JARQ 57 (3), 217-224 (2023) https://www.jircas.go.jp

# Analysis of Scent Emission in Cut Flowers of *Tulipa gesneriana* L. 'Niigata 13 go,' Known as Koshiharuka

**Kyutaro KISHIMOTO[1]* and Yusuke WATANABE[2]**

[1] Institute of Vegetable and Floriculture Science, National Agriculture and Food Research Organization, Tsukuba, Japan
[2] Horticultural Research Center, Niigata Agricultural Research Institute, Seiro, Niigata, Japan

## Abstract

To utilize scent as an added value of cut tulip flowers, it is necessary to reveal how the scent changes during anthesis. This study investigated the daily changes in scent emission of cut flowers under different temperatures (13℃, 18℃, and 23℃), using *Tulipa* 'Niigata 13 go.' At 23℃, the total emission was high and decreased with tepal senescence. The total emissions at 18℃ increased later than those at 23°C. The lowest temperature (13°C) resulted in overall low scent emissions compared to those at the highest temperature of 23°C. Additionally, as the tepals matured, the scent composition changed from monoterpene to benzenoid. These changes in the quantity and composition of scents were observed earlier at higher temperatures. One of the underlying factors is presumed to be the rapid maturation and senescence of flowers at high temperatures. Therefore, both flower maturation and temperature are required for sufficient scent emission. Furthermore, the emissions of scent components with the same biosynthetic pathway tended to behave similarly. The scent of cut tulip flowers changed both quantitatively and qualitatively during anthesis, and these changes were affected by temperature. This result suggests that the scent of cut tulip flowers can be partially controlled by artificial temperature management.

**Discipline:** Horticulture
**Additional key words:** benzenoid, β-ocimene, phenylacetaldehyde, terpenoid, tulip

## Introduction

Scent is a desired characteristic of flowers, and ~10% to 25% of Japanese general consumers cite "scent" as a decision-making factor when purchasing cut flowers (Kaneko 2009, 2012; Tsuji 2000). In a questionnaire survey on flower scents conducted with 870 general consumers in Japan, ~30% of the respondents stated that they would like a scent to be added to tulips (Kishimoto 2012). This percentage was one of the highest in the survey, along with that for carnations and roses. This suggests that the desire for tulips to emit a scent is relatively high in Japan. In addition, tulip cultivars have been shown to have a wide variety of scents (Oyama-Okubo & Tsuji 2019). Based on these data, scent is expected to create an added value of cut tulip flowers.

To utilize scent as an added value of cut flowers, it is necessary to reveal how scent changes during anthesis. Various cut flowers, including one tulip cultivar, have been reported to exhibit large changes in scent emissions during anthesis (Ikeura et al. 2013, Kishimoto & Shibuya 2021, Kishimoto & Watanabe 2023). Several young and mature flowers are known to emit different odors in response to changes in their principal components (Pragadheesh et al. 2017, Robertson et al. 1995). Floral scent emissions are also affected by temperature. For instance, temperature considerably affects the quantity of scent emitted from wild petunias (*Petunia axillaris* Britt.) and carnations (*Dianthus caryophyllus* L.) (Kishimoto 2022, Sagae et al. 2008). The vase life of cut tulip flowers is strongly influenced by temperature (Ichimura et al. 2011); therefore, the scent emissions are also expected to

Present address:
[2] Tokamachi Regional Development Bureau, Toka, Niigata, Japan
*Corresponding author: cucumber@affrc.go.jp
Received 30 August 2022; accepted 14 November 2022.

be temperature sensitive.

This study investigated the basic characteristics of the scent emissions of cut tulip flowers of *Tulipa* 'Niigata 13 go,' which is registered as a cultivar from Niigata Prefecture, Japan, as a model. This cultivar, commonly known as koshiharuka, has a unique scent. First, the daily change in scent emission from cut flowers was revealed at 23°C, which is a common temperature used in quality confirmation tests for cut flowers (Ichimura et al. 2011, Pun et al. 2016). Next, by comparing the results of the same investigation at different temperatures (18°C and 13°C), the response of the emissions to temperature was revealed. Based on these results, this study discusses the effects of visible flower development and temperature on scent emissions from cut tulip flowers.

## Materials and methods

### 1. Materials

Koshiharuka tulips were cultivated at the Horticultural Research Center, Niigata Agricultural Research Institute (37°59′ N, 139°17′ E), Seiro, Niigata, Japan. Vernalized bulbs were planted in containers (H 25 cm × W 40 cm × L 60 cm) containing potting soil and incubated in a glass greenhouse. Vernalization treatment and cultivation of the bulbs were performed according to the method of Kishimoto and Watanabe (2023).

