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Effects of Deflowering and Defoliating on the Postharvest Characteristics of Individual Organs in Cut Dahlias

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Cut dahlia (*Dahlia* Cav.) flowers have recently become popular, but their marketability has been limited due to their poor vase life. The purposes of this study were to clarify the roles of leaves and inflorescences in the senescence of cut dahlias and to discuss the sink-source relationship between vegetative organs and inflorescences. The leaf life was maintained much longer (16.7 days) than the inflorescence life (7.4 days). The inflorescence life was not affected by removal of leaves, while leaf life was prolonged (19.6 days) by removal of inflorescences. Sucrose, glucose, fructose and small quantities of *myo*-inositol were detected in florets, and in addition to these sugars, nystose and 1-kestose were detected in stems and leaves. Total sugar levels of the middle florets (14.5 mg·g^{-1} FW on day 0) declined rapidly before their senescence. Total sugar levels of leaves (20.5 mg·g^{-1} FW on day 0) and stems (19.0–22.5 mg·g^{-1} FW on day 0) also decreased gradually during the postharvest period, but the levels decreased more slowly in deflowered cut stems. Sugar leakage from stem bases into vase water occurred during the initial few days. Removal of inflorescences increased sugar leakage significantly and promoted callus formation on the stem base. From these results, the inflorescence is considered to be a strong sink for carbohydrates, and stems and leaves serve as source organs. Heat girdling applied to the flower necks and petioles, also increased sugar concentrations of stem bases, thus resulting in higher sugar leakage and callus formation, although both heat girdling treatments shortened the leaf life. The sharp decrease in sugar levels of florets and an insufficient sugar supply are considered to be responsible for the short vase life of cut dahlias. It is suggested that these effects might be partly due to the blockage of sugar flows into petals through abscission layer development in the petal-ovary boundaries. Based on these results, we illustrate the senescing process of cut dahlia flowers in relation to sugar dynamism.

Key Words: callus formation, heat girdling, sink-source relationship, sugar dynamism, sugar leakage.

Introduction

Dahlia (*Dahlia* Cav.), a member of the Asteraceae family, has recently become a popular cut flower in Japan and Europe. However, the cut flowers have a vase life of a week or less. The senescence starts with wilting and discoloration of the outermost petals due to abscission layer formation (Yang et al., 2021). With inflorescence senescence, the stem basal portion becomes thin and pale. Furthermore, without adding bactericides to the vase water, stem bases gradually rot and the vase water becomes turbid. The leaves, which

are damaged through postharvest sugar treatment, are removed during commercial trade. However, removal of leaves decreases the ornamental value of cut dahlia flowers.

Besides, leaves on cut flowers have physiological functions such as water uptake and as a carbohydrate source (Horibe et al., 2014; Mightak et al., 1974). Because cut flowers are usually maintained under low light conditions, little or no net carbon gain can be obtained through photosynthesis and consequently these cut flowers rely on stored carbohydrate reserves for flower opening and life maintenance. Carbohydrate supply is mainly obtained from stem and leaves (Adachi et al., 1999; Mor and Halevy, 1979). In cut roses and peony, soluble sugars decline in leaves and stems with flower opening during the vase period (Marissen and La Brijn, 1995; Walton et al., 2010). If the leaves also serve as carbohydrate sources in cut

dahlias, these leaves could improve the inflorescence life. Furthermore, the removal of a sink organ, i.e., inflorescences, is also likely to greatly extend the leaf life.

Although there are many studies focusing on the inflorescence senescence of cut dahlias (Azuma et al., 2019, 2020; Shimizu-Yumoto and Ichimura, 2013; Shimizu-Yumoto et al., 2020), the life of its vegetative organs and their interactions with inflorescences have rarely been studied. The purposes of this study were to clarify the roles of leaves and inflorescences in the senescence of cut dahlias and to discuss the sink-source relationship between vegetative organs and inflorescences.

