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Influence of Growing Temperature on Dry Matter Accumulation in Plant Parts of 'Siberia' Oriental Hybrid Lily

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Abstract

'Siberia' Oriental hybrid lily plants were grown under conditions of changing day temperature (DT) and night temperature (NT). Plants were grown under three fluctuating temperature conditions (average 25.8°C, 23.4°C, and 19.9°C) in a temperature gradient growth chamber (TGC), and under three DT/NT levels (28/23°C, 24/19°C, and 20/15°C) in constant temperature growth chambers (CGCs). In the CGC experiment, 35 days after planting (at the visible bud stage), the plants grown under low temperature conditions had high fresh weight (FW) of the stem and stem roots. At the flowering stage in both TGC and CGC experiments, the plants grown under low temperature conditions had a longer stem length and higher FW of the stem, flower buds, stem roots, and bulb compared than those of plants grown under high temperature conditions. The plants grown under low temperature conditions had high dry weight (DW) of the total plant, stem, and bulb, and a high DW/FW ratio of the stem and bulb. In both TGC and CGC experiments, the plants grown under the low temperature conditions showed a high relative growth rate (RGR) and net assimilation rate (NAR) from planting to flowering. These data demonstrate that cooler growing temperatures are advantageous for the accumulation of dry matter in 'Siberia' lilies. The low growing temperature enhances the accumulation of dry matter in 'Siberia' lily plants via the promotion of photosynthesis by leaves and the absorption of nutrients by well-developed stem roots.

Discipline: Horticulture
Additional key words: growth analysis, photosynthesis, stem roots

Introduction

The cut flowers of Oriental hybrid lilies (*Lilium* hybrids) are very popular in markets for their colorful and gorgeous appearance. However, basic data on the relations between environmental conditions during the forcing and growth of Oriental hybrid lilies are limited. There have been many reports describing the temperature and light conditions for other important commercial varieties such as *L. longiflorum* Thunb. (Easter lily), especially regarding the production of potted plants. Although information from these reports occasionally applies to Oriental hybrid lilies as cut flowers, it may not necessarily be appropriate in view of genetic differences and production goals. The quality of cut flowers is essentially based on the accumulation and distribution of dry matter (DM) among the shoots and floral organs. For example, the cut flower quality of tulips is determined by DM allocation at the flowering stage, as influenced by temperature and the duration of bulb storage and forcing temperature[5,6]. We studied the effects of the growing environment (e.g. temperature, irradiance, CO_2 concentration) on DM accumulation and distribution in a typical Oriental lily cultivar ('Sibelia'). This report is part of a study dealing with the effects of growing temperature where both day temperature (DT) and night temperature

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(NT) were changed simultaneously. We also applied growth analysis to this study as previously applied to other ornamental plants such as roses[16,17] and tulips[5].

Materials and methods

1. General methods

We conducted experiments in a temperature gradient growth chamber (TGC) and natural light constant temperature growth chambers (CGCs; Koitotron S153A; Koito Industry Co., Yokohama, Japan) at the NARO Tohoku Agricultural Research Center in Morioka, Japan. Bulbs (18–20 cm in circumference) produced in the Netherlands and stored at subzero temperature, were obtained from an importer. The bulbs were thawed at 2–5°C for 1–2 weeks before pre-rooting treatment. The pre-rooting treatment of bulbs at 10°C with sphagnum peat moss to encourage root development[1, 14] began on May 28, 2008. The bulbs were planted in pots on June 18. One bulb was planted per plastic pot (21 cm in diameter) filled with a growing medium containing slow-release fertilizer. Bulbs were planted at ca. 10 cm from the surface of the medium to ensure adequate stem root growth[2]. At planting time, the plants were sampled, and with both the fresh weight (FW) and dry weight (DW) being measured. In both experiments, plants were grown under natural day length.

We conducted two sub-experiments.

