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**A THESIS FOR THE DEGREE OF MASTER OF SCIENCE**

**Vegetative Growth and Inflorescence Emergence of  
*Phalaenopsis* ‘Mantefon’ as Affected by  
Photoperiod, Light Intensity, and Daily Light Integral**

**일장, 광도, 일적산광량에 따른 호접란의 영양생장 및 꽃대 출현 변화**

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**FEBRUARY, 2018**

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# **Vegetative Growth and Inflorescence Emergence of *Phalaenopsis* ‘Mantefon’ as Affected by Photoperiod, Light Intensity, and Daily Light Integral**

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## **ABSTRACT**

This study was conducted to determine how photoperiod, light intensity, and daily light integral (DLI) influence vegetative growth (Experiment 1) and inflorescence emergence (Experiment 2) in *Phalaenopsis*. In Experiment 1, five-month-old plants were treated with a combination of three photoperiods [8 (short day, SD), 12 (medium day, MD), and 16 h (long day, LD)] and three light intensities (50, 100, and 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), resulting in 7 DLIs ranging from 1.44 to 11.52  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . Each light treatment was maintained for 20 weeks at constant 28°C. It was observed that plants grown under longer photoperiod and high light intensity resulted in shorter, wider, and thicker leaves, respectively. Number of new leaves, total leaf area, and shoot and root weights were increased with increasing photoperiod and light intensity. DLI showed higher correlation coefficients with vegetative growth parameters than with photoperiod and light intensity. The regression analysis indicated that increased DLIs promoted vegetative growth.

However, it was observed that when DLI reached  $11.52 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , response slope gradually decreased.

In Experiment 2, twelve-month-old plants were used to investigate the effects of photoperiod, light intensity, and DLI on inflorescence emergence. Plants were treated with combinations of three photoperiods [8/16 (day/night, SD), 8+8 (DE;  $10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for 8 h extension right after the SD), and 16/8 h (LD)] and three light intensities (75, 150, and  $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Each light treatment was maintained for 12 weeks at constant  $20^{\circ}\text{C}$ . Inflorescence emergence percent, the days to emergence, and the number of inflorescences were generally more promoted under LD treatments than SD and DE treatments, indicating that the effect of photoperiod on flower induction of *Phalaenopsis* was insignificant. Comparing the light intensities, inflorescence emergence was generally promoted as the light intensity was increased. Correlation coefficients of DLIs with days to emergence and number of inflorescences showed the highest values. Regression analysis indicated that as DLI increase from 2 to  $17 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , the days to inflorescence emergence was shortened by about one month, and average number of the inflorescence was increased more than 2 times. However, they seemed not to be promoted beyond DLI of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , suggesting that the DLI reached the maximum (or saturation) point. Thus, inflorescence emergence was promoted with increasing DLI, but the DLI above  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  was less promotive for inflorescence emergence.

**Additional key words:** *Doritaenopsis*, orchid, chlorophyll fluorescence, leaf color, day extension, correlation coefficient, regression analysis

**Student number:** 2016–21450

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# INTRODUCTION

*Doritaenopsis*, an intergeneric hybrid between the *Doritis* and *Phalaenopsis*, belongs to Orchidaceae, one of the most diverse flowering plant families (Sun et al., 2012). Meanwhile, *Doritis* was considered as a synonym of *Phalaenopsis* in the monophyly of the genus, which was supported by ample amount of molecular data (Christenson, 2001; Tsai et al., 2010). *Phalaenopsis* hybrids, which generally include *Doritaenopsis*, are becoming increasingly popular for their ornate flower shapes, and longer flowering period than the traditional *Phalaenopsis* (Chen and Chen, 2011; Christenson, 2001; De et al., 2014).

Production time of the *Phalaenopsis* (i.e., *Doritaenopsis* in this paper) is approximately 50 to 70 weeks from small *in vitro* cultivated plantlets until flowering and can be divided into three phases (1) period of vegetative growth, (2) flower bud initiation (cooling phase), and (3) inflorescence development (finishing phase) (Hückstädt and Torre, 2013). In addition, it is necessary to find the production method of the multiple inflorescences, because they are paid higher than the single inflorescence plant. Therefore, new cultivation methods that shorten the length of cultivation period and controlling inflorescence numbers are needed to improve the economic efficiency of this plant.