Materials and Methods

Plant materials and vase conditions

Dalia (*Dalia* Cav.) 'Kokuchou' plants were propagated through cutting and grown in an open field at Kyoto University in 2021. Cut inflorescences were harvested at commercial maturity, which was determined by the horizontal position of the outermost petals. The cut inflorescences were trimmed to 40 cm, leaving leaves on the two upper nodes. Then, they were held in deionized water (DIW) containing $1 \text{ mL} \cdot \text{L}^{-1}$ Kathon™ CG (Rohm and Haas Japan K. K., Tokyo, Japan) as a bactericide for at least two hours before use in experiments. Postharvest environmental conditions were controlled at 20°C with 12-h lighting of $30 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ using day-white fluorescent tubes and 50–60% RH.

Exp. 1. Effects of removing leaves and inflorescences
Exp. 1.1 Vase life

Three types of cut dahlias, intact cut flowers (cut stems with both an inflorescence and leaves), defoliated cut flowers (cut stems with an inflorescence) and deflowered cut stems (cut stems with leaves) were prepared. These cut stems were held in vessels containing DIW supplemented with $0.2 \text{ mL} \cdot \text{L}^{-1}$ bactericide, which allowed the subsequent analysis of the vase water. Each vessel contained one cut flower with 60-mL vase water. The cut flowers were transferred to a vase with new water every 24 h.

The inflorescence life was determined when petals on the first to fifth whorls showed wilting or discoloration. The leaf life was determined when the half area of lower leaves turned yellow. Callus formation on the stem bases was observed visually.

Exp. 1.2 Changes in sugar concentrations of individual organs

Soluble carbohydrates in the middle florets (florets on the third to fourth whorls, without their ovaries), the flower necks (1 cm below the inflorescence), the lowermost leaves, and the basal portion of stems (1 cm from the cut ends) were analyzed on day 0, 5, 10, and 15. Sugars were then extracted following the modified protocol of Ichimura and Hisamatsu (1999). These tissues

(0.2 g fresh weight, FW) were frozen using liquid nitrogen and ground to pieces. The pieces were then immersed in 4 mL of 80% ethanol and heated in a water bath at 75°C for 20 min. Next, samples were centrifuged at 9,000 rpm for 5 min, after which supernatants were collected and heated at a temperature not exceeding 80°C until dried. Pellets were resolved in 1 mL DIW and then centrifuged at 12,000 rpm for 5 min. Finally, supernatants were collected for analysis using high performance liquid chromatography (HPLC).

Sugars were separated using an HPLC system (LC-10A; Shimadzu Corp., Kyoto, Japan) equipped with a refractive index detector (RID-10A; Shimadzu) on a column (SUGAR SC1011; Showa Denko K. K., Tokyo, Japan) maintained at 80°C. Carbohydrates were subsequently eluted using 5% acetonitrile at a flow rate of $1 \text{ mL} \cdot \text{min}^{-1}$. The identity of each peak was confirmed using authentic standards.

Exp. 1.3 Sugar leakage into the vase water

The vase water was collected daily and evaporated to 1 mL through heating at 80°C. Sugars that leaked from dahlia stems into the vase water were then analyzed by HPLC as mentioned above.

Exp. 2. Effects of heat girdling on sugar flow and vase life

To block phloem transport cut flowers were subjected to heat girdling treatments. The flower necks (3 cm below the inflorescence) or petioles (1 cm above the basal portions attaching to the stem) were heated using a hot sealer (HS-40; Taiyo Electric Ind. Co., Ltd., Fukuyama, Japan). The flower necks were treated for approximately 20 s by rotating the sealer around the stem surface, and the petioles were treated for 5 s by attaching the sealer to the abaxial side. Following these treatments, two cut flowers were kept in 150 mL DIW containing $0.2 \text{ mL} \cdot \text{L}^{-1}$ bactericide.

