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Growth and Flowering Responses of Korean Native *Veronica rotunda* and *Veronica longifolia* to Cold Treatment and Light Conditions

저온 처리와 광 환경에 따른 한국 자생식물인
산꼬리풀과 긴산꼬리풀의 생육 및 개화 반응

BY

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UNDER THE DIRECTION OF DR. KI SUN KIM
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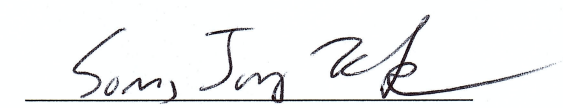
MEMBER 
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ABSTRACT

Mountain spike speedwell [산꼬리풀, *Veronica rotunda* var. *subintegra* (Nakai) T.Yamaz.] and long-leaf spike speedwell (긴산꼬리풀, *V. longifolia* L.) are Korean native plants that were selected as potential new ornamental crops due to their unique appearance and flowering time. This study was conducted to examine the effects of cold treatment, photoperiod, and daily light integral (DLI) on the growth and flowering of two *Veronica* species. In Experiment I, seedlings were grown under 9 h photoperiod at 22°C. The plants (seedlings) with four or five nodes were stored at 5°C for 0, 3, 6, 9, or 12 weeks, then forced under six photoperiod conditions [9, 12, 14, 16, or 24 h of continuous light or 9 h with a 4 h night interruption (NI; 22:00 to

02:00 $_{HR}$)] in a greenhouse. Regardless of the duration of cold treatment, there were no significant differences between photoperiods in all growth parameters in both species. Cold treatment was not required for the flowering of two *Veronica* species, and photoperiod also did not affect the flowering of both species. These results indicate that two *Veronica* species can be classified as day-neutral plants without vernalization requirement. In Experiment II, seedlings with four or five nodes were grown under five DLI conditions (3.6, 6.6, 8.1, 14.7, and 18.3 $mol \cdot m^{-2} \cdot d^{-1}$) to determine the effect of DLI. The plants grown under DLI conditions of 8.1 to 18.3 $mol \cdot m^{-2} \cdot d^{-1}$ showed the lower maximum quantum efficiency (F_v/F_m) than those grown under DLI conditions of 3.6 and 6.6 $mol \cdot m^{-2} \cdot d^{-1}$ after 2 weeks of treatments. However, these differences diminished at 6 weeks after treatments. The net CO_2 assimilation rates (A_n) for the light intensity of 200 to 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased with increasing DLI. Most growth parameters of both species increased with increasing DLI. Increasing DLI did not affect flowering percentage in both species. However, the number of nodes below the first inflorescence was lower under higher DLI conditions, and the number of visible inflorescences (VI) and inflorescence length at the first open flower showed a similar trend as growth parameters. Days to VI, from VI to the first open flower, and to the first open flower decreased as DLI increased. These results suggest that high DLI condition can promote the growth and flowering of two *Veronica* species, and it can be used to force flowering of these plants in commercial production.

Additional keywords: daily light integral, herbaceous perennial, photoperiod, photosynthesis, vernalization

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INTRODUCTION

Veronica is a genus of the Plantaginaceae (APG, 2003) and contains about 450 species distributed over much of the Northern Hemisphere (Albach et al., 2004). Some *Veronica* plants are hardy in USDA zones 4-6 and commonly produced and marketed as flowering potted plants or cut flowers (Nau, 2011). We selected two *Veronica* plants as promising new ornamental crops: mountain spike speedwell [산꼬리풀, *V. rotunda* var. *subintegra* (Nakai) T.Yamaz.] and long-leaf spike speedwell (긴산꼬리풀, *V. longifolia* L.). These species are native to Korea and have ornamental potential at the basis of unique tail-shaped floral structure, blue flower color, and flowering season. However, it is difficult to produce them in commercial greenhouses because detailed information for growth and flowering of them have not been published. In many herbaceous perennials, flowering is influenced by environmental factors such as temperature, photoperiod, and irradiance (Whitman et al., 1996; Runkle et al., 1998; Runkle et al., 1999; Mattson and Erwin, 2005). Therefore, determination of the environmental requirements related to flowering can make growers get commercial benefits including accurate scheduling, reducing production time and costs, and enhancing crop quality (Whitman et al., 1996; Heins et al., 1997; Runkle et al., 1999; Hamrick, 2003; Fausey et al., 2005; Faust et al., 2005).

Vernalization and photoperiodic flowering responses of *Veronica* plants have been studied in many types of research. Fausey and Cameron (2007) identified that *V.*

spicata ‘Red Fox’ required a minimum of 4 weeks at –2.5 and 0°C, 6 weeks at 2.5°C, and 8 weeks at 5 and 7.5°C for complete flowering. In another study by Heins et al. (1997), *V. longifolia* ‘Sunny Border Blue’ also required the cold treatment for flowering, and flowering of *V. spicata* ‘Blue’ was improved after the cold treatment. In case of photoperiod response, all *Veronica* plants exhibited identical photoperiodic response. *V. longifolia* ‘Sunny Border Blue’ and *V. spicata* ‘Blue’ flowered regardless of photoperiod following the cold treatment (Heins et al., 1997). Enfield et al. (2004) also found *V. spicata* ‘Red Fox’, ‘Icicle’, and ‘Goodness Grows’ to be day-neutral plants with the vernalization requirements.

Daily light integral (DLI) can affect plant growth and development through photosynthesis (Nemali and van Iersel, 2004; Cheon et al., 2006; Oh et al., 2009; Zhao et al., 2012). Many studies reported that increasing DLI promoted plant growth and flowering including the number of branches, stem diameter, biomass accumulation, and flower initiation and quality in various horticultural crops (Niu et al., 2000; Warner and Erwin, 2003; Fausey et al., 2005; Islam et al., 2005; Mattson and Erwin, 2005; Cheon et al., 2006; Oh et al., 2009; Currey and Erwin, 2011). For example, high DLI reduced the number of nodes (or leaves) below the first open flower in *Eustoma grandiflorum* ‘Echo Blue’ and ‘Fuji Deep Blue’ and *Hibiscus cisplatinus* (Islam et al., 2005; Warner and Erwin, 2003). Fausey and Cameron (2007) also found that average time to the first flower of *V. spicata* ‘Red Fox’ was almost 2 weeks faster under higher air temperature and DLI conditions.

The objectives of this study were 1) to investigate growth and flowering of Korean

native *V. rotunda* and *V. longifolia* under different photoperiod conditions after different durations of cold treatment in order to determine vernalization and photoperiod requirements for flowering and 2) to examine the effects of DLI on growth and flowering of these plants for forcing flowering.

LITERATURE REVIEW

Flowering Response to Vernalization

Exposure to a period of low temperature, called as vernalization, alleviates repression of flowering, given to a hydrated seed or to a growing plant (Taiz et al., 2015). Vernalization requirements of herbaceous perennials for flowering vary with species (Heins et al., 1997). Some herbaceous perennials such as *Lavandula angustifolia* 'Munstead' (Whitman et al., 1996), *Oenothera fruticosa* 'Youngii-lapsley' (Clough et al., 2001), and *Dianthus gratianopolitanus* 'Bath's Pink' (Padhye and Cameron, 2008) required a cold treatment for flowering (obligate or qualitative vernalization requirement). In addition, the cold treatment was not absolutely required but hastened or improved flowering (facultative or quantitative vernalization requirement) in *Phlox paniculata* 'Eva Cullum' (Runkle et al., 1998) and *Rudbeckia fulgida* 'Goldsturm' (Runkle et al., 1999). There were also plants that flower regardless of cooling (Runkle et al., 1999). In general, the effective duration and temperature range for vernalization are several weeks with a broad optimum between about 1 and 7°C (Taiz et al., 2015). For example, *Laurentia axillaris* and *Campanula* 'Birch Hybrid' required a minimum of 5 weeks at 5 to 10°C, 7.5 weeks at 12.5°C, and 10 weeks at 2.5°C and a minimum of 5 weeks at 2.5 to 7.5°C, 7 weeks at 0 and 12.5°C, and 9 weeks at 10°C for complete flowering, respectively (Fausey and Cameron, 2007; Padhye and Cameron, 2009). In some *Veronica* species, vernalization requirements have been investigated. *V. spicata* 'Red Fox' exhibited

obligate vernalization requirement for flowering and required a minimum of 4 weeks at –2.5 and 0°C, 6 weeks at 2.5°C, and 8 weeks at 5 and 7.5°C for complete flowering (Fausey and Cameron, 2007). Heins et al. (1997) identified that other *Veronica* species also required the cold treatment for flowering (*V. longifolia* 'Sunny Border Blue') or improvement of flowering (*V. spicata* 'Blue'). Vernalization response of *V. longifolia* 'Sunny Border Blue' that is the same species as Korean native *V. longifolia* has been investigated, but two *V. longifolia* may not show identical vernalization requirement because vernalization response can vary within cultivars of a species (Heins et al., 1997; Fausey and Cameron, 2007).

Flowering Response to Photoperiod

Photoperiod is also an environmental factor to control plant responses such as initiation of flowering (Taiz et al., 2015). Photoperiodic flowering responses are usually divided into three categories: short-day, long-day, and day-neutral plants (Thomas and Vince-Prue, 1997). Short-day and long-day plants flower under a certain day length, and day-neutral plants flower under any day length (Thomas and Vince-Prue, 1997). Herbaceous perennials showed diverse photoperiodic flowering responses (Heins et al., 1997; Mattson and Erwin, 2005), and these photoperiodic responses are often linked to vernalization requirement (Whitman et al., 1996; Runkle et al., 1998; Runkle et al., 1999). Photoperiodic flowering responses of *Veronica* plants have been studied in many research papers. *V. longifolia* 'Sunny Border Blue' and *V. spicata* 'Blue' flowered regardless of photoperiod following the

cold treatment (Heins et al., 1997). Enfield et al. (2004) also found *V. spicata* 'Red Fox', 'Icicle', and 'Goodness Grows' to be day-neutral plants with the vernalization requirements.

