

## METHYL JASMONATE TREATMENT DELAYS FLOWER OPENING AND PETAL WILTING OF THREE CUT ROSE CULTIVARS

Takanori HORIBE\*, Maho MAKITA  
 Chubu University, College of Bioscience and Biotechnology  
 1200 Matsumoto-cho, 487-8501, Kasugai-shi, Aichi, Japan

Received: June 2019; Accepted: November 2019

### ABSTRACT

Developing a method for the control of cut flower opening and improvement of cut flower quality is important to meet consumer demand. In this study, we investigated the effects of methyl jasmonate (MeJA) on flower opening of three rose cultivars: ‘Red Star,’ ‘Princes Meg,’ and ‘Madrid’. Shoot bases of cut roses were immersed in water solutions containing 100- or 1000- $\mu$ M MeJA in addition to 2% weight/volume (w/v) sucrose and 0.02% w/v 8-hydroxyquinoline monohydrate. Subsequently, the vase life, flower opening, petal wilting, petal weight, water uptake, and water evaporation were measured. Flower opening of all three cultivars was clearly delayed following the treatment with MeJA, resulting in prolonged vase life compared with control. In addition, flower wilting was suppressed in all cultivars. Moreover, 7 days following treatment, the petal fresh weight was maintained high in the ‘Red Star’ and ‘Princes Meg’ cultivars. However, there was no significant difference in the ‘Madrid’ cultivar versus control. In all three cultivars, there was a minimal difference in the total amount of water uptake and evaporation. Thus, it is suggested that the total amount of water uptake and evaporation have limited relevance to the changes in the relative fresh weight of cut roses and petal fresh weight observed following treatments. Despite the difference in the sensitivity of the rose cultivars to treatment with MeJA, we conclude that MeJA has high potential as a quality retention agent for cut roses.

**Keywords:** vase life, cut flower quality, water absorption, plant growth regulator

### INTRODUCTION

The rose is one of the most important ornamental plants appreciated as cut flowers and gardening plants, holding an important position in the ornamental flower industry. The quality of a cut rose flower is dependent on the external characteristics of the plant (i.e., color, length, volume, freshness, and fragrance) and perishability, which is determined by the duration of the aforementioned characteristics. In particular, vase life is a critical factor in determining the market value of cut flowers.

Owing to continued efforts for the improvement of the quality of cut flowers and prolongation of their vase life, numerous agents – e.g., ethylene production/action inhibitors (van Doorn & Woltering 2008) have been developed to preserve the quality of flower.

It has been reported that ethylene in rose flower regulates its opening and petal expansion, as well as its senescence (Ma et al. 2006; Tan et al. 2006). In addition, several studies have reported that sugars are involved in extending the vase life of cut flowers of rose and carnation (Paulin 1979; Paulin & Jamain 1982; Ichimura et al. 2003), suggesting that soluble carbohydrates play an important role in regulating osmotic pressure in petal cells. However, most research studies performed thus far have focused on the mechanism of senescence to prolong the vase life of flowers (van Doorn & Woltering 2008). For ornamental plants, especially for roses, their value lies in the process of blooming from its buds. Therefore, it is also important to establish methods for controlling the rate of flower opening, as well as flower senescence.

\*Corresponding author:  
 e-mail: t-horibe@isc.chubu.ac.jp

Methyl jasmonate (MeJA) is a naturally occurring fragrant volatile ester form of jasmonic acid. Recently, an increasing number of studies have investigated the effects and potential uses of MeJA in agriculture (Reyes-Díaz et al. 2016). For example, it has been suggested that MeJA may be used to enhance the quality of grape and wine (Portu et al. 2015) and to increase the concentration of anthocyanins in blackberries (Wang et al. 2008) and apples (Shafiq et al. 2013). Although few studies have investigated the effect of MeJA on flower opening, the only promotion was found in *Eustoma* (Ochiai et al. 2013; Mizuno et al. 2017). In addition, our previous study assessed the flower opening of rose ‘Meivildo’, characterized with a short vase life. The results showed that flower opening was delayed by approximately 1–2 days following the treatment with MeJA versus control (Horibe et al. 2013). Hence, we hypothesized that MeJA is a potential agent for controlling the rate of flower opening. However, the effects of plant growth regulators on cut flowers vary widely among species and cultivars. For example, in cut roses, the effect of ethylene on flower opening is cultivar dependent. There are three types of reactions to ethylene treatment: inhibition or acceleration of petal opening and lack of effect on petal opening (Reid et al. 1989; Yamamoto et al. 1994). There is limited evidence regarding the reaction of cut roses following the treatment with MeJA, including flower opening, petal growth, water balance, and differences between cultivars. Thus, in the present study, we investigated the effects of two concentrations of MeJA on flower opening, petal growth, and water balance using three cut rose cultivars.

## MATERIALS AND METHODS

### Plant material

Three rose cultivars were used in the experiments: ‘Red Star’, ‘Princes Meg’, and ‘Madrid’. These flowers were obtained at the commercial harvest stage from a commercial nursery in Aichi Prefecture, Japan. Cut flowers were transported in a dry, cool condition to our laboratory within 1 day.

