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Research Report

Different Day and Night Temperature Responses in *Lilium hansonii* in Relation to Growth and Flower Development

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Abstract. Temperature is one of the most important factors that directly affect the possibility and the rate of flower differentiation in many geophytes such as *Lilium*. In this experiment, different day and night temperatures were used to determine the required day and night temperature for flower bud development in *Lilium hansonii*. After low temperature exposure for breaking bulb dormancy, the bulbs were planted in pots, and placed in designated growth chambers each with a specific temperature. The plants were exposed to different temperatures for 30 days, and 15 days after planting sample plants were collected in each treatment for observation of flower bud development using the scanning electron microscope (SEM). Responses of plant height, number of leaves, and stem diameter were also measured as affected by difference between day and night temperature (DIF) and average daily temperature (ADT). The results showed that average daily temperature and high day temperature had a direct effect on the quality, quantity, and time required for flower bud development. They also affected the stem elongation, number of leaves, and stem diameter. Higher ADT and DT (25°C) promoted stem elongation and increased leaf unfolding rate (LUR), but with less number of leaves produced. As ADT and DT increased, stem diameter decreases. In lower ADT and DT (15°C) treatment, greater stem diameter and higher number of flower buds (2-7 buds) were produced. Higher ADT and DT promoted early flower bud initiation, but lower number of flower buds with higher possibilities of flower bud abortion, while lower ADT and DT showed slower flower bud initiation and development with higher flower bud formation.

***Additional key words*:** DIF, flower abortion, flowering physiology, scanning electron microscope (SEM)

Introduction

The genus *Lilium* contains ~110 species that are distributed in the northern hemisphere, mainly Asia, North America, and Europe (Liang and Tamura, 2000). Korea is known as an important distribution center for the genus *Lilium*, with diverse germplasm and twelve native lily species found in the mountainous areas in the country including *L. hansonii* representing the most primitive species (Lighty, 1969). In Korea, *L. hansonii* is growing in mountainous areas of Ulleung Island at elevation of 300-800 meters above sea level (van Tuyl et al., 2011). Generally, it has many flowers with long vase life, with unpleasant odor, and vigorous stem (Lim and van Tuyl, 2006). The *L. hansonii* has basically 3 layered whorled leaves and down facing scented florets. The flower color is yellow or golden yellow and very distinctive as compared to other lilies in native habitat. Nowadays, it is usually used as a genetic resource in commercial breeding programs for the development of new resistant cultivars against various biotic and abiotic stresses (Rhee et al., 2005; Sultana et al., 2011).

Previous experiment showed that for 65 days of exposure to cold temperature (4°C) was effective in breaking dormancy of *L. hansonii* (Lucidos, 2013). After dormancy breaking, stem elongation and further flowering are regulated by environmental conditions, mainly by air temperature (Kamenetsky et al., 2003). Temperature is a major determinant factor that exerts inductive effects on the phenotypical characteristics such as plant height as well as physiological factors, i.e. flower initiation by stimulating internal plant hormones

(Craufurd and Wheeler, 2009; Halliday et al., 2003; Lim, 1996; Younis et al., 2009). In some bulbous plant species, thermo-periodic fluctuations are required for flower induction and temperatures favorable to flower differentiation generally inhibit root initiation and differentiation (Halevy, 1990). It might also affect morphological growth in relation to flower bud development and flower bud abortion in geophytes (Hu and Willson, 2000). Apical meristem continues to produce leaves during harvesting, packaging, shipping, cold storage programming, planting of bulbs, shoot emergence, and even up to the flower initiation stage (Kodaira and Fukai, 2005). The flowering process involves five successive stages starting from flower bud induction, followed by initiation, organogenesis that involves differentiation of floral parts, maturation and growth of floral parts, and lastly flower anthesis. The successive steps are more or less easy to separate, but knowledge on the factors that control them and the determination of the period of the growth cycle during which they take place in the bulb are essential (De Hertogh and Le Nard, 1993). In *Lilium*, flower formation starts during or towards the end of storage period, but has to be completed after planting (Anderson et al., 2010).

Present experiment was conducted in order to determine an appropriate temperature for the flower bud development after dormancy breaking avoiding flower bud abortion by temperature. This will help to produce healthy and well developed plants with a good quality of flowers formed to be used for breeding and other physiology related studies.

