Difference in Flower Longevity and Endogenous Ethylene Production of *Portulaca umbraticola* Cultivars

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Portulaca umbraticola Kunth, with ephemeral flowers, has become an important summer bedding plant in Japan. A lot of new cultivars have recently been bred with different flowering characteristics, but there is little information about *P. umbraticola* cultivars. In this study, we investigated the differences in flower longevity, endogenous ethylene production and ethylene sensitivity between a conventional cultivar, ‘Single Red’ (SR), and a newly released cultivar, ‘Sanchuraka Cherry Red’ (SCR). The flowers of SR opened and closed earlier than those of SCR and the flower longevity of SCR was significantly longer than that of SR. The effects of pollination, filament wounding and pistil removal on flower longevity were also investigated in both cultivars. Pollination, filament wounding and pistil removal significantly accelerated senescence in both cultivars, but filament wounding was much more significant in accelerating senescence. Endogenous ethylene production from flower opening to closure was significantly higher in SR than in SCR. The peak ethylene production in SR occurred 2 h earlier than that in SCR. Exogenous ethylene treatments of 0.5, 1, and 2 $\mu\text{L}\cdot\text{L}^{-1}$ significantly accelerated the rate of senescence in both SR and SCR. The use of ethylene action inhibitor 1-methylcyclopropene (1-MCP) and ethylene biosynthesis inhibitor aminoethoxyvinylglycine (AVG) significantly improved flower longevity in both cultivars, with the latter being much more effective. The better flower longevity of SCR seems to be related to lower endogenous ethylene production. The senescence of *P. umbraticola* cultivars seems to be ethylene-dependent.

Key Words: bedding plant, ephemeral, filament wounding, flower closure, senescence.

Introduction

Portulaca umbraticola Kunth is an annual summer bedding plant with morphological characteristics that resemble those of common purslane (*P. oleracea* L. subsp. *sativa* DC.). Although the flower shape of *P. umbraticola* resembles that of *P. grandiflora* Hook., its leaf morphology highly resembles that of common purslane. As a result, *P. umbraticola* cultivars were named “Hanasuberihyu” in Japanese, which means ornamental *P. oleracea*, or were simply called *Portulaca*, which is its genus name. *Portulaca umbraticola* cultivars are frequently mislabeled as *P. oleracea* or *P. grandiflora*, or as hybrids of these species. A strain called wildfire has been offered as both *P. grandiflora* and *P. oleracea*, but it is actually a strain of *P. umbraticola* cultivars (Matthews et al., 1992). Re-

cently, Ocampo and Columbus (2012) illustrated that *P. umbraticola*, formerly referred to as *Portulaca* hybrid or *P. oleracea* subsp. *sativa*, belongs to the *Umbraticola* clade within the genus *Portulaca* and is indeed *P. umbraticola*.

The genus *Portulaca* consists of many species with a wide range of functions, some of which are considered as invasive weeds, while *P. oleracea* is used as a vegetable: purslane is one of the richest green plant sources of omega-3 fatty acids (Uddin et al., 2014). Methanolic extracts of *P. oleracea* have been reported to have antioxidant activity (Sanja et al., 2009), and it is also considered to have antiphlogistic, bactericidal, antidiabetic, anaphrodisiac, and diuretic effects, as well as being a refreshing agent (Boulous, 1983).

In the genus *Portulaca*, two species are mainly used for ornamental purposes, that is, *P. grandiflora* and *P. umbraticola*. The flowers of *Portulaca* are ephemeral and generally open early in the morning and wilt in the afternoon; the flowers do not fully open on cloudy or relatively cool days (Ichimura and Suto, 1998a). Al-

Received; June 8, 2015. Accepted; July 31, 2015.

First Published Online in J-STAGE on September 15, 2015.

