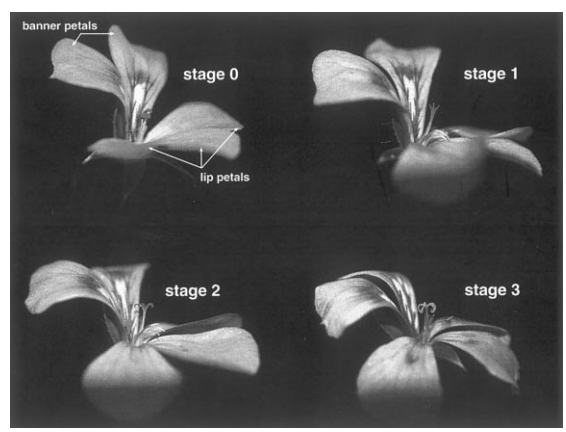

Fig. 1. Four stages of development during flower development in *Pelargonium peltatum* 'Pink Blizzard' as defined in the current study. Descriptions of each stage are given in Table 1. Note the abscission of the pollen sacs and the appearance of the stigmatic lobes during stage 1. During stage 2, the stigmatic lobes are clearly separated.

2.5. 1-MCP effectiveness after time and temperature treatments

In the first experiment, 12 plants were treated with 1-MCP as described above and returned to the greenhouse. At various intervals after 1-MCP treatment, flowers were harvested at stage 2, and ethylene-induced petal abscission and separation force was determined. In the second experiment, 36 plants were treated as described above. Twelve plants were returned to the greenhouse, while two other groups of 12 were put in controlled environment chambers set at 12 or 25°C, respectively. About 16 h photoperiods were provided in both growth chambers at ≈ 180 μmol s^{-1} m^{-2}. Temperature in the greenhouse and in each chamber was measured every 2 min by using Hobo XT temperature loggers (Pocasset, MA). The ADT was calculated from the combined data and is reported for each experiment. For each experiment, flowers were harvested at various intervals after 1-MCP treatment, and ethylene-induced petal abscission and separation force was determined.

2.6. Multiple applications of 1-MCP

Twenty-four plants were treated with 1-MCP as described above and returned to the greenhouse. At various intervals after 1-MCP treatment, flowers were harvested at stage 2, and ethylene-induced petal abscission was determined. After 70 h, 12 plants were re-treated with 1-MCP, and returned to the greenhouse. At various intervals after the second 1-MCP treatment, flowers were harvested at stage 2, and ethylene-induced petal abscission was determined.

2.7. Measurement of ethylene-induced petal abscission and separation force

As a general test of ethylene-induced petal abscission, individual flowers were harvested at stage 2 and placed into 0.7 ml microfuge tubes containing water that served as miniature vases. Flowers (16 per microfuge rack) were placed in aquarium chambers (35.9-l volume). Just after sealing, 0.05 ml pure ethylene was injected into the headspace to rapidly establish $\approx 1.5 \pm 0.5$ μl l^{-1}. A constant flow of a gas mixture containing 1.5 ± 0.5 μl l^{-1} ethylene in air was then established at a flow rate of ≈ 6 l min^{-1}. A 3-ml gas sample was taken periodically and analyzed using Carle AGC 111 gas chromatograph fitted with an Hnu PI-51 photo-ionization detector to ensure the correct ethylene level.

After 2 h, unless otherwise stated, flowers were removed from ethylene exposure and petal abscission and separation force were determined immediately. Since, in some cases, petals remained attached very loosely to the flower, abscission was counted when a petal abscised readily when it was lightly pulled (< 3 cN separation force), and the separation force was recorded as zero. If the petal did not abscise readily, the specific separation force was determined by using a force transducer (Interface, Scotsdale, AZ) using an alligator clip to each individual petal. In separate experiments, the separation force measured by the force transducer was compared with the force required to cause abscission by using known weights. Generally, the values were similar (data not shown). Due to the variability in measurements, the lower limit of detection of the force transducer was ≈ 3 cN. All the remaining petals were measured on each of the 16 flowers per treatment, and the data was categorized by petal type, since the two upright 'banner' petals (Fig. 1) required significantly more separation force than the three lower 'lip' petals, as was noted for *P. xhortorum* (Evensen et al., 1991). In a separate study, the separation force of lip and banner petals was determined at each stage of maturity for 16 flowers.