Cut flowers, ~40-cm long, were placed in tap water and incubated at 5°C. After 3 h, the cut flowers were wrapped in newspaper, packed in a cardboard box, and kept at 5°C for ~1 day. The box containing the cut flowers was shipped by a private courier to the Institute of Vegetable and Floriculture Science, NARO (36°02′ N, 140°05′ E), Tsukuba, Japan. The temperature and relative humidity during transportation in the box, measured using a data logger, were 2°C-10°C and >80%, respectively.

### 2. Temperature treatment

The maintenance conditions for the cut flowers were in accordance with those described by Kishimoto and Watanabe (2023). Each flower was cut back to a stem length of ~30 cm and placed in a glass flask containing 500-mL distilled water. Subsequently, the cut flowers were maintained under a 12-h light-dark photoperiod, at a light intensity of ~10 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and at a relative humidity of 70%. The cut flowers were maintained at 23°C for 3 h to ensure that their physiological conditions were similar. The cut flowers were then divided into three groups and maintained at 13°C, 18°C, and 23°C for 7 days.

### 3. Collection of emitted scents and gas chromatography–mass spectrometry (GC-MS) analysis

The scent emitted from the tulip flowers was collected using the dynamic headspace method (Kishimoto & Watanabe 2023). The collections were consistently performed at 09:30 h to reduce any effects of the circadian rhythm on scent emission. The tulip flowers were wrapped in 1-L Tedlar bags (GL Science Inc., Tokyo, Japan), which were then sealed with tape. A constant stream of air (500 $mL \cdot min^{-1}$) was filtered through activated charcoal and piped into the bags. The volatiles were collected for 1 h using a Tenax-TA tube (180 mg, 60 × 80 mesh; Gerstel GmbH & Co. KG, Mülheim, Germany).

The components collected in the Tenax-TA tubes were analyzed via gas chromatography–mass spectrometry (GC-MS) using an Agilent 6890 N GC system connected to an Agilent 5930 N mass-selective detector (Agilent Technologies, Inc., Santa Clara, CA, USA). A cooled injection system (Gerstel GmbH & Co. KG) and DB-WAX capillary column (Agilent 122–7032; Agilent Technologies) were used for GC. Helium was used as the carrier gas at a flow rate of 1.0 $mL \cdot min^{-1}$. The temperature conditions of the GC-MS were as described by Kishimoto and Watanabe (2023). Ionization was performed in the electron impact mode at 70 eV, and a mass scan range of 30-350 *m/z* was monitored.

The detected scent components were identified using the Wiley 9$^{th}$/NIST 2011 library search system (Agilent Technologies), and the mass spectra and retention times of the standards were determined (purity >90%) (Fujifilm Wako Pure Chemical Co., Ltd., Osaka, Japan; Kanto Chemical Co., Inc., Tokyo, Japan; Sigma-Aldrich Co., LLC, St. Louis, MO, USA; and Tokyo Chemical Industry Co., Ltd., Tokyo, Japan). The amount of each scent compound in each standard was calculated based on the peak areas of 5, 25, 50, 250, and 1,000 ng on the ion chromatograms. The mean values of three independent plants are presented for each condition.

To determine whether there were differences in the quantities of scent emissions, we used two-way randomized block analysis of variance (ANOVA), considering temperature treatments and measurement days as the independent variables (fixed factors), individual cut flowers as the block (random factors), and scent component emissions as the dependent variable. If a significant difference was detected in the interaction by ANOVA, all treatments were compared by multiple testing [Tukey–Kramer honestly significant difference (HSD) test]. Statistical analyses were performed using the free statistical analysis software EZR version 1.55

(available at https://www.jichi.ac.jp/saitama-sct/SaitamaHP.files/statmedEN.html), which was referenced by Kanda (2013).

## Results

### 1. Changes in scent emission at 23°C

Fifty-five scent components emitted from the cut flowers were identified using GC-MS (Table 1). Other minor components could not be accurately identified because of the difficulty in obtaining their standards. These 55 compounds accounted for 87%-94% of the total peak area in the GC-MS chromatogram. The emission changes of these compounds and the appearance of the cut flowers at 23°C are shown in Figure 1 a and Table 1 (or Fig. 2 a), respectively. The koshiharuka scent is composed of benzenoid aromatic compounds, fatty acid derivatives, monoterpenes, and sesquiterpenes. The principal components were benzenoids, benzaldehyde, benzyl alcohol, phenylacetaldehyde, and the monoterpene β-ocimene. The total quantity of scent emission remained high until the 4$^{th}$ day of flower opening and then decreased rapidly. These decreases in scent emission appeared to be synchronized with flower senescence, such as tepal discoloration and wilting (Figs. 1 c, 2 a).