### Treatment of cut flowers and determination of vase life, flower opening, and fresh weight of cut roses and petals

Promptly after arrival at our laboratory, the flowers were cut to 30-cm length and the stem bases were continuously held in 2% weight/volume (w/v) sucrose with 0.02% w/v 8-hydroxyquinoline monohydrate (Wako Pure Chemical Industries Ltd., Japan) – control, or with the addition 100 or 1,000  $\mu\text{M}$  of MeJA (Wako Pure Chemical Industries Ltd., Japan). Cut flowers were maintained in the plant growth chamber (BioTron; Nippon Medical & Chemical Instruments Co., Japan) at 25 °C, 60% relative humidity, and a 12-h photoperiod (photosynthetic photon flux density: 20–30  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Once every 2 days, changes in the fresh weight were evaluated during the experimental periods. Vase life was defined as the period from the start of the treatment to petal wilting (Norikoshi et al. 2012). The condition of the flowers was visually assessed every day at the same time of the day. Five outermost petals (outer petals) and five inner petals (16th to 20th; inner petals) under control and treatment with 1,000  $\mu\text{M}$  of MeJA were sampled. Their fresh weight was evaluated at third and seventh day following treatment.

### Water uptake and evaporation from cut flowers

The fresh weight of cut roses and the volume of water were recorded every 2 days during the experimental period. Water evaporation was also measured from a beaker containing an equal volume of water as the beaker containing the cut roses. For the calculation of the water uptake, the determined value was subsequently subtracted from the total amount of water lost from the beaker containing the cut roses. From this water uptake, we subtracted the changes in fresh weight of cut roses to calculate the amount of water evaporated from them.

### Experimental design and statistical analysis

Eight flowers were used for each treatment (control, 100- $\mu\text{M}$  MeJA, and 1,000- $\mu\text{M}$  MeJA) and for the measurement of vase life and the changes in the fresh weight of cut roses. Another three flowers were used for the measurement of fresh weight of petals in control and in 1,000- $\mu\text{M}$  MeJA treatments. In addition, four flowers were used for the measurement of water uptake and evaporation in each treatment.

All experiments were repeated twice. The data were subjected to analysis of variance, and differences across means were determined using the t-test and Tukey’s test, with significance defined as  $p \leq 0.05$ .

RESULTS

**Effect of treatment with MeJA on vase life, flower opening, and fresh weight of cut roses and petals**

The vase life of cut roses of all cultivars was significantly longer in flowers maintained in the solution containing 1,000- $\mu$ M MeJA than in the control (Table 1). There was no significant difference between the control and the 100- $\mu$ M MeJA treatment in ‘Red Star’ and between 100- and 1,000- $\mu$ M MeJA treatments in ‘Madrid’. Vase life became longer as the concentration of MeJA increased in ‘Princes Meg’.

Table 1. Vase life (days) of rose cultivars in each treatment

Cultivar	Treatment	Vase life
‘Red Star’	control	5.50 $\pm$ 0.13 <sup>a</sup>
	100 $\mu$ M	5.85 $\pm$ 0.12 a
	1,000 $\mu$ M	8.88 $\pm$ 0.19 b
‘Princes Meg’	control	6.38 $\pm$ 0.17 a
	100 $\mu$ M	8.25 $\pm$ 0.17 b
	1,000 $\mu$ M	9.38 $\pm$ 1.19 c
‘Madrid’	control	6.25 $\pm$ 0.17 a
	100 $\mu$ M	9.38 $\pm$ 0.28 b
	1,000 $\mu$ M	9.69 $\pm$ 0.19 b

Means followed by a different letter within same cultivar are significantly different, according to the least significant difference (Tukey’s test,  $p \leq 0.05$ ). Values are means  $\pm$  SE (n = 16).

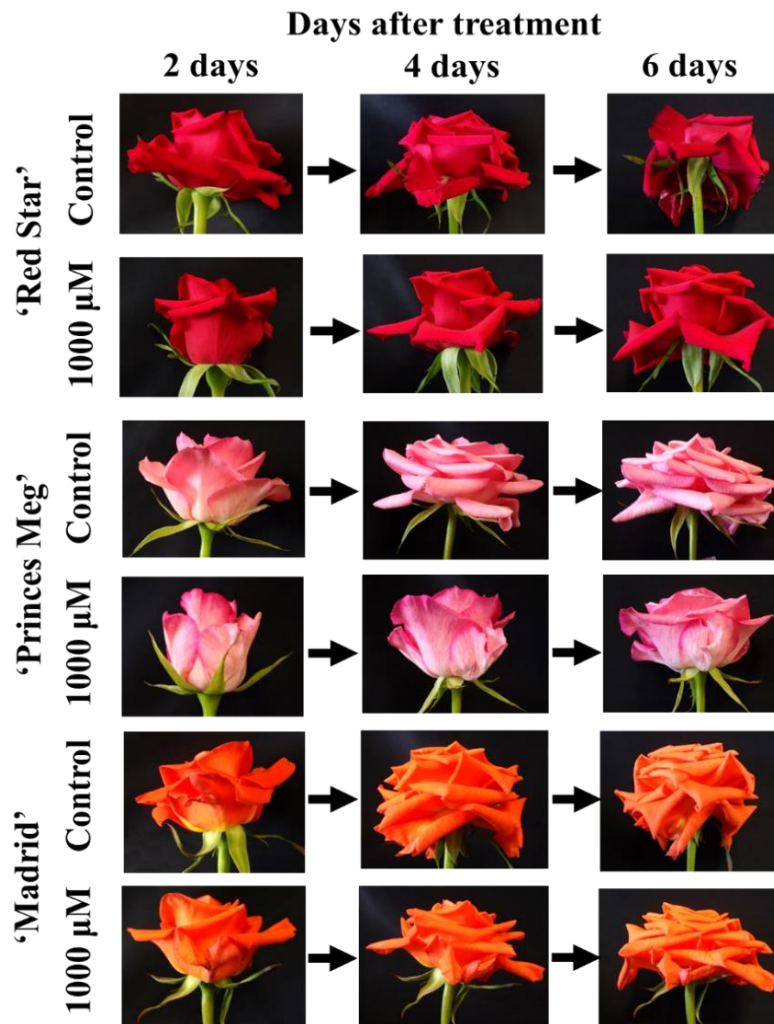


Fig. 1. Pattern of flower opening and petal wilting of cut roses from days 2 to 6 after treatment of three rose cultivars