2.8. Statistical analysis

Statistical analyses were performed by using SAS procedures (SAS Institute, 1988). Abscission percentage versus time was fit to the Gompertz equation of the form

$$\% \text{ abscission} = a \exp(-b \exp(-ct))$$

where a, b and c are constants and t is time (h). The change in separation force with time was fit to linear regression analysis by using SigmaPlot 2000.

3. Results

3.1. Ethylene sensitivity and stage of flower development

Sensitivity of *P. peltatum* 'Pink Blizzard' petals to ethylene-induced abscission was strongly influenced by stage of flower development (Fig. 2). Flowers harvested 1 day prior to full opening (stage 1) were almost insensitive to a 3-h exposure to 1.5 μl l^{-1} ethylene (Fig. 2). Even overnight ethylene exposure did not consistently cause petal abscission (data not shown). Ethylene sensitivity increased as flowers first opened (stage 0), though complete abscission of petals was not observed within the 3-h treatment period (Fig. 2). Only after several hours of constant exposure to 1.5 μl l^{-1} ethylene did all petals from flowers at stage 0 abscise (data not shown). Petal abscission after a 1 h exposure increased from 0% at stage 1 to over 70% at stage 3. Flowers at stages 1, 2 and 3 were extremely ethylene sensitive, since petals completely abscised within 2 h of ethylene exposure. A similar level of ethylene sensitivity and an increase in ethylene sensitivity with flower age was observed in *P. domesticum* (Deneke et al., 1990; Evensen, 1991; Evensen and Olson, 1992) and *P. xhortorum* (Evensen et al., 1991).

In the greenhouse (ADT ≈ 21°C) petal abscission from untreated flowers typically occurred 12–18 day after they first opened (stage 0; Table 1). There was little evidence of pollination, since < 1% of flowers developed fruit. Pollination can induce endogenous ethylene production and has been linked to natural petal abscission in other *Pelargonium* species (Phillippi, 1961; Deneke et al., 1990; Clark et al., 1997).

3.2. Inhibition of ethylene $_2H_4$-induced petal abscission by 1-MCP

Ethylene-induced petal abscission was completely inhibited by a 1 μl l^{-1} 1-MCP exposure, when flowers were challenged with ethylene immediately after the 1-MCP treatment, except for a few petals, harvested at stage 3, that abscised largely before the ethylene treatments had begun (Fig. 2). Even a 3 h exposure to 100 μl l^{-1} ethylene did not induce petal abscission from stage 2 flowers when ethylene was applied immediately after the 1-MCP treatment (data not shown). Thus, 1-MCP was an effective inhibitor of ethylene-induced petal abscission in *P. peltatum*.

3.3. Separation force and stage of development

There was actually relatively little change in separation force with flower age between stage-1 and 2 (Fig. 3) and there appeared to be no correlation between initial separation force and ethylene sensitivity (compare with Fig. 2). The two upright 'banner' petals (Fig. 1) initially required about four–five times more separation

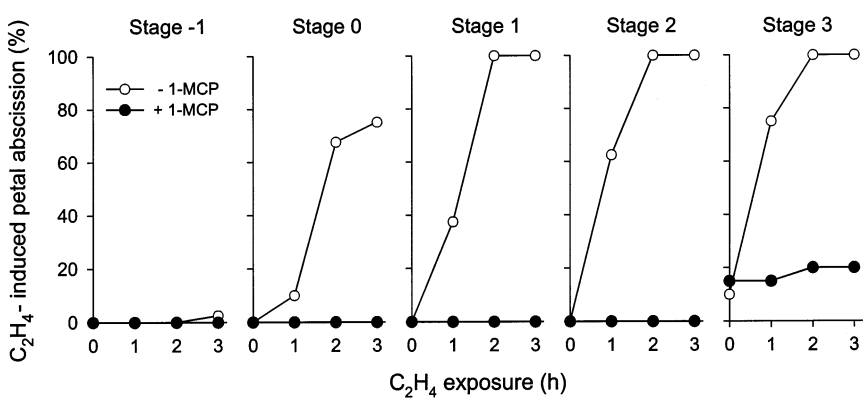

Fig. 2. Petal abscission percentage as a function of exposure time to 1.5 μl l^{-1} ethylene and stage of flower development with and without a 2-h 1 μl l^{-1} 1-MCP pretreatment.