2. Fluctuating temperature conditions (TGC experiment)

On the day of bulb planting (June 18), the plants were transferred to the TGC. The temperatures in the TGC fluctuated under control according to ambient temperature[10] (Fig. 1). The TGC was designed to create a temperature gradient along its longitudinal axis, resulting in the highest temperature furthest from the air inlet. In the TGC, 10 plants each were arranged at interval of 1 m (low temperature, L), 12 m (moderate temperature, M), and 23 m (high temperature, H) from the air inlet. The TGC was covered by transparent plastic film allowing the transmission of sunlight; no shading was installed. The plants were then sampled for measurement at the flowering stage as described below.

3. Constant temperature conditions (CGC experiment)

On the day of bulb planting (June 18), the plants were transferred to the CGCs. Twenty plants were arranged in each of the three chambers. From the date of bulb planting, the temperature in all CGCs was set to 22°C at day (06:00–18:00) and to 17°C at night (18:00–06:00). From June 30 (12 days after planting), the DT/NT in each CGC was set to 28/23°C, 24/19°C, or 20/15°C. On July 23, at the visible bud stage (35 days after planting, day 35) and at the flowering stage of each experimental plot, 10 plants from each chamber were sampled. The relative humidity (RH) in the growth chambers was maintained at >70%. The outer glass surface of the CGCs was covered with black cheesecloth, giving a shading rate of 40% to avoid leaf tip burn disorder caused by high irradiance[3].

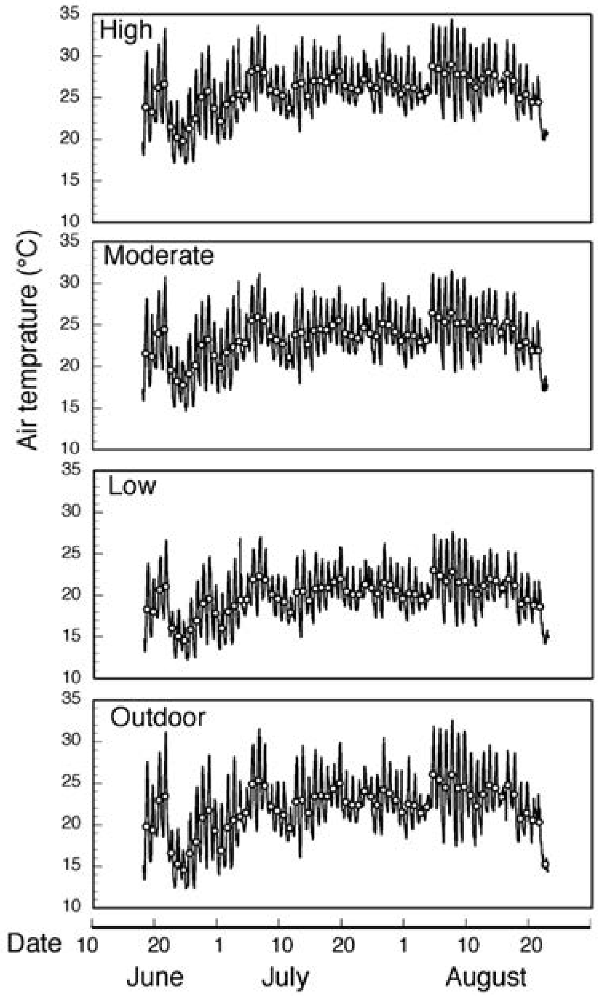

Fig. 1. Temperatures in the temperature gradient chamber (TGC)
Temperatures were measured at 1 m (for low temperature), 12 m (moderate temperature), and 23 m (high temperature) from the air inlet.
Circles show average daily temperatures.