Materials and Methods

Plant Materials

The bulbs of *Lilium hansonii* were collected from Ulleung Island, Korea and were used for the bulb dormancy experiment during year 2012. After the experiment, the bulbs were then stored at 4°C temperature for 65 days to break dormancy. Before conducting this experiment, such initial data were gathered as bulb circumference, number of bulb scales, number of leaves, and the initiation of flower buds.

Exposure to Different Day and Night Temperatures

The bulbs were planted in insert pot size (such as 10 cm) square pots filled with a commercial soil mixture (Nongwoo Bio Co., Ltd., Suwon, Korea) combined with coarse vermiculite (SunGro Horticulture, Bellevue, Inc., North Bloomfield, OH, USA). The pots were placed in designated growth chambers set to have either 15, 20, or 25°C air temperature. After emergence, plants were exposed to different day/night temperatures (15/15, 15/20, 15/25, 20/15, 20/20, 20/25, 25/15, 25/20, and 25/25°C). A long day length of 13 hours per day was provided with light intensity of 2,500 lux (Fluorescent lamp and high pressure sodium lamp), because *Lilium* plants are relatively long day plants. After exposures to different temperatures for 30 days and the plants were transferred to a greenhouse with 25°C day and 20°C night temperatures. The standard management practices for growing lilies, such as watering, fertilization, and pest management, were applied.

Observation Using a Scanning Electron Microscope (SEM)

In order to clearly observe and identify the effect of day and night temperatures on flower bud development, scanning electron microscopy (SEM) was conducted. Fifteen days after planting, samples were collected from each treatment and brought to the laboratory for dissection using a light microscope (CKX41, Olympus, Tokyo, Japan). After dissection, the flower bud samples were subjected to a series of procedures starting from fixation. For fixation, the Karnovsky's fixative solution (8% paraformaldehyde, 25% glutaraldehyde, and 0.2M cacodylate buffer) was used, wherein the samples were fixed for 24 hours. After fixation, the samples were washed using a 0.05 M cacodylate buffer for 10 minutes for three times. Then the samples were placed in 1% osmic acid for 2 hours at 4°C for post-fixation. After post-fixation, the samples were washed in a series starting from a 0.05 M cacodylate buffer (3 times for 10 minutes), a series of ethanol [2x 50% ethanol (30 minutes), 75% ethanol (30 minutes), 90% ethanol (30 minutes), 95% ethanol (30 minutes) and 2x 100% ethanol (30 minutes)], and one time with amylacetate for 30 minutes. Then the samples were stored in amylacetate in preparation for SEM observations. After the fixation process, the samples were dried using the critical point dryer (HCP-2, Hitachi, Tokyo, Japan) wherein the samples were placed first in a 50-80% liquid carbon dioxide (L-CO_2) at 20°C for 20 minutes and then at 38°C for 5 minutes. The dried samples were put in a specimen holder and placed in an ion sputter (E-1030, Hitachi, Tokyo, Japan) for white gold coating. A scanning electron microscope (S-4300, Hitachi, Tokyo, Japan) was used for observation.

Phenotypic Characteristics

Temperature is not only important in flower bud development, but also for expression of morphological characteristics of the plants. Before, during, and after exposing the plants to different day and night temperatures, plant height, number of leaves, stem diameter, and number of flower buds formed were measured. Days to flowering, number of flowers, and flower diameter (mm) were also recorded.

Statistical Analysis

In order to validate the relevance of each treatment from

the other in response to temperature, all data including the plant height, number of leaves, stem diameter, and number of flower buds formed at 15 days after planting were analyzed using Duncan's multiple range test (DMRT) at $p < 0.05$ with SPSS (version 19.0, SPSS Inc., Chicago, USA).

Results

Based on the initial data gathered after harvest, the average bulb used had 12.3 cm circumference with 51 scales and 18.8 mm nose size. It was also observed that leaf formation in the bulbs was already started, but no flower bud initiation observed under scanning electron microscope (SEM).