Growth and Flowering in Response to DLI

DLI is the light quantity (photosynthetically active photons) that is delivered to a specific area for a 24 h period and an important environmental factor to affect plant growth and development through photosynthesis (Nemali and van Iersel, 2004; Cheon et al., 2006; Oh et al., 2009; Zhao et al., 2012). Increasing irradiance generally increases net photosynthesis rate up to light saturation point, and plants grown under high DLI condition have higher net CO_2 assimilation rates (A_n) at light saturation point than those grown under low DLI condition (Cheon et al., 2006; Matsuda, 2016). For this reason, many studies reported that increasing DLI promoted plant growth including the number of leaves and branches, stem diameter, and biomass accumulation in various horticultural crops (Fausey et al., 2005; Islam et al., 2005; Mattson and Erwin, 2005; Cheon et al., 2006; Oh et al., 2009; Currey and Erwin, 2011). DLI also affects flowering responses. In most plants, days to visible bud or flowering decreased, and flower quality such as the number of flowers (or inflorescences) and flower diameter increased as DLI increased (Niu et al., 2000; Warner and Erwin, 2003; Fausey et al., 2005; Islam et al., 2005; Cheon et al., 2006; Oh et al., 2009). Fausey and Cameron (2007) also found that average time to the first flower of *V. spicata* 'Red Fox' was almost 2 weeks faster under higher air

temperature and DLI conditions. However, the effect of DLI on the number of nodes below the first open flower was reported differently among species (Mattson and Erwin, 2005; Warner and Erwin, 2005; Currey and Erwin, 2011). For example, DLI did not affect leaf number below the first flower in *Calendula officinalis* 'Calypso Orange', *Impatiens walleriana* 'Super Elfin White', *Torenia fournieri* 'Clown Burgundy', and *Mimulus* ×*hybridus* 'Mystic Yellow' (Warner and Erwin, 2005). However, high DLI reduced the number of nodes below the first open flower by 0.7-1.7 nodes compared to low DLI in *Eustoma grandiflorums* 'Echo Blue' and 'Fuji Deep Blue' (Islam et al., 2005). In *Hibiscus cisplatinus* which is a day-neutral plant and flowers during high irradiance periods such as spring and summer in their natural habitats, leaf number below the first open flower decreased with increasing DLI (Warner and Erwin, 2003).

MATERIALS AND METHODS

Vernalization and Photoperiod Requirements (Experiment I)

Plant materials. Seeds of *V. rotunda* var. *subintegra* and *V. longifolia* from Korea National Arboretum (Yangpyeong, Korea) were sown on 19 May 2017 in 105-cell plug trays filled with a commercial soilless media (Bio Green, FarmHannong Co., Seoul, Korea). Seeds were covered with a thin layer of vermiculite to maintain moisture and germinated on 28 May 2017. Seedlings were grown under 9 h photoperiod at 22°C in a closed plant production system at the university farm (Seoul National University, Suwon, Korea). The light intensity was maintained at 110 ± 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ using fluorescent lamps. After the population had four or five nodes, they were transferred to a cold storage room or a greenhouse for cold or photoperiod treatments, respectively.

Cold treatments. On 14 July 2017, the plants except no cold treatments were placed in the cold storage room at the university farm at 5°C. During cold treatment, plants were illuminated with 5 ± 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 9 h photoperiod using commercially available white LEDs (12V SMD 5050 LED, CamFree Co., Ltd., Seoul, Korea). While in the cold storage room, plants were irrigated when substrate appeared dry using hand-drip irrigation. A quarter of each species was removed from the cold storage room at 3-week intervals for 12 weeks and transferred to a greenhouse for photoperiod treatments.

Photoperiod treatments and growth conditions. On 14 July 2017, eighty-four

and sixty plants without the cold treatment were randomly selected and transplanted into 7-cm round plastic pots with the above media in *V. rotunda* var. *subintegra* and *V. longifolia*, respectively. The plants were then placed in each greenhouse bench of the university farm in a completely randomized design. The number of plants per treatment was fourteen for *V. rotunda* var. *subintegra* and ten for *V. longifolia*. Plants removed from the cold storage room were also treated as no cold treatment described above. Photoperiods were 9, 12, 14, 16, or 24 h of continuous light or 9 h with a 4 h night interruption (NI; 22:00 to 02:00 $_{HR}$). Continuous photoperiods consisted of 9 h natural day lengths supplemented by day extension lighting. Opaque black cloth was pulled at 18:00 $_{HR}$ and opened at 09:00 $_{HR}$ every day on all benches so that plants received a similar DLI within each cold treatment. The black cloth was opened at 22:00 $_{HR}$ and closed at 03:00 $_{HR}$ for air ventilation. Day extension and NI lighting were provided by the same white LEDs as the cold storage room at 2 ± 1 μmol·m^{-2}·s^{-1} at canopy level.

Plants were transplanted into 10-cm round plastic pots eight weeks after photoperiod treatment. During photoperiod treatment, plants were irrigated as necessary with tap water using a sprinkler. Air temperature on one bench was monitored every 30 min with a data logger (Watch Dog Model 1000, Spectrum Technologies, Inc., Plainfield, IL, USA) from July 2017 to January 2018 (Fig. 1). To avoid dormancy during winter, the air temperature was maintained at 10°C or above by an automated controlled oil heater from November 2017 to January 2018. Pesticides were applied at their recommended rates as needed throughout the

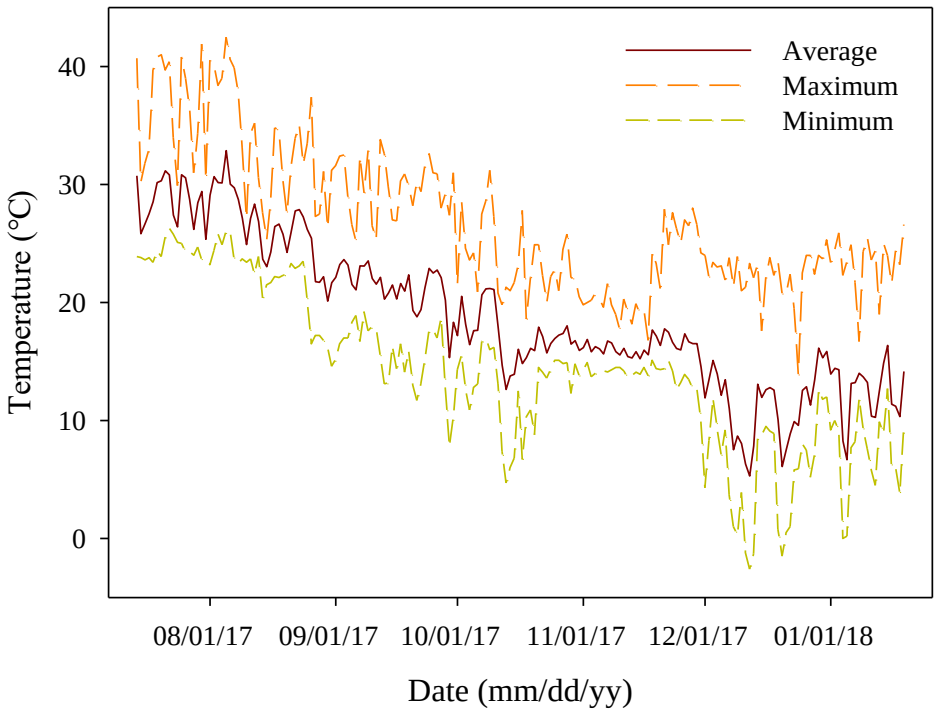

Fig. 1. Average, maximum, and minimum daily air temperatures in a greenhouse during photoperiod treatment (from 14 July 2017 to 19 January 2018)

growing period.

Data collection and statistical analysis. Total plant height (height from the medium to the top of the plant), the number of branches (1 cm or longer), and leaf (the longest leaf) length and width were recorded for each plant. The date when the first inflorescence was visible (5 mm or longer) and the date when the first flower opened were recorded. The number of nodes below the first inflorescence and the number of VIs at the first open flower were measured. For harvesting, rooting medium was carefully washed off, and shoot and root were separated. Shoot and root dry weight were measured after drying at 80°C for 3 d. Data collection was ended when the experiment was terminated 15 weeks after photoperiod treatment. Few plants that did not grow normally during the experiment were discarded and not included in the results.

Collected data were analyzed using ANOVA in the SAS system for Windows version 9.3 (SAS Institute Inc., Cary, NC, USA). Mean separation by Duncan's multiple range test at $p < 0.05$ was performed for all data. Graph modules were analyzed using SigmaPlot software version 10.0 (Systat Software, Inc., Chicago, IL, USA).

Response to Daily Light Integral (Experiment II)

Plant materials and growth conditions. *V. rotunda* var. *subintegra* and *V. longifolia* seeds from Korea National Arboretum (Yangpyeong, Korea) were sown on 23 March 2018 in 105-cell plug trays filled with a commercial soilless media (Bio Green, FarmHannong Co., Seoul, Korea). Seeds were covered with a thin layer of vermiculite to maintain moisture and placed into a closed plant production system in the university farm (Seoul National University, Suwon, Korea). Temperature and photoperiod were 22°C and 12 h, respectively. The light intensity was maintained at 110 ± 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ using fluorescent lamps. Seeds germinated on 30 March. Seedlings were fertilized every second week with water-soluble fertilizer (EC 0.5 $mS \cdot cm^{-1}$; Hyponex professional 20N-20P-20K, Hyponex Japan, Osaka, Japan) using sub-irrigation.

When the seedlings had produced 4 or 5 nodes, they were transplanted into 12-cm round plastic pots in another soilless media (Baroker, Seoul Bio Co., Eumseong, Korea). Plants were then transferred to a greenhouse under one of five different lighting treatments. Air temperature of the greenhouse was monitored with a data logger (Watch Dog Model 1000, Spectrum Technologies, Inc., Plainfield, IL, USA), and the average air temperature in a greenhouse was 22.7°C. Plants were irrigated as necessary with tap water using a sprinkler. Three grams of a controlled release fertilizer (Osmocote Plus 15N-4.8P-10.8K+12.Mg+TE, Everris Int'l BV, Heerlen, Netherlands) were placed at the media after 4 weeks of treatment. Pesticides were applied at their recommended rates as needed throughout the growing period.

Daily light integral treatments. Plants were grown under one of five irradiance levels: 55% shading of ambient irradiance, 55% shading of ambient plus average 137 μmol·m^{-2}·s^{-1} supplemental irradiances, ambient irradiance, ambient plus average 137 μmol·m^{-2}·s^{-1} supplemental irradiances, and ambient plus average 209 μmol·m^{-2}·s^{-1} supplemental irradiances (Fig. 2). All supplemental irradiance was provided by high-pressure sodium lamps only during the day to prevent confounding effects of photoperiod on flower induction. Ambient irradiance on one bench was measured every 30 min with a quantum sensor (LightScout, Spectrum Technologies, Inc., Plainfield, IL, USA) connected to the data logger. The average DLI of the ambient irradiance treatment was calculated for each week from 4 May to 26 July 2018 (Fig. 3). DLIs for the other treatments except the ambient irradiance were calculated from the ambient DLI (Fig. 3). The irradiance treatments resulted in average DLIs of 3.6, 6.6, 8.1, 14.7, and 18.3 mol·m^{-2}·d^{-1} at canopy level. A completely randomized design with twelve plants in each treatment for both species was used.