4. Measurement and growth analysis

When several plants had reached the flowering stage in each experimental plot, all plants from those plots were simultaneously harvested for measurement. The sampled plants were then separated into their various constituents, with their size, FW, DW, and leaf area (LA) being recorded. From the data of DW and LA data, we calculated the leaf area ratio (LAR, LA per unit of total plant DW, $cm^2 g^{-1}$),

Table 1. Number of leaves and flower, stem length, fresh weight, and fresh/dry weight ratio of 'Siberia' lily grown under 3 fluctuating temperature levels in a temperature gradient chamber (TGC) estimated at the flowering stage

Temperature level	Date of sampling at the flowering stage[1)]	Days from plating to sampling	Number of		Length of stem[3)] (cm)	Fresh weight of					Dry/fresh weight ratio of		
			intact leaves[2)]	flower buds		leaves (g)	stem (g)	flower buds (g)	stem roots (g)	bulb (g)	leaves ($g\ g^{-1}$)	stem ($g\ g^{-1}$)	bulb ($g\ g^{-1}$)
High	Aug. 18	61	61.8 a[4)]	7.2 a	70.1 a	71.9 a	70.1 a	86.6 a	122.7 a	45.5 a	0.154 a	0.177 a	0.208 a
Moderate	Aug. 19	62	62.9 a	7.5 a	72.0 a	70.9 a	76.3 ab	97.1 ab	115.1 a	52.6 b	0.159 a	0.178 a	0.213 a
Low	Aug. 21	64	60.5 a	7.2 a	77.3 b	82.3 b	85.5 b	107.1 b	170.6 b	56.1 b	0.153 a	0.197 b	0.232 b

1): All plants were sampled when several plants had well-colored flower buds in each plot.
2): Intact leaves on the stem and peduncles.
3): Length between basal plate and peduncle of top flower bud.
4): Values with the same letter are not significantly different by Tukey's multiple range test at 5% level.

specific leaf area (SLA, LA per unit of leaf DW, $cm^2\ g^{-1}$), relative growth rate (RGR, rate of increase in total plant DW per unit of plant DW, $mg\ g^{-1}\ day^{-1}$), and net assimilation rate (NAR, rate of increase in total plant DW per unit of LA, $g\ m^{-2}\ day^{-1}$) as follows:

$$LAR = \frac{A_{leaf}}{W_{total}}$$

$$SLA = \frac{A_{leaf}}{W_{leaf}}$$

$$RGR = \frac{\ln W_{total\ 2} - \ln W_{total\ 1}}{t_2 - t_1}$$

$$NAR = RGR \times \frac{W_{total\ 2} + W_{total\ 1}}{A_{leaf\ 2} + A_{leaf\ 1}}$$

Where, W_{total} denotes total plant DW (g or mg), W_{leaf} is leaf DW (g), A_{leaf} is LA (cm^2 or m^2), t is time (day), and subscript numerals represent time (1 = initial, 2 = final).

Results

The total FW at planting was 104.6 g (bulb, 75.0 g; shoot, 25.7 g; and bulb roots, 3.9 g). The total DW at planting was 29.2 g (bulb, 25.5 g; shoot, 3.2 g; and bulb roots, 0.5 g).

1. Fluctuating temperature conditions (TGC experiment)

The daily maximum, minimum and average temperatures from planting to flowering for H plants were 30–34°C, 20–25°C, and 25.8°C, respectively; those for M were 25-30°C, 17-22°C, and 23.4°C; and those for L were 17-22°C, 14-20°C, and 19.9°C (Fig. 1). Average RH was 56.0% for H, 62.9% for M, and 75.5% for L. Consequently, the average vapor pressure deficits (VPDs) were 1.51 kPa for H, 1.11 kPa for M, and 0.61 kPa for L.