Fig. 2. Influence of MeJA on flowers of rose after 8 days of treatment

Also flowers' opening of all cultivars was markedly delayed following the treatment with 1,000- $\mu$ M MeJA versus control. However, the observed differences in the speed of flower opening were small between the 100- $\mu$ M MeJA treatment and the control (Fig. 1). 'Red Star' roses in control tended to wilt faster than other cultivars. Eight days after treatment, cut flowers under control were wilted or pistils were visible. In contrast, there were no wilted flowers or visible pistils after treatment with 1,000- $\mu$ M MeJA (Fig. 2). Leaf abscission was not observed after the treatment with 100- and 1,000- $\mu$ M MeJA.

Changes in the relative fresh weight of cut roses for each treatment are shown in Figure 3. For 'Red Star' and 'Princes Meg', the relative fresh weight in the control increased from 1 to 4 days and decreased subsequently (Fig. 3A, B), whereas in 'Madrid' roses, it increased from 1 to 6 days and decreased subsequently (Fig. 3C). After 6 days, the relative fresh weight of 'Red Star' cut roses treated with 1,000- $\mu$ M MeJA was higher versus that observed in other treatments (Fig. 3A). However, the observed difference between control and 100- $\mu$ M MeJA treatment was not significant. The relative fresh weight of 'Princes Meg' after treatment with 100- and 1,000- $\mu$ M MeJA was higher than that in control at days 8 and 10 (Fig. 3B). For 'Madrid' roses, the relative fresh weight after treatment with 100- and 1,000- $\mu$ M MeJA was higher than that observed in the control at day 10. Notably, the relative fresh weight was high in control at days 4 and 6 than those measured for the other treatments (Fig. 3C).

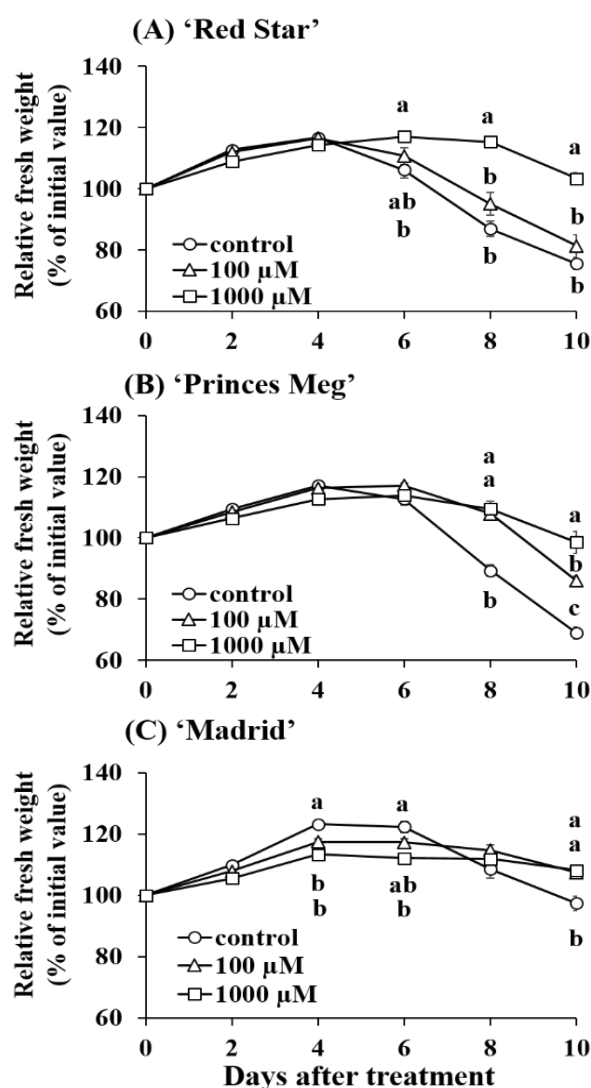


Fig. 3. Influence of MeJA on fresh weight of cut roses of three cultivars. Means followed by a different letter within each day are significantly different, according to the least significant difference (Tukey's test,  $p \leq 0.05$ ). Values are means  $\pm$  SE ( $n = 16$ ).

Changes in the petal fresh weight for each treatment are shown in Figure 4. In ‘Red Star’ and ‘Princess Meg’, the fresh weights of outer and inner petals of roses treated with 1,000- $\mu$ M MeJA were significantly higher versus those reported in the control at day 7 (Fig. 4A, B, C, D, respectively). In ‘Princes Meg’ roses, the fresh weights

of outer and inner petals after treatment with 1,000- $\mu$ M MeJA were significantly lower than those in the control at day 3. (Fig. 4C, D). In ‘Madrid’ roses, there was no significant difference in the fresh weights of outer and inner petals between the control and the plants treated with 1,000- $\mu$ M MeJA (Fig. 4E, F).

