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Effects of Intermittent Low-temperature Storage Duration and Cycle on the Bolting and Flowering of *Delphinium elatum* in Summer

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Early-bolting in summer is a major problem when growing delphinium seedlings in summer to produce cut flowers that will be shipped in autumn and winter. In this study, an intermittent low-temperature storage (ILTS) treatment that induces flower bud differentiation in strawberry and prevents rosette formation in *Eustoma* significantly increased the *Delphinium elatum* cut flower length. Moreover, ILTS was as effective as growing seedlings under cool conditions at preventing early-bolting. We analyzed the effects of six ILTS treatments that differed regarding the treatment temperature (5 and 10°C) and treatment cycle (3 days/3 days, 6 days/6 days, and 12 days/12 days; ambient conditions/cool and dark). Cut flowers were significantly longer with the 6 days/6 days treatment at 10°C than for the control treatment. Furthermore, repeating the ILTS treatment cycle (6 days ambient conditions/6 days at 10°C) a total of four times produced high-quality cut flowers regardless of the cultivar. Therefore, this ILTS treatment may be ideal for preventing early-bolting in *D. elatum*.

Key Words: cool storage, cut flower quality, high ambient temperature, long day, *Ranunculaceae*.

Introduction

Delphinium species are perennial plants in the family *Ranunculaceae*. Three of these species (*Delphinium grandiflorum*, *D. elatum*, and *D.* × *belladonna*) are grown mainly for the production of cut flowers. There is a demand for delphinium cut flowers for bouquets and arrangements because they are blue, which is a relatively rare flower color. There are several delphinium cultivars, including early- to late-season cultivars. Rosette formation is a problem for late-season cultivars because their seedlings are usually sown in September and cut flowers are harvested from January to March when they are grown by forcing culture. Therefore, previous studies examined the environmental factors that induce rosette formation (Hirai and Mori, 1999; Katsutani et al., 2002b, c). To produce cut flowers in autumn and winter, the seedlings of early-season cultivars must be grown during the high-temperature period from July to August. However, delphinium plants are quantitative long-day species (Katsutani and Ikeda, 1997), and early-season cultivars often experience a phenomenon known as "early-bolting", which occurs when young seedlings are exposed to high temperatures that induce bolting, resulting in a decrease in the seedling growth rate. Cut flowers from early-bolting seedlings have relatively few florets and short stem lengths, which are undesirable traits for commercial production. Notably, *D. elatum* is characterized by spike inflorescences, but early-bolting leads to decreases in the number of florets and spike length, which adversely affects its commercial value. Growing seedlings under cool conditions (20°C day/10°C night) using a heat pump reportedly inhibited early-bolting (Katsutani et al., 2002a). However, because of the high cost and environmental impact associated with the required cooling, alternative methods for controlling early-bolting are required.

Intermittent low-temperature storage (ILTS) effectively induces flower bud differentiation in strawberry (Yoshida et al., 2012) and prevents rosette formation in *Eustoma* (Phan et al., 2020). During ILTS, seedlings are maintained under cool conditions (e.g., in a refrigerator)

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for a certain period, after which they are kept under ambient conditions for the same period. This cycle between cool and ambient conditions is repeated. Because refrigerators for storing cut flowers can be used, ILTS may have lower initial costs than methods requiring air-conditioning systems. Earlier research indicated that ILTS promoted flowering in *Begonia* × *hiemalis*, which is a quantitative short-day plant (Nakajima and Goto, 2018, 2019), but another study revealed the positive effects of ILTS on *D. grandiflorum*, which is a quantitative long-day plant species (Goto et al., 2015). However, there are various delphinium species. Accordingly, potential differences in the effects of ILTS on the flowering of these species should be investigated. Moreover, the effects of different ILTS temperatures and treatment cycles on the growth and flowering of delphinium plants need to be thoroughly investigated. In this study, we examined the effects of ILTS on the growth and flowering of *D. elatum*, which is particularly susceptible to early-bolting, to determine the optimal temperature and treatment cycle to prevent early-bolting. In Experiment 1, *D. elatum* seedlings maintained under ILTS conditions were compared with seedlings grown under cool conditions. In Experiments 2 and 3, the ideal ILTS temperature and treatment cycles were determined.