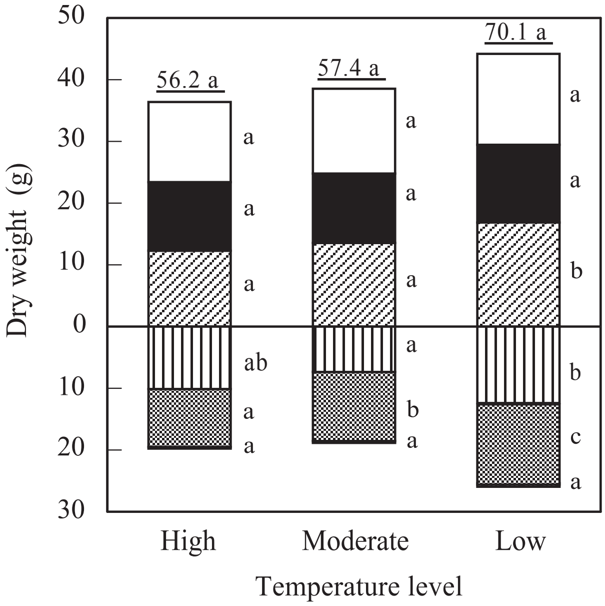

Fig. 2. Dry matter distribution at the flowering stage of 'Siberia' lilies grown under 3 fluctuating temperatures in a TGC
□: Flower buds, ■: Leaves, ▨: Stem, ▥: Stem roots, ▦: Bulb, ▩: Bulb roots
Figures above the bars indicate total dry weight.
Mean separation within organs and total dry weight by Tukey's multiple range test at 5% level.

The date of sampling at the flowering stage was a little earlier for the H plants than for the M and L plants (Table 1). At the flowering stage, the L plants showed increased stem length and increased FW of the leaves, stem, flower buds, stem roots, and bulb (Table 1). The L plants also showed increased DW of the total plant, stem, stem roots, and bulb (Fig. 2), increased DW/FW ratios of the stem and bulb (Table1), and increased LA (Table 2). No significant difference was detected in LAR and SLA at the flowering stage (Table 2). RGR and NAR from planting were higher in the M and L plants than in the H plants (Table 2).

Table 2. Leaf area, leaf area ratio, specific leaf area, relative growth rate, and net assimilation rate of 'Siberia' lily grown under 3 fluctuating temperature levels in a TGC estimated at the flowering stage

Temperature level	Leaf area		LAR[1)]	SLA[2)]	RGR[3)]	NAR[4)]
	Total (cm^2)	Per leaf (cm^2)	(cm^2 g^{-1})	(cm^2 g^{-1})	from planting (mg g^{-1} day^{-1})	from planting (g m^{-2} day^{-1})
High	1474 a[5)]	23.9 a	26.4 a	134.0 a	6.1 a	0.894 a
Moderate	1468 a	23.4 a	25.8 a	130.8 a	10.7 b	1.598 b
Low	1711 b	28.4 b	24.4 a	140.4 a	13.6 c	1.983 b

1): Leaf area ratio.
2): Specific leaf area.
3): Relative growth rate.
4): Net assimilation rate.
5): Values with the same letter are not significantly different by Tukey's multiple range test at 5% level.

Table 3. Number of leaves and flower, stem length, fresh weight, and fresh/dry weight ratio of 'Siberia' lily grown under 3 day/night temperature levels in constant temperature growth chambers (CGCs) estimated at the visible bud stage (35 days after planting)

Temperature (Day/Night)	Number of		Length of stem[2)] (cm)	Fresh weight of					Dry/fresh weight ratio of		
	intact leaves[1)]	flower buds		leaves (g)	stem (g)	flower buds (g)	stem roots (g)	bulb (g)	leaves (g g^{-1})	stem (g g^{-1})	bulb (g g^{-1})
28/23°C	58.4 a[3)]	6.7 a	80.1 a	75.6 b	69.2 a	5.4 b	52.6 a	44.6 a	0.108 ab	0.112 a	0.152 a
24/19°C	61.0 a	6.5 a	90.0 b	70.0 ab	73.9 ab	5.2 b	52.7 a	50.9 a	0.105 a	0.116 a	0.134 a
20/15°C	60.4 a	7.3 a	85.6 ab	62.1 a	79.9 b	3.5 a	78.9 b	59.8 b	0.112 b	0.119 a	0.137 a

1), 2), 3): See footnote of Table 1.

2. Constant temperature conditions (CGC experiment)

On day 35 (at the visible bud stage), the 28/23°C plants showed low FWs of the stem, stem roots, and bulb (Table 3) and high leaf FW (Table 3), and large individual LA (data not shown). At this stage, the FW of flower buds at 20/15°C was less than that under other temperature conditions (Table 3). On day 35, the total DW of plants grown under the three temperature conditions was similar to that at planting (29.2 g); at the same time, bulb DW decreased markedly from that at planting (25.5 g) (Fig. 3A).