The vase life of individual organs and callus formation were recorded. Subsequently, sugar leakage into the vase water during the initial 24 h and sugar concentrations in the stem bases on day 0 and day 5, were measured by HPLC.

Statistical analysis

Data were subjected to the *t*-test and Tukey's test using Costat software (v.6.4, Cohort Software, UK).

Results

Exp. 1. Effects of removing leaves and inflorescences
Exp. 1.1 Vase life

The inflorescence life of intact cut flowers was 7.4 days. Compared with the inflorescence life, the leaf life was 9.3 days longer (16.7 days). The inflorescence life of defoliated cut flowers was not different (7.8 days). On the other hand, deflowered cut stems with leaves exhibited a longer leaf life of 19.6 days and higher percentages of callus formation on the stem bases (Table

1). Separately from this experiment, the vase life of detached inflorescences with 5 cm stems (flower necks) and no leaves, which was evaluated under same conditions, was also unchanged (7.5 days) (data not shown).

Exp. 1.2 Changes in sugar concentrations in individual organs

In 'Kokuchou', sucrose, glucose, fructose and small quantities of *myo*-inositol were detected in all organs. Two types of low degree of polymerization (DP) fructan, 1-kestose (a trisaccharide consisting of one glucose and two fructose molecules, G-F2) and nystose (a tetrasaccharide consisting of one glucose and three fructose molecules, G-F3), were only detected in its leaves and stems.

At the start of the postharvest periods, the total concentration of soluble sugars ranged from 14.5–22.5 mg·g^{-1} FW, exhibiting the lowest value in the middle florets (Fig. 1A–D). Total sugar concentrations in the middle florets on day 5 sharply decreased to 5 mg·g^{-1} FW or lower (Fig. 1A). Total sugar concentrations of leaves in intact cut flowers decreased with time and reached 10 mg·g^{-1} FW on day 10, whereas those of deflowered cut stems were maintained at a higher level (Fig. 1B). In intact and defoliated cut flowers, total

sugar concentrations of flower necks declined to 10 mg·g^{-1} FW on day 5, reached 8 mg·g^{-1} FW on day 10, and remained unchanged afterwards (Fig. 1C). Changes in total sugar concentrations of stem bases showed a similar tendency to the flower necks; however, those of intact and defoliated cut flowers fell more rapidly to 5 mg·g^{-1} FW on day 5 (Fig. 1D). In leaves and stems, deflowered cut stems had much higher total sugar concentrations as compared with the two types of cut stems with inflorescences (Fig. 1B–D).

In the middle florets, glucose and fructose are the major sugars. All detected sugars decreased to less than half on day 5, and were still decreasing on day 10 (Fig. 2A–F).

In leaves, nystose, 1-kestose, sucrose and glucose were mainly detected. Nystose was around 7 mg·g^{-1} FW on day 0 sharply decreased to around 1 mg·g^{-1} FW on day 5, and then increased slightly on day 15 (Fig. 2G). 1-Kestose was around 3 mg·g^{-1} FW on day 0, increased to 6 mg·g^{-1} FW on day 5, but decreased again to 3 mg·g^{-1} FW on day 10 (Fig. 2H). Sucrose remained at constant levels at around 2 mg·g^{-1} FW throughout the postharvest period (Fig. 2I). Glucose showed the high concentrations of

Table 1. Effects of removal of inflorescences or leaves on the vase life of 'Kokuchou'.

Cut stem types	Inflorescence life[z] (days)	Leaf life[y] (days)	Callus formation (%)
Intact cut flowers	7.4±0.4	16.7±0.8	14
Defoliated cut flowers	7.8±0.3	—	0
Deflowered cut stems	—	19.6±0.3	71
Significance[x]	NS	**	

[z] Inflorescence life was determined when petals on the first to fifth whorls showed wilting or discoloration.

[y] Leaf life was determined when half the area of lower leaves turned yellow.