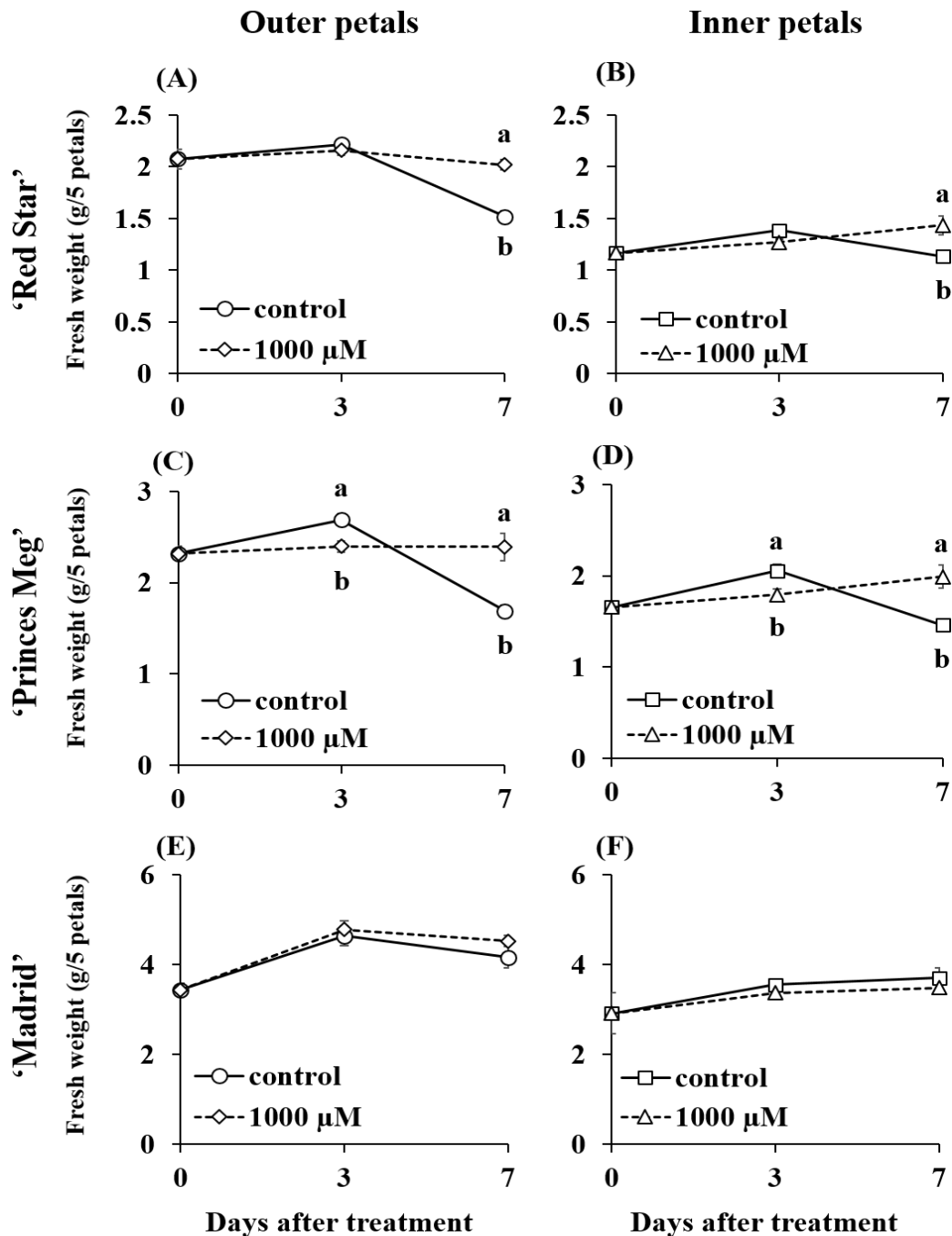


Fig. 4. Influence of MeJA on fresh weights of petals during flower opening of three cultivars. Means followed by a different letter within each day are significantly different, according to the least significant difference (t-test,  $p \leq 0.05$ ). Values are mean  $\pm$  SE ( $n = 6$ ).