Morphological characteristics and flower buds formed at 15 days after exposure to different day and night temperatures are presented in Table 1. Based on these results, it was found that temperature had a significant effect on the plant height, number of leaves, stem diameter, and number of flower buds developed. These parameters were directly affected by the average daily temperature (ADT) and high day temperature (DT). As the day temperature increases (20-25°C) or with a positive DIF, stem elongation was promoted, while the low day temperature (15°C) slowed down the growth of the stem. Plant height was also monitored starting from emergence to flower bud maturation at a 5 day interval. It was found that higher average daily temperature and day temperature promoted stem elongation until 35 days after planting. After that, the growth became constant. Lower temperatures slowed down stem elongation, drastically increased it at the flowering stage. The plants exposed to 15°C in first 30 days and then transferred to greenhouse condition (25/20°C) showed least stem elongation. However, stem length on this treatment surpassed that of the plant exposed to 25°C at the flower bud maturation stage, and persisted until anthesis. Leaf formation and leaf unfolding rate (LUR) were also affected by temperature. Higher temperatures increased LUR, but caused to produce less numbers of leaves, while the low temperature (15°C) decreased LUR, but caused to produce more numbers of leaves. Stem diameter was also significantly affected by temperature. Higher temperatures produced plants with thinner stem diameters as compared with lower temperatures. This was also related to the development of flower buds; thicker stems had bigger apical meristems, and thus higher numbers of flower buds formed.

All morphological characteristics and flower bud development in *L. hansonii* were affected by temperature. Higher ADTs and DTs promoted stem elongation and LUR, but suppressed number of leaves produced and stem diameter, thus resulting in lesser numbers of flower buds as compared to lower ADTs and DTs.

As illustrated in Fig. 1, flower bud development was highly affected by average daily temperature (ADT) when observed with a scanning electron microscope (SEM). The lowest temperature (DT/NT = 15/15°C) treatment had the slowest flower bud development, but the greater number of flower buds. In the moderate temperature (DT/NT = 20/15°C) treatment, the flower buds developed faster and produced more flower buds than in the 15°C treatment. The DT/NT = 25/15°C treatment had the fastest flower initiation and development among three different temperatures, and at the same time had more flower bud abortion or blasting. Higher day temperatures increased the possibility of flower bud abortion or blasting and produced only one flower bud. The flower bud development observed through the SEM is illustrated in Fig. 2.

In terms of flowering time, plants at the lowest temperature (15°C) produced 5 flower buds, and had delayed flowering time (78 DAP) and shorter flower diameter (51.7 mm) as

Table 1. Morphological characteristics and flower buds formed at 15 days after planting.

Day temp. (°C)	Night temp. (°C)	Average daily temp. (°C)	Difference between DT and NT (°C)	Plant height (cm)	Number of leaves	Stem diameter (mm)	Number of flowers
15	15	15	0	5.5 g[z]	35.0 d	7.1 b	5.0 b
	20	17.5	-5	8.4 e	44.3 c	7.2 b	2.0 e
	25	22.5	-10	9.8 d	47.7 a	7.4 b	4.0 c
20	15	17.5	5	5.8 g	43.0 c	5.6 c	3.0 d
	20	20	0	9.7 d	36.7 d	5.6 c	2.0 e
	25	22.5	-5	6.6 f	45.7 b	8.1 a	7.0 a
25	15	20	10	24.7 a	19.3 e	3.5 d	1.0 ef
	20	22.5	5	20.7 b	15.7 e	2.9 e	1.0 ef
	25	25	0	19.5 c	18.3 e	2.7 e	0.6 f

[z]Means with the same letters are not significantly different by Duncan's multiple range test (DMRT) at $p < 0.05$.