The date of sampling at the flowering stage was earlier for plants grown under the high temperature conditions (Table. 4). At the flowering stage, the plants grown under low DT/NT conditions showed increased stem length and increased FW of the stem, flower buds, stem roots, and bulb (Table 4). The total plant DW increased between planting and flowering under all DT/NT conditions, and was particularly large under low DT/NT conditions (Fig. 3B). Plants grown under low temperature conditions also showed increased DW of the flower buds, stem, and bulb (Fig. 3B), and high DW/FW ratios of the leaves, stem, and bulb (Table 4).

While there were no significant differences between temperature conditions regarding LA at the flowering stage, LAR and SLA for the 20/15°C plants were both low (Table 5). Plants grown under the low DT/NT conditions showed a high RGR from planting, as well as a high NAR from planting and from day 35 to flowering (Table 5).

Discussion

The growth of green plants basically depends on the assimilation of carbon dioxide by photosynthesis and the absorption of mineral nutrition and water from the roots. Most varieties of *Lilium* are categorized as bulbous crops; cut flower production is characterized by starting from a bulb that stores abundant nutrient reserves. Most of the DM in the developing part of the tulip, which is also a bulbous plant, originates from the storage materials in the bulb scales[4,6,11]. In our experiments, the total plant DW was 29 g at planting and in the range of 36–70 g (Figs. 2 and 3) at the flowering stage. From these data, 20–60% of DM at the flowering stage had been accumulated after planting, by photosynthesis and the absorption of nutrients depending on the temperature conditions. However, the total plant DW at the visible bud stage (on day 35) in the CGC experiment was identical to that at planting. The elongation of shoot and roots from planting to the visible bud stage of 'Siberia' lilies may depend on reserves in the mother bulb, and the

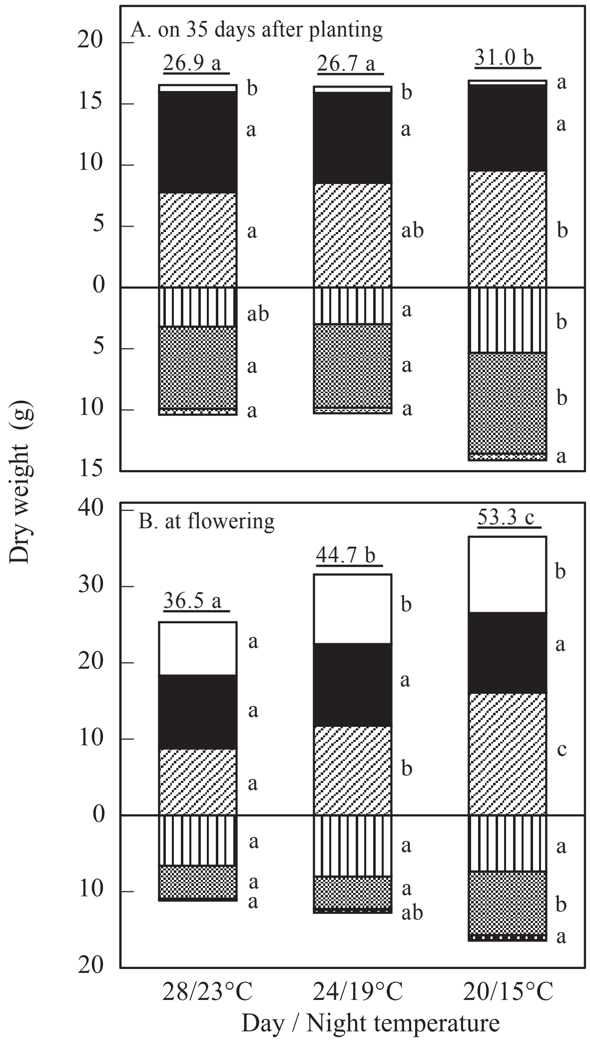

Fig. 3. Dry matter distribution of 'Siberia' lilies grown under 3 day/night temperature conditions in constant temperature growth chambers (CGCs)

□: Flower buds, ■: Leaves, ▨: Stem, ▥: Stem roots, ▦: Bulb, ▩: Bulb roots

A: 35 days after planting (at the visible bud stage); B: at the flowering stage.