Chlorophyll fluorescence measurement. Chlorophyll fluorescence was measured with a mature leaf attached to the third node from the top after 2 and 6 weeks of treatments. Seven plants from each treatment were randomly collected and the chlorophyll fluorescence was measured from 12:00 $_{HR}$ to 14:00 $_{HR}$ using a PAM chlorophyll fluorometer (PAM 2000, Heinz Walz, Effeltrich, Germany). After 20 min of dark adaptation, the minimum fluorescence (F_o) was induced by a measuring light of 0.6kHz and less than 0.1 μmol·m^{-2}·s^{-1} PPF. Then a saturating light pulse at about 8,000 μmol·m^{-2}·s^{-1} was irradiated for 0.8 s to obtain the maximum

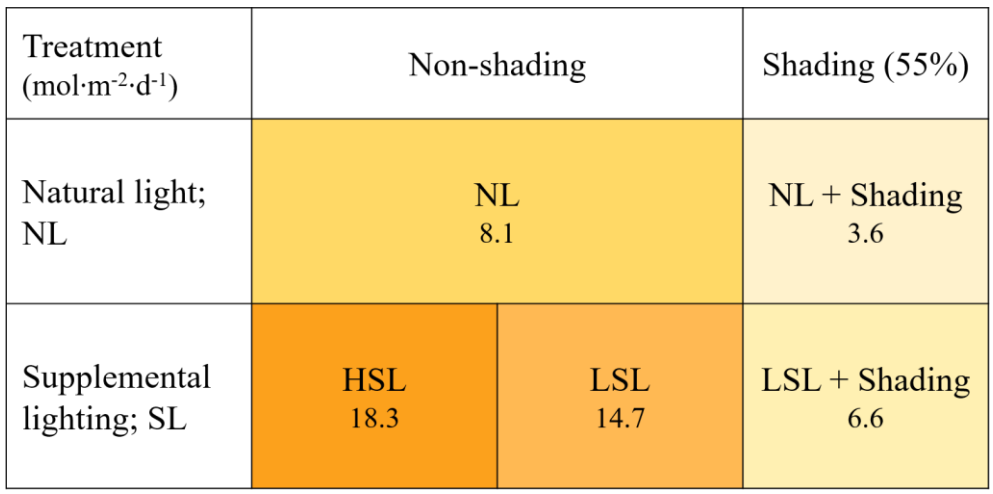

Fig. 2. Schematic diagram of greenhouse daily light integral (DLI) settings used in Experiment II. Supplemental lighting (SL) had two supplemental irradiances: average 137 μmol·m^{-2}·s^{-1} (LSL) and average 209 μmol·m^{-2}·s^{-1} (HSL). Numbers below treatment indicate average DLI during the experiment period.

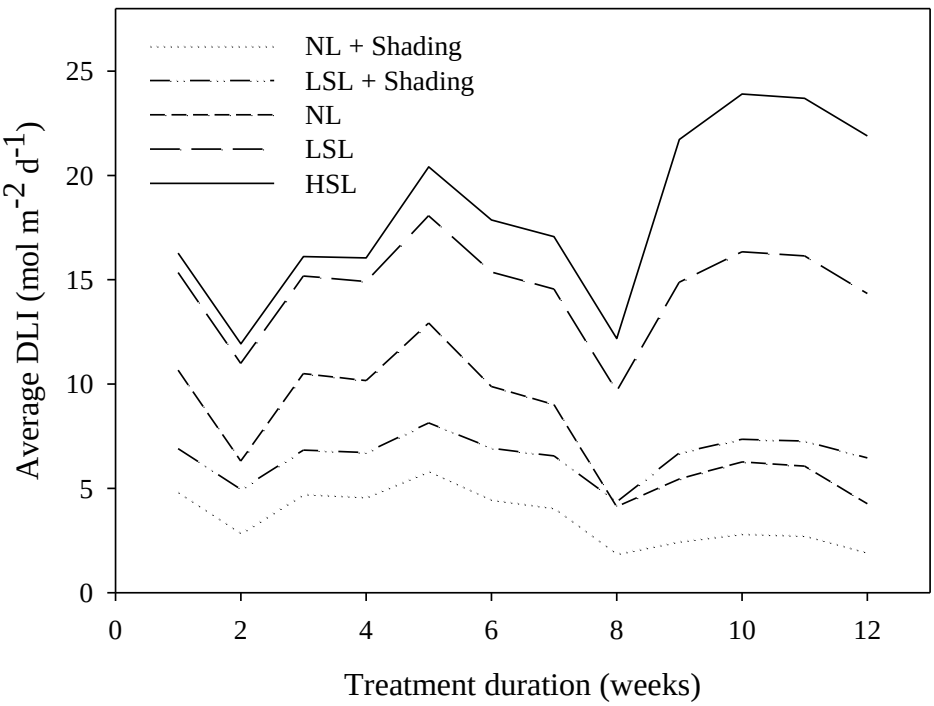

Fig. 3. Average daily light integral (DLI) during 12 weeks of treatments (from 4 May to 26 July 2018). The average DLIs were calculated for each week. Refer to Fig. 2 for the light treatments.

fluorescence (F_m). The variable fluorescence (F_v) was defined by the difference between F_m and F_o and used to estimate the maximum quantum efficiency (F_v/F_m).

Net CO_2 assimilation rates measurement. Net CO_2 assimilation rates (A_n) was measured with three plants randomly selected in each treatment after 5 weeks of treatments. A portable photosynthesis system (LI-6400XT, Li-Cor Co., Inc., Lincoln, NE, USA) equipped with an infrared gas analyzer was used. Mature leaf attached the third node from the top was clamped on to a 6 cm^2 LED chamber. Before the measurement, leaves were acclimated to 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for at least 20 min. The irradiance levels in the leaf chamber were set at 1200, 900, 600, 300, 200, 100, 80, 60, 40, 20, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for the A_n in response to light intensity. A minimum and maximum wait time for each step were set to be 60 and 180 s, respectively. The temperature, relative humidity, and CO_2 concentration inside the leaf chamber were maintained at 25℃, 60%, and 400 ppm during the measurement, respectively. The light response curves were fitted to a rectangular hyperbola; $y = y_0 + ax/(b + x)$.

Data collection and statistical analysis. Total plant height (height from the medium to the top of the plant), the number of branches (1 cm or longer), and leaf (the longest leaf) length and width were recorded for each plant. Stem diameter was measured at the fourth internode from the root using a digital caliper (ABS Digimatic Caliper; Mitutoyo Co., Ltd., Tsukuba, Japan). The relative chlorophyll content of mature leaf on the third node from the top was also measured using a chlorophyll meter (SPAD 502, Konica Minolta Sensing Inc., Sakai, Japan). The date when the first inflorescence was visible (5 mm or longer) and the date when the first flower

opened were recorded. The number of nodes below the first inflorescence and the number of VIs and the first inflorescence length at the first open flower were measured. Collection of the growth parameters was ended when the experiment was terminated after 12 weeks of the treatment. At this time, four plants per treatment were randomly collected, the rooting medium was carefully washed off, and inflorescence, shoot (except inflorescences), and root were separated. Inflorescence, shoot, and root dry weight were measured after drying at 80°C for 3 d. The remaining plants were grown until flowering. Few plants that did not grow normally during the experiment were discarded and not included in the results.

Collected data were analyzed using ANOVA in the SAS system for Windows version 9.3 (SAS Institute Inc., Cary, NC, USA). Mean separation by Duncan's multiple range test at $p < 0.05$ was performed for all data. Regression analysis and graph modules were analyzed using SigmaPlot software version 10.0 (Systat Software, Inc., Chicago, IL, USA).

RESULTS AND DISCUSSION

Vernalization and Photoperiod Requirements (Experiment I)

Growth parameters. *V. rotunda* var. *subintegra* and *V. longifolia* grown under different photoperiod conditions without cold treatment did not show significant differences in all growth parameters including plant height, leaf length and width, the number of branches, and shoot and root dry weight (Tables 1 and 2). After the cold treatment for 3, 6, 9, or 12 weeks, although two *Veronica* species showed significant differences between photoperiods in some parameters, the parameters did not show any tendency with increasing photoperiod (Tables 1 and 2). Therefore, the growth parameters were not influenced by photoperiod in both species (Tables 1 and 2). On the other hand, plant height and shoot and root dry weight were significantly ($p < 0.001$) reduced as the duration of cold treatment increased in both species, and leaf length and width of *V. longifolia* also significantly decreased with increasing duration of cold treatment (Tables 1, 2, and 3). However, it might not be the effect of the cold treatment because seasonal change by the longer duration of cold treatment caused different greenhouse environments such as temperature and DLI. According to Hatfield et al. (2011) and Cheon et al. (2006), air temperature and DLI can affect plant growth. In this experiment, average air temperatures in the greenhouse during each photoperiod treatment gradually decreased from average 23 to 14°C as the duration of cold treatment increased (Fig. 1). Because this pattern of temperature change was similar to the reduction of growth parameters (Fig. 1 and

Table 1. Growth characteristics of *V. rotunda* var. *subintegra* grown for 15 weeks under different photoperiod conditions after 0, 3, 6, 9, or 12 weeks of cold treatment.

Cold treatment[z] (weeks)	Photoperiod (h)	Plant height (cm)	Leaf (cm)		No. of branches	Dry weight (g)	
			Length	Width		Shoot	Root
0	9	53.41	11.13	5.15	2.2	2.67	2.68
	12	51.38	11.29	4.68	3.5	2.70	2.92
	14	56.28	12.26	5.01	2.9	2.82	2.84
	16	47.03	11.46	4.69	4.2	2.57	2.70
	24	46.33	11.42	4.97	3.5	2.61	2.32
	NI[y]	48.83	11.27	4.68	5.5	2.53	2.28
	Significance	NS	NS	NS	NS	NS	NS
3	9	23.01 ab[x]	11.05	4.91	1.9 a	1.97	2.96 b
	12	28.09 a	11.30	4.71	0.9 b	1.97	3.77 a
	14	21.61 ab	11.13	4.69	0.7 b	1.59	2.37 bc
	16	27.62 a	11.56	4.82	0.4 b	1.85	2.49 bc
	24	20.70 b	10.47	4.60	0.2 b	1.57	2.10 c
	NI	19.34 b	10.72	4.92	1.1 ab	1.57	2.61 bc
	Significance	*	NS	NS	**	NS	***
6	9	15.12	9.78	4.27 ab	1.0	1.38	1.81 a
	12	14.45	9.83	4.65 a	1.2	1.28	1.93 a
	14	14.76	8.93	4.17 ab	0.7	1.19	1.22 b
	16	15.89	9.58	4.26 ab	1.1	1.49	1.29 b
	24	13.54	9.43	4.18 ab	1.2	1.19	1.13 b
	NI	14.41	8.74	3.76 b	1.3	0.99	1.25 b
	Significance	NS	NS	*	NS	NS	***
9	9	12.58 b	9.88	4.49	1.0 bc	0.96	0.90
	12	17.11 a	10.17	4.31	1.7 abc	1.17	1.10
	14	13.27 b	9.16	4.31	2.1 a	1.07	0.95
	16	16.36 a	10.37	4.55	1.2 abc	1.14	1.24
	24	16.95 a	10.04	4.45	0.7 c	1.12	1.22
	NI	12.62 b	8.79	3.88	2.1 ab	0.82	0.93
	Significance	**	NS	NS	*	NS	NS
12	9	15.03 b	10.75	4.50	3.2	1.23	1.08 ab
	12	19.14 a	10.39	4.06	3.4	1.18	0.80 b
	14	19.79 a	10.92	4.46	2.7	1.23	0.78 b
	16	22.04 a	11.11	4.45	1.9	1.35	1.16 a
	24	21.04 a	10.74	4.42	3.5	1.16	0.73 b
	NI	20.21 a	10.66	4.55	3.8	1.12	0.78 b
	Significance	*	NS	NS	NS	NS	*

[z]Duration of 5°C cold treatment
[y]9 h with a 4 h night interruption (22:00-02:00)
[x]Means within columns followed by different letters are significantly different by Duncan's multiple range test at $p < 0.05$.
NS, *, **, *** Non-significant or significant at $p < 0.05$, 0.01, 0.001, respectively.