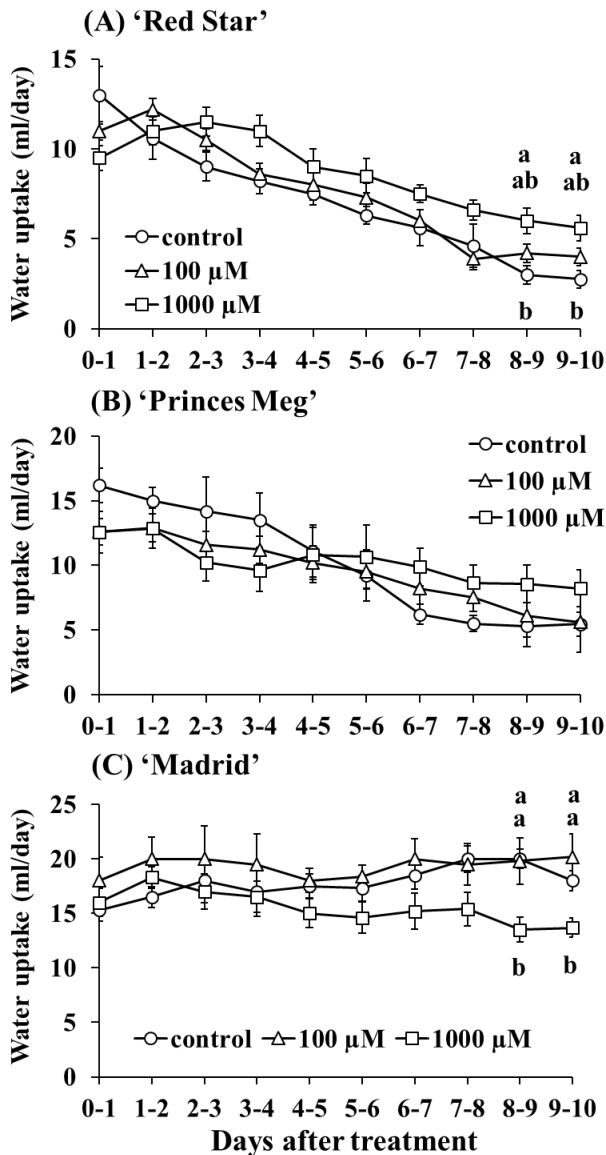


Fig. 5. Influence of MeJA on the water uptake by cut roses of three cultivars. Means followed by a different letter within each day are significantly different, according to the least significant difference (Tukey's test,  $p \leq 0.05$ ). Values are means  $\pm$  SE ( $n = 8$ ).

#### Effect of treatment with MeJA on water uptake and evaporation of cut roses

Water uptake for each treatment is shown in Fig. 5. In 'Red Star' and 'Princes Meg', the amount of water uptake in the control and plants treated with MeJA tended to decrease with time. However, the highest water uptake was recorded in plants treated with 1,000- $\mu$ M MeJA, although differences in 'Princes Meg' were not always significant (Fig. 5A, B). In 'Madrid' roses, the amount of water uptake was more stable with time and decreased only in the plants treated with 1,000- $\mu$ M MeJA (Fig. 5C).

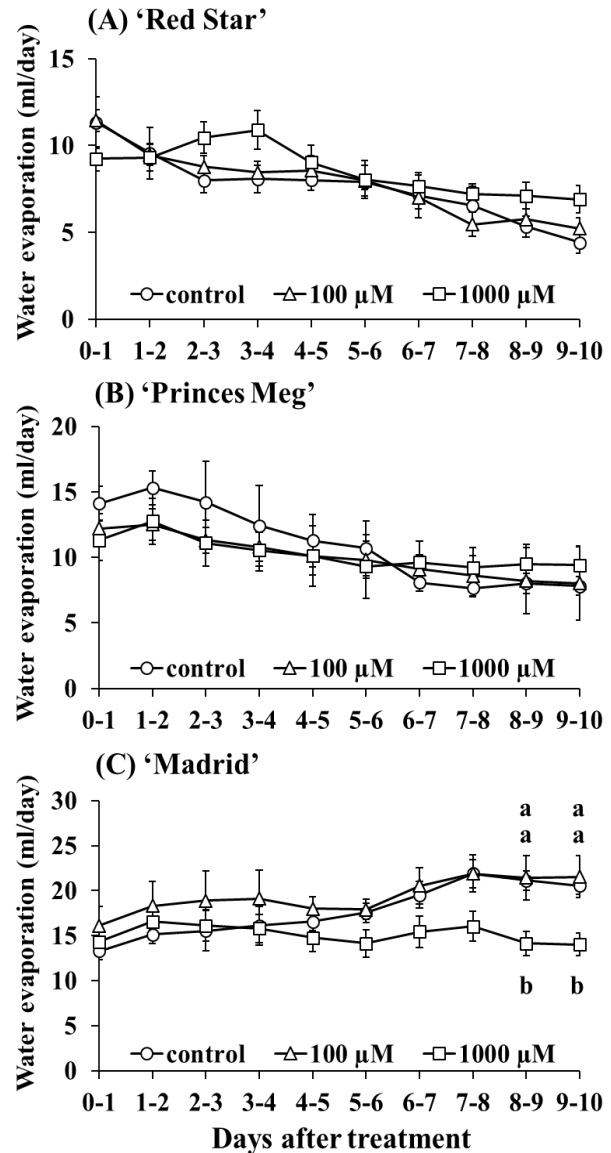


Fig. 6. Influence of MeJA on water evaporation of three cultivars of cut roses. Means followed by a different letter within each day are significantly different, according to the least significant difference (Tukey's test,  $p \leq 0.05$ ). Values are means  $\pm$  SE ( $n = 8$ ).

Changes in the water evaporation from cut flowers for each treatment are shown in Fig. 6. Water evaporation showed similar patterns as those observed for water uptake. In 'Madrid' roses, the amount of water evaporation from cut flowers after treatment with 1,000- $\mu$ M MeJA from days 8 to 10 was significantly lower versus that reported for other treatments (Fig. 6C). In 'Red Star' and 'Princes Meg' roses, no significant differences were observed between the treatments (Fig. 6A, B).

## DISCUSSION

Flowers attract the interest of people and are now essential in our daily lives. Thus, understanding the mechanisms of flower opening may benefit commercial horticulture as well as plant science in general. In the present study, whose aim was to find a way to extend vase life, we discovered the beneficial role of MeJA, which when added to the water solution containing 2% w/v sucrose and 100  $\mu\text{M}$  w/v 8-hydroxyquinoline monohydrate, markedly delayed flower opening, suppressed a decrease in relative fresh weight of cut flower and petals, and inhibited the process of water loss, resulting in an extension of vase life. The above statements mostly refer to a concentration of 1,000- $\mu\text{M}$  MeJA and two of three cultivars. Cut roses of three cultivars had different sensitivity to MeJA. Also, they differed in their reaction to maintaining in control solution, containing sucrose and 8-hydroxyquinoline. For example, 'Madrid' lost only 10% of its fresh weight, whereas 'Red Star' and 'Princes Meg' lost about 30% of fresh weight. The same kind of difference was recorded in fresh mass of petals, as an initial mass of 'Madrid' was higher and practically was not changed during experiment. Moreover, roses of 'Madrid' took up more water and evaporated less.