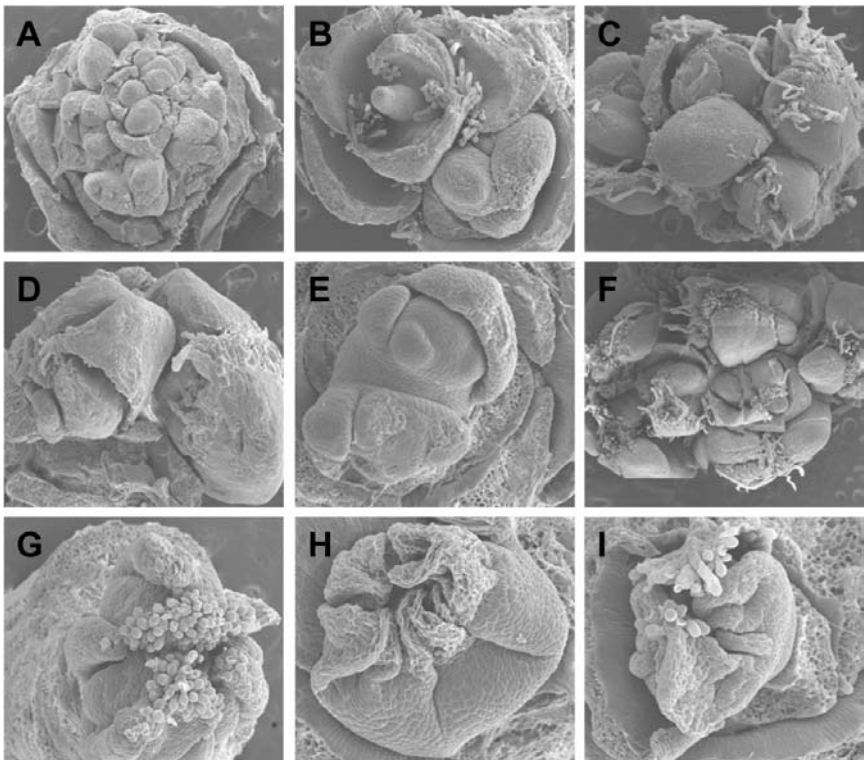

Fig. 1. Scanning electron microscopic (SEM) observation of *L. hansonii* flower buds (15 DAP) exposed to different day/night temperatures: A, 15/15 (x25); B, 15/20 (x40); C, 15/25 (x30); D, 20/15 (x35); E, 20/20 (x40); F, 20/25 (x30); G, 25/15 (x60); H, 25/20 (x90); and I, 25/25 (x80). Figures A to F show flower bud formation without abortion. However, Figs. G to I indicate flower abortion due to high day temperature (25°C).

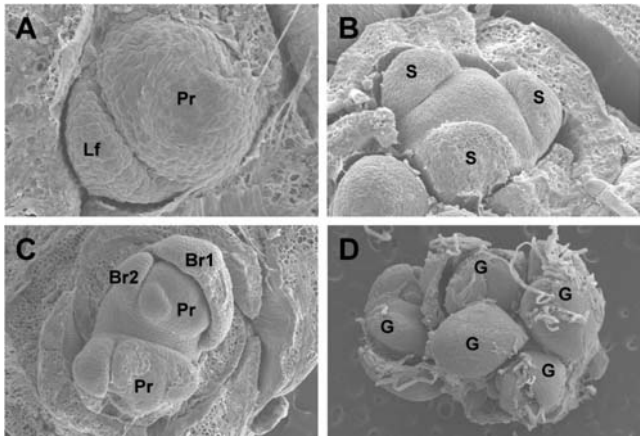

Fig. 2. Flower bud development in *L. hansonii* observed using a scanning electron microscope: A, vegetative stage; B, reproductive stage (P1 stage); C, reproductive stage (A1-A2 stages with bracts visible); and D, reproductive stage (G stage). Pr, Primordia; Lf, Leaf; S, Sepal; Br1, Bract 1; Br2, Bract 2; and G, Gynoecium (G stage).

compared to with those at a moderate temperature (20°C) which produced only two flower buds and earlier flower time (73 DAP) and longer flower diameter (61.4 mm) (Table 2). High temperature (25°C) promoted flower bud abortion. Based on the results, 1°C decreased in temperature delayed the flowering time by about 1 day (Fig. 3).

Table 2. Effect of average daily temperature (ADT) on flowering characteristics of *L. hansonii*.

ADT (°C)	Number of flowers	Days to flowering	Flower diameter (mm)
15	5 a[z]	78 a	51.7 b
20	2 b	73 b	61.4 a
25	Not flowered	Not flowered	Not flowered

[z]Means with the same letters are not significantly different by Duncan's multiple range test (DMRT) at $p < 0.05$.