Table 2. Growth characteristics of *V. longifolia* grown for 15 weeks under different photoperiod conditions after 0, 3, 6, 9, or 12 weeks of cold treatment.

Cold treatment[z] (weeks)	Photoperiod (h)	Plant height (cm)	Leaf (cm)		No. of branches	Dry weight (g)	
			Length	Width		Shoot	Root
0	9	48.64	12.55	5.56	4.1	2.71	2.68
	12	45.43	11.87	5.28	4.5	2.49	2.82
	14	41.09	13.07	5.14	5.0	2.39	2.53
	16	56.30	13.57	6.07	4.7	2.77	3.45
	24	46.88	12.68	5.06	5.0	2.67	2.58
	NI[y]	46.08	13.50	5.58	3.3	2.79	3.23
	Significance	NS	NS	NS	NS	NS	NS
3	9	18.56	12.36	5.38	1.4	1.56	2.35
	12	28.61	13.85	5.58	1.1	2.10	3.10
	14	24.41	13.59	5.74	0.0	1.91	2.67
	16	27.60	13.41	5.65	0.3	1.66	2.07
	24	17.40	12.05	5.13	0.8	1.49	2.04
	NI	23.63	14.06	5.81	0.5	1.81	2.76
	Significance	NS	NS	NS	NS	NS	NS
6	9	14.51	11.41	4.74	0.9	1.48 ab	2.12 ab
	12	14.86	12.00	4.95	0.8	1.53 ab	2.22 a
	14	14.97	11.53	4.98	0.5	1.55 ab	1.77 abc
	16	12.69	11.87	4.87	1.1	1.59 a	1.94 ab
	24	13.22	11.30	4.94	0.3	1.09 c	1.09 c
	NI	11.06	10.86	4.71	0.4	1.18 bc	1.43 bc
	Significance	NS	NS	NS	NS	*	**
9	9	15.24 b[x]	9.55	4.04	4.0 a	1.23	1.24
	12	13.82 b	10.73	4.70	2.8 ab	1.24	1.31
	14	15.14 b	10.39	4.16	1.9 b	1.16	1.05
	16	14.67 b	10.29	4.08	2.2 b	1.10	1.23
	24	12.78 b	9.25	4.05	1.1 b	0.85	1.00
	NI	18.73 a	11.70	4.68	1.7 b	1.40	1.59
	Significance	*	NS	NS	*	NS	NS
12	9	13.36	9.07	3.57	3.0	0.98	0.90
	12	15.44	10.60	3.86	2.9	1.17	1.12
	14	14.42	9.68	3.99	4.4	1.18	0.89
	16	15.80	10.70	4.30	3.5	1.12	0.91
	24	17.85	11.15	4.01	4.0	1.12	1.06
	NI	15.58	10.18	3.71	2.8	1.09	1.01
	Significance	NS	NS	NS	NS	NS	NS

[z]Duration of 5°C cold treatment
[y]9 h with a 4 h night interruption (22:00-02:00)
[x]Means within columns followed by different letters are significantly different by Duncan's multiple range test at $p < 0.05$.
[NS, *, **] Non-significant or significant at $p < 0.05$, 0.01, respectively.

Table 3. Analysis of variance of the impact of cold treatment on growth characteristics of *V. rotunda* var. *subintegra* and *V. longifolia* grown for 15 weeks under different photoperiod conditions after 0, 3, 6, 9, or 12 weeks of cold treatment.

Photoperiod (h)	Plant height	Leaf		No. of branches	Dry weight	
		Length	Width		Shoot	Root
V. rotunda var. *subintegra*						
9	***	NS	NS	*	***	***
12	***	NS	NS	***	***	***
14	***	***	*	**	***	***
16	***	**	NS	***	***	***
24	***	***	NS	***	***	***
NI[z]	***	***	***	***	***	***
V. longifolia						
9	***	***	***	**	***	***
12	***	**	**	***	***	***
14	***	***	***	***	***	***
16	***	*	***	**	***	***
24	***	*	**	***	***	***
NI	***	***	***	**	***	***

[z]9 h with a 4 h night interruption (22:00-02:00)
[NS, *, **, ***] Non-significant or significant at $p < 0.05$, 0.01, 0.001, respectively.

Tables 1 and 2), it seems that air temperature decrease during the photoperiod treatment delayed plant growth. These results indicated that cold treatment, as well as photoperiod, has no effect on the growth of two *Veronica* species.

Flowering characteristics. Flowering occurred under all photoperiod conditions without exposure to the low temperature in both species (Figs. 4 and 5). In non-cooled *V. rotunda* var. *subintegra*, percentages of VI and flowering showed above 90.9 and 85.7 in all photoperiods, respectively (Table 4). *V. longifolia* also showed VI above 80.0% in all photoperiods, and the flowering percentage was 80.0, 66.7, 70.0, 85.7, 71.4, or 100.0 under photoperiod conditions of 9, 12, 14, 16, 24 h, or NI, respectively (Table 5). Both species did not flower 100% under any photoperiod because data collection was ended at 15 weeks of the photoperiod treatments (Tables 4 and 5). However, both plants flowered completely under all photoperiod conditions in a repeated experiment, which was ended when all plants flowered (data not shown). In addition, significant differences in the number of nodes below the first inflorescence and VIs at the first open flower and days to VI were not observed between photoperiod treatments in both species (Tables 4 and 5 and Fig. 6). Therefore, cold treatment was not required for the flowering of two *Veronica* species, and photoperiod also had no influence on the flowering of both species. These flowering tendencies of them were also observed in the repeated experiment (data not shown).

For two species treated at 5°C for 3 weeks, all flowering parameters including a percentage of VI were not affected by photoperiod, similar to non-cooled plants

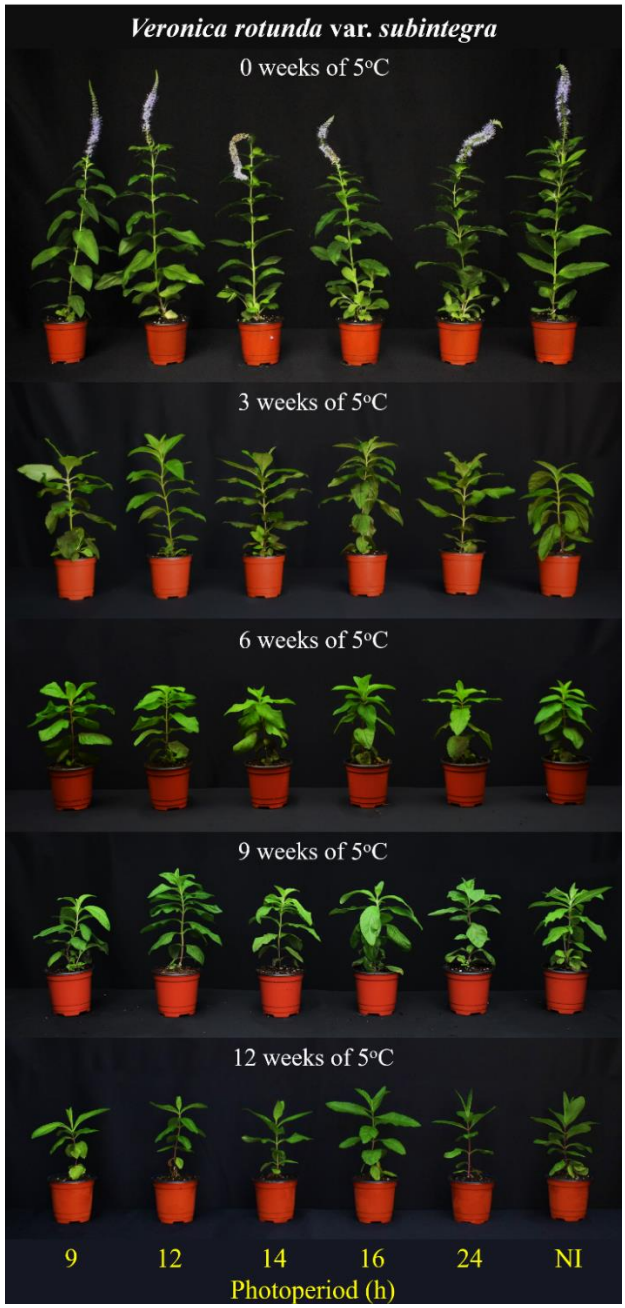

Fig. 4. Growth and flowering of *V. rotunda* var. *subintegra* grown for 11 weeks under different photoperiod conditions after 0, 3, 6, 9, or 12 weeks of cold treatment.