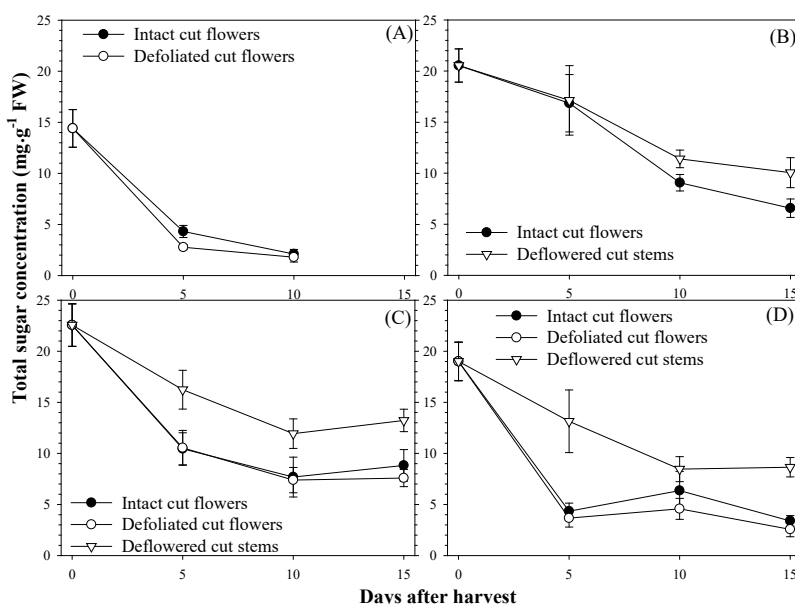[x] NS and ** indicate non-significant or significant at $P < 0.01$ by *t*-test (n=7).

Fig. 1. Total sugar concentrations (sum of sucrose, glucose, fructose, *myo*-inositol, nystose and 1-kestose) of the middle florets (A), leaves (B), flower necks (C) and stem bases (D) of 3 types of 'Kokuchou' cut stems. Bars indicate SEs (n = 6).
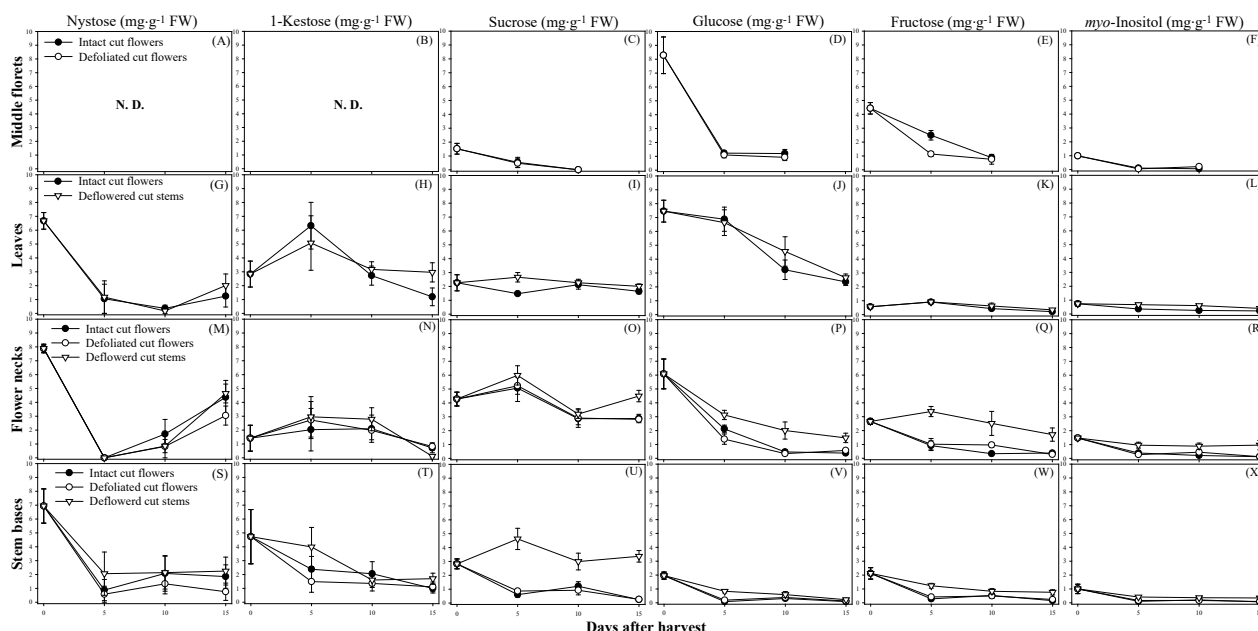
Fig. 2. Sugar concentrations of the middle florets (A–F), leaves (G–L), flower necks (M–R) and stem bases (S–X) in 3 types of 'Kokuchou' cut stems. N. D. means non-detected. Bars indicate SEs (n = 6).