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though there has been an increase in the sales of floricultural *Portulaca*, there is little information about the flowering characteristics of this plant. The ephemeral nature of its flowers has greatly affected its use as an ornamental plant. *Portulaca* hybrid, namely, *P. umbraticola*, grows well under very hot and dry conditions typical of a Japanese summer (Ichimura and Suto, 1998b). Recent trends have shown an increase in the sales of ornamental *Portulaca* spp., with *Portulaca* being ranked as the 9th most grown summer bedding plant in Japan as of 2009 (Japan Flower Promotion Center Foundation; <http://www.jfpc.or.jp/bunseki/2009.html>, September 1, 2010). The average life of *Portulaca* hybrid is greatly affected by light and temperature (Ichimura and Suto, 1998b), with high temperature and light facilitating rapid flower opening but also early closing. In *Portulaca* hybrid (*P. umbraticola*), pollination, filament wounding and pistil removal significantly accelerated senescence, with filament wounding being much more effective. Filament wounding increased ethylene production (Ichimura and Suto, 1998a). Iwanami and Hoshino (1963) also reported that filament wounding in *P. grandiflora* accelerated senescence.

The main objective of this research was to identify the main differences between a conventional cultivar, ‘Single Red’ (SR), and a newly released cultivar, ‘Sanchuraka Cherry Red’ (SCR), in relation to ethylene sensitivity, senescence and flower longevity. SCR belongs to the Sanchuraka series, which are cultivars newly released by Sakata Seed Co. Ltd. SR, a conventional cultivar used in this experiment, is the same as *Portulaca* hybrid ‘ANR1’ used by Ichimura and Suto (1998a, b), the only difference being the name used. General observations have shown that Sanchuraka series cultivars last longer than conventional cultivars; however, there is no specific information on their longevity as well as the mechanism used for their selection. This research should provide the basic information necessary for future improvement of ornamental *Portulaca* as well as providing an insight into the possible mechanism used for the selection of cultivars with better flower longevity.

Materials and Methods

Plant materials and growth conditions

Portulaca umbraticola cultivars ‘Single Red’ (SR) and ‘Sanchuraka Cherry Red’ (SCR) were raised in a phytotron at 28/23°C day and night temperatures, respectively. The plants were grown in 15-cm plastic pots filled with a 3:1 mixture of granular soil and peat-based soil mix (Metro-Mix 360; Sun Gro, Agawam, MA, USA). The plants were grown in a phytotron under natural light in Tokyo, Japan.

The experiment was divided into two parts.

1. Flowering characteristics

1.1 Determination of flower longevity

The flower buds of SR and SCR were harvested a day before anthesis and then placed into test tubes containing distilled water. The buds were stored in a refrigerator overnight at 10°C. The following morning at 8 a.m., the flowers were transferred into the phytotron and the time taken from opening to closing was recorded using a digital camera at 5-min intervals. A total of five flower buds were used for each experiment.

Apart from that, the effects of temperature on flower opening were also evaluated. The above procedure was followed until the following morning. In the morning, the buds were then subjected to different temperatures (22.5°C–40°C) in a growth chamber (LH-240NPFLD; Nippon Medical and Chemical Instruments Co. Ltd., Osaka, Japan) with light intensity of 100–105 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The time taken to full opening was recorded. A total of five flower buds were used for each experiment.

1.2 Effects of pollination, pistil removal and filament wounding on flower longevity

The above procedure was followed and most flowers opened within three hours. The flowers that did not open within this time period were discarded. The flowers were then subjected to self/cross-pollination; for pistil removal, the pistil was carefully pulled out by hand. The filaments were wounded by carefully cutting them to about 1/3 from their base using a pair of tweezers, following the method used by Ichimura and Suto (1998a). Untreated plants were used as a control. A total of five flower buds were used for each experiment.