Materials and Methods

General procedures

All seedlings used in this study were grown in a greenhouse belonging to the School of Agriculture, Okayama University. More specifically, seeds sown in cell trays containing Excel soil (Minoru Sangyo Co., Ltd., Okayama, Japan) were covered with vermiculite and subirrigated with water. The cell trays were incubated at 20°C until at least one seed germinated, after which they were transferred to a greenhouse and incubated under humid conditions provided by a mist spraying system. After cotyledons expanded, the trays were transferred to another part of the greenhouse for subirrigation with water when the growth medium was dry. After the first leaf expanded, the seedlings were fertilized during each subirrigation using the OAT A solution (1/6 concentration; 43.3 ppm N, 20 ppm P_2O_5, 67.5 ppm K_2O, 38.3 ppm CaO, and 10 ppm MgO; OAT Agrio Co., Ltd., Tokyo, Japan). For the ILTS treatment (x days/x days cycle × number of repeats) conducted from July (sowing) to September (transplanting), the seedlings were cycled between a refrigerator (10°C) and a greenhouse under ambient conditions and incubated for a set number of days. The cycle was repeated several times depending on the total number of cool storage days for each experiment. The ILTS treatments are summarized in Figure 1. During the cool storage period, seedlings were maintained in darkness, with no subirrigation.

After completing the ILTS treatments, the seedlings that had not bolted were transplanted to planters (soil capacity: 12 L) filled with sandy loam mixed at Okayama University. Each planter containing five seedlings was grown in a greenhouse with a 16-h daylength (04:00–20:00), a minimum temperature of 15°C, and a ventilation temperature of 28°C. The transplanted seedlings in each planter were fertilized weekly with 1 L OAT A solution (1/6 concentration).

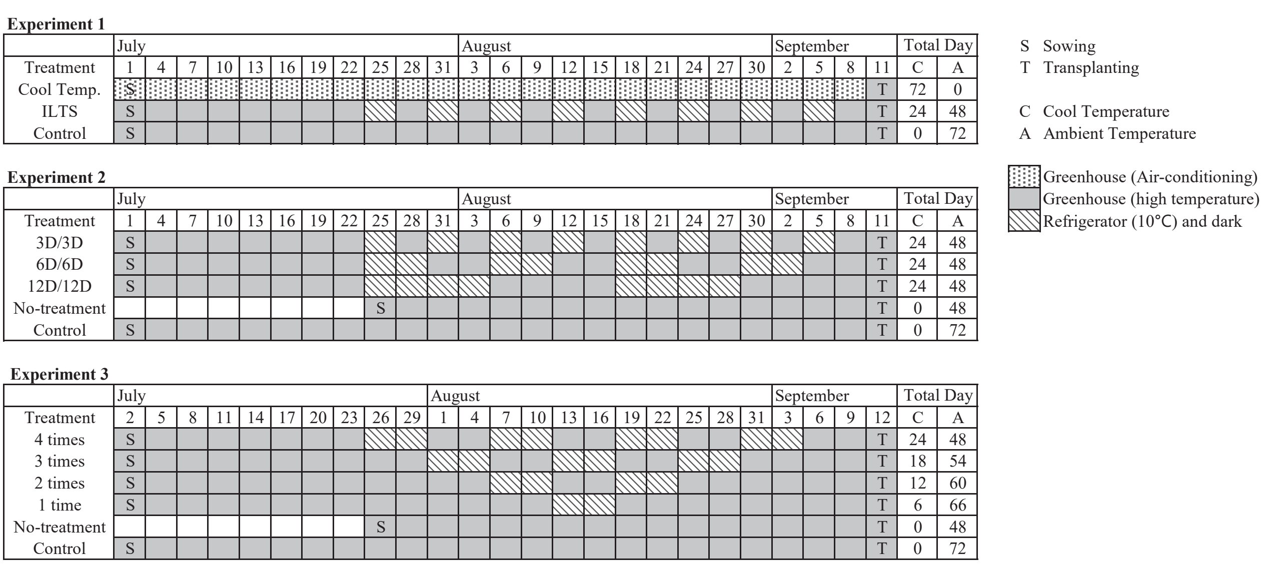

Fig. 1. Overview of intermittent low-temperature storage (ILTS) treatments. The number under months means date and only the first day of the three-day period (one block) is listed. Seedlings were placed in a refrigerator (10°C) for x days and then transferred to a greenhouse (ambient conditions) for x days. Seedlings grown in a greenhouse for the duration of the experimental period were used as controls. Seedlings derived from seeds sown on July 25 (Experiment 2) or 26 (Experiment 3) and grown in a greenhouse for the duration of the experimental period were used as no-treatment (NT) controls and compared with the ILTS-treated seedlings that were maintained under ambient conditions for the same duration.