There are many environmental factors affecting the growth and development of plants, and amongst which light condition is one of the most important variables (Inada and Yabumoto, 1989). The daily light integral (DLI) is the function of photosynthetic photon flux (PPF) and photoperiod per day or the summation of PPF in the course of 24

h. It is often used in place of PPF as a light parameter in plant growth and development models (Faust and Heins, 1993; Kitaya et al., 1991), because it describes the amount of light more accurately in some plant species. Several studies have described the effect of DLI on the growth and development of bedding plants (Kaczperski et al., 1991; Niu et al., 2000; White and Warrington, 1984). However, no researches on the effect of DLI on *Phalaenopsis* have been published to my knowledge. Therefore, it is necessary to investigate the effect of DLI, in addition to examine the effects of light intensity and photoperiod.

The effect of photoperiod on growth and development of *Phalaenopsis* was different according to cultivars (Blanchard and Runkle, 2006). Short days have caused advanced inflorescence initiation and the days of flowering in *Phalaenopsis* regardless of temperature or cultivars (Griesbach, 1985; Rotor, 1952; Went, 1957; Yoneda et al., 1991). However, Ichihashi (1997) and Sakanishi et al. (1980) reported that *Phalaenopsis* was non-photoperiodic plant when they were grown at the critical temperature for inflorescence emergence.

Previous studies have shown that increased light intensity promoted the growth and development of *Phalaenopsis*, and it is believed that the growth-promoting effect only works well within a certain range of light intensity from 100 to 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Guo et al., 2012; Kubota and Yoneda, 1993; Lin and Hsu, 2004; Lootens and Heursel, 1998; Wang, 1995). When light intensity was too high, there was reduced growth as caused by faded leaf color, spots or a band running diagonal to the “indentation” on the fully grown leaf. Thus, increasing light intensity too high in order to increase DLI cannot be advantageous for growth and development. In order to examine the response of DLIs,

various combinations of photoperiod and light intensity are necessary. However, it is not clear whether the DLI affect the vegetative growth in *Phalaenopsis*, because the effect of photoperiod was not well understood.

This study was conducted to examine the effects of light intensity, photoperiods, and their interaction on the promotion of vegetative growth (Experiment 1) and inflorescence emergence (Experiment 2) of *Phalaenopsis* orchids.

# LITERATURE REVIEW

## Characteristics of *Phalaenopsis*

**Distribution.** The *Phalaenopsis* orchids can be found all over the world from the arctic and temperate regions to the tropics. However, the greatest diversity of species is found in the tropics where orchids usually grow epiphytically or lithophytically (Baker and Baker, 1991). The *Phalaenopsis* genus is originated from the tropical region of Asia. The western frontier of its area of distribution lies in Sri Lanka and Southern India. While the eastern frontier lies in Papua New Guinea and a section of neighboring Australia. They also grow in Southern China (Yunnan), Taiwan, and the Philippines in the north. They are also native to Thailand, Malaysia, Vietnam, and Indonesia. Approximately 66 different species are known. The *Phalaenopsis* subgenus is originated mainly from the Philippines, Taiwan, and from Indonesia to Australia (Van der Knaap, 2005).

**Morphology.** Roots of *Phalaenopsis* have the characteristic of developing a new plant from the root primordium on a piece of root material that has remained behind but is no longer connected to the mother plant. Roots are not only used for absorbing water and nutrients, but also functioned as anchorage organs to get a good grip on tree trunks. The root tissue contains some amounts of chlorophyll and has the photosynthetic capability (Van der Knaap, 2005).

Leathery succulent-like leaves of *Phalaenopsis* provide an alternative for pseudobulbs that are used to store water during dry periods. And these orchids perform crassulacean acid metabolism (CAM) to fix CO<sub>2</sub> (Guo, 1999; Hew and Yong, 2004). In the CAM plants, CO<sub>2</sub> is fixed at night and stored as malate in the vacuole. During the

daytime, the malate is decarboxylated in the chloroplast and the released CO<sub>2</sub> is incorporated to the C3 cycle (Taiz and Zeiger, 2015).

Inflorescences are green colored, contain chlorophyll, and have the photosynthetic ability. However, the capacity of assimilation is not enough for the development of spikes and blossoms. The flower structure of orchid family, including the *Phalaenopsis* orchid, is characterized by the figure three: three sepals, three petals and a triangular ovary (Van der Knaap, 2005).