Ethylene is a major contributor in the aging of many plants, including some rose cultivars (Reid et al. 1989; Yamamoto et al. 1994). Its role in flower senescence was reported as different and dependent on the species. Porat et al. (1993) stated that treatment with MeJA increased ethylene production and accelerated senescence of petunia and dendrobium. Although MeJA demonstrated its potential as a quality retention agent for controlling the speed of cut rose flower opening, appropriate treatment concentration should be investigated by using more cultivars henceforth. Mizuno et al. (2017) reported that uneven coloration of cut *Eustoma* was reduced by treatment with MeJA and that 1 day of this treatment was sufficient to achieve the effect. Thus, shortening the duration of treatment with MeJA in cut roses may be effective in reducing the occurrence of adverse effects. In this study, leaf abscission was not observed after treatment with 100- and 1,000- $\mu\text{M}$  MeJA.

In cut rose (*Rosa hybrida*) flower stems, the leaves play an important role in maintaining the rates of water uptake through their transpiration (Halevy & Mayak 1981). Adverse water relations lead to incomplete flower opening, premature petal wilting, and bending of the pedicel in roses (Doi et al. 1999). In the present study, the amount of water uptake did not significantly differ among treatments, except for days 8 and 10 in 'Red Star' and 'Madrid' roses. The amount of water evaporation from the cut flowers did not differ significantly among treatments, except for days 8–10 in 'Madrid' roses. This discrepancy might be caused by the difference in water path though cut rose when the water evaporated. We surmise that a larger amount of water reached the petals after treatment with 1,000- $\mu\text{M}$  MeJA versus control despite the limited difference observed between treatments in the total amount of water evaporation from the cut roses. Our results suggest that the total amount of water uptake and evaporation had limited relevance to the observed changes in the relative fresh weight of cut roses and petal fresh weight.

Currently, the physiological mechanisms involved in the response of flower opening to treatment with MeJA remain to be identified. The process of rose bud development and subsequent flower opening involves irreversible petal growth and reflection, in which existing cells expand and fresh and dry weights increase (Evans & Reid 1986, 1988; Faragher et al. 1984). In carnation flowers, the amount of DNA in the petals does not increase once the petals emerge from the calyx, suggesting that cells also stop dividing at an early stage (Kenis et al. 1985). In *Gaillardia grandiflora*, petal cells appear to stop dividing at a much earlier flowering stage, and no increase observed in the number of abaxial epidermal cells was observed (Koning 1984). These reports indicate that petal growth related to flower opening depends mainly on cell expansion. Cells in rose petals almost completely stop dividing even when the petals remain covered by the calyx (Roberts et al. 1985; Yamada et al. 2009a). This finding suggests that petal growth associated with flower opening depends on cell expansion. Thus, there is a possibility that treatment with MeJA inhibited the growth of petals in cut roses, leading to the delayed flower opening observed in the present study.

However, there was no significant difference observed in the relative fresh weight between treatments until day 4 in ‘Red Star’ and until day 6 in ‘Princes Meg’) when the speed of flower opening differed on the appearance. In addition, in ‘Red Star’ and ‘Madrid’, the fresh weights of outer and inner petals did not differ significantly between control and treatment with 1,000- $\mu$ M MeJA at day 3. Of note, the fresh weights in ‘Princes Meg’ roses after treatment with 1,000- $\mu$ M MeJA were significantly lower compared with those measured in control. These results show that, when petals become enlarged, the petal fresh weight after treatment with 1,000- $\mu$ M MeJA is not always lower versus that reported in the control. This implies that the growth of petals is not inhibited by treatment with MeJA. However, the structure of petal cells (including the width, volume, and shape) may be affected by the treatment with MeJA, leading to a delay in flower opening even though the petal fresh weight remains unchanged. Li et al. (2018) reported that the treatment with MeJA caused significant changes in trichome density, cuticle composition, and thickness of leaves in sunflower, tomato, and soybean. The adaxial and abaxial epidermal cells in the cut roses show marked expansion during rose flower opening. Moreover, adaxial epidermal cells become corn shaped when the flower is fully open (Yamada et al. 2009a). In addition, the parenchyma cells of rose petals showed unique growth into a tetrapod-like shape that resembles the mesophyll cells of leaves (Yamada et al. 2009a). Differences in the patterns of expansion among the cell types and locations, including adaxial and abaxial epidermal cells, are thought to cause petal reflection during rose flower opening. More detailed analysis of the petal structure is necessary to verify the relationship between delayed flower opening and petal growth.

Furthermore, the accumulation of sugar in vacuoles, cell wall loosening, and the subsequent water flow into the cells are thought to be important for the enlargement of rose petals (Horibe & Yamada 2017). Regarding the function of carbohydrates in the process of rose flower opening, it is considered that the accumulation of sugar in petal cells