The time required for flower bud development was also affected by temperature, especially by the average daily temperature and day temperature. Exposure to high temperature (25°C) starting from planting caused the plant to have a shorter time at the vegetative stage, and thus formation of leaves was limited and stem was thin and weak. In contrast, the plants exposed to lower temperature (15-20°C) had a longer vegetative stage to produce more leaves and a thicker stem. Since the high temperature caused a shorter vegetative stage, the plants in that treatment had earlier flower development (flower initiation, flower differentiation) with only one flower bud formed and with high possibility of flower bud abortion or blasting (Fig. 4). The plants exposed to the

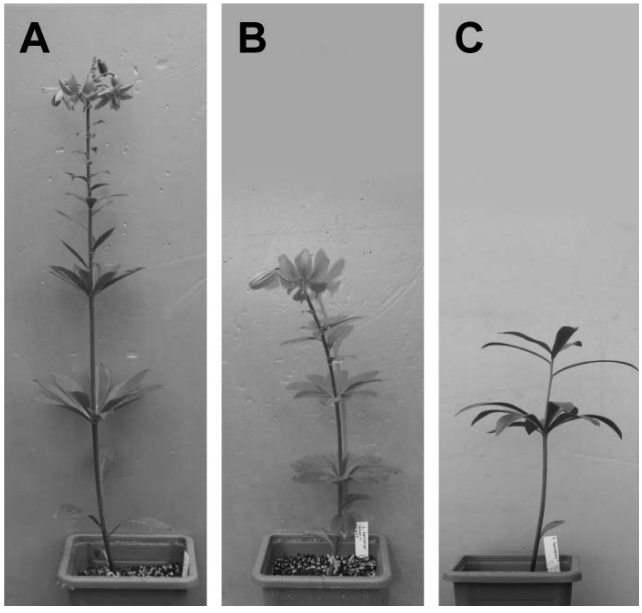

Fig. 3. Flowering of *L. hansonii* in response to day time (DT)/night time (NT) temperatures: A, DT/NT = 15/15°C; B, DT/NT = 20/15°C; and C, DT/NT = 25/15°C.

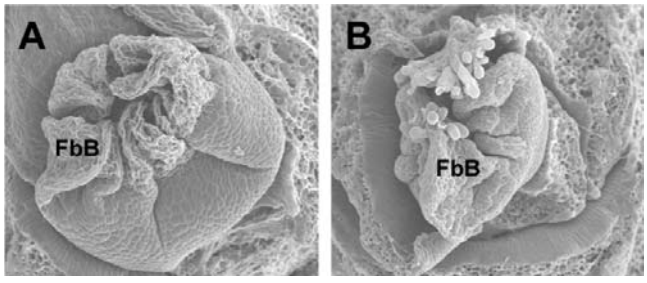

Fig. 4. Flower bud abortion in *L. hansonii* at 25°C: A, early stage of flower bud blasting (FbB); and B, severe stage of flower bud blasting.

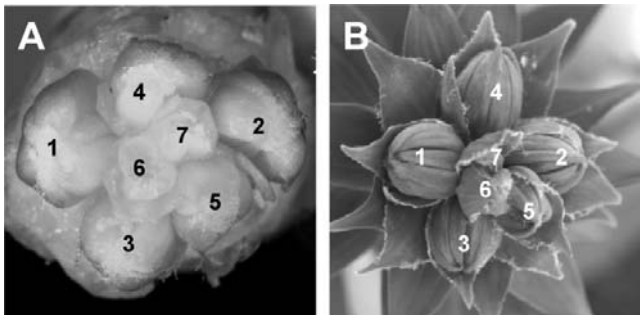

Fig. 5. Pattern of the flower bud formation in *Lilium hansonii* observed at early stage (A) and late stage (B). Numbers on flower buds indicate that showing clockwise orientation.

low temperature had a longer vegetative stage, and thus flower bud developed gradually to have more flowers of higher quality and low possibility of flower bud abortion.

With all environmental factors favorable for flower bud development, the plants produced 2-7 flower buds in a clockwise orientation of flower bud formation (Fig. 5). Based on flower bud size, first flower bud developed on the left side, followed by the second flower bud on the right side of the primodium. The third flower bud developed at the lower center of the meristem which was followed by the fourth flower bud in the upper center of the meristem. The four flower buds developed formed the first set of a cross-like pattern. This was confirmed at anthesis by a visual observation. The flower buds formed in a criss-cross pattern, and were further completed with their clockwise orientation of flower formation. A clockwise orientation of flower bud formation was observed under the light microscope and SEM (Fig. 5). This pattern of flower bud formation is the same of genus *Lilium*.