Focusing on the composition of the scent emissions, the ratio markedly changed mainly due to the increase and decrease in the principal scent components (Table 1; Fig. 2 b). Until the 2$^{nd}$ day, the composition was dominated by β-ocimenes. However, the benzenoids gradually increased, and on the 4$^{th}$ day, the composition changed to a benzenoid-based compound, such as phenylacetaldehyde and benzyl alcohol. In addition, on the 6$^{th}$ day, the decrease in monoterpenes and increase in sesquiterpenes made these proportions comparable. On the 8$^{th}$ day, the proportion of fatty acid derivatives increased due to the greater reduction in other scent components, but the total quantity of scent emitted was very low (Fig. 2 b). The monoterpene-based scent exhibited a gentle herbaceous aroma, derived from β-ocimene. In contrast, when the scent was benzenoid-based, the flowers exhibited a fruity sweet odor derived from benzenoids.

### 2. Comparison of scent emission under different temperatures

Figures 1 and 2 show comparisons of the changes in flower appearance, total scent emission, and scent composition in cut flowers at 13°C, 18°C, and 23°C. The cut flowers were kept at 23°C for the 1$^{st}$ day and then subjected to each temperature. The elongation and bending of the flower stalks progressed faster at higher temperatures (Fig. 1 a). Tepal expansion also progressed faster at higher temperatures (Fig. 1 c). Tepal senescence, such as discoloration and wilting, occurred more quickly at 23°C than at 18°C. At 13°C, no visible senescence was observed during the experimental period.

The change in total scent emissions differed depending on the temperature (Fig. 2 a). The emissions at 23°C remained high until the 4$^{th}$ day, but then declined rapidly. Until the 2$^{nd}$ day, the scent emission at 18°C was significantly lower than that at 23°C. However, on the 4$^{th}$ day, it reached the same level as that at 23°C. Subsequently, the scent emission at 18°C leveled off, with a decreased beginning at 23°C, and on the 6$^{th}$ day, the emission at 18°C significantly exceeded that at 23°C. At 13°C, the changes in scent emission were relatively minor, and even after the tepals were visibly mature (the 6$^{th}$-8$^{th}$ day in Fig. 1), they did not show scent emissions as high as at 23°C and had little scent emission.

The scent composition was also affected by the different temperatures (Fig. 2 b). At all temperatures, the proportion of monoterpenes decreased and the proportion of benzenoids increased each day. Reversal of the monoterpene and benzenoid ratios was observed on the 4$^{th}$ day at 23°C and on the 6$^{th}$ or 8$^{th}$ day at 18°C. At 13°C, no apparent proportion reversal was observed during the investigation period. Thus, the rate of change in the scent composition differed depending on the temperature.

Figure 3 shows the changes in the emissions of the principal components from each group, which shared a common metabolic pathway at each temperature. At 23°C, the benzenoids, including benzaldehyde, benzyl alcohol, and phenylacetaldehyde, increased until the 4$^{th}$ day and then decreased. At 18°C and 13°C, these benzenoids tended to increase gradually until the 6$^{th}$ or 8$^{th}$ day. For the monoterpene geranylacetone, higher temperatures were related to earlier peaks in the emission and earlier declines. In contrast, the monoterpenes β-ocimene and α-terpineol at 23°C had the highest emissions on the 1$^{st}$ and 2$^{nd}$ day and then decreased rapidly. At 18°C and 13°C, the emissions of these two monoterpenes decreased slowly or remained at similar levels after the 2$^{nd}$ day. The patterns of emission change for the fatty acid derivatives, (*Z*)-3-hexenol and (*Z*)-3-hexenyl acetate, were relatively similar to those of the monoterpenes (β-ocimene and α-terpineol). For the sesquiterpenes, the emission of compounds other than caryophyllene was very small (Table 1). At 23°C, caryophyllene exhibited the highest emission on the 6$^{th}$ day. A significant increase in the sesquiterpene emissions was observed only on the 8$^{th}$ day at 18°C. Although the changes in the two monoterpenes and fatty acid derivatives were similar, the other groups exhibited unique daily changes and temperature responses. In

**Table 1. Changes in emission quantities (nmol $h^{-1}$/flower) of 55 scent components in cut flowers of koshiharuka tulips at 23°C**