Bolting was considered to have occurred when the first internodes elongated more than 5 mm. The bolting date was recorded after transplanting for Experiments 2 and 3. The following dates were also recorded: visible flower bud, first floret anthesis, and harvest. After harvesting, the cut flower length, number of florets, number of nodes to the first floret, spike length, and cut flower weight were determined. Cut flowers were harvested when one-third of the florets had flowered. Data were analyzed using EXCEL Toukei Ver. 7.0 (ESUMI Co., Ltd., Tokyo, Japan).

Experiment 1: Effects of ILTS on early-bolting in D. elatum

D. elatum 'Triton Light Blue' (Miyoshi Co., Ltd., Tokyo, Japan) seeds were sown in cell trays (200 cells with a root zone volume of 12 mL) on July 1, 2015. The ILTS treatment, which was started on July 25, involved a 3 days/3 days cycle, with the temperature during the cool storage period set at 10°C. Seedlings placed in an air-conditioned greenhouse in which the temperature was controlled using a heat pump (day: 30°C; night: 20°C) were referred to as cool Temp. Seedlings placed in a greenhouse maintained under ambient conditions were referred to as control. Although 20°C/10°C (day/night temperatures) is recommended for growing seedlings under cool conditions, even 30°C/20°C is less likely to cause early-bolting than ambient conditions for seedlings with fewer than six unfolding leaves (Katsutani et al., 2002a). Seedlings were transplanted on September 11.

Experiment 2: Effects of ILTS temperatures and cycles on early-bolting in D. elatum

D. elatum 'Triton Light Blue' seeds were sown in cell trays (72 cells with a root zone volume of 46 mL) on July 1 and 25, 2016. The ILTS treatments, which were started on July 25, were completed using seedlings derived from seeds sown on July 1. The effects of the ILTS temperatures (5 and 10°C) were assessed using the following cycles (ambient conditions/cool and dark): 3 days/3 days, 6 days/6 days, and 12 days/12 days. A total of six ILTS treatments were established. Control and no-treatment seedlings were derived from seeds sown on July 1 and 25, respectively. The no-treatment seedlings were incubated under ambient conditions for the same number of days as the ILTS-treated seedlings to clarify whether the effects derived from the number of days they were placed under natural conditions or from interrupting the high temperature period with the chilling period of ILTS. Seedlings were transplanted on September 11.

Experiment 3: Effects of the number of ILTS cycle repeats on early-bolting in D. elatum

D. elatum 'Ariel Light Blue' (Miyoshi Co., Ltd.) and 'Triton Light Blue' seeds were sown in cell trays (128 cells with a root zone volume of 20 mL) on July 2 and 26, 2020. The ILTS treatments, which were started on July 26, were completed using seedlings derived from the seeds sown on July 2. More specifically, the ILTS treatment (6 days under ambient conditions/6 days at 10°C in darkness) was repeated for a total of 1–4 times. Control and no-treatment seedlings were derived from seeds sown on July 2 and 26, respectively; these seedlings were incubated under ambient conditions for the same number of days as the ILTS-treated (four times) seedlings. Seedlings were transplanted on September 12.

Results

Experiment 1

The average daily temperature in the greenhouse during the seedling growth period was 22.0–32.8°C (Fig. 2). The average daily, maximum, and minimum temperatures during the seedling growth period were