2. Ethylene treatments

2.1 Determination of ethylene produced from flower opening to closing by the two cultivars

The flower buds were harvested a day before anthesis and then stored in a plant growth chamber (FLI-2000H; EYELA, Tokyo, Japan) of 28/25°C day and night temperatures, respectively, with cool fluorescent light (315–325 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and 70% RH. The lights were turned on at 7 a.m. and turned off at 7 p.m. Ethylene production was measured at 2-h intervals from opening to closing. Two flowers per cultivar were sealed in a 25-mL flask and incubated for 30 min at the above temperature. Head space gas samples (2 mL) were taken and injected into a gas chromatograph (GC-7A; Shimadzu, Kyoto, Japan) equipped with an alumina column and a flame ionization detector. This was replicated three times giving a total of six flowers per measurement.

2.2 Exogenous ethylene treatment

Flower buds were held under the above conditions and fully open flowers were selected at 9 a.m. The flowers were placed in sealed incubation chambers with a small circulating fan. Designated ethylene concentrations (0.5, 1, and 2 $\mu\text{L}\cdot\text{L}^{-1}$) were introduced by a syringe through an inlet rubber-sealed pipe. The flowers

were incubated for 1 h. Untreated plants were used as a control. A digital camera was used to record the time taken to wilting. A total of eight flowers were used for each experiment.

2.3 Ethylene action and biosynthesis inhibitor treatments (AVG and 1-MCP)

Flower buds were held under the above conditions until they were fully open. For aminoethoxyvinylglycine (AVG) treatments, $5 \mu\text{L} \cdot \text{L}^{-1}$ AVG (Sigma-Aldrich, St. Louis, MO, USA) was spread on the filaments of the flowers using a syringe (5 mL/flower). For 1-methylcyclopropene (1-MCP), flowers with their cut ends immersed in distilled water were placed in an acrylic chamber (53 L), and then Ethyl Bloc TM (Rohm and Haas Japan, Tokyo, Japan) was added to the distilled water to evolve 1-MCP at a concentration of $2 \mu\text{L} \cdot \text{L}^{-1}$ and held at 28°C for 1 h. Untreated plants were used as a control. Time taken to wilting was recorded using a digital camera. A total of five flower buds were used for each experiment.

Statistical analysis

The data were subjected to analysis of variance (ANOVA) using a statistical package, R-Console (Rx64 3.0.2) (<https://www.r-project.org/>).

Results

1. Difference in flower longevity

The flowers of SR took 1.2 h to open fully from the bud stage, while those of SCR took 2.5 h. However, SR took 10.3 h from the bud stage to closing, while SCR took 15.3 h (Table 1). SR and SCR significantly differed in their flower longevity, having averages of 9.1 and 12.8 h, respectively.

At 22.5 and 25°C , the flowers of both cultivars did not fully open. After 6 h at 25°C , SR was at a more advanced opening stage than SCR, but the flowers never

reached the fully open stage (data not shown). A temperature of 27.5°C was the minimum threshold for opening as both cultivars reached the fully open stage; SR took 3.3 h while SCR took 4.4 h. The difference in opening time between the two cultivars decreased with an increase in temperature. At 30°C , SR took 3.2 h to open fully while SCR took 4 h. At 32.5°C , SR took 3.0 h while SCR took 3.5 h. At 35°C , 37.5°C , and 40°C , the differences in time taken to full opening were not significant (Table 2), with SR taking 2.6, 2.9, and 2.5 h, respectively, while SCR took 2.7, 3.2, and 2.8 h. At 40°C , the petals appeared slightly droopy, indicating that the temperature was too high for the flowers.

2. Effects of pollination, pistil removal, and filament wounding on flower longevity

Pollination and pistil removal significantly accelerated senescence in both cultivars. However, filament wounding was much more effective in accelerating the rate of senescence. In SR, the control recorded 9 h, while the cases with pollination and pistil removal recorded 6 and 6.9 h, respectively (Table 3). Filament wounding had the greatest effect, recording 3.9 h. In SCR, the control recorded 11.9 h, while the cases with pollination and pistil removal recorded 7.8 and 8 h, respectively. Just like in SR, filament wounding also had the greatest effect in SCR, reducing the flower longevity to 5.4 h (Table 3).