7.5 mg·g^{-1} FW on day 0, decreased gradually and reached around 3 mg·g^{-1} FW on day 15 (Fig. 2J). Both fructose and *myo*-inositol had initial levels lower than 1 mg·g^{-1} FW and gradually decreased with time (Fig. 2K, L).

The two soluble fructans accounted for more than half of the total sugar concentrations of stems. In flower necks, nystose was about 8 mg·g^{-1} FW on day 0, sharply decreased to 0–2 mg·g^{-1} FW on day 5 and then increased again on day 10 (Fig. 2M). 1-Kestose in flower necks maintained a level of 1–3 mg·g^{-1} FW until day 10 and then declined slightly (Fig. 2N). Sucrose in the flower necks showed no significant decline and ranged from 3–6 mg·g^{-1} FW throughout the vase period (Fig. 2O). Flower necks had initial levels of 6, 3, and 2 mg·g^{-1} FW in glucose, fructose and *myo*-inositol, respectively. These three sugars decreased to lower than half on day 5 in the two types of cut stems with inflorescences, while the decreases were slower or insignificant in the deflowered cut stems (Fig. 2P–R).

In stem bases, all the sugar levels declined with time, except for sucrose in deflowered cut stems. Nystose ranged about 7 mg·g^{-1} FW on day 0, sharply decreased to 1–2 mg·g^{-1} FW on day 5 and then stopped decreasing (Fig. 2S). 1-Kestose in stem bases ranged from around 5 mg·g^{-1} FW on day 0, declined with time and then reached 2 mg·g^{-1} FW on day 10 (Fig. 2T). Sucrose in stem bases decreased from 3 mg·g^{-1} FW on day 0 to 1 mg·g^{-1} FW on day 5 in the two types of cut stems with inflorescences, while it maintained the initial level in the deflowered ones (Fig. 2U). Stem bases had initial levels of 1–2 mg·g^{-1} FW for glucose, fructose and *myo*-inositol, and these levels had a tendency to be lower

than those of flower necks. These three sugars decreased with time to less than 0.5 mg·g^{-1} FW on day 5 in intact and defoliated cut flowers, while the decrease was much slower in deflowered cut stems (Fig. 2V–X).

Exp. 1.3 Sugar leakage into the vase water

Sucrose, glucose, fructose and small quantities of *myo*-inositol were detected in the vase water where 'Kokuchou' cut stems were placed. The highest value was obtained for the first 24 h. Compared with the sugar leakage from intact and defoliated cut flowers (1.0–2.5 mg·day^{-1}), deflowered cut stems released sugars more abundantly (2.0–10.0 mg·day^{-1}) during the first three days. However, sugar leakage declined to low levels ranging from 0.5–1.0 mg·day^{-1} after day 4 (Fig. 3).