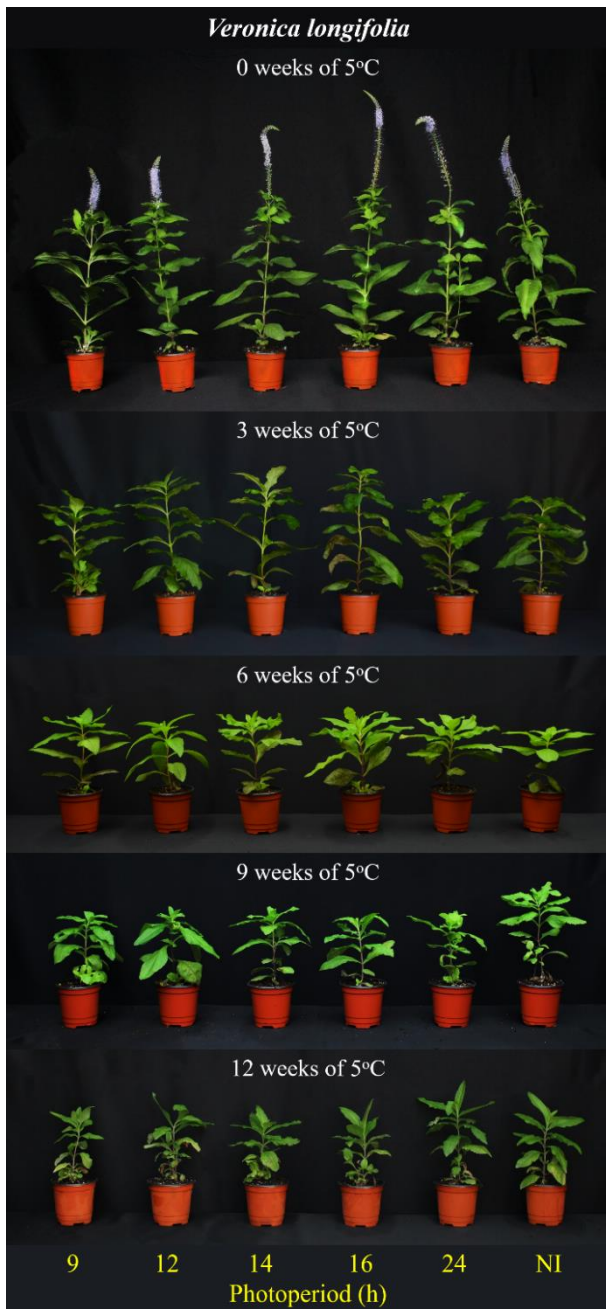

Fig. 5. Growth and flowering of *V. longifolia* grown for 11 weeks under different photoperiod conditions after 0, 3, 6, 9, or 12 weeks of cold treatment.

Table 4. Flowering characteristics of *V. rotunda* var. *subintegra* grown for 15 weeks under different photoperiod conditions after 0, 3, or 6 weeks of cold treatment.

Cold treatment[z] (weeks)	Photoperiod (h)	VI (%)	Flowering (%)	No. of nodes below first inflorescence	No. of VIs at first open flower
0	9	92.9	85.7	14.2 bc[x]	1.17
	12	92.9	92.9	14.2 bc	1.38
	14	100.0	100.0	14.6 abc	1.43
	16	92.9	92.9	13.7 c	1.08
	24	100.0	100.0	13.6 c	1.00
	NI[y]	90.9	90.9	14.1 bc	1.30
3	9	50.0	14.3	15.5 abc	1.00
	12	57.1	35.7	16.3 a	1.40
	14	25.0	16.7	15.0 abc	1.00
	16	71.4	42.9	15.8 ab	1.00
	24	30.8	15.4	16.0 ab	1.00
	NI	30.8	15.4	16.3 a	1.00
6	9	0.0	0.0	-	-
	12	0.0	0.0	-	-
	14	8.3	0.0	-	-
	16	15.4	7.7	-	-
	24	0.0	0.0	-	-
	NI	0.0	0.0	-	-
Significance					
Cold treatment (C)		-	-	***	NS
Photoperiod (P)		-	-	NS	NS
C * P		-	-	NS	NS

[z]Duration of 5°C cold treatment
[y]9 h with a 4 h night interruption (22:00-02:00)
[x]Means within columns followed by different letters are significantly different by Duncan's multiple range test at $p < 0.05$.
NS, *** Non-significant or significant at $p < 0.001$, respectively.

Table 5. Flowering characteristics of *V. longifolia* grown for 15 weeks under different photoperiod conditions after 0, 3, or 6 weeks of cold treatment.

Cold treatment[z] (weeks)	Photoperiod (h)	VI (%)	Flowering (%)	No. of nodes below first inflorescence	No. of VIs at first open flower
0	9	90.0	80.0	13.4 ab[x]	1.1
	12	88.9	66.7	12.2 b	1.2
	14	80.0	70.0	13.4 ab	2.1
	16	85.7	85.7	13.4 ab	2.2
	24	85.7	71.4	12.4 b	1.5
	NI[y]	100.0	100.0	12.4 b	1.1
3	9	37.5	12.5	15.3 a	1.0
	12	62.5	25.0	15.2 a	1.5
	14	44.4	22.2	14.8 a	1.0
	16	75.0	37.5	15.0 a	2.7
	24	33.3	0.0	13.5 ab	-
	NI	37.5	37.5	14.3 ab	1.0
6	9	0.0	0.0	-	-
	12	12.5	12.5	-	-
	14	0.0	0.0	-	-
	16	0.0	0.0	-	-
	24	0.0	0.0	-	-
	NI	0.0	0.0	-	-
Significance					
Cold treatment (C)		-	-	***	NS
Photoperiod (P)		-	-	NS	NS
C * P		-	-	NS	NS

[z]Duration of 5°C cold treatment
[y]9 h with a 4 h night interruption (22:00-02:00)
[x]Means within columns followed by different letters are significantly different by Duncan's multiple range test at $p < 0.05$.
NS, *** Non-significant or significant at $p < 0.001$, respectively.

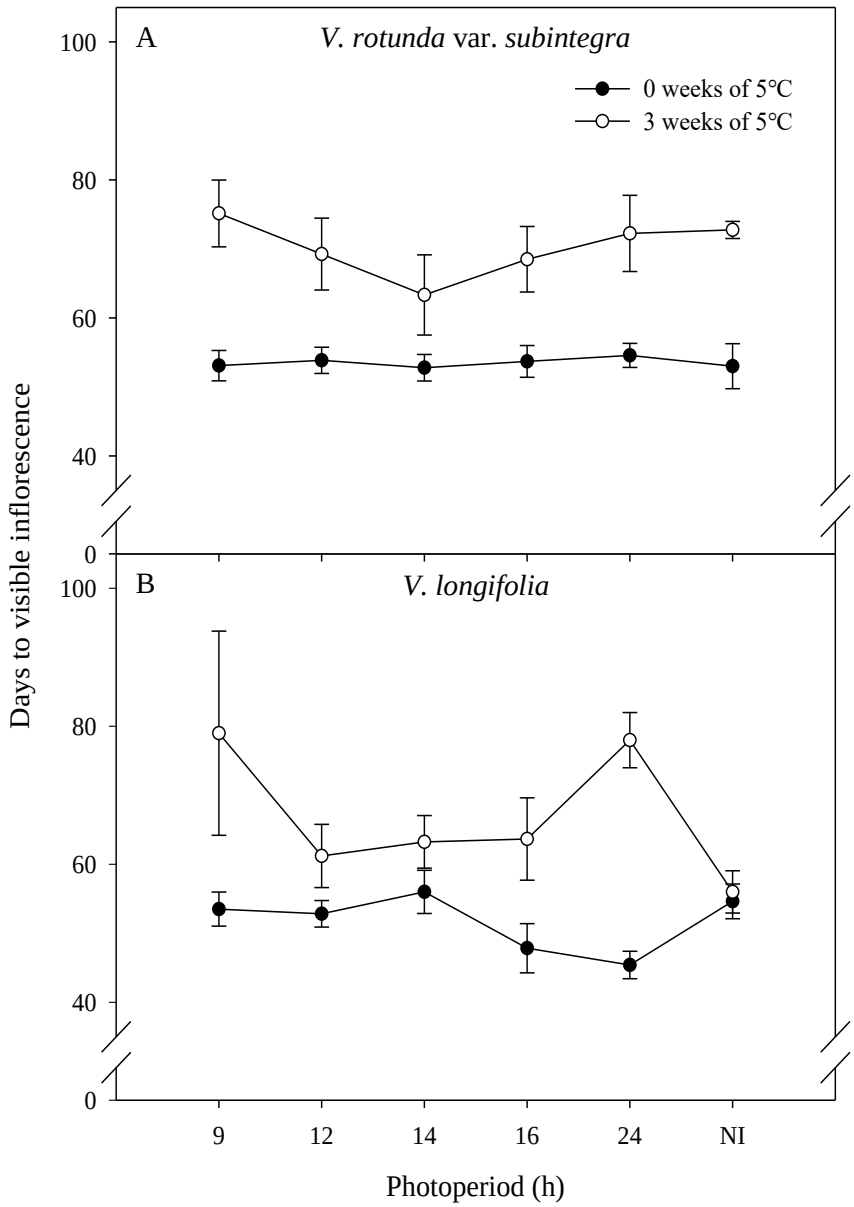

Fig. 6. Days to visible inflorescence of *V. rotunda* var. *subintegra* (A) and *V. longifolia* (B) plants grown for 15 weeks under different photoperiod conditions after 0 or 3 weeks of cold treatment.

(Tables 4 and 5 and Fig. 6). However, the percentage of VI and flowering were lower, and the number of nodes below the first inflorescence and days to VI were higher than those of non-cooled plants, regardless of photoperiod (Tables 4 and 5 and Fig. 6). Moreover, plants treated at 5°C for over 6 weeks hardly flowered within 15 weeks of photoperiod treatments. These results may be attributed to not the cold treatment but seasonal change of greenhouse environments during the photoperiod treatment, similar to the growth parameters. In case of percent VI and flowering, both plants treated at 5°C in the repeated experiment flowered 100% under all photoperiod conditions, demonstrating that the cold treatment did not affect flowering percentage (data not shown). Delayed flowering has been observed under lower temperature and DLI conditions in many studies (Heins et al., 1997; Niu et al., 2000; Warner and Erwin, 2003; Warner and Erwin, 2005; Fausey and Cameron, 2007). In a study by Fausey and Cameron (2007), an average time to the first flower of *V. spicata* 'Red Fox' was almost 2 weeks slower under decreased daily temperature and DLI conditions. In addition to days to flowering, Warner and Erwin (2005) reported low DLI increased leaf number below the first flower in *Antirrhinum majus* and *Calendula officinalis*. In this experiment, the average daily temperature for photoperiod treatment after 3 weeks of 5°C was lower than that for photoperiod treatment without cold treatment (Fig. 1), but DLI during the photoperiod treatment period was not collected. Thus, it is difficult to identify which factor had more influence on the flowering of *Veronica* plants between temperature and DLI, and further studies are needed to understand the effects of temperature and

DLI on the flowering of two *Veronica* species.

In conclusion, *V. rotunda* var. *subintegra* and *V. longifolia* can be classified as day-neutral plants without vernalization requirement because the growth and flowering of two species were not affected by cold and photoperiod treatments. This photoperiodic response is consistent with that of other *Veronica* species such as *V. longifolia* 'Sunny Border Blue', *V. spicata* 'Red Fox', 'Blue', 'Icicle', and 'Goodness Grows' (Heins et al., 1997; Enfield et al., 2004). However, the vernalization requirement of Korean native *Veronica* plants is not identical to that of other *Veronica* species. In other studies, *V. spicata* 'Red Fox' and *V. longifolia* 'Sunny Border Blue' exhibited obligate vernalization requirement, and *V. spicata* 'Blue' showed facultative vernalization requirement for flowering (Heins et al., 1997; Fausey and Cameron, 2007). This indicates that the flowering response of the same species can vary depending on their natural habitats.