### **Vegetative Growth in Response to Light Intensity and Photoperiod**

The recommended light intensity levels for *Phalaenopsis* during vegetative growth varied from 60 to 400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and the wide interval was thought to be due to hybrid differences (Konow and Wang, 2001; Lin and Hsu, 2004; Lopez and Runkle, 2005; van der Knaap, 2005). Several studies have found that the photosynthetic rate of *Phalaenopsis* was saturated at about from 130 to 180  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Lootens and Heursel, 1998; Ota et al., 1991), and exposure to the intensity higher than 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  has resulted in significant photo-inhibition (Lin and Hsu, 2004). By increasing the intensity from 50 to 125  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  during the vegetative growth phase, the total production time was substantially reduced, mainly by shortening the vegetative growth phase. The light intensity during the vegetative growth phase could influence the number of inflorescences per plant, time for cooling to visible inflorescence emergence, or inflorescence morphology (Hückstädt and Torre, 2013).

The effect of photoperiod on flowering of orchids appeared to be very diverse among orchid species (Newton, 2008). Some orchids such as *Dendrobium* (Sheenhan et al.,

1965) and *Vanda* (Murashige et al., 1967) have vegetative response to photoperiod. But no report has been found, to my knowledge, on the effects of photoperiod in the vegetative growth rate of *Phalaenopsis*.

### **Reproductive Growth in Response to Light Intensity and Photoperiod**

The bud primordium become active and develops into new tissues only at a certain stage, and after which it becomes dormant (Rotor, 1952). The inflorescence usually emerged from the third or often the fourth node below the apical leaf (Sakanishi et al., 1980). Because an increased price is paid for a multiple-stem over a single-stem plant, production of the multiple-stem plant is desirable, but it is not well understood how the inflorescence number is environmentally regulated in *Phalaenopsis*. However, the ability to generate multiple inflorescences was controlled genetically because certain hybrids have tendencies to generate preferably single or multi inflorescence plants. Some environmental factors during the cooling period have been also found to influence the number of inflorescence. High light intensity during the cooling period was necessary to induce an inflorescence (Kataoka et al., 2004), while plants did not develop inflorescences at all when exposed to low light intensity or kept in complete darkness (Wang, 1995). Several studies also indicated that photoperiod played an important role in flowering in terms of the flower initiation and development. The short photoperiod promoted both early inflorescence initiation and the number of days to flowering in *Phalaenopsis* hybrids, regardless of temperature (An et al., 2013; Griesbachm, 1985; Rotor, 1952; Went, 1957). However, Ichihashi (1997) and Sakanishi et al. (1980) suggested that the effect of photoperiod was the secondary to those of temperature.

## **Growth and Development in Response to Daily Light Integral (DLI)**

Recommendation for light requirement during commercial greenhouse crop production has been often expressed in the unit of  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , an instantaneous measurement of light intensity (Dole and Wilkins, 2005; Faust, 2003). However, light intensity varies widely within a single day and over the course of a growing season, as well (Lambers et al., 2008; Larcher, 2003). Therefore, the integrated photosynthetic DLI as expressed in the unit of  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  was suggested to be a more accurate description of light condition during crop production, since it was the cumulative light amount received over the course of a daily basis (Faust et al., 2005).

Several studies have described the effect of DLI on the growth and development of bedding plants. Plant growth measured in terms of dry mass accumulation, leaf area, and plant height was affected by DLI. For example, White and Warrington (1984) observed an increase in geranium plant dry mass from 2.9 to 3.4 g as the DLI was increased from 6.5 to 19.4  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , while the leaf area per plant decreased from 10,647 to 820  $\text{cm}^2$  as the DLI increased from 8.7 to 20.5  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . Niu et al. (2000) reported that the dry mass of pansy ‘Delta Yellow Blotch’ increased by 40% as the DLI increased from 4.1 to 10.6  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . Kaczperski et al. (1991) reported that petunias grown at 6.5  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  were up to 6 cm taller than plants grown under 13.0  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . The DLI also affected flowering in terms of the rate of flower development and flower size. For example, increasing the DLI to geraniums from 3.2 to 24.3  $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  resulted in a 29 day decrease in time to visible bud; however, the DLI did not affect the time from visible bud to flower (Armitage, 1981). Time to flower for petunia decreased by 3 weeks as DLI

increased from 6.5 to 13.0 mol·m<sup>-2</sup>·d<sup>-1</sup> (Kaczperski et al., 1991). However, no researches on the effect of DLI on *Phalaenopsis* have been published to my knowledge.