Exp. 2. Effects of heat girdling

Cross sections of the flower neck and petioles to which heat girdling was applied were photographed microscopically. The phloem and cortices were stained by toluidine blue, indicating a loss of cell membrane function (Fig. S1). Heat girdling treatments on flower necks and petioles did not affect the inflorescence life, but significantly shortened the leaf life. Heat girdling on the flower necks promoted callus formation (Table 2). Moreover, sugars released into the vase water were increased significantly after heat girdling on the petioles (Table 3). The sugar level in stem bases on day 0 was 22.5 mg·g^{-1} FW and decreased to 6 mg·g^{-1} FW on day 5. The heat girding treatments, especially those on petioles, tended to maintain stem-base sugar levels of 1.5–2.0 times higher on day 5 (Fig. 4).

Discussion

In the intact cut flowers of 'Kokuchou', the florets kept opening and were still fresh on day 5. Then, the inflorescences began to wilt on day 6 from the outermost florets. Stems and leaves stayed green for more than 15 days. The presence of leaves on the cut stems had little effect on their inflorescence life, while the presence of inflorescences shortened the leaf life (Table 1). Based on these vase life data for cut dahlias, we discuss the postharvest characteristics of cut dahlias as follows.

Sugar concentrations in individual organs result not only from catabolic and anabolic carbohydrate processes, but also from their translocation. Although these are many factors affecting these processes, sugar dynamism is still an important aspect for the postharvest physiology of cut flowers. Total sugars in the middle florets reduced to one-third or less on day 5 in cut flowers with or without leaves. When inflorescences were present, total sugars decreased to one-half in leaves and to one-third or lower in stems on day 10, while the sugar level in deflowered cut stems decreased more slowly (Fig. 1). These results indicate that the inflorescence is the major sink organ for carbohydrates and that the stems and leaves are the source organs. In many cut flowers, stems and leaves serve as source organs to provide carbohydrates to flowers (Carvalho et al., 2006; Ichimura et al., 2005). This idea is also supported by the fact that the level of the transport sugar, i.e., sucrose, remained unchanged in flower necks during the postharvest period even in the intact cut flowers. On the other hand, glucose, fructose and *myo*-inositol declined rapidly with time in the stems of those two types with inflorescence (Fig. 2). Glucose and fructose were the major sugars in dahlia petals and may serve as respiration substrates. *myo*-Inositol was reported to be a reserve substance and a precursor of other sugars (Loewus and Loewus, 1983). These sugars may be consumed for metabolism for inflorescence opening. The
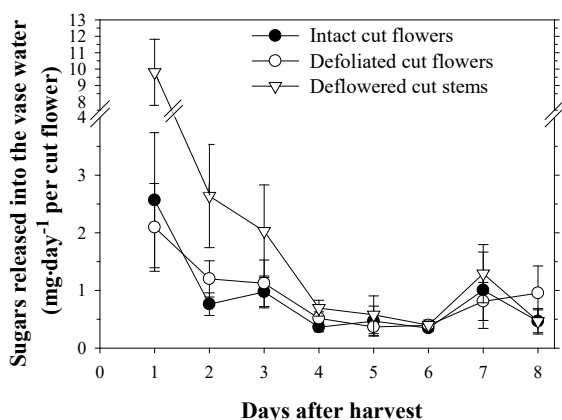

Fig. 3. Sugars released into the vase water from 3 types of 'Kokuchou' cut stems. Bars indicate SEs (n = 5).
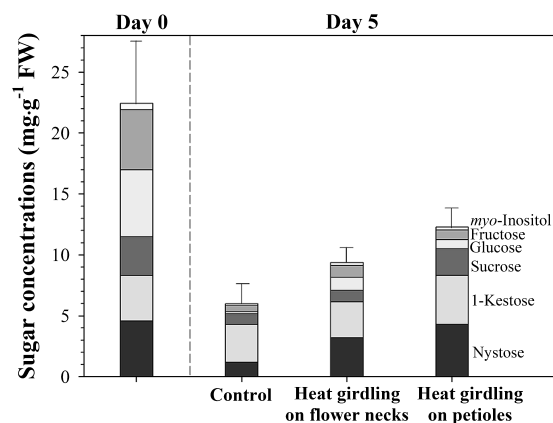

Fig. 4. Effects of heat girdling on the sugar concentrations of 'Kokuchou' stem bases. Bars indicate SEs for total sugars (n = 6).