Response to Daily Light Integral (Experiment II)

Chlorophyll fluorescence. *V. rotunda* var. *subintegra* and *V. longifolia* grown under DLI conditions from 8.1 to 18.3 mol·m^{-2}·d^{-1} showed the lower maximum quantum efficiency (F_v/F_m) than those grown under DLI conditions of 3.6 and 6.6 mol·m^{-2}·d^{-1} after 2 weeks of treatments ($p < 0.001$) (Fig. 7). High irradiance as abiotic stress can reduce the F_v/F_m value by damaging the photosynthetic apparatus in many cases (Mishra and Singhal, 1992; Lichtenthaler et al., 2005). However, the F_v/F_m values of plants grown under DLIs from 8.1 to 18.3 mol·m^{-2}·d^{-1} were average 0.81 in *V. rotunda* var. *subintegra* and 0.79 in *V. longifolia* (Fig. 7). The F_v/F_m value generally ranges from 0.74 to 0.85 when plants do not suffer from abiotic or biotic stresses in the light (Lichtenthaler et al., 2005; Baker, 2008). Therefore, DLI conditions from 8.1 to 18.3 mol·m^{-2}·d^{-1} also might not affect photochemical efficiency and stress both plants. In addition, these differences of the F_v/F_m between high DLI and low DLI treatments diminished at 6 weeks after treatments in both species through acclimation (Fig. 7). The F_v/F_m values of all treatments were about 0.83, which is a mean value under optimal conditions (Baker, 2008).

Net CO_2 assimilation rates and chlorophyll content. Regardless of DLI treatments, net CO_2 assimilation rates (A_n) increased rapidly as light intensity increased to 100 μmol·m^{-2}·s^{-1} and then increased slightly slowly to 1200 μmol·m^{-2}·s^{-1} in both species (Fig. 8). Although light compensation points did not show any significant difference between DLI treatments, plants grown under lower DLI treatments have lower light compensation points. The lower light compensation

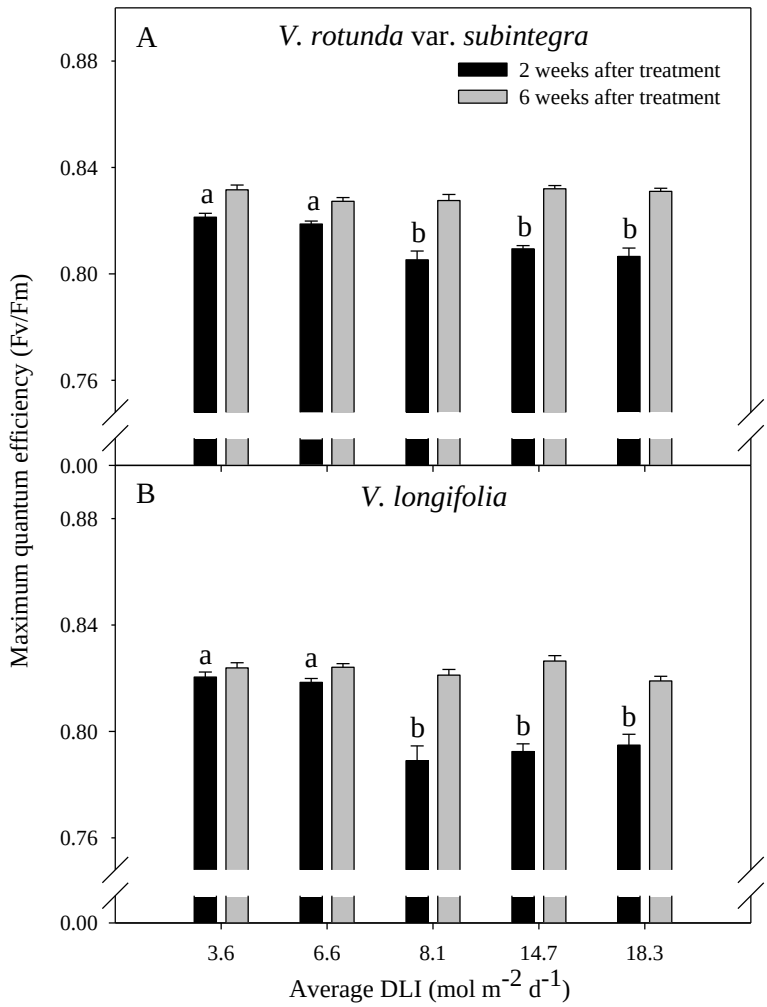

Fig. 7. Maximum quantum efficiency (F_v/F_m) of a mature leaf on the third node from the top of *V. rotunda* var. *subintegra* (A) and *V. longifolia* (B) plants grown under different daily light integral (DLI) conditions. The measurements were conducted after 2 and 6 weeks of each treatment. Letters indicate mean separation within a species across DLIs by Duncan's multiple range test at $p < 0.05$. The data shown are the mean ± SE (n = 7).

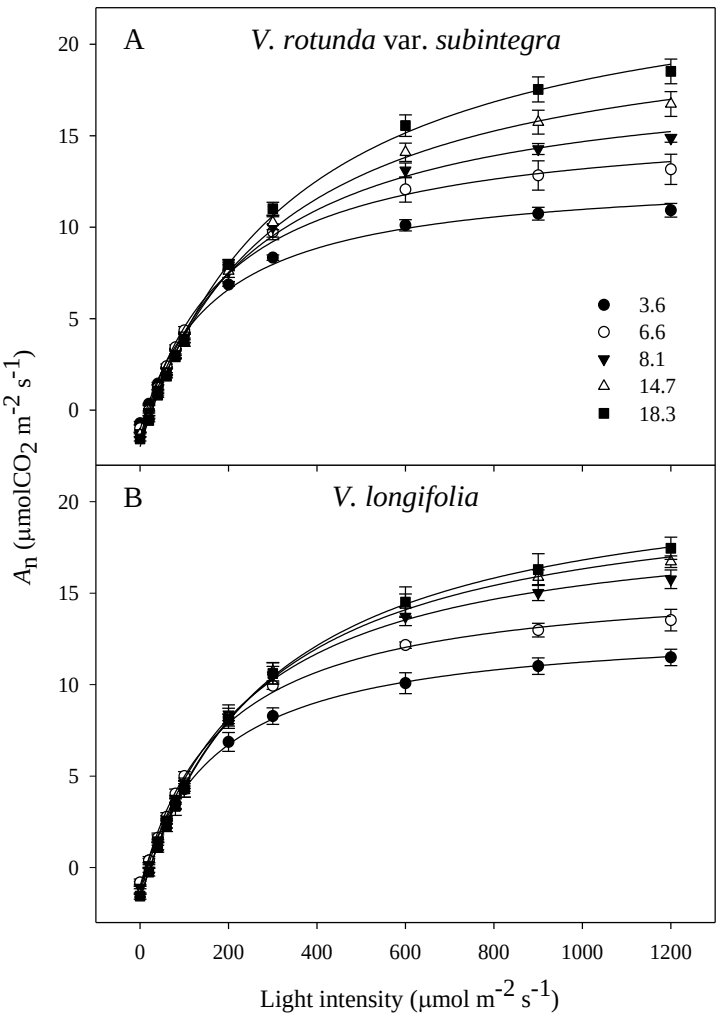

Fig. 8. Net CO_2 assimilation rates (A_n) in response to the light intensity of a mature leaf on the third node from the top of *V. rotunda* var. *subintegra* (A) and *V. longifolia* (B) plants grown under different daily light integral (DLI) conditions. The measurement was conducted after 5 weeks of each treatment. The data shown are the mean ± SE (n = 3). The lines were fitted to a rectangular hyperbola; $y = y_0 + ax/(b + x)$.

points and relatively higher A_n at the low light intensity in plants grown under the low DLI conditions could be due to their lower respiration rates per leaf area (Lambers et al., 2008). However, the specific A_n for the light intensity of 200 to 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased with increased DLI in both species (Fig. 8). Compared with plants grown under low irradiance, plants grown under conditions of high light generally have exhibited relatively higher A_n values with the increase of light intensity because of photosynthetic acclimation (Murchie and Horton, 1997; Lambers et al., 2008; Cai, 2011; Zhao et al., 2012; Matsuda, 2016). Lambers et al. (2008) suggested many components including larger amounts of photosynthetic enzymes, more chloroplasts, and larger stroma volume could enhance the A_n of high irradiance-acclimated leaves.

In addition to the A_n, chlorophyll contents also significantly ($p < 0.001$) increased with increasing DLI from 3.6 to 8.1 and to 14.7 $mol \cdot m^{-2} \cdot d^{-1}$ in *V. rotunda* var. *subintegra* and *V. longifolia*, respectively, but there was no further increase under higher DLI conditions (Table 6). In a study by Murchie and Horton (1997), the relationship between chlorophyll content and light environment showed species variation. For example, chlorophyll contents were higher under shade condition for optimizing light absorption in some shade tolerant plants (Murchie and Horton, 1997; Dai et al., 2009; Zhao et al., 2012). However, in other plants, not only higher chlorophyll contents under the condition of high irradiance but also a positive correlation between chlorophyll contents and light-saturated A_n have been identified (Murchie and Horton, 1997; Jiang et al., 2006). Therefore, these *Veronica* plants are

Table 6. Growth characteristics of *V. rotunda* var. *subintegra* and *V. longifolia* plants grown for 12 weeks under different daily light integral (DLI) conditions.

Average DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Plant height (cm)	Leaf (cm)		No. of branches	Stem diameter (mm)	SPAD
		Length	Width			
			Veronica rotunda var. *subintegra*			
3.6	55.52 c[z]	13.81 b	5.03 b	0.0 c	2.99 d	33.36 c
6.6	74.86 b	16.09 a	5.95 a	3.6 c	3.77 c	38.54 b
8.1	90.59 a	16.03 a	5.14 b	11.9 ab	5.47 b	49.14 a
14.7	96.21 a	14.82 ab	5.23 b	9.8 b	5.55 b	51.58 a
18.3	98.16 a	16.31 a	5.65 ab	15.5 a	6.29 a	51.28 a
Significance	***	*	*	***	***	***
			Veronica longifolia			
3.6	65.24 c	16.95	5.97	1.3 b	3.35 c	34.86 c
6.6	77.97 b	18.00	6.09	3.9 b	4.48 b	41.88 b
8.1	95.63 a	17.04	5.82	12.7 a	5.66 a	45.06 b
14.7	102.74 a	16.12	5.87	12.5 a	5.97 a	49.53 a
18.3	101.81 a	16.43	5.51	15.9 a	6.01 a	52.71 a
Significance	***	NS	NS	***	***	***

[z]Means within columns followed by different letters are significantly different by Duncan's multiple range test at $p < 0.05$.
[NS, *, ***] Non-significant or significant at $p < 0.05$, 0.001, respectively.

not shade-tolerant plants but high irradiance demanding species, and increased chlorophyll contents might affect the enhanced A_n in this study.