| Scent compound | | Flower opening days | | | | |
|---|---|---|---|---|---|---|
| | | 1 day | 2 days | 4 days | 6 days | 8 days |
| Benzenoid aromatic compound | Acetophenone | trace | trace | 0.1 ± 0.0[z] | 0.1 ± 0.1 | — |
| | Benzaldehyde | 0.1 ± 0.0 | 2.7 ± 0.7 | 5.1 ± 0.8 | 1.9 ± 0.9 | trace |
| | Benzyl acetate | — | — | 0.1 ± 0.0 | trace | trace |
| | Benzyl alcohol | 0.1 ± 0.1 | 1.2 ± 0.4 | **9.2 ± 1.6** | 1.1 ± 0.5 | 0.1 ± 0.0 |
| | Benzyl benzoate | 0.1 ± 0.1 | 0.2 ± 0.1 | 0.1 ± 0.1 | 0.1 ± 0.0 | 0.1 ± 0.1 |
| | Benzyl tiglate | — | 0.2 ± 0.1 | 0.0 ± 0.0 | — | — |
| | 3,5-Dimethoxytoluene | trace | trace | trace | trace | trace |
| | Elemicin | — | — | — | — | trace |
| | Eugenol | 0.1 ± 0.1 | — | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 |
| | Ethylhexyl benzoate | trace | trace | trace | trace | trace |
| | (*Z*)-3-Hexenyl benzoate | — | — | 0.0 ± 0.0 | trace | — |
| | Methyl benzoate | — | — | trace | trace | — |
| | 4-Methoxybenzyl alcohol | — | — | trace | | — |
| | Methyl salicylate | — | trace | trace | — | — |
| | Pentyl benzoate | — | — | trace | — | — |
| | Phenethyl acetate | — | — | — | trace | trace |
| | Phenylacetaldehyde | 0.4 ± 0.1 | 1.4 ± 0.4 | 4.2 ± 1.7 | **3.4 ± 0.7** | **0.4 ± 0.0** |
| | 2-Phenylethanol | 0.0 ± 0.0 | 0.3 ± 0.1 | 0.9 ± 0.5 | 0.9 ± 0.2 | 0.1 ± 0.0 |
| | Thymol | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | trace | — |
| Fatty acid derivative | Eicosane | — | — | — | trace | trace |
| | Heneicosane | trace | — | trace | — | trace |
| | Heptadecane | — | — | 0.1 ± 0.0 | 0.1 ± 0.0 | trace |
| | Hexadecane | 0.1 ± 0.1 | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | 0.1 ± 0.0 |
| | n-hexanol | 0.1 ± 0.1 | 0.1 ± 0.1 | trace | — | — |
| | (*E*)-2-Hexenal | 0.4 ± 0.0 | 0.3 ± 0.0 | trace | — | — |
| | (*Z*)-3-Hexenol | 1.0 ± 0.2 | 0.6 ± 0.1 | 0.2 ± 0.2 | trace | trace |
| | (*Z*)-3-Hexenyl acetate | 0.2 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 | trace | trace |
| | 6-Methyl-5-heptene-2-one | trace | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | — |
| | Nonadecane | trace | — | trace | trace | trace |
| | Nonanal | 0.1 ± 0.1 | 0.3 ± 0.2 | 0.2 ± 0.0 | 0.3 ± 0.0 | 0.2 ± 0.0 |
| | Octadecane | trace | trace | trace | trace | trace |
| | Octanal | 0.1 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 | — |
| | (*Z*)-2-Pentenol | — | 0.4 ± 0.0 | 0.1 ± 0.1 | — | — |
| | Tetradecane | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | trace |
| | Tridecane | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | — |
| Monoterpene | Borneol | — | trace | trace | — | — |
| | Carveol | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | trace |
| | 3-Carene | — | — | trace | — | — |
| | Citronellal | trace | trace | trace | trace | — |
| | Geranylacetone | trace | 0.3 ± 0.0 | 0.1 ± 0.0 | trace | trace |
| | D-Limonene | — | — | — | — | trace |
| | Linalool | — | — | trace | trace | — |
| | β-Myrcene | 0.2 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 | trace | — |
| | β-Ocimene | **15.8 ± 3.1** | **16.7 ± 3.4** | 5.2 ± 1.7 | 0.6 ± 0.3 | trace |
| | Pinocarveol | 0.1 ± 0.0 | 0.1 ± 0.0 | — | — | — |
| | α-Terpineol | 0.5 ± 0.2 | 0.4 ± 0.2 | 0.1 ± 0.1 | trace | — |
| | Safranal | 0.1 ± 0.0 | 0.1 ± 0.0 | trace | — | — |
| | Sabinene | trace | — | — | trace | trace |
| Sesquiterpene | β-Caryophyllene | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.3 ± 0.1 | 0.5 ± 0.2 | 0.1 ± 0.0 |
| | Caryophyllene oxide | trace | trace | trace | 0.1 ± 0.0 | — |
| | Farnesene | — | — | trace | trace | — |
| | Farnesol | trace | 0.1 ± 0.1 | trace | trace | — |
| | Germacrene D | 0.1 ± 0.1 | — | 0.1 ± 0.0 | 0.1 ± 0.0 | — |
| | Humulene | — | — | 0.1 ± 0.1 | 0.2 ± 0.1 | — |
| | Nerolidol | — | trace | trace | 0.1 ± 0.1 | trace |
| Total | | 20.4 ± 3.5 | 26.7 ± 2.9 | 27.1 ± 3.4 | 10.2 ± 2.4 | 1.6 ± 0.3 |
| | | 92%[y] | 94% | 94% | 91% | 87% |

Numbers in bold represent the highest value on each measurement day.
Dashes represent that the scent was not detected.
trace <0.05
[z] mean ± SE, n = 3
[y] Mean percentage of these scent compounds in the total peak area of the GC-MS chromatogram