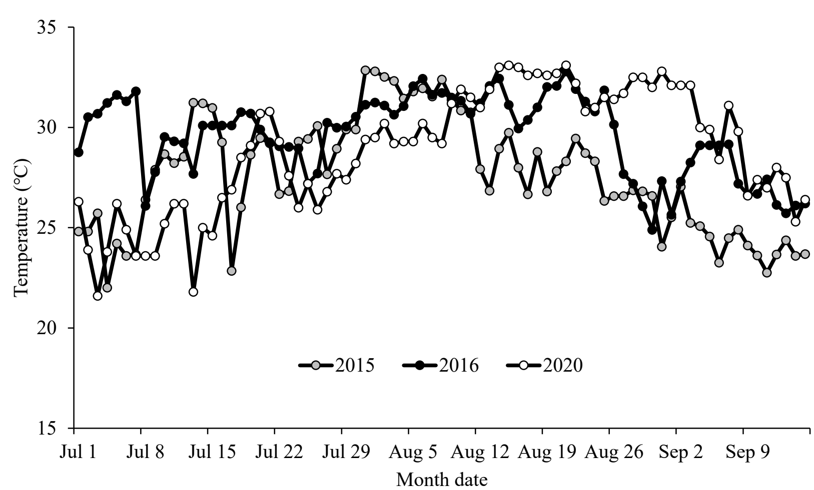

Fig. 2. Average daily temperatures during the seedling growth period from July 1 to September 15 in 2015, 2016, and 2020 (Experiments 1, 2, and 3, respectively).

27.6, 34.1, and 23.0°C, respectively. Table 1 summarizes the effects of air-conditioning and ILTS on *D. elatum* growth and flowering. Flower buds were visible on control plants on October 19, which was earlier than the corresponding date for the plants that underwent the other treatments. The cut flowers of the control plants were shorter (34.8 cm) than the cut flowers of the plants grown under cool conditions (i.e., air-conditioned greenhouse) (83.1 cm) and the plants that underwent the ILTS treatment (83.3 cm). There was no significant difference between the cut flower lengths of the plants grown in an air-conditioned greenhouse and the plants that underwent the ILTS treatment. The control plants also had the fewest florets and nodes to the first floret, shortest spikes, and lowest cut flower weight. There were no significant differences in the number of florets, number of nodes to the first floret, spike length, or cut flower weight between the plants grown in an air-conditioned greenhouse and the plants that underwent the ILTS treatment.

Experiment 2

The average daily temperature in the greenhouse during the seedling growth period was 24.9–32.8°C (Fig. 2). The average daily, maximum, and minimum temperatures during the seedling growth period were 29.6, 36.4, and 24.2°C, respectively. Table 2 provides details regarding the effects of ILTS temperatures and cycles. The bolting date was September 28 for the control, which was significantly earlier than the corresponding date for the other treatments (October 8–11), which did not differ significantly. Control plants were harvested approximately 25 days earlier than the ILTS-treated plants, with significant decreases in the cut flower length, number of nodes to the first floret, spike length, and cut flower weight. There were no significant differences among the ILTS-treated seedlings. The number of florets tended to be higher for the 10°C treatment than for the 5°C treatment. The percentage of cut flowers that were longer than 80 cm (Fig. 3) was approximately 7.7% for the control plants and 40.0% for the no-treatment plants, whereas the percentage was higher for the ILTS-treated plants (e.g., 100% for the plants that underwent the 6 days/6 days treatment at 10°C).

Experiment 3

The average daily temperature in the greenhouse during the seedling growth period was 21.6–33.1°C (Fig. 2). The average daily, maximum, and minimum temperatures during the seedling growth period were 28.8, 35.8, and 24.1°C, respectively. The effects of the number of ILTS cycle repeats on 'Ariel Light Blue' and 'Triton Light Blue' growth and flowering are presented in Tables 3 and 4, respectively. For 'Ariel Light Blue', the control treatment resulted in a significantly earlier bolting date (September 23) than the ILTS treatments completed four and three times (October 2 and September 28, respectively). For 'Triton Light Blue', the bolting date was significantly earlier (September

Table 1. Effects of air-conditioning and ILTS on *D. elatum* 'Triton Light Blue' plant growth and cut flower quality (Experiment 1). Details regarding ILTS are provided in Figure 1.

Treatment	Flower bud date	Flowering date	Harvesting date	Cut flower length (cm)	Number of florets	Number of nodes to the first florets	Spike length (cm)	Cut flower weight (g)
Cool Temp.	Nov-1 b[z]	Nov-20 ab	Nov-21 ab	83.1 b	23.1 b	9.3 b	37.7 b	51.4 b
ILTS	Nov-6 b	Nov-24 b	Nov-25 b	83.3 b	19.6 b	8.5 b	34.4 b	47.9 b
Control	Oct-19 a	Nov-10 a	Nov-10 a	34.8 a	4.2 a	5.7 a	14.1 a	9.3 a

[z] Mean values (n = 10) followed by different letters indicate significant differences among treatments ($P < 0.05$, Tukey's HSD test).