leads to the reduction of the water potential and promotes water influx, which may lead to cell enlargement and flower opening (Ho & Nichols 1977; van Doorn et al. 1991; Ichimura et al. 2003). Numerous studies have indicated a relationship between the activity of invertase – an enzyme that metabolizes sucrose translocated from the source to sink tissues – and the strength of the sink tissues (Tang et al. 1999; Balibrea et al. 2004; Roitsch & González 2004). Horibe et al. (2013) reported that treatment with MeJA activates invertase in petals. Moreover, this activation appears to promote the translocation of sucrose from leaves to petals during petal growth, resulting in delayed senescence. Furthermore, sugar metabolism in petals and leaves may also be affected by the treatment with MeJA. Cell expansion is regulated by the accumulation of sugars and water influx, as well as cell wall pressure, which is determined by the strength of the cell wall. When the cell wall of petals remains rigid, water cannot influx into the cell and the cell cannot expand. Ochiai et al. (2013) reported that MeJA accelerates the expression of genes related to cell wall loosening (*EgEXPA2*, *EgEXPA3*, and *EgXTH1*) and the accumulation of expansin and xyloglucan endotransglucosylase/hydrolase in *Eustoma* petals. In roses, genes related to cell wall loosening (*RhEXPA1* and *RhXTH1*) are thought to be mainly involved in petal expansion (Takahashi et al. 2007; Yamada et al. 2009b). These cell-wall-loosening proteins in rose petals may also be affected by the treatment with MeJA. Further research regarding the roles of these proteins in response to the treatment with MeJA is warranted.

In conclusion, the present study showed that the treatment with MeJA delays flower opening and petal wilting in three cut rose cultivars, resulting in longer vase life. It is important to establish the methods for controlling the rate of flower opening and senescence in ornamental plants. We think that MeJA has high potential as a quality retention agent for cut roses. It is of interest to verify the effect of MeJA on flowering using other cultivars and species. Additional studies are warranted to investigate the relationship between treatment with MeJA and flower opening.



### Acknowledgments

We would like to thank Prof. Shohei Yamaki of Nagoya University and Prof. Kunio Yamada of Gifu University for their professional advice.

### REFERENCES

- Balibrea Lara M.E., Gonzalez Garcia M.-E., Fatima T., Ehness R., Lee T.K., Proels R., Tanner W., Roitsch T. 2004. Extracellular invertase is an essential component of cytokinin-mediated delay of senescence. *Plant Cell* 16(5): 1276–1287. DOI: 10.1105/tpc.018929.
- Doi M., Miyagawa M., Inamoto K., Imanishi H. 1999. Rhythmic changes in water uptake, transpiration and water potential of cut roses as affected by photoperiods. *Journal of the Japanese Society for Horticultural Science* 68(4): 861–867. DOI: 10.2503/jjshs.68.861.
- van Doorn W.G., Woltering E.J. 2008. Physiology and molecular biology of petal senescence. *Journal of Experimental Botany* 59(3): 453–480. DOI: 10.1093/jxb/erm356.
- van Doorn W.G., Groenewegen G., van de Pol P.A., Berkholst C.E.M. 1991. Effects of carbohydrate and water status on flower opening of cut ‘Madelon’ roses. *Postharvest Biology and Technology* 1(1): 47–57. DOI: 10.1016/0925-5214(91)90018-7.
- Evans R.Y., Reid M.S. 1986. Control of petal expansion during diurnal opening of roses. *Acta Horticulturae* 181: 55–64. DOI: 10.17660/actahortic.1986.181.5.
- Evans R.Y., Reid M.S. 1988. Changes in carbohydrates and osmotic potential during rhythmic expansion of rose petals. *Journal of the American Society for Horticultural Science* 113(6): 884–888.
- Faragher J.D., Mayak S., Tirosh T., Halevy A.H. 1984. Cold storage of rose flowers: Effects of cold storage and water loss on opening and vase life of ‘Mercedes’ roses. *Scientia Horticulturae* 24(3-4): 369–378. DOI: 10.1016/0304-4238(84)90122-5.
- Halevy A.H., Mayak S. 1981. Senescence and postharvest physiology of cut flowers: Part 2. *Hort. Reviews* 3: 59–143. DOI: 10.1002/9781118060742.ch5.
- Ho L.C., Nichols R. 1977. Translocation of <sup>14</sup>C-sucrose in relation to changes in carbohydrate content in rose corollas cut at different stages of development. *Annals of Botany* 41(1): 227–242. DOI: 10.1093/oxfordjournals.aob.a085272.
- Horibe T., Yamada K. 2017. Petal growth physiology of cut rose flowers: progress and future prospects. *Journal of Horticultural Research* 25(1): 5–18. DOI: 10.1515/johr-2017-0001.
- Horibe T., Yamaki S., Yamada K. 2013. Effects of auxin and methyl jasmonate on cut rose petal growth through activation of acid invertase. *Postharvest Biology and Technology* 86: 195–200. DOI: 10.1016/j.postharvbio.2013.06.033.
- Ichimura K., Kawabata Y., Kishimoto M., Goto R., Yamada K. 2003. Shortage of soluble carbohydrates is largely responsible for short vase life of cut ‘Sonia’ rose flowers. *Journal of the Japanese Society for Horticultural Science* 72(4): 292–298. DOI: 10.2503/jjshs.72.292.
- Kenis J.D., Silvente S.T., Trippi V.S. 1985. Nitrogen metabolism and senescence-associated changes during growth of carnation flowers. *Physiologia Plantarum* 65(4): 455–459. DOI: 10.1111/j.1399-3054.1985.tb08673.x.
- Koning R.E. 1984. The roles of plant hormones in the growth of the corolla of *Gaillardia grandiflora* (Asteraceae) ray flowers. *American Journal of Botany* 71(1): 1–8. DOI: 10.2307/2443617.
- Li C., Wang P., Menzies N.W., Lombi E., Kopitke P.M. 2018. Effects of methyl jasmonate on plant growth and leaf properties. *Journal of Plant Nutrition and Soil Science* 181(3): 409–418. DOI: 10.1002/jpln.201700373.
- Ma N., Tan H., Liu X., Xue J., Li Y., Gao J. 2006. Transcriptional regulation of ethylene receptor and CTR genes involved in ethylene-induced flower opening in cut rose (*Rosa hybrida*) cv. Samantha. *Journal of Experimental Botany* 57(11): 2763–2773. DOI: 10.1093/jxb/erl033.
- Mizuno T., Fukuta N., Shimizu-Yumoto H. 2017. Nonuniform coloration of harvested flower buds of double-flowered *Eustoma* is reduced by methyl jasmonate treatment. *The Horticulture Journal* 86(2): 244–251. DOI: 10.2503/hortj.okd-001.
- Norikoshi M., Imanishi H., Ichimura K. 2012. Effects of vase solution and air temperatures and isothiazolonic germicides on the vase life of cut rose flowers. *Environmental Control in Biology* 50(4): 329–334. DOI: 10.2525/ecb.50.329.
- Ochiai M., Matsumoto S., Yamada K. 2013. Methyl jasmonate treatment promotes flower opening of cut *Eustoma* by inducing cell wall loosening proteins in petals. *Postharvest Biology and Technology* 82: 1–5. DOI: 10.1016/j.postharvbio.2013.02.018.