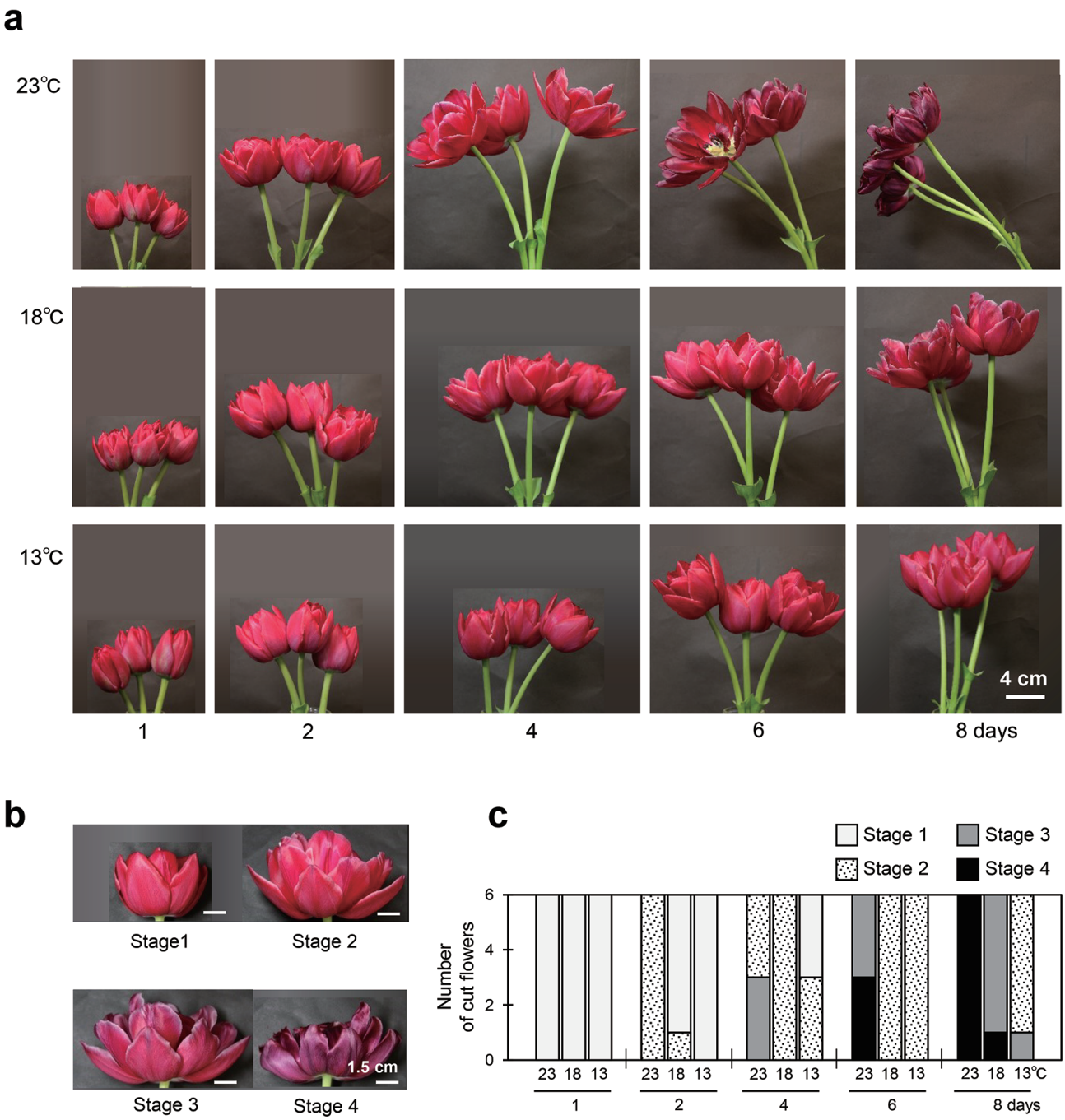


**Fig. 1. Changes in the flower appearance in cut flowers of koshiharuka tulips at different temperatures**
In Panel a, the cut flowers were kept at 23°C for the 1st day and then subjected to different temperatures. In Panel b, flower maturity during the observation period was categorized into four stages. Stage 1, the flowers not fully open; Stage 2, flowers open and no discoloration of tepals; Stage 3, >50% of the tepals are discolored with no noticeable wilting; and Stage 4, significant wilting of the tepals. In Panel c, changes in the number of cut flowers at each maturity stage under each temperature condition are shown.

contrast, except for geranylacetone, the patterns of change were relatively similar for scent components within the same group at the same temperature.