3. Ethylene produced from flower opening to closing

The flowers reached the fully open stage after 2 h, which is when ethylene measurement started. At 2 h, SR produced $1.97 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$ ethylene, while SCR produced $1.95 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$. At 4, 6, and 8 h, SR produced slightly less ethylene than SCR, recording 2.40, 2.40, and $3.80 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$, while at those times, SCR produced 3.36, 3.50, and $3.96 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$, respectively (Fig. 1). Thereafter, SR had a sharp and significant rise at 10 h, when it reached its peak of 13.65, while SCR recorded $3.67 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$. SCR reached its peak 2 h later at 12 h, which was 5.36; at this point, SR was fully closed and produced its last recorded amount of ethylene, which was $10.14 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$ and was also significantly higher than the SCR peak. SCR was almost closed at 14 h, when it produced its last recorded amount of ethylene, which was $4.42 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$ (Fig. 1). Both SR and SCR pro-

Table 1. Difference of flower longevity of *P. umbraticola* cultivars.

Cultivar	Time taken to open (h)	Time taken to close (h)	Flower longevity (h)
SR	1.2 ± 0.3	10.3 ± 0.1	9.1 ± 0.2
SCR	2.5 ± 0.1	15.3 ± 0.2	12.8 ± 0.3

** indicates significant difference in *t*-test ($P < 0.01$, $n = 5$). The times taken to open and to close are also shown; this time is from the bud stage.

Table 2. Effects of temperature on flower opening of *P. umbraticola* cultivars.

Cultivar	Time to open at different temperatures (h)					
	27.5°C	30°C	32.5°C	35°C	37.5°C	40°C
SR	3.3 ± 0.1	3.2 ± 0.2	3.0 ± 0.1	2.6 ± 0.6	2.9 ± 0.3	2.5 ± 0.2
SCR	4.4 ± 0.3	4.0 ± 0.2	3.5 ± 0.1	2.7 ± 0.2	3.2 ± 0.7	2.8 ± 0.4
	*	*	*	NS	NS	NS

* indicates significant difference in *t*-test ($P < 0.05$, $n = 5$); NS indicates no significant difference.

Table 3. The effects of pollination, pistil removal and filament wounding on flower longevity of *P. umbraticola* cultivars.

Cultivar	Treatment	Time taken to close (h)
SR	Control	9.0±0.4 a
	Pollination	6.0±0.3 c
	Pistil removal	6.9±0.3 b
	Filament wounding	3.9±0.2 d
SCR	Control	11.9±0.5 a
	Pollination	7.8±0.3 b
	Pistil removal	8.0±0.3 b
	Filament wounding	5.4±0.2 c

Different letters indicate significant differences in Tukey's multiple range test ($P < 0.01$, $n = 5$).

Fig. 1. Endogenous ethylene production from flower opening to closure of *P. umbraticola* cultivars. SR: 'Single Red', SCR: 'Sanchuraka Cherry Red'. The flowers of SR were fully closed at 12 h, while those of SCR were almost closed at 14 h. Data are presented as the mean ± SE ($n = 3$).

duced detectable amounts of ethylene from opening to closure. The peak levels of ethylene production by the two cultivars were significantly different, with SR producing more ethylene than SCR. The peak ethylene production in SR occurred at 10 h, which was 2 h earlier than the peak of SCR, occurring at 12 h (Fig. 1).