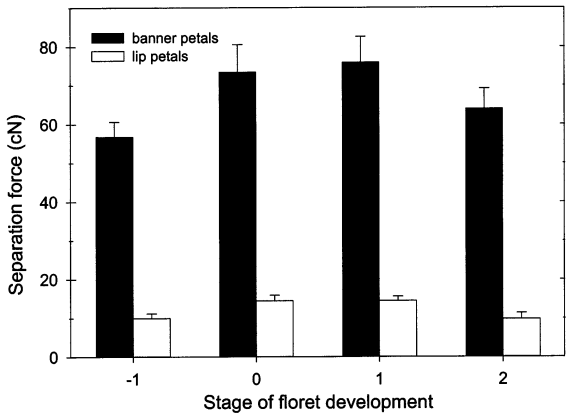

Fig. 3. Petal separation force as a function of petal type and stage of flower development. Separation force was measured as grams required to cause petal detachment.

force than the three lower 'lip' petals, independent of stage of development (Fig. 3). Evensen et al. (1991) monitored separation force for flowers of *P. xhortorum* following exposure to ethylene and noted a similar difference in separation force between the upright and lower petals. They also observed that before ethylene exposure, there was little difference in separation force of flowers harvested at developmental stages comparable to those we define as stage 0 and 2 (Evensen et al., 1991).

3.4. 1-MCP effectiveness after time and temperature treatments

Although 1-MCP treatment consistently prevented ethylene-induced petal abscission, the effect was transient because abscission percentage increased and separation force decreased with time after 1-MCP treatment at all temperatures (Fig. 4). As judged by abscission percentage, stage 2 flowers harvested 40 h after 1-MCP treatment from plants grown at 20.7°C were almost completely ethylene insensitive, while stage 2 flowers harvested 65 h after 1-MCP treatment were completely ethylene sensitive (Fig. 4C). There was essentially no difference between abscission percentages for banner and lip petals, even though there was initially a substantial difference in separation force (Fig. 4A, C and E). Separation force was somewhat variable even within a treatment, but generally declined in what appears to be a linear pattern starting after the end of the 1-MCP treatment at all temperatures (Figs. 4 and 5).

Based on percent abscission after a 2 h ethylene exposure, the half-life of 1-MCP activity was about 2, 3, and 6 days after 1-MCP treatment at 25, 20.7 and 12°C, respectively (Fig. 4). There was no evidence for a residual effect after 4 or 5 day at 25 or 20.7°C, respectively.

When treated plants were grown at 12°C, ethylene-induced petal abscission from harvested flowers was variable and never completely returned to 100%, even 10 days after 1-MCP treatment. However, this pattern of response may not be completely attributable to 1-MCP, since reduced production temperatures alone significantly reduced flower development rate of *P. xhortorum* (Armitage et al., 1981) and ethylene-induced petal abscission from *P. domesticum* flowers (Evensen and Olson, 1992).

A second application of 1-MCP completely prevented abscission from stage 2 flowers and reestablished the beneficial effect with a subsequent pattern similar to that observed after the first 1-MCP application (Fig. 5). The half-life of 1-MCP effectiveness was about 50 h for the first and second application of 1-MCP. Abscission percentages of banner and lip petals were very similar.

4. Discussion

It has been proposed that 1-MCP covalently binds to the ethylene binding site and disables binding permanently (Sisler and Serek, 1997). As judged by the lack of petal abscission in the presence of exogenous ethylene, it appears that all ethylene binding sites were blocked shortly after 1-MCP treatment (Fig. 2). However, the capacity of flowers to respond to ethylene increased with time after 1-MCP treatment. Thus, it follows that new binding sites were likely being synthesized or 1-MCP was not permanently attached. In these experiments, flowers were consistently harvested at stage 2. At 21°C, it took about 4.5 day for flowers to progress from stage-1 to stage 2 (Table