Table 2. Effects of ILTS temperatures and cycles on *D. elatum* 'Triton Light Blue' plant growth and cut flower quality (Experiment 2). Details regarding ILTS are provided in Figure 1.

	Refrigerator temperature	Treatment	Bolting date	Flower bud date	Flowering date	Harvesting date	Cut flower length (cm)	Number of florets	Number of nodes to the first florets	Spike length (cm)	Cut flower weight (g)
ILTS	5°C	3D/3D	Oct-10 b[z]	Oct-31 bc	Nov-26 b	Nov-28 b	92.6 bc	24.9 ab	6.7 b	46.7 b	57.4 b
		6D/6D	Oct-11 b	Nov-1 bc	Nov-28 b	Nov-29 b	94.0 bc	27.6 ab	6.9 b	45.9 b	60.2 b
		12D/12D	Oct-8 b	Oct-29 bc	Nov-25 b	Nov-26 b	83.9 bc	21.6 ab	6.5 b	38.8 b	50.7 ab
	10°C	3D/3D	Oct-11 b	Nov-4 c	Nov-30 b	Dec-1 b	92.1 bc	28.4 b	7.4 b	46.0 b	61.1 b
		6D/6D	Oct-11 b	Oct-31 bc	Nov-28 b	Nov-29 b	101.9 c	35.7 b	7.1 b	52.4 b	69.8 b
		12D/12D	Oct-11 b	Oct-30 bc	Nov-27 b	Nov-28 b	96.9 bc	28.9 b	6.9 b	49.5 b	61.0 b
	No-treatment		Oct-8 b	Oct-24 b	Nov-21 b	Nov-23 b	80.6 b	21.3 ab	5.9 ab	37.9 b	48.9 ab
	Control		Sep-28 a	Oct-9 a	Nov-2 a	Nov-5 a	46.9 a	11.4 a	4.2 a	21.3 a	22.1 a

[z] Mean values (n = 15) followed by different letters indicate significant differences among ILTS temperatures and cycles ($P < 0.05$, Tukey's HSD test).

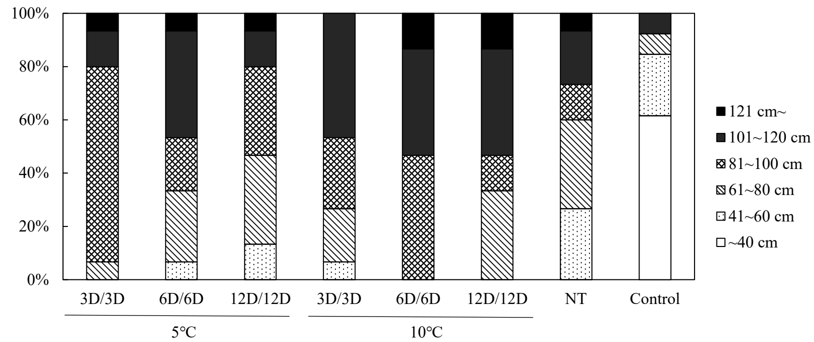

Fig. 3. Effects of ILTS temperatures and cycles on the *D. elatum* 'Triton Light Blue' cut flower length (Experiment 2).

Table 3. Effects of ILTS cycle repeats on *D. elatum* 'Ariel Light Blue' plant growth and cut flower quality (Experiment 3). Details regarding ILTS are provided in Figure 1.

Treatment	Bolting date	Flower bud date	Flowering date	Harvesting date	Cut flower length (cm)	Number of florets	Number of nodes to the first florets	Spike length (cm)	Cut flower weight (g)
4 times	Oct-2 d[z]	Oct-27 c	Nov-15 c	Nov-17 b	67.5 c	17.9 b	4.9 c	32.5 b	59.4 c
3 times	Sep-28 cd	Oct-21 bc	Nov-9 bc	Nov-12 ab	57.8 bc	13.7 ab	4.0 bc	25.4 ab	42.1 bc
2 times	Sep-24 abc	Oct-14 ab	Nov-2 ab	Nov-4 a	48.6 ab	10.3 ab	3.4 ab	22.8 a	32.7 ab
1 time	Sep-21 a	Oct-7 a	Oct-27 a	Oct-29 a	40.8 a	6.3 a	2.8 ab	21.7 a	22.6 a
No-treatment	Sep-26 bc	Oct-23 a	Nov-2 ab	Nov-5 a	40.9 a	6.3 a	2.5 a	22.4 a	24.8 ab
Control	Sep-23 ab	Oct-10 a	Oct-31 a	Nov-3 a	37.1 a	5.5 a	2.8 ab	17.8 a	16.8 a

[z] Mean values (n = 15) followed by different letters indicate significant differences among ILTS cycle repeats ($P < 0.05$, Tukey's HSD test).