Table 2. Effects of heat girdling on the vase life of 'Kokuchou' cut flowers.

Treatment	Inflorescence life[z] (days)	Leaf life[y] (days)	Callus formation (%)
Control	6.7±0.3 a[x]	16.1±0.6 a	0
Heat girdling on the flower necks	7.3±0.3 a	13.4±1.0 b	42
Heat girdling on the petioles	7.3±0.3 a	13.1±0.4 b	14

[z] Inflorescence life was determined when petals on the first to fifth whorls showed wilting or discoloration.
[y] Leaf life was determined when half the area of lower leaves turned yellow.
[x] Means are separated by Tukey's test at $P < 0.05$ (±SEs, n = 7).

Table 3. Effects of heat girdling on sugar leakage into the vase water on day 1.

Treatment	Sugars released in the vase water (mg·day⁻¹ per cut flower)				
	Sucrose	Glucose	Fructose	*myo*-Inositol	Total
Control	1.1±0.2 a[z]	0.2±0.1 b	0.1±0.1 b	0.1±0.04 a	1.6±0.3 b
Heat girdling on the flower necks	1.8±0.6 a	1.7±0.5 ab	1.5±0.4 ab	0.1±0.03 a	5.1±0.3 ab
Heat girdling on the petioles	1.5±0.2 a	3.0±0.6 a	2.4±0.7 a	0.1±0.02 a	6.9±1.2 a

[z] Means are separated by Tukey's test at $P < 0.05$ (±SEs, n = 5).

sugar leakage from the stem bases was elevated by removal of inflorescences, also implying that inflorescences absorb a lot of these soluble sugars from their stems (Fig. 3).

Two low DP fructans, 1-kestose and nystose, were detected only in vegetative organs and changed differently from the other four sugars. Many Asteraceae species store carbohydrates as fructans (Kriukova et al., 2017; Vergauwen et al., 2003; Vilhalva et al., 2011). Compared with tuberous roots of dahlias grown under a short day (9 h light) condition, those grown under a long day (9 h light with a 4 h night break) condition contained more reducing sugars and lower amounts of fructans (DP3-25), especially the high DP (> 20) fructans (Legnani and Miller, 2001). Cut dahlias used in this study were grown under natural 14 h light and moved to a 12 h light condition. These photoperiodic conditions may partly affect the characteristic changes in nystose and 1-kestose. Although nystose and 1-kestose both showed re-ascension during the post-harvest period, implying the hydrolysis of other high DP fructans, fructose levels did not increase correspondingly. This indicates that fructose may be exhausted rapidly for floret opening and respiration of petals and leaves, or be readily transformed to other sugars. Further investigations should clarify the role of fructan in cut dahlias because it is a major storage carbohydrate.

Sugar leakage into vase solutions was also reported in some other cut flower species (Chuang and Chang, 2013; Tonooka et al., 2021; Woltering, 1987). In cut dahlias, sugar leakage was mainly detected on day 1, declined with time and reached trace levels after the inflorescences started senescing (Fig. 3). These results imply that basipetal sugar flows only occur in the initial few days and that the major sugar flows in cut stems are acropetal during the vase period. Furthermore, these results also suggest that carbohydrate redistribution from senescing petals to other organs rarely occurs.