Discussion

In *Lilium*, flower development is one of the most important stages to consider, since lilies are widely known cut flowers with the greatest diversity in terms of kind of flowers, shape, size, and color. Environmental factors, such as photoperiod and temperature, exert inductive effects on flowering by stimulating internal plant hormones (Sarathum et al., 2010). In *Lilium,* temperature is one of the factors that highly affect flower bud development and growth, and lilies generally require vernalization for flower initiation, although non-vernalization lilies were also reported (Anderson et al., 2009, 2011). In terms of plant height, higher average daily and day temperatures promoted stem elongation. According to Erwin et al. (1989), as day temperature (DT) increased, plant height also increased; as night temperature (NT) increased, plant height decreased. It was the difference (DIF) between day and night temperatures (DIF equals DT minus NT), not the absolute temperature that controlled plant height or internode length. In *Lilium hansonii*, the high temperature (25°C), as compared to low temperature (15°C), promoted early flower bud initiation, but caused the plants to have less leaves, thinner stems, and only one flower bud due to increased flower bud abortion. The lower temperature (15°C) treatment caused slower flower initiation and development, slower stem elongation, but more leaves, thicker stem, and about 2-7 flower buds with lower possibilities of flower bud abortion. This supports the results of Roh and Wilkins (1973) in that warmer temperature tended to produce taller plants and increased flower abortion. Boontjes (1982) also reported that bud abortion of 'Connecticut King' can be caused by high temperatures during summer. Roh (1990) found that although flowering in 'Red Carpet', 'Cherub', 'Sunray', and 'Connecticut Lemonglow' was accelerated at 26/24°C as compared to 16/13°C day/night temperatures, the number of aborted flower buds was higher at the higher temperatures. According to Karlsson et al. (1988), leaf unfolding was a linear function of the average daily tem-

perature, within the approximate commercial limits of photoperiod and temperature. In terms of stem diameter, De Hertogh et al. (1976) reported that the number of flowers formed was correlated with meristem diameter. In the case of Easter lily, greenhouse temperature of 13°C promoted the formation of primary flowers, while 21°C promoted the formation of secondary flowers (De Hertogh et al., 1976).

In present experiment, the flower bud formation pattern of *L. hansonii* occurred in a clockwise orientation with 4-5 flower buds per set. In Asiatic hybrid 'Rouge Pixie' a whorl of flower buds, usually four or five, is initiated first around the perimeter of the meristem. Then another whorl of several buds (usually three or four) may be initiated on a scape that arises from the middle of the meristem (De Hertogh and Le Nard, 1993).

Lilium hansonii which belongs to the section Martagon is second in terms of time of flower initiation and flower development among four *Lilium* groups. A study conducted by Ohkawa (1989) divided the *Lilium* into four groups depending on their time of flower bud initiation. In the first group, flower buds initiation starts in early fall, before the bulbs sprouted, and completes after shoot emergence. Asiatic hybrid lilies belongs to the first group, wherein some Asiatic hybrids start their flower bud initiation as early as inside the bulb during cold storage, and others starts and completes the flower initiation and flower development after shoot emergence (Ohkawa et al., 1990). The second group is *L. hansonii* wherein as a result of this experiment; the flower bud initiation starts at 5-10 days after shoot emergence and completes its flower maturation in 20-30 days after planting. The third group is Oriental hybrid lilies which start initiate flower initiation and development at 10-15 days after planting, and the last group is *Longiflorum* hybrids which start flower initiation and development at 20-30 days after planting. The results of these experiments can be applied for proper temperature management for Hanson lily (*L. hansonii*) to get its maximum potential in terms of bulb dormancy breaking, morphological characteristics, and flower quality and quantity, and also to minimize flower bud abortion. The development of good quality flowers of *L. hansonii* can be used for further studies such as breeding, production, and physiology related studies to understand the evolution and potential of *L. hansonii* in the floriculture industry and in horticulture in general.

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