Table 4. Effects of ILTS cycle repeats on *D. elatum* 'Triton Light Blue' plant growth and cut flower quality (Experiment 3). Details regarding ILTS are provided in Figure 1.

Treatment	Bolting date	Flower bud date	Flowering date	Harvesting date	Cut flower length (cm)	Number of florets	Number of nodes to the first florets	Spike length (cm)	Cut flower weight (g)
4 times	Oct-5 d[z]	Nov-1 c	Nov-22 c	Nov-24 b	90.2 cd	34.5 bc	6.0 b	48.3 cd	67.5 c
3 times	Oct-2 cd	Oct-28 bc	Nov-19 bc	Nov-21 b	95.7 d	45.1 c	5.9 b	54.6 d	65.9 c
2 times	Sep-28 bc	Oct-22 b	Nov-13 b	Nov-15 b	81.3 bcd	28.5 abc	4.8 ab	45.9 bcd	56.2 bc
1 time	Sep-23 ab	Oct-13 a	Nov-4 a	Nov-6 a	62.0 ab	19.3 ab	3.5 a	35.2 ab	37.2 ab
No-treatment	Oct-2 cd	Oct-23 bc	Nov-13 bc	Nov-16 b	69.9 abc	24.3 abc	3.9 a	38.4 bc	47.6 bc
Control	Sep-21 a	Oct-7 a	Oct-29 a	Oct-31 a	49.2 a	9.2 a	3.6 a	20.6 a	18.9 a

[z] Mean values (n = 15) followed by different letters indicate significant differences among ILTS cycle repeats ($P < 0.05$, Tukey's HSD test).

21) for the control treatment than for the ILTS treatments completed four, three, and two times (October 5, October 2, and September 28, respectively). The quality of cut flowers increased if bolting was delayed, which is consistent with the finding of an earlier study (Katsutani et al., 2002a) and the results of Experiments 1 and 2. The percentage of cut flowers that were longer than 60 cm exceeded 90% for the 'Ariel Light Blue' plants that underwent the ILTS treatment four times (Fig. 4). For 'Triton Light Blue', the percentage of cut flowers that were longer than 80 cm exceeded 80% for the plants that underwent the ILTS treatment four and three times, respectively (Fig. 5).

Discussion

High-quality delphinium cut flowers can be produced in autumn and winter by growing early-season cultivar seedlings that can avoid rosette formation; however, early-bolting must be prevented. Air-conditioning systems are often used during the seedling growth period to reduce the chances of early-bolting, but these systems are expensive to introduce and run and may have harmful effects on the environment due to heavy power consumption. Therefore, inexpensive and eco-friendly methods for suppressing early-bolting are needed. In this study, we investigated the effects of ILTS on early-bolting in *D. elatum*.

An average daily temperature of 20°C or higher

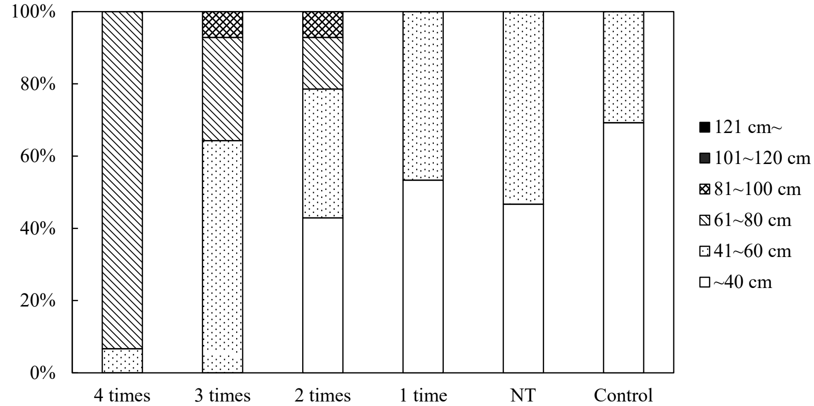

Fig. 4. Effects of ILTS cycle repeats on the *D. elatum* 'Ariel Light Blue' cut flower length (Experiment 3).