4. Exogenous ethylene treatment

In SR, exogenous ethylene treatment accelerated senescence. A level of $0.5 \mu\text{L}\cdot\text{L}^{-1}$ resulted in flowers wilting at 6.5 h, while cases with 1 and $2 \mu\text{L}\cdot\text{L}^{-1}$ recorded 6.4 h (Table 4). Exogenous ethylene was much more effective at accelerating senescence than the control, for which the time of wilting was 9.3 h. In SCR, the trends were almost the same as for SR. SCR control recorded 11.9 h, while 0.5 and $1 \mu\text{L}\cdot\text{L}^{-1}$ had the same flower longevity of 8.5 h. The case of $2 \mu\text{L}\cdot\text{L}^{-1}$ had slightly shorter flower longevity, recording 8.4 h (Table 4). Exogenous ethylene treatments significantly accelerated senescence in both cultivars. There was no

Table 4. The effects of exogenous ethylene treatment on flower longevity of *P. umbraticola* cultivars.

Cultivar	Ethylene treatment ($\mu\text{L}\cdot\text{L}^{-1}$)	Time taken to close (h)
SR	Control	9.3±0.2 a
	0.5	6.5±0.6 b
	1	6.4±0.6 b
	2	6.4±0.4 b
SCR	Control	11.9±0.6 a
	0.5	8.5±0.3 b
	1	8.5±0.3 b
	2	8.4±0.3 b

Different letters indicate significant differences in Tukey's multiple range test ($P < 0.01$, $n = 8$).

Table 5. The effects of ethylene inhibitor treatments on flower longevity of *P. umbraticola* cultivars.

Cultivar	Ethylene inhibitor	Time taken to close (h)
SR	Control	9.0±0.3 c
	AVG	22.1±2.0 a
	1-MCP	13.8±0.4 b
SCR	Control	10.4±0.3 c
	AVG	24.6±3.0 a
	1-MCP	13.0±0.7 b

Different letters indicate significant differences in Tukey's multiple range test ($P < 0.01$, $n = 5$). AVG: aminoethoxyvinylglycine, 1-MCP: 1-methylcyclopropene.

significant difference among the three concentrations used (0.5 , 1 , and $2 \mu\text{L}\cdot\text{L}^{-1}$).

5. Ethylene action and biosynthesis inhibitor treatments (AVG and 1-MCP)

1-MCP, an ethylene action inhibitor, significantly improved flower longevity in both cultivars. It seems its effect was much greater in SR, which averaged 13.8 h compared with 9 h for the control. In SCR, it recorded 13.0 h, compared with 10.4 h for the control. AVG, an ethylene biosynthesis inhibitor, had a much more significant effect, improving the longevity of both cultivars. In SR, AVG-treated flowers had average flower longevity of 22.1 h, while in SCR, they had 24.6 h (Table 5).

Discussion

SCR and SR had different flower longevity of 12.8 and 9.1 h, respectively. The flowers of SR opened earlier than those of SCR (Table 1). In flowering plants, flower longevity is species-specific and is closely linked to reproductive strategy (Shibuya et al., 2014). The newly released 'Sanchuraka' cultivars also showed some slight variation in flower longevity among themselves (data not shown). The difference in flower longevity between SR and SCR might have been due to the

difference in the amount of endogenous ethylene produced. In carnation, the long-lasting cultivars produced less ethylene than short-lived conventional cultivars (Nukui et al., 2004; Onozaki et al., 2006). In *P. umbraticola*, SR produced more ethylene (with peak ethylene production of $13.65 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$) than SCR ($5.36 \text{ nL} \cdot \text{g}^{-1} \text{ FW} \cdot \text{h}^{-1}$) (Fig. 1). The flowers of SCR opened and closed later than those of SR. SCR took 15.3 h from opening to closure, while SR took 10.3 h (Table 1). SCR requires a high temperature to open compared with SR (Table 2); at 25°C , although SR did not fully open, it was at a more advanced opening stage than SCR, probably showing that, at a lower temperature than for SCR, SR can accumulate enough heat to open.