1) and at stage 1, flowers were almost insensitive to ethylene (Fig. 2). The 1-MCP effect was almost completely lost after 4 days at 21°C (Fig. 4). Thus, stage-1 flowers treated with 1-MCP, but exposed to ethylene after they had developed to stage 2, completely regained sensitivity to ethylene. During the same time period, it appeared that separation force consistently decreased (Figs. 4 and 5), which could imply that new binding sites were synthesized at least during stages 0 and 1. This result emphasizes that in *P. peltalum*, abscission is an indirect measure of ethylene binding and occurs only if adequate binding sites are present. The change in separation force was markedly delayed at lower temperatures (Fig. 4), which would be consistent with a reduced rate of protein synthesis.

In apples, 1-MCP blocked ethylene action for up to several months, even at room temperature (Fan and Mattheis, 1999). This infers that in apples, 1-MCP dissociated slowly, if at all, from apple binding protein with time. If 1-MCP binds irreversibly in *P. peltatum*, then the loss in effect with time is better explained by the appearance of new binding protein, but this remains unresolved.

The capacity to respond to ethylene develops just as the flower is opening (stage 0) and maximizes only after the stigmatic surface has appeared (stage 2; Figs. 1 and 3) which is consistent with the role of ethylene as a messenger in pollination-induced senescence. However, ETR1 homolog transcripts were expressed consistently even in flowers in the tight bud stage for *P.*

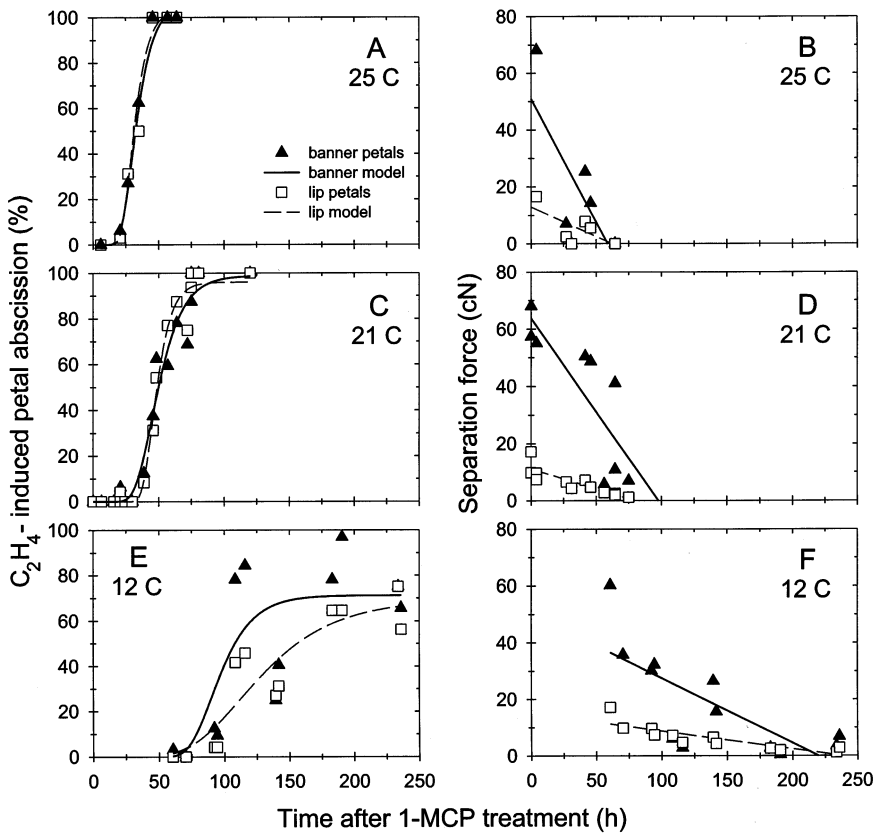

Fig. 4. Change in ethylene-induced petal abscission percentage and separation force of *Pelargonium peltatum* 'Pink Blizzard' as a function of time after 1-MCP treatment. After a 2-h 1 μl l^{-1} 1-MCP treatment, the plants were held at 25, 21 or 12°C. Stage 2 flowers were harvested from plants and exposed to 1.5 μl l^{-1} ethylene for 2 h at various times after 1-MCP treatment before measurement of petal abscission percentage and separation force.