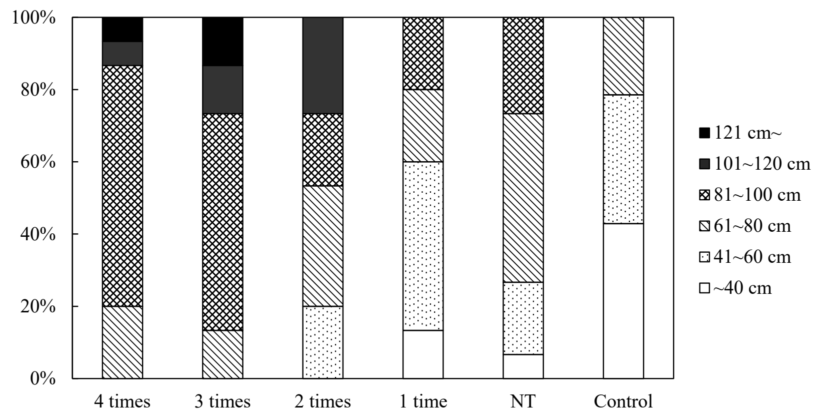

Fig. 5. Effects of ILTS cycle repeats on the *D. elatum* 'Triton Light Blue' cut flower length (Experiment 3).

markedly accelerated bolting in *D. elatum* (Katsutani, 2004). The average daily greenhouse temperatures during the seedling growth period exceeded 20°C in 2015 (Experiment 1), 2016 (Experiment 2), and 2020 (Experiment 3). More specifically, after July 25 or 26, when ILTS treatments were initiated, the average daily temperatures in the greenhouses were higher than 25°C, thereby providing conditions conducive to *D. elatum* flower bud differentiation.

In Experiment 1, the visible bud date was 18 days later for the ILTS-treated seedlings (November 6) than for the control seedlings, suggesting ILTS may prevent early-bolting in *D. elatum*. The visible bud date for the seedlings grown in an air-conditioned greenhouse (November 1) did not differ significantly from the visible bud date for the ILTS-treated seedlings. When seedlings that did not undergo early-bolting were transplanted, they grew without problems until harvest. However, the cut flower quality was significantly higher for the ILTS-treated plants than for the controls. Therefore, ILTS may be an alternative approach to growing *D. elatum* seedlings under cool conditions.

Analyses of the effects of ILTS temperatures (5 and 10°C) and cycles (3 days/3 days, 6 days/6 days, and 12 days/12 days) revealed a lack of significant differences in cut flower quality among ILTS-treated plants. The percentage of cut flowers longer than 80 cm was highest (100%) following the 6 days/6 days treatment at 10°C (Fig. 3), implying this may be the ideal treatment for the stable production of high-quality cut flowers.

A comparison of the number of ILTS cycle repeats during the 6 days/6 days treatment at 10°C indicated the 'Ariel Light Blue' cut flowers were significantly longer when the treatment was completed four times (67.5 cm) than when the treatment was completed two, one, or zero (control) times. For 'Triton Light Blue', the cut flowers were significantly longer when the ILTS treatment was completed four and three times (90.2 and 95.7 cm, respectively) than when the ILTS treatment was conducted one or zero (control) times. For both cultivars, cut flower quality tended to be higher for the ILTS-treated plants than for the controls. Considering the percentage of high-quality cut flowers (in terms of length), the ILTS treatment should ideally be completed four times for 'Ariel Light Blue' and three or four times for 'Triton Light Blue'. These results suggest four times may be the optimal number of treatment cycles regardless of the cultivar.

In 2016, when the average daily temperature in the two weeks before transplanting was less than 30°C, plants grown only under natural conditions produced cut flowers that were similar to those of ILTS-treated plants if the sowing date was delayed (Experiment 2). The diversity in the results for the ILTS-treated and no-treatment plants maintained under natural conditions for the same duration in different years may reflect the effects of the temperatures in the late seedling growth period. In 2016 (Experiment 2), the average daily temperature after August 27 was less than 30°C, whereas in 2020, most of the average daily temperatures from August 9 to September 7 exceeded 30°C. Delphinium flower buds do not form until approximately four unfolding leaves have expanded (Katsutani and Ikeda, 1997). Thus, high temperatures during the late seedling growth period are believed to contribute to early-bolting. Because of increasing summer temperatures due to global warming, ILTS may be useful for the stable production of high-quality *D. elatum* cut flowers.