Figures above the bars indicate total dry weight.

Mean separation within organs and total dry weight by Tukey's multiple range test at 5% level.

bulk of new DM accumulation apparently occurs after this stage. In experiments determining ^{14}C translocation in 'Nellie White' (an Easter lily)[18] and 'Star Gazer' (an oriental lily)[15], the sink activity of flowers before anthesis was very high and bulb scales were markedly competitive with flowers as a sink. This dominant DM accumulation in the flower buds and bulb between the visible bud stage and flowering stage was also observed in the experiments (Fig. 3A and B).

Our experiments were conducted under conventional constant DT/NT conditions in the CGCs, and under fluctuating temperature conditions simulating natural temperature changes in the TGC. The results obtained by both approaches were generally similar. Although plants grown under the high temperature conditions flowered earlier, there was little difference recorded except for the 20/15°C plants in the CGC experiment (Tables 1 and 4), a result different from that in Easter lilies as reported by Karlsson et al.[7]. The marked reduction in bulb DW under high temperature conditions observed at the visible bud stage on day 35 (Fig. 3A) may reflect a rapid mobilization of storage in the bulb for newly developing organs. The flower bud FW of low DT/NT of the 20/15°C plants on day 35 was lower than that of plants grown under high temperature conditions (Table 3), and thus indicates a delay in the reproductive developmental stage due to low temperature conditions. However, FW (Table 3) and DW (Fig. 3A) of the stem and stem roots of the 20/15°C plants at this stage were high in spite of low leaf FW (Table 3) and individual LA (data not shown), thus suggesting an intensive distribution of DM originating from the bulb to these parts. At the flowering stage, the plants grown under low temperature conditions had a long stem length and high FWs of the stem, flower buds, and bulb in both TGC (Table 1) and CGC experiments (Table 4). These results were derived from a sufficient accumulation of DM in all plant parts (Figs. 1 and 2). The DW/FW ratios of the stem, bulb, and/or leaves were high in plants grown under low temperature conditions (Tables 1 and 4), implying that massive plants suitable for cut flowers were obtained. In the CGC experiment, in which RH was maintained at >70%, the low DT/NT of the 20/15°C plants had thick leaves with low SLA and LAR (Table 5). Reduced SLA and LAR under a low temperature environment were also observed in sweet pepper[8] and roses[16,17]. In the TGC experiment, no differences in SLA and LAR were observed (Table 2). It is thus possible that the large VPD gradient in the TGC[10] affected leaf extension. The influence of air humidity on LA was also observed in some crops[12].

Plants grown under the low temperature conditions (e.g. L plants in TGC, 20/15°C plants in CGCs) showed increased total DW at the flowering stage (Figs. 1 and 2), and high RGR from planting to flowering (Tables 2 and 5). Two factors may have influenced these results. One is the development of stem roots that play a key role in absorbing water and nutrients, and which significantly affect the growth of aerial parts[2]. As high temperatures strongly inhibit stem root development in Oriental hybrid lilies just after planting, we conducted "pre-rooting" treatment[1, 14] before bulb planting. And in the CGC experiment, the plants were grown at 22/17°C for 12 days after planting to avoid exposure to high temperature. However, the stem roots of plants grown under low temperature conditions had a high FW (Tables 1, 3, and 4), and these well-developed roots may have contributed to the growth of shoot and flow-

Table 4. Number of leaves and flower, stem length, fresh weight, and fresh/dry weight ratio of 'Siberia' lily grown under 3 day/night temperature levels in CGCs estimated at the flowering stage