Growth parameters. Most growth parameters showed an increasing tendency with increasing DLI in both species (Table 6). In *V. rotunda* var. *subintegra*, plant height, the number of branches, and stem diameter significantly ($p < 0.001$) increased as increasing DLI although there was no further increase of plant height under DLIs from 8.1 to 18.3 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 6). Leaf length and width of *V. rotunda* var. *subintegra* also showed significant differences ($p < 0.05$) between DLI treatments, but any tendency with increasing DLI was not observed in these parameters. In case of *V. longifolia*, plant height, the number of branches, and stem diameter significantly ($p < 0.001$) increased as DLI increased from 3.6 to 8.1 $mol \cdot m^{-2} \cdot d^{-1}$. Enhanced plant growth has been observed under high DLI condition in many other horticultural crops including *Eustoma grandiflorum* (Islam et al., 2005), *Cyclamen persicum* (Cheon et al., 2006; Oh et al., 2009), and *Kalanchoe* species (Currey and Erwin, 2011). In addition, these growth patterns of plant height, the number of branches, and stem diameter were similar to A_n patterns in both species (Fig. 8 and Table 6), suggesting that increasing DLI may promote plant growth through enhanced photosynthesis. Zhao et al. (2012) also reported that growth parameters were higher in herbaceous peony grown under high irradiance, which showed higher A_n values.

Dry weight. Shoot (except inflorescences), and root dry weight significantly ($p < 0.001$) increased with increasing DLI in both species, similar to other growth

parameters such as plant height and stem diameter (Table 6 and Fig. 9). Inflorescence dry weight also showed an increasing tendency with increasing DLI, but significant difference among DLI treatments was not observed in this parameter. *V. rotunda* var. *subintegra* showed a continuous increase of dry weight as DLI increased from 3.6 to 18.3 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 9). Increased dry weight under high DLI condition was observed previously for a number of plants (Fausey et al., 2005; Faust et al., 2005; Islam et al., 2005; Mattson and Erwin, 2005; Warner and Erwin, 2005; Cheon et al., 2006; Oh et al., 2009; Currey and Erwin, 2011). For example, Fausey et al. (2005) reported that root, shoot, and flower dry weight increased as DLI increased from 5 to 43 $mol \cdot m^{-2} \cdot d^{-1}$ for many floriculture crops such as *Ageratum houstonianum* and *Tagetes erecta*. On the other hand, there was no further increase in dry weight of *V. longifolia* under DLIs from 8.1 to 18.3 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 9). This difference of dry weight pattern between both *Veronica* species under DLIs from 8.1 to 18.3 $mol \cdot m^{-2} \cdot d^{-1}$ might be affected by the difference between the maximum A_n of both species. *V. longifolia* grown under high DLI conditions showed the lower specific A_n for the light intensity of 200 to 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ than *V. rotunda* var. *subintegra* (Fig. 8). Vidal et al. (1990) and Cheon et al. (2006) also reported that *Fatsia japonica* and *Cyclamen persicum* grown under high DLI conditions exhibited the higher maximum A_n than that grown under low DLI conditions, resulting in increasing dry weight.

Flowering characteristics. In addition to growth, flowering was also promoted under high DLI condition in both species (Fig. 10). Although a flowering percentage

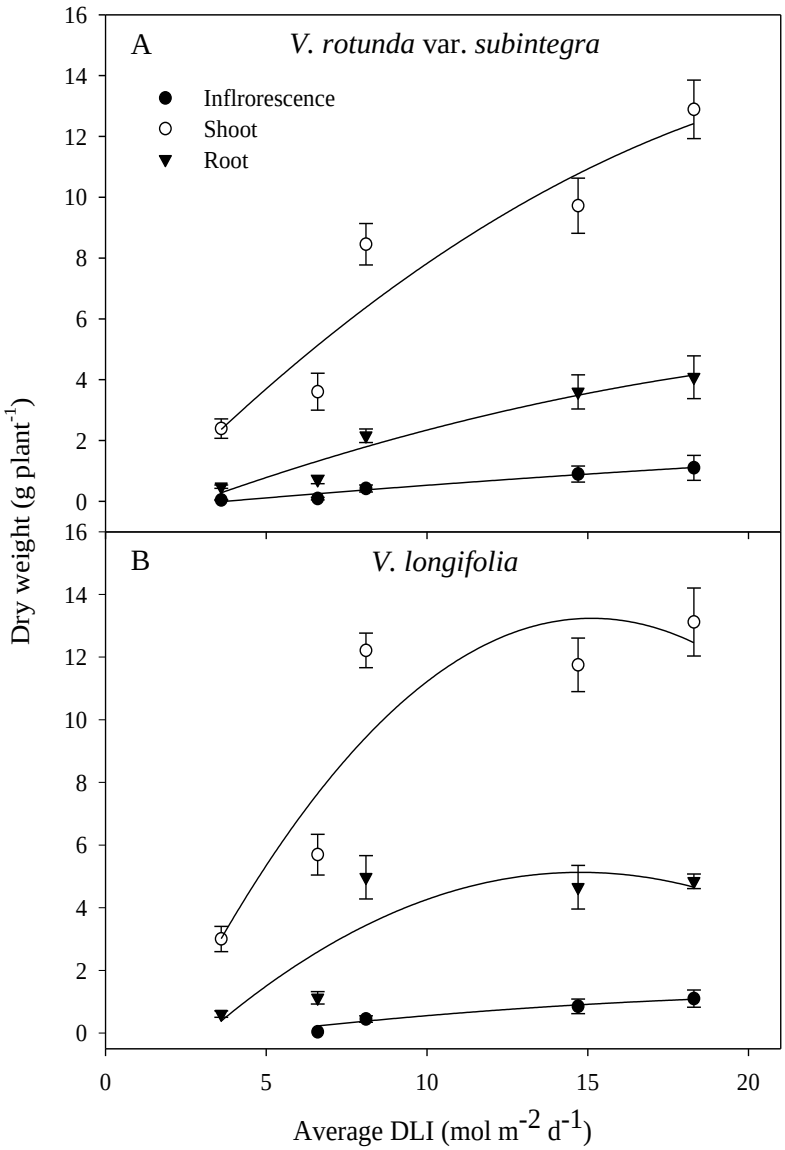

Fig. 9. Inflorescence, shoot (except inflorescences), and root dry weight of *V. rotunda* var. *subintegra* (A) and *V. longifolia* (B) plants grown for 12 weeks under different daily light integral (DLI) conditions. The data shown are the mean ± SE (n = 4). The lines were fitted to a quadratic polynomial; $y = y_0 + ax + bx^2$.

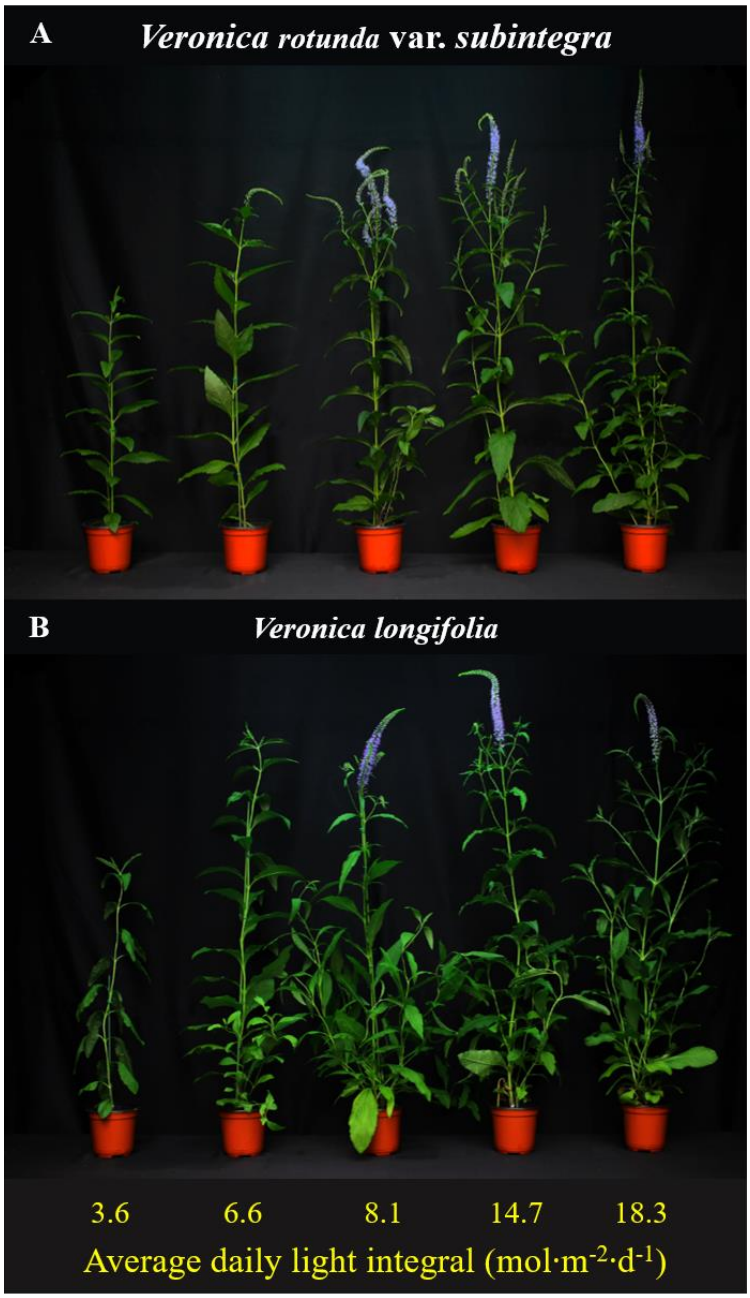

Fig. 10. Growth and flowering of *V. rotunda* var. *subintegra* (A) and *V. longifolia* (B) grown for 12 weeks under different daily light integral (DLI) conditions.

of two species was 100% under all DLI conditions except 3.6 mol·m^{-2}·d^{-1} in *V. longifolia*, the number of nodes below the first inflorescence of both species was lower under higher DLIs from 8.1 to 18.3 mol·m^{-2}·d^{-1} (Table 7). The number of nodes below the first inflorescence generally shows the rate of flower initiation (Warner and Erwin, 2003; Mattson and Erwin, 2005). Mattson and Erwin (2005) divided the flowering response to irradiance into three groups: facultative irradiance response (reduced leaf number below the first flower with increasing irradiance), irradiance indifferent response (increasing irradiance did not reduce leaf number below the first flower), and detrimental irradiance response (increased leaf number below the first flower with increasing irradiance). From the data of this experiment, the flowering response to the irradiance of both *Veronica* plants can be classified as facultative irradiance response because they flowered earlier developmentally with increasing DLI. Moreover, increasing DLI enhanced the number of VI and inflorescence length at the first open flower in both *Veronica* plants (Table 7). These results indicate that DLI can affect flower quality in addition to the rate of flower initiation. Similarly, Fausey et al. (2005) reported that the number of lateral inflorescences increased as DLI increased 5 to 20 mol·m^{-2}·d^{-1} in *Gaura lindheimeri* and *Achillea ×millefolium*, which is consistent with results reported for other plants such as *Hibiscus radiatus* (Warner and Erwin, 2003) and *Eustoma grandiflorums* (Islam et al., 2005).