# MATERIALS AND METHODS

## Vegetative Growth (Experiment 1)

**Plant materials and acclimation conditions.** Tissue cultured clones of five-month-old *Phalaenopsis* Queen Beer ‘Mantefon’ were purchased from Sangmione nursery, Taean, Korea (37°71'S, 126°29'E) and were cultivated for this study at a closed plant production system in the Seoul National University Farm (Suwon, Korea). The plants were transplanted into 10 cm pots filled with 100% sphagnum moss. The plants were acclimatized at 28°C, relative humidity of 70%, and the photoperiod was 12 h (from 08:00 to 20:00) with  $100 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  using warm-white LEDs for 4 weeks. Nutrient solution had EC of  $0.8 \text{ mS}\cdot\text{cm}^{-1}$  by using water soluble fertilizer (Hyponex professional 20N–20P–20K, Hyponex Japan, Osaka, Japan) with conductivity of  $0.8 \text{ mS}\cdot\text{cm}^{-1}$ . Plants were watered once a week by a drip irrigation system.

**Light treatments.** After the acclimatization period, thirteen plants were placed in each compartment of treatment and grown for an additional 20 weeks under the light treatments. At the beginning of treatment, the plants had three to four fully developed leaves, the average leaf span, the distance between the tips of the longest leaves, was 17.1 cm.

Plants were treated with three different photoperiods [8 (short day, SD), 12 (medium day, MD), and 16 h (long day, LD)] with a combination of three light intensities ( $50 \pm 5$ ,  $100 \pm 10$ , and  $200 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) for a total of 9 treatments. The resultant DLIs were ranged between 1.44 and  $11.52 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . In order to avoid redundancy, the treatments are abbreviated as LD/200 treatment for the 16 h photoperiod under  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$

light intensity, for example. The light intensity levels were measured by using spectrum solar electric quantum meter (3415FSE, Spectrum Technologies, Aurora, IL, USA) at the top-level of plant canopy.

***Growth parameters.*** For vegetative growth measurement, the leaf length, width (measured at the middle of the leaf), thickness of the uppermost mature leaves, and number of new leaf appearance were measured from thirteen plants every 4 weeks. The total leaf area of each plant was measured with a leaf area meter (Li-Cor 3100, Li-Cor, Lincoln, NE, USA). Fresh weights of leaf and root were measured after the media were rinsed off, and the dry weights were measured after drying at 80°C for 4 days after 20 weeks of treatment. The relative chlorophyll content of the uppermost mature leaf was also measured using a chlorophyll meter (SPAD 502, Konica Minolta Sensing, Osaka, Japan) after 20 weeks of the treatment.

***Chlorophyll fluorescence.*** Photosynthetic activities were measured using a chlorophyll fluorometer (PAM-2000, Heinz Walz, Effeltrich, Germany). After 30 min dark adaptation period, a measuring light of 0.6kHz and less than  $0.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PPFD was irradiated to obtain the minimum fluorescence in the dark-adapted state ( $F_o$ ) and then a saturating light pulse at about  $8,000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PPFD was irradiated for 0.8s to induce maximum fluorescence in the dark-adapted state ( $F_m$ ). After the first saturating light pulse, an actinic light intensity of  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  was irradiated to obtain the maximum ( $F_m'$ ) and the minimum fluorescence ( $F_o'$ ) in the light-adapted state. During actinic light adaptation, the saturating light pulse was irradiated 20 times with a 20 s interval. Then,  $F_m'$ ,  $F_o'$ , and fluorescence at steady state ( $F_s$ ) at the 20th saturating light pulse was recorded, regarding it as a steady state of fluorescence. With these

fluorescence parameters, photosystem II (PSII) activities were estimated. Potential quantum yields in the dark- and light-adapted states were estimated from  $(F_m - F_o)/F_m = F_v/F_m$  and  $(F_m' - F_o')/F_m' = F_v'/F_m'$ , respectively, representing the efficiency of energy captured by open PSII (Genty et al., 1989). The coefficient for photochemical quenching,  $qP$ , representing the fraction of open PSII reaction center was calculated as  $(F_m' - F_s)/(F_m' - F_o')$ . The actual quantum yield of PSII ( $qP$ ), described as the fraction of absorbed light utilized through photochemistry, was estimated from  $(F_m' - F_s)/F_m'$  (Genty et al., 1989).