Temperature (Day/Night)	Date of sampling at the flowering stage[1)]	Days from plating to sampling	Number of		Length of	Fresh weight of					Dry/fresh weight ratio of		
			intact leaves[2)]	flower buds	stem[3)] (cm)	leaves (g)	stem (g)	flower buds (g)	stem roots (g)	bulb (g)	leaves $(g\ g^{-1})$	stem $(g\ g^{-1})$	bulb $(g\ g^{-1})$
28/23°C	Aug. 18	61	57.4 a[4)]	6.1 a	77.9 a	79.3 a	71.6 a	59.9 a	89.8 a	25.4 a	0.120 a	0.122 a	0.170 a
24/19°C	Aug. 21	64	62.4 a	6.8 a	92.5 b	84.0 a	84.7 b	80.2 b	103.4 ab	24.9 a	0.128 b	0.139 b	0.170 a
20/15°C	Sep. 1	75	60.7 a	6.7 a	102.6 c	72.9 a	94.8 b	83.7 b	121.3 b	33.9 b	0.143 c	0.169 c	0.243 b

[1), 2), 3), 4)]: See footnote of Table 1.

Table 5. Leaf area, leaf area ratio, specific leaf area, relative growth rate, and net assimilation rate of 'Siberia' lily grown under 3 day/night temperature levels in CGCs estimated at the flowering stage

Temperature (day/night)	Leaf area		LAR[1)] $(cm^2\ g^{-1})$	SLA[2)] $(cm^2\ g^{-1})$	RGR[3)] $(mg\ g^{-1}\ day^{-1})$		NAR[4)] $(g\ m^{-2}\ day^{-1})$	
	Total (cm^2)	Per leaf (cm^2)			from planting	from 35 days after planting[5)]	from planting	from 35 days after planting
28/23°C	1843 a[6)]	32.0 a	50.9 b	193.9 b	3.4 a	11.2 a	0.305 a	0.504 a
24/19°C	1964 a	31.4 a	44.6 b	184.2 ab	6.4 b	17.3 b	0.605 b	0.833 b
20/15°C	1802 a	29.7 a	36.0 a	173.4 a	7.8 b	13.1 ab	0.895 c	0.834 b

[1), 2), 3), 4), 6)]: See footnote of Table 2.
[5)]: At the visible bud stage.

ers.

The other factor is the efficiency of photosynthesis. NAR is a parameter reflecting the photosynthetic rate per LA; in plants grown under low temperature conditions, NAR was high in both the TGC and CGC experiments (Tables 2 and 5). Low LAR and SLA alone may lead to a reduction of photosynthesis. Photosynthetic assimilation in rose plants grown under low temperatures with low LAR and SLA was compensated by increased NAR through high ribulose-1, 5-bisphosphate carboxylase/oxygenase content and/or high stomatal leaf conductance in leaves[16,17]. The results of the few studies conducted on photosynthesis in Oriental hybrid lilies are not in accord. Yamaguchi and Kamijo[19] reported the optimum photosynthesis temperature of 'Star Gazer' as being 15–20°C, while Sorrentino et al.[13]. claimed that of 'Casa Blanca' to be 31–32°C. The difference between their data stands in marked contrast, and the findings from neither of those studies are in accord with ours. Hence, more information is needed regarding photosynthesis in Oriental lilies. Accelerated respiratory loss due to high NT may also affect the accumulation of DM at the flowering stage.

In conclusion, low growing temperature helps enhance the accumulation of DM in 'Siberia' lilies via the promotion of photosynthesis by leaves and the absorption of nutrients by well-developed stem roots. The plants grown under low temperature had massive shoots and/or bulbs with a high DW/FW ratio, which are advantageous quality for commercial production. These results support the advantages of the culturing Oriental lilies under cooler conditions in summer. In warmer districts, a heat pump cooling system is expected to be available for cooling growing temperatures in forcing facilities during summer[9]. Shading is an effective method of lowering DT, but at the same time may inhibit photosynthesis. For instance, shading apparently caused the total DW in the CGC experiment (Fig. 3B) to be lower than that in the TGC experiment (Fig. 2). Our next report will address the influence of shading on DM accumulation by the 'Siberia' Oriental hybrid lily. The individual effects of DT and NT also demand further investigation.

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