## Discussion

This study attempted to reveal the basic nature of scent emissions from cut tulip flowers using koshiharuka as a model. To ensure data accuracy, this study targeted only 55 scent compounds that could be identified using

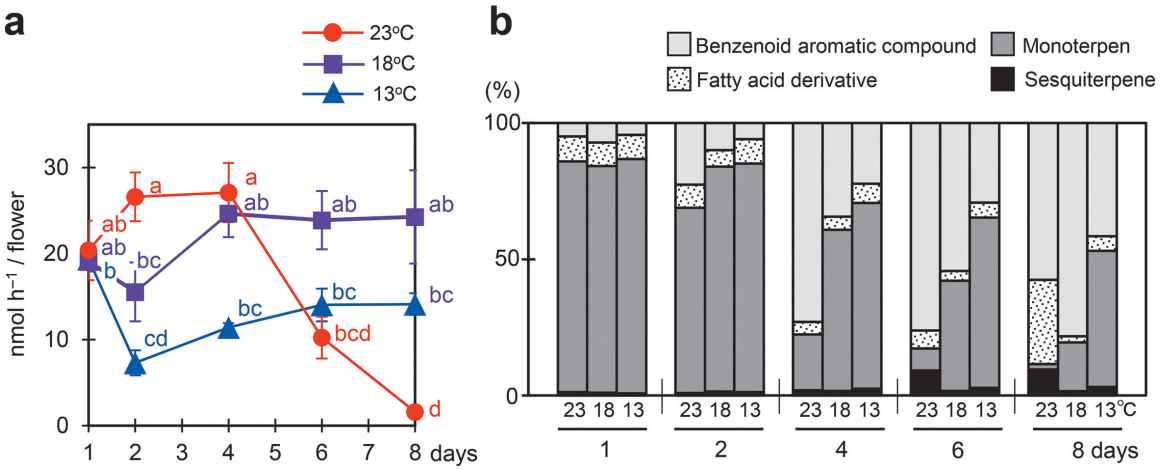


**Fig. 2. Changes in the quantity (Panel a) and composition (Panel b) of scent emissions in cut flowers of koshiharuka tulips at different temperatures**

The cut flowers were kept at 23°C for the 1st day and then subjected to different temperatures. In Panels a and b, the total emissions of the 55 scent components, which accounted for 87%-94% of the total peak area in the GC-MS chromatogram, were investigated. In Panel a, all data were analyzed using two-way ANOVA, following the Tukey–Kramer HSD test. The differences were considered statistically significant at $P<0.05$. Error bars indicate SE (n = 3). Different letters indicate significant differences.

their standards, accounting for >87% of the GC-MS chromatogram peak area. In addition, the temperature conditions considered were in the temperature range commonly used for cut flower management (Cevallos & Reid 2001, Ichimura et al. 2011), which was sufficient to induce clear differences in the appearance and vase life of the cut flowers (Fig. 1). Therefore, we believe that it is possible to discuss changes in the scent of the tulips based on the results under these limited conditions.

The quantity and composition of scent emissions from tulip cut flowers changed during anthesis, and these changes were affected by temperature (Fig. 2). Changes also occurred in visible flower development, such as with the expansion and senescence of tepals (Fig. 1). Thus, scent emission is affected by the degree of flower maturation or senescence (Macnish et al. 2010, Schade et al. 2001, Underwood et al. 2005). Changes in scent emission, maturation, and senescence in flowers were induced earlier at higher temperatures. As the temperature of cut flowers increased, sugar utilization for respiration also increased, and flower maturation and senescence were promoted (Gupta & Dubey 2018). Therefore, difference in scent emissions caused by temperature changes may be partially attributable to the effects of temperature on flower maturation and senescence.

In contrast, at 13°C, the high scent emission accompanying flower development that occurred at other temperatures was not observed (Figs. 1 c, 2 a). Therefore, a certain temperature is required to achieve sufficient scent emission. A study using petunia (*Petunia* × *hybrida* Vilm. 'Mitchell') as a model suggested that ~50% of the scent components in the flowers were accumulated in the cuticle on the petal surface (Liao et al. 2021). At low temperatures, such as 13°C, the volatilization of scent components from the cuticle may have been inactive. However, further investigations are required to confirm this hypothesis.

These results suggest that scent emissions from cut tulip flowers can be controlled by artificial temperature management. For cut koshiharuka flowers, 18°C appeared to be relatively suitable for both scent emission and vase life (Figs. 1 c, 2 a). For carnation cut flowers, presale management at a low temperature of 10°C is suggested to improve the scent emission and vase life, assuming a room temperature of 23°C after sale (Kishimoto 2022). In the future, by conducting research that incorporates changes in temperature, more suitable management methods for tulip cut flower scent emissions can be identified.