Days to VI, from VI to first open flower, and to the first open flower decreased as DLI increased from 3.6 to 8.1 mol·m^{-2}·d^{-1} although a further increase of DLI had only a small effect on flowering time (Fig. 11). *V. rotunda* var. *subintegra* and *V.*

Table 7. Flowering characteristics of *V. rotunda* var. *subintegra* and *V. longifolia* plants grown for 12 weeks under different daily light integral (DLI) conditions.

Average DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Flowering (%)	No. of nodes below first inflorescence	At first open flower	
			No. of VIs	Inflorescence length (cm)
		Veronica rotunda var. *subintegra*		
3.6	100.0	19.3 a[z]	2.3 c	13.65 c
6.6	100.0	18.4 a	3.5 bc	15.54 bc
8.1	100.0	15.3 b	6.2 a	20.08 ab
14.7	100.0	16.4 b	5.9 ab	22.37 a
18.3	100.0	16.4 b	7.9 a	20.45 ab
Significance	-	***	***	*
		Veronica longifolia		
3.6	87.5	19.3 a	2.2 c	9.17 b
6.6	100.0	19.4 a	4.0 bc	10.93 b
8.1	100.0	17.0 b	6.7 ab	18.39 a
14.7	100.0	16.1 b	7.7 a	19.91 a
18.3	100.0	16.5 b	8.6 a	19.66 a
Significance	-	**	***	***

[z]Means within columns followed by different letters are significantly different by Duncan's multiple range test at $p < 0.05$.
[NS, *, **, ***] Non-significant or significant at $p < 0.05$, 0.01, 0.001, respectively.

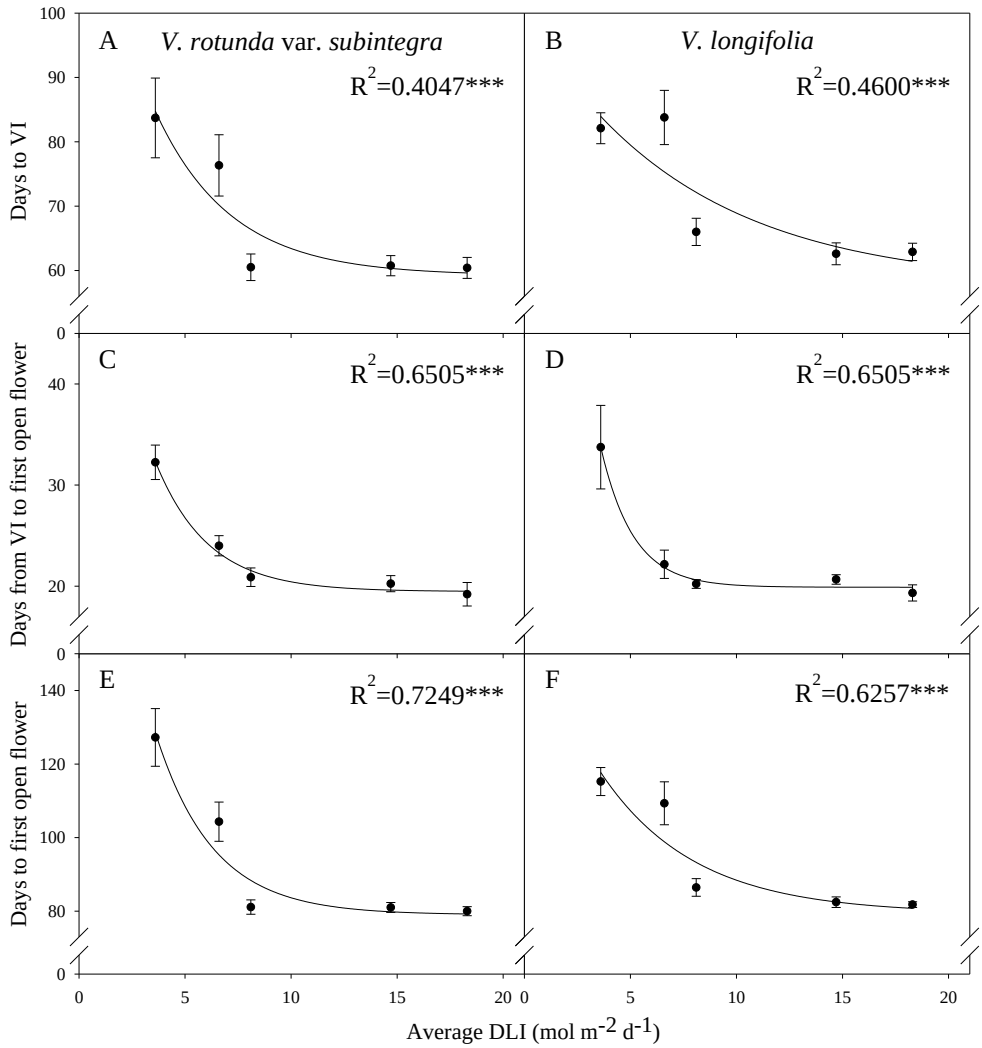

Fig. 11. Days to visible inflorescence (VI), from VI to the first open flower, and to the first open flower of *V. rotunda* var. *subintegra* (A, C, E) and *V. longifolia* (B, D, F) plants grown for 12 weeks under different daily light integral (DLI) conditions. The data shown are the mean ± SE. The lines were fitted to a quadratic polynomial; $y = y_0 + ae^{-bx}$.

longifolia grown under DLI condition of 8.1 $mol \cdot m^{-2} \cdot d^{-1}$ flowered 46 and 29 days earlier than those grown under DLI condition of 3.6 $mol \cdot m^{-2} \cdot d^{-1}$, respectively (Fig. 11). These results agree with the reports for other horticulture crops including *Pelargonium ×domesticum* (Loehrlein and Craig, 2004), *Cyclamen persicum* (Cheon et al., 2006; Oh et al., 2009) and *Kalanchoe* species (Currey and Erwin, 2011). In a study for *Kalanchoe* species, time to the first open flower of some species such as *K. laciniata* was reduced with increasing DLI from 4.3 to 17.2 $mol \cdot m^{-2} \cdot d^{-1}$ (Currey and Erwin, 2011). Reduced days to VI of both species can result from many of the aforementioned factors including promoted growth rate and flower initiation rate (Table 7 and Fig. 11). Similarly, Warner and Erwin (2003) reported that leaf number below the first open flower decreased with increasing DLI in *Hibiscus cisplatinus* which is day-neutral plant and flowers during high irradiance periods in their natural habitats, contributing to the reduction of time to flowering. Thus, both *Veronica* plants may choose DLI as a method to flower under proper environments such as summer because two species are day-neutral plants without the vernalization requirement. In addition, reduced days from VI to the first open flower suggests that high DLI condition also can decrease time to flowering by increasing flower development rate.

Although Korean native *Veronica* species without the vernalization requirement can have more advantages in commercial production than other *Veronica* species in terms of saving time and money, growers may not prefer Korean native *Veronica* plants. The reason can be attributed to the difficulty in controlling flowering of plants

to meet preferred market dates. However, our results suggested that a high DLI condition can promote growth and flowering of two *Veronica* species. Therefore, this observation can be used to control the flowering of two *Veronica* plants in commercial production, contributing to the industrialization of Korean native plants.

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ABSTRACT IN KOREAN

산꼬리풀과 긴산꼬리풀은 독특한 형태와 개화 시기로 인하여 새로운 관상식물 후보로 선정된 한국의 자생식물이다. 본 연구에서는 이러한 두 꼬리풀의 생육과 개화에 있어서 저온 처리, 일장, 일일적산광량의 영향을 알아보았다. 첫 번째 실험에서 9시간 일장, 평균 온도 22°C의 환경에서 육묘를 진행하였다. 유묘의 마디수가 4~5개가 되었을 때 각각 0, 3, 6, 9, 12주간 5°C에서 저온 처리 후 온실로 옮겨 9, 12, 14, 16, 24시간 그리고 9시간+4시간 야파처리까지 총 6개의 일장 조건 하에 배치하였다. 두 종 모두 저온 처리 기간에 상관없이 일장 처리 간의 유의한 생육 차이는 나타나지 않았으며 저온 처리 없이 모든 일장 조건 하에서 개화하였다. 따라서 산꼬리풀과 긴산꼬리풀은 저온요구도가 없는 중성식물로 확인되었다. 두 번째 실험에서는 일일적산광량의 영향을 알아보기 위하여 5개의 일일적산광량 처리(3.6, 6.6, 8.1, 14.7, 18.3mol·m^{-2}·d^{-1})를 진행하였으며 마찬가지로 마디가 4~5개인 유묘를 이용하였다. 최대양자수율의 경우 처리 2주 후에 관찰했을 때 8.1에서 18.3mol·m^{-2}·d^{-1} 사이의 일일적산광량 하에 있던 식물이 3.6과 6.6mol·m^{-2}·d^{-1}의 일일적산광량 하에서 자란 식물보다 더 낮은 값을 나타냈으나 처리 6주 후에는 처리 간의 차이가 관찰되지 않았다. 두 종

모두 일일적산광량이 증가할수록 광합성 능력이 향상되었으며 대부분의 생육 지표가 증가하였다. 개화 반응의 경우 개화율에는 차이가 없었으나 일일적산광량의 증가가 개화시 마디수를 감소시켰으며 개화시 화서수와 화서장이 증가하였다. 또한 화아유도 소요일수, 화아유도부터 개화까지의 소요일수, 총 개화 소요일수가 모두 일일적산광량이 증가함에 따라 감소하였다. 따라서 높은 일일적산광량이 산꼬리풀과 긴산꼬리풀의 생육과 개화를 촉진할 수 있으며 이를 통하여 실제 농가에서 두 식물의 개화 촉진이 가능할 것으로 생각된다.

추가 주요어: 일일적산광량, 다년생 초본, 일장, 광합성, 춘화

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