## **Inflorescence Emergence (Experiment 2)**

***Plant materials and acclimation conditions.*** Twelve-month-old plants were acclimatized at 28°C, relative humidity of 70%, and the photoperiod was 12 h (from 08:00 to 20:00) with  $100 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  using warm-white LEDs for 4 weeks. The same nutrient solution listed above was irrigated once a week by a drip irrigation system.

***Light treatment.*** After the acclimatization, sixteen plants were placed in each compartment of treatments and grown for an additional 12 weeks under the light treatments. At the beginning of treatment, the plants had six or seven fully developed leaves, the average leaf span was 18.2 cm.

The plants were treated three different photoperiods [8 (short day, SD), 8+8 (day extension, DE;  $10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for additional 8 h after the SD), and 16 h (long day, LD)] with a combination of three levels of light intensities (75, 150, and  $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). This combination has resulted in 6 DLIs ranging from 2.16 to  $17.28 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . DE treatments were included to compare the photoperiod effects between 8 and 16 h at the

very similar DLI levels under the same light intensity. The treatments were also abbreviated in the text as SD/150 treatment for the SD photoperiod with  $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , for example.

The temperature was reduced to  $20^{\circ}\text{C}$  with relative humidity of 70%. Plants were watered and fertilized at the same manner as described above.

***Leaf growth and inflorescence emergence parameters.*** For leaf measurement of leaf growth, total and new leaf number and relative chlorophyll contents were measured. Chlorophyll fluorescence of  $F_v/F_m$  was measured as described earlier. The days to inflorescence and number of the inflorescence were counted when the 1st and 2nd inflorescence was about 0.5 cm in length. The inflorescence emergence was recorded every two days. The percentage of the inflorescence was calculated by dividing the total number of the inflorescence by number of plant. The duration of the experiment was 12 weeks because an inflorescence usually emerges after from 3 to 5 weeks after exposure to an inductive temperature less than  $25^{\circ}\text{C}$  (Lee and Lin, 1987).

***Statistical analysis.*** The experimental design was a factorial design of photoperiods and light intensity of 3 levels each and each treatment had thirteen (experiment 1) or sixteen (experiment 2) plants as replications. Comparisons of treatment means were performed using Duncan's multiple range test at  $p < 0.05$  using the SAS system for Windows version 9.3 (SAS Institute, Cary, NC, USA). Partitioning of the sum of square (%SS) was also presented to examine the contribution from each factor to the treatment means of each parameter. Correlation and regression analyses were performed by using the Sigma Plot (version 10.0; Systat Software, Chicago, IL, USA).

## RESULTS AND DISCUSSION

### Vegetative Growth (Experiment 1)

**Leaf growth.** A tendency of leaf growth and shape with shorter, wider, and thicker leaves was observed under the longer photoperiod and higher light intensity (Table 1). Number of new leaves and total leaf area were increased with increasing photoperiod and light intensity. The photoperiod treatments had no effect on the leaf length. However, leaf length showed an increasing trend with increasing light intensity. Thus, the shortest leaf length was observed at the  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments. Both photoperiod and light intensity treatments did not show significant effect on the leaf width, but it still showed some increasing trend. Therefore, due to the reduction in the leaf length as accompanied by broadening width, the L/W ratios showed decreasing values by both increasing photoperiod and light intensity, resulting in broad shaped leaves. The leaf thickness was not significantly affected by the photoperiod treatments, but was getting thicker as the light intensity increased. Though insignificant, there was some tendency of increasing leaf thickness by the increasing photoperiod.

Hückstädt and Torre (2013) also found that a similar tendency of longer, narrower, and thinner leaves was found under  $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  condition, as compared to 125 or  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  condition. However, the plants at the MD or LD and the 100 or  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments were not seen more compact, because the leaf span (defined as the distance in between the two largest leaves of the plant) was not significantly different (data not shown).