The results shown in Figure 3 reveal that the principal scent components derived from the same metabolic pathway tend to behave similarly. These benzenoids, fatty acid derivatives, monoterpenes, and sesquiterpenes are biosynthesized via the phenylpropanoid/benzenoid biosynthetic, oxylipin metabolic, plastidial methylerythritol phosphate, and cytosolic mevalonic acid pathways, respectively (Matsui 2006, Muhlemann 2014). Although geranylacetone behaved differently from other monoterpenes, it has also been reported to be biosynthesized through a unique

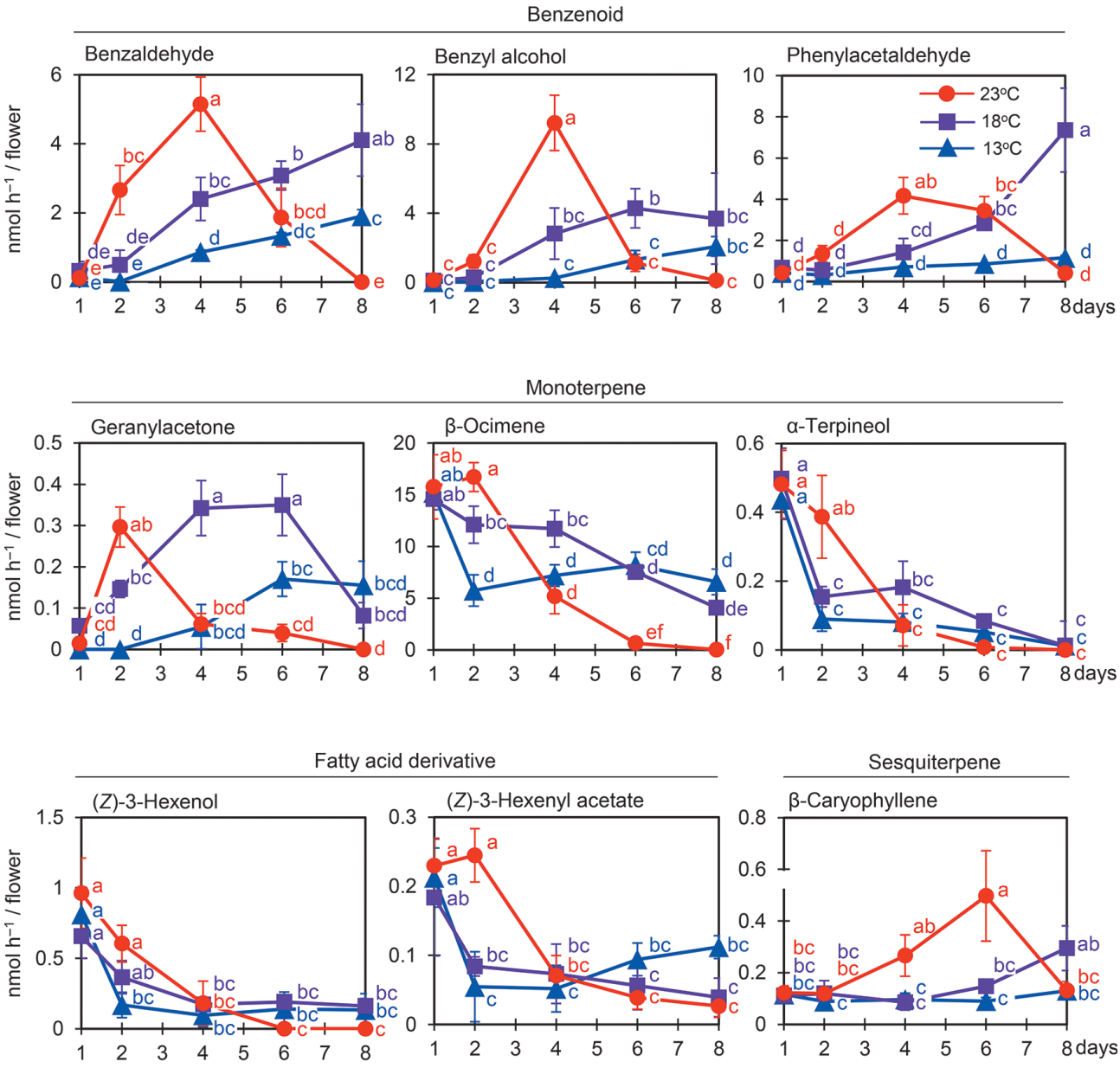


**Fig. 3. Changes in the emissions of principal scent components in cut flowers of koshiharuka tulips at different temperatures**
The cut flowers were kept at 23°C for the 1st day and then subjected to different temperatures. All the data were analyzed using two-way ANOVA, followed by the Tukey–Kramer HSD test. The differences were considered statistically significant at $P < 0.05$. Error bars indicate SE (n = 3). Different letters indicate significant differences.

metabolic pathway using carotenoids as substrates (Simkin et al. 2004). These results suggest that scent emission, which changes with flower development or temperature, is differentially regulated or influenced at the biochemical level. Owing to the wide variety of principal scent components in tulip cultivars (Oyama-Okubo & Tsuji 2019), different cultivars may exhibit altered scent emission behaviors. Therefore, to understand the basic nature of changes in the scent of cut tulip flowers, comparative experiments using more cultivars are necessary.