The findings of this study suggest a 6 days/6 days treatment at 10°C completed four times is the optimal ILTS treatment for *D. elatum*. Yoshida et al. (2012) and Nakajima and Goto (2018) determined that ILTS promotes flower bud differentiation and flowering because it is a short-day treatment (according to the duration of the exposure to cool and dark conditions and the duration of the exposure to ambient conditions before and after the treatment). Delphinium is a quantitative long-day plant for which bolting is reportedly delayed in response to short-day treatment (Sugawara et al., 2023). Therefore, it is likely that the short-day effect of the ILTS treatment helps suppress bolting. Katsutani (2004) reported that a short-day treatment during cool storage can prevent early-bolting, which is consistent with the effect of ILTS (i.e., low temperature and short day). In addition, delphinium flower bud differentiation is accelerated by continuous exposure to high temperatures (Katsutani, 2004). ILTS may repress early-bolting because the exposure to high temperatures is interrupted during the treatment period. Ogasawara et al. (1996) observed that *D. elatum* 'Blue bird' flower buds do not form during a period of cool conditions. Combining a short-day treatment with low temperatures can inhibit early-bolting, which is consistent with the findings of an earlier study by Kuroshima (2018) that concluded a short-day and night chilling treatment had suppressive effects on early-bolting in *D. grandiflorum*. Going forward, a more precise determination of the appropriate time to initiate the ILTS treatment, as well as clarifying the effect of the discontinuation timing of the exposure to high temperatures on *D. elatum* flower bud differentiation will be needed. Yano et al. (2022) reported that exposure to high temperatures during a non-refrigerated ILTS treatment influenced when the apical flower of strawberry blooms, suggesting that the temperature difference between the cool and ambient conditions during ILTS affects flowering. Higashiura et al. (2020) suggested that carnation flowering time was affected by the temperature difference between day and night during a nighttime cooling treatment, likely because of changes in flowering-related gene expression at different time points. Therefore, the expression of genes related to delphinium flower development should be investigated because the time of day when these genes are expressed may change during ILTS.

According to Experiment 3, the cut flowers of both cultivars were significantly longer for the plants that underwent the ILTS treatment four times ('Ariel Light Blue') or three times ('Triton Light Blue') than for the no-treatment plants derived from seeds sown on July 26. Notably, for 'Triton Light Blue', the bolting date was October 2 for the no-treatment plants and the plants that underwent the ILTS treatment three times, but the cut flowers of the ILTS-treated plants were significantly longer than the cut flowers of the no-treatment plants. This may be related to differences in the number of leaves at the transplanting stage. Specifically, for both cultivars, the no-treatment plants, which had a relatively short growth period, had one or two fewer leaves than the control and ILTS-treated plants. The observed increase in cut flower quality as the number of leaves at the transplanting stage increased is in accordance with the findings of a previous study by Kikuchi et al. (2000) and Katsutani (2004). Hence, ILTS can suppress early-bolting without decreasing the number of leaves.

Earlier research confirmed ILTS also affects *D. grandiflorum* (Goto et al., 2015), suggesting that ILTS may inhibit early-bolting in all delphinium species. In addition, we also determined that ILTS can prevent early-bolting in larkspur (*Consolida ajacis*), which belongs to the family *Ranunculaceae*, as well as in delphinium (data not published). Accordingly, the effects of ILTS on other *Ranunculaceae* species will need to be examined.

Various methods have been developed to suppress early-bolting in delphinium. For example, seedlings can be grown under cool conditions (Katsutani et al., 2002a) and/or may undergo a short-day and night chilling treatment (Kuroshima, 2018). One potential advantage of ILTS for cut flower production over alternatives is that it may be completed using refrigerators that have already been purchased for storing cut flowers, making it a low-cost and easy-to-adopt technology. ILTS is also more eco-friendly system than air-conditioning by heat pump. Rising temperatures due to global warming may lead to the increased occurrence of early-bolting, even in areas where early-bolting is currently not a problem. Early-bolting in *D. elatum* may be suppressed by ILTS, which is an easy-to-implement technology that can optimize delphinium flower production. The practical or commercial application of ILTS to suppress early-bolting in delphinium species will require further elucidation of the underlying molecular mechanism.

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