As mentioned above, inflorescences absorb sugars from the vegetative organs resulting in a shortened leaf life and thinned stem bases. We applied heat girdling to two portions, the flower neck and petioles, to substitute for the removal of inflorescences and leaves, respectively. However, these two treatments both shortened the leaf life but had little effect on inflorescence life (Table 2). It is unclear why heat girdling on the flower necks shorted the leaf life; however, some other compounds which translocate through the xylem, such as cytokinin (Kiba and Sakakibara, 2016), may contribute to this phenomenon. Although the results of heat girdling on the flower necks were inconsistent with those of deflowering, heat girdling treatments could alter the direction of sugar flow and promote sugar accumulation in the stem bases resulting in increased sugar leakage (Table 3; Fig. 4). Callus formation on the stem-base surface, which was also observed in the deflowered stems, occurred in the flower neck heat-girdled stems (Table 2). Callus formation prevents thinning of stem bases and it may be protective response against sugar leakage induced by abiotic injurious stress.

The sharp decreases in sugar levels of florets in cut dahlias is considered to be responsible for their short vase life. Although the sugars in source organs are absorbed by the inflorescences, the amount may be insufficient to maintain floret respiration and life. In addition, sugar movement into petals may be limited once the abscission layer has formed (Yang et al., 2021). Compared with cut chrysanthemums, which have a longer vase life, sugar concentrations increased in the capitulum of dahlias under a 20°C condition (Adachi et al., 1999, 2000). Although dahlias and chrysanthemums are both members of the Asteraceae family, the changes in sugar levels of inflorescences during the postharvest period are different, and these may be linked to their different vase lives. It was reported that dahlia cultivars with high sugar levels (10–18 mg·g^{-1} FW) in stems exhibited longer vase life (Nakajima et al., 2019). Cut defoliated dahlias with long stems (60 and 80 cm) also had longer vase life than those with short stems (8 and 40 cm) (Fujimoto and Onozaki, 2021; Onozaki et al., 2018). This indicates that abundant carbohydrate sources in stems are beneficial for the inflorescence life in cut dahlias. Treat-
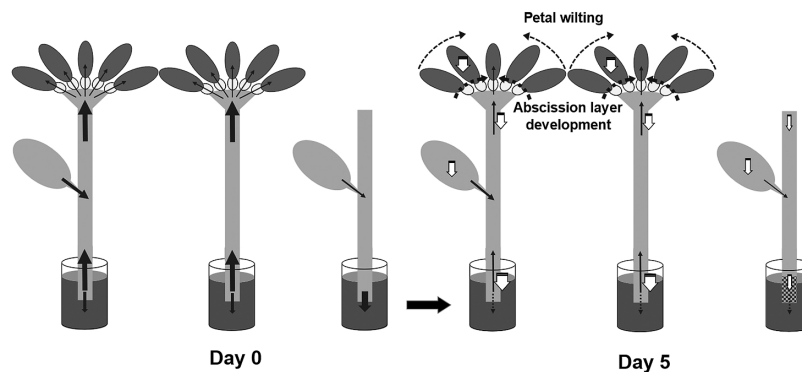

Fig. 5. Sugar dynamism in the intact cut flowers, defoliated cut flowers and deflowered cut stems. Solid-line arrows indicate sugar flows. Open downward arrows indicate decreases in sugar levels in the individual organs. A mesh pattern indicates callus initiation on stem bases.

ments with 2–5% glucose, fructose or sucrose also improved vase life (Azuma et al., 2019; Takahashi et al., 2016). In addition to the results obtained in this study, these results indicate the importance of carbohydrate supply for the maintenance of inflorescence life.

Results obtained from this study are illustrated in Figure 5. They suggest that 1) inflorescences serve as a strong sink for carbohydrates from stems and leaves, 2) sugar leakage from stem bases into vase water decreased with time, 3) carbohydrates hardly redistribute from senescing petals to other organs, and 4) these sink-source relationships are reflected in the sugar levels of the individual organs, and may contribute to their senescing process. In addition, callus formation on the stem bases may be closely correlated with sugar dynamism in the stems during the postharvest period.

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