## Acknowledgements

This research was supported by grants from the Project of the NARO Bio-oriented Technology Research Advancement Institution (Research Program on Development of Innovative Technology, 26103C), Japan. We thank Dr. Katsuhiko Sumitomo (Institute of Vegetable and Floriculture Science, NARO, Tsukuba, Japan) for his advice on the statistical analysis.

## References


Cevallos, J. C. & Reid, M. S. (2001) Effect of dry and wet storage at different temperatures on the vase life of cut flowers. *HortTechnology*, **11**, 199-202.

Gupta, J. & Dubey, R. K. (2018) Factors affecting post-harvest life of flower crops. *Int. J. Curr. Microbiol. App. Sci*., **7**, 548-557.

Ichimura, K. et al. (2011) Investigation of the vase life of cut flowers in different seasons. *Kakikenkyūsyo Kenkyūhōkoku* (*Bull. Natl. Inst. Flor. Sci*.), **11**, 49-65 [In Japanese with English abstract].

Ikeura, H. et al. (2013) Effect of silver thiosulfate complex (STS) in combination with sucrose on the post-harvest fragrance of cut sweet pea flowers. *Acta Hortic*., **970**, 197-204.

Kaneko, N. (2009) One consideration of "cut-flowers" consumption and consumer needs. *Matumoto Daigaku Kenkyū Kiyō* (*J. Matsumoto Univ.*), **7**, 33-47 [In Japanese].

Kaneko, N. (2012) One consideration of "cut-flowers" consumer needs: The case of a direct sales store. *Matumoto Daigaku Kenkyū Kiyō* (*J. Matsumoto Univ.*), **10**, 271-299 [In Japanese].

Kishimoto, K. (2012) Characteristics of floral scent components in Dianthus; Evaluation as a breeding material for fragrant carnations. *Syokutyō* (*SHOKUCHO*), **46**, 291-299 [In Japanese].

Kishimoto, K. (2022) Effect of temperature on scent emission from carnation cut flowers. *JARQ*, **56**, 163-170.

Kishimoto, K. & Shibuya, K. (2021) Scent emissions and expression of scent emission-related genes: a comparison between cut and intact carnation flowers. *Sci. Hortic*., **281**, 109920.

Kishimoto, K. & Watanabe, Y. (2023) Effect of pre- and post-transport preservative treatments to extend vase life on scent emission of tulip cut flowers. *JARQ*, **57**, 47-54.

Liao, P. et al. (2021) Cuticle thickness affects dynamics of volatile emission from petunia flowers. *Nat. Chem. Biol*., **17**, 138-145.

Macnish, A. J. et al. (2010) Physiological and molecular changes during opening and senescence of *Nicotiana mutabilis* flowers. *Plant Sci*., **179**, 267-272.

Matsui, K. (2006) Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. *Curr. Opin. Plant Biol*., **9**, 274-280.

Muhlemann, J. K. (2014) Floral volatiles: from biosynthesis to function. *Plant Cell Environ*., **37**, 1936-1949.

Oyama-Okubo, N. & Tsuji, T. (2019) Diversity of floral scent of tulips. *Acta Hortic*., **1237**, 259-267.

Pragadheesh, V. S. et al. (2017) Scent from *Jasminum grandiflorum* flowers: Investigation of the change in linalool enantiomers at various developmental stages using chemical and molecular methods. *Phytochemistry*, **140**, 83-94.

Pun, U. K. et al. (2016) Effect of sucrose on sensitivity to ethylene and enzyme activities and gene expression involved in ethylene biosynthesis in cut carnations. *Postharvest Biol. Technol*., **121**, 151-158.

Robertson, G. W. et al. (1995) Changes in the chemical composition of volatiles released by the flowers and fruits of the red raspberry (*Rubus idaeus*) cultivar glen prosen. *Phytochemistry*, **38**, 1175-1179.

Sagae, M. et al. (2008) Effect of temperature on the floral scent emission and endogenous volatile profile of *Petunia axillaris*. *Biosci. Biotechnol. Biochem*., **72**, 110-115.

Schade, F. et al. (2001) Fragrance volatiles of developing and senescing carnation flowers. *Phytochemistry*, **56**, 703-710.

Simkin, A. J. et al. (2004) The tomato *carotenoid cleavage dioxygenase 1* genes contribute to the formation of the flavor volatiles β-ionone, pseudoionone, and geranylacetone. *Plant J*., **40**, 882-892.

Tsuji, K. (2000) The trends of cut-flowers consumption and consumer's buying behavior. *Wakayamaken Nōrinsuisansōgōgizyutusentā Kenkyū Hōkoku* (*Bull. Wakayama Res. Cent. Agri. Forest. Fish*.), **1**, 111-119.

Underwood, B. A. et al. (2005) Ethylene-regulated floral volatile synthesis in petunia corollas. *Plant Physiol*., **138**, 255-266.