- Paulin A. 1979. 1979. Évolution des glucides dans les différents organes de la rose coupée (var. Carina) alimentée temporairement avec une solution glucosée. *Physiologie Végétale* 17: 129–143. [in French]
- Paulin A., Jamain C. 1982. Development of flowers and changes in various sugars during opening of cut carnations (*Dianthus caryophyllus*). *Journal American Society for Horticultural Science* 107(2): 258–261.
- Porat R., Borochoy A., Halevy A.H. 1993. Enhancement of petunia and dendrobium flower senescence by jasmonic acid methyl ester is via the promotion of ethylene production. *Plant Growth Regulation* 13(3): 297–301. DOI: 10.1007/bf00024851.
- Portu J., Santamaría P., López-Alfaro I., López R., Garde-Cerdán T. 2015. Methyl jasmonate foliar application to Tempranillo vineyard improved grape and wine phenolic content. *Journal of Agricultural and Food Chemistry* 63(8): 2328–2337. DOI: 10.1021/jf5060672.
- Reid M.S., Evans R.Y., Dodge L.L., Mor Y. 1989. Ethylene and silver thiosulfate influence opening of cut rose flowers. *Journal of the American Society for Horticultural Science* 114(3): 436–440.
- Reyes-Díaz M., Lobos T., Cardemil L., Nunes-Nesi A., Retamales J., Jaakola L., et al. 2016. Methyl jasmonate: an alternative for improving the quality and health properties of fresh fruits. *Molecules* 21(6): 567. DOI: 10.3390/molecules21060567.
- Roberts I.N., Lloyd C.W., Roberts K. 1985. Ethylene-induced microtubule reorientations: mediation by helical arrays. *Planta* 164(4): 439–447. DOI: 10.1007/bf00395959.
- Roitsch T., González M.-C. 2004. Function and regulation of plant invertases: sweet sensations. *Trends in Plant Science* 9(12): 606–613. DOI: 10.1016/j.tplants.2004.10.009.
- Shafiq M., Singh Z., Khan A.S. 2013. Time of methyl jasmonate application influences the development of ‘Cripps Pink’ apple fruit colour. *Journal of the Science of Food and Agriculture* 93(3): 611–618. DOI: 10.1002/jsfa.5851.
- Takahashi R., Fujitani C., Yamaki S., Yamada K. 2007. Analysis of the cell wall loosening proteins during rose flower opening. *Acta Horticulturae* 755: 483–488. DOI: 10.17660/actahortic.2007.755.66.
- Tan H., Liu X., Ma N., Xue J., Lu W., Bai J., Gao J. 2006. Ethylene-influenced flower opening and expression of genes encoding *Etrs*, *Ctrs*, and *Ein3s* in two cut rose cultivars. *Postharvest Biology and Technology* 40(2): 97–105. DOI: 10.1016/j.postharvbio.2006.01.007.
- Tang G.Q., Lüscher M., Sturm A. 1999. Antisense repression of vacuolar and cell wall invertase in transgenic carrot alters early plant development and sucrose partitioning. *Plant Cell* 11(2): 177–189. DOI: 10.1105/tpc.11.2.177.
- Wang S.Y., Bowman L., Ding M. 2008. Methyl jasmonate enhances antioxidant activity and flavonoid content in blackberries (*Rubus* sp.) and promotes antiproliferation of human cancer cells. *Food Chemistry* 107(3): 1261–1269. DOI: 10.1016/j.foodchem.2007.09.065.
- Yamada K., Norikoshi R., Suzuki K., Nishijima T., Imanishi H., Ichimura K. 2009a. Cell division and expansion growth during rose petal development. *Journal of the Japanese Society for Horticultural Science* 78(3): 356–362. DOI: 10.2503/jjshs1.78.356.
- Yamada K., Takahashi R., Fujitani C., Mishima K., Yoshida M., Joyce D.C., Yamaki S. 2009b. Cell wall extensibility and effect of cell-wall-loosening proteins during rose flower opening. *Journal of the Japanese Society for Horticultural Science* 78(2): 242–251. DOI: 10.2503/jjshs1.78.242.
- Yamamoto K., Komatsu Y., Yokoo Y., Furukawa T. 1994. Delaying flower opening of cut roses by cis-propenyl phosphonic acid. *Journal of the Japanese Society for Horticultural Science* 63(1): 159–166. DOI: 10.2503/jjshs.63.159.