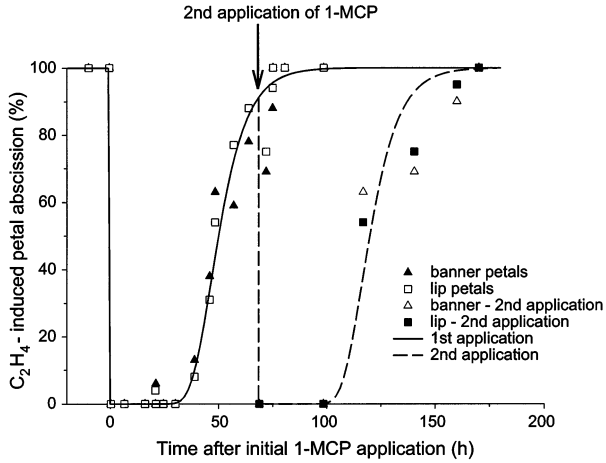

Fig. 5. Ethylene-induced petal abscission percentage and separation force of *Pelargonium peltatum* 'Pink Blizzard' following two treatments with 1-MCP at time zero and 70 h after the first application. Except during 1-MCP treatment, plants were held at ≈ 21°C (average daily temperature) in a glass greenhouse. Stage 2 flowers were harvested from plants and exposed to 1.5 μl l^{-1} ethylene for 2 h before measurement of petal abscission percentage and separation force.

xhortorum (Dervinis et al., 2000), which does not correlate with the differential ethylene response of flowers at different developmental stages as observed in the current study. Presumably, this lack of correlation could be due to post-translational modification, presence of other undiscovered binding sites that do increase with flower opening, or development of other response elements during flower development. However, the presence of ETR1 transcripts would be consistent with renewed synthesis of ethylene binding sites after 1-MCP treatment.

Higher levels of 1-MCP did not provide additional protection against ethylene-induced petal abscission of *P. peltatum* (data not shown). It is likely that 1 μl l^{-1} was far in excess of that required to saturate the response as based on the results of earlier studies with apples (Fan and Mattheis, 1999), bananas (Golding et al., 1999) and flowers. As little as 25 nl l^{-1} effectively prevented ethylene-induced abscission of phlox flowers (Porat et al., 1995), and the 1-MCP binding constant for potted flowering begonia was calculated to be about 10 nl l^{-1} (Serek et al., 1994) 100 times less than that used in these experiments. In no case did we observe any toxicity symptoms on *P. peltatum*.

The transient nature of the beneficial affect of 1-MCP may limit its usefulness for pelargonium species. For instance, in preliminary trials, we found that there was no observable increase in postharvest life when *P. xhortorum* plants were treated with 1-MCP and then grown in the greenhouse or held in a postharvest environment but not exposed to exogenous ethylene. Petals abscised at the same time (14 to 18 days after stage 0) from untreated and 1-MCP-treated plants (data not shown). Serek et al. (1994) found that 1-MCP protected begonia when challenged immediately with ethylene, but provided no postharvest life extension in an interior environment. When not exposed to ethylene, all potted flowering begonia plants lasted for several weeks without significant petal abscission. Macnish et al. (2000) found a dramatic increase in the vase life of cut flowers from a few species of native Australian plants treated with 1-MCP and exposed to 10 μl l^{-1} ethylene. However, in the absence of exogenous ethylene, there was no observable increase in vase life. Yet, 1-MCP effectively increased the life of cymbidium flowers for 15 days, even after three successive challenges with ethylene at 5-day intervals (Heyes and Johnston, 1998). It possible that orchid flowers develop new binding sites more slowly than pelargoniums and begonia.

A second application of 1-MCP completely prevented abscission from stage 2 flowers and reestablished the beneficial effect (Fig. 5). This response is consistent with the idea that, as new binding sites are synthesized, continual or at least sequential treatments with 1-MCP would be necessary to block their activity. Practical methods for multiple 1-MCP applications may help circumvent some of these limitations imposed by the transient effect but currently could be costly and inconvenient. If 1-MCP is to be used commercially, the plants should be continually cooled after application to maximize the protective period.

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