Pollination and pistil removal significantly accelerated senescence of both SCR and SR; however, filament wounding was much more effective in accelerating senescence. In *P. umbraticola*, filament wounding accelerated senescence by increasing ethylene production (Ichimura and Suto, 1998b). Pollination has been reported to accelerate senescence in many flowers such as orchids (Porat et al., 1994) and *P. grandiflora* (Iwanami and Hoshino, 1963). In *Petunia*, pollination and wounding of pistils stimulated senescence (Whitehead et al., 1984). The effects of pollination, pistil removal and filament wounding may be attributable to an increase in ethylene production since there will be small chances of wounding, which in turn can cause ethylene production. Our results agree with the findings of Ichimura and Suto (1998b) using the conventional cultivar ANR1, although this previous paper refers to it as *Portulaca* hybrid.

Exogenous ethylene treatments at 0.5, 1, and $2 \mu\text{L} \cdot \text{L}^{-1}$ significantly accelerated the rate of senescence in both cultivars (Table 4). There was no significant difference between the three ethylene concentrations used. Since exogenous ethylene accelerated senescence in both cultivars, this implies that the long vase life of SCR might not be associated with ethylene sensitivity, but rather with its lower ethylene production. In carnations, flowers of lines selected for a long vase life produced very low levels of ethylene during senescence, whereas the ethylene sensitivity of the selected lines was generally high (Onozaki et al., 2006). Although *P. umbraticola* is ephemeral in nature, our results can be compared to those of carnations. The use of AVG and 1-MCP significantly improved flower longevity in both cultivars. Since exogenous ethylene accelerated senescence and AVG and 1-MCP delayed senescence, this confirmed that the senescence of *P. umbraticola* cultivars SR and SCR is ethylene-dependent. In *Hibiscus rosa-sinensis*, treatment with ACC and 1-MCP confirmed that flower senescence in *Hibiscus* is ethylene-dependent (Trivellini et al., 2011). In *Portulaca* hybrid, treatment with ethylene for one hour significantly accelerated flower senescence, and the senescence of both intact

and filament-wounded flowers was markedly delayed by exposure to norbornadiene (NBD), an inhibitor of ethylene action (Ichimura and Suto, 1998a). In *Ipomoea nil* 'Violet', exogenously applied ethylene accelerated petal senescence; however, AVG and 1-MCP did not delay senescence (Yamada et al., 2006). On the basis of these observations, petal senescence of *I. nil* 'Violet' is considered to be regulated independently of endogenous ethylene (Shibuya, 2012; Yamada et al., 2006). Although the senescence of both *P. umbraticola* cultivars and *I. nil* 'Violet' is accelerated by exogenous ethylene, their senescence pathways tend to differ since they respond differently to ethylene action and ethylene biosynthesis inhibitors. The plant growth hormone ethylene is known to hasten the senescence of many cut flowers such as carnations (Mayak et al., 1976; Satoh, 2011) and *Portulaca* hybrid (Ichimura and Suto, 1998a). This was almost the same scenario as how exogenously applied ethylene accelerated senescence of both SR and SCR. Senescence of *P. umbraticola* cultivars is ethylene-dependent, so ethylene inhibitors prolonged vase life while exogenous ethylene accelerated senescence.

In conclusion, flower longevity of SCR might have been selected on the basis of endogenous ethylene production rather than ethylene sensitivity. Both SR and SCR were sensitive to exogenous ethylene, but SCR produced less ethylene than SR, thereby probably explaining the difference in their flower longevity. However, the mechanism through which SCR produces lower endogenous ethylene than SR is still not clear. Furthermore, analysis of ethylene-associated genes from flower opening to closure might be crucial for understanding the senescence process. To obtain a deep understanding of this there is a need for information specific to each cultivar, rather than generalizing the findings across the species. With the current trend of a global rise in temperature, *P. umbraticola* provides a realistic adaptation option in the ornamental industry, so basic information on this ornamental plant is promising for promoting the future of the industry.

Acknowledgements

Our sincere gratitude goes to NARO Institute of Floricultural Science and its staff for providing all of the necessary support towards this work.

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