The number of new leaves showed an increasing tendency to the increasing

photoperiod hours, thus the least and greatest numbers were observed at the SD and LD treatments, respectively. The 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments resulted in the greatest new leaf numbers, while those plants under the 50  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment had the least numbers. As a combination of these results, the greatest new leaf number was observed under the LD/200 treatments.

Total leaf area showed an increasing trend with photoperiod hours, and the greatest numbers were observed at 16 h treatment. Plants under the light intensity of 100 and 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments had 15% greater total leaf area than those under the 50  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments. An et al. (2013) suggested that the increased number of leaves was found in plants grown under long photoperiod conditions such as 16 h. Many researchers also showed that both cell division and cell expansion were involved in the promotional effect of long-day on leaf size and this greater leaf expansion increased light interception rate (Arney, 1956; Humphries and Wheeler, 1963; Milford and Lenton, 1976). Konow and Wang (2001) reported that increased light intensity from about 50 to 250  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  resulted in plants with more leaf number and larger total leaf area. From these previous researches, it could be expected that greater leaf numbers had resulted in the larger leaf area because leaf size usually increased in successive younger leaves. In all, increased growth rates and leaf size would lead to accelerated flowering phase and, subsequently, reduce the total production time and production cost.

***Chlorophyll content.*** Chlorophyll content was increased continuously until 20 weeks after treatment and then stayed constant. Plants under the LD treatments had greater chlorophyll contents than those under the SD or MD treatments for 20 weeks.

Typically, the chlorophyll content was related to the rate of plant growth (Brougham,

1960; Son and Oh, 2013). Langton et al. (2003) found that long-day increased chlorophyll contents in four bedding plant species, geranium, impatiens, pansy and petunia. This result caused the author to speculate that long-day could have affected the chlorophyll content by modifying the rates of chlorophyll synthesis and/or breakdown. Chlorophyll synthesis could only occur when a plant was illuminated, as the reduction process of protochlorophyllide was dependent on light (Suzuki and Bauer, 1995; Thompson and White, 1991).

In case of light intensity, the chlorophyll content showed an increasing trend as the growth period was extended, except the result at 4 weeks under  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment (data was not shown). Under the  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment, chlorophyll content was exceptionally reduced at 4 weeks, but was recovered to the similar level to other treatments from 8 weeks. Though not significant, the chlorophyll content was the lowest under  $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and the highest under  $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment. Interestingly, the chlorophyll content was middle under the  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment. These results implied that the  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment has a light inhibition effect on the *Phalaenopsis* leaf.

This might be also attributed to the stress at high light intensity. Several studies have found that the photosynthesis of *Phalaneopsis* saturates at about  $130\text{-}180 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Lootens and Heursel, 1998; Ota et al., 1991), and exposure to light intensity higher than  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  resulted in a significant photo-inhibition (Lin and Hsu, 2004). However, the plants recovered after 2 months.

In leaf growth responses, a significant interaction between photoperiod and light intensity was observed in leaf width and total leaf area. That meant the treatment of

photoperiod and light intensity influenced independently in controlling the leaf growth of *Phalaenopsis* orchids.



Table 1. Leaf growth and chlorophyll content of *Phalaenopsis* 'Mantefon' after 20 weeks of light treatment

Photoperiod (h)	Light intensity ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	Length (cm)	Width (mm)	Length/Width ratio	Thickness (mm)	No. of new leaves	Total leaf area ( $\text{cm}^2$ )	Chlorophyll content (SPAD value)
8	50	13.0 a	4.9 c	2.7 a	1.6 c	2.3 d	174.9 b	71.06 c
	100	13.9 a	5.5 bc	2.5 a	1.9 ab	2.6 cd	235.1 a	72.60 abc
	200	12.5 a	5.9 ab	2.1 bcd	2.0 ab	2.8 bc	234.9 a	71.36 c
12	50	13.8 a	5.7 abc	2.4 ab	1.9 ab	2.3 d	228.4 a	69.18 d
	100	13.6 a	5.2 bc	2.6 a	1.8 abc	2.8 bc	232.1 a	70.89 c
	200	9.9 b	5.6 abc	1.8 d	2.1 a	3.3 ab	237.3 a	69.11 abc
16	50	13.4 a	5.5 abc	2.5 ab	1.8 bc	2.3 d	229.0 a	71.94 bcd
	100	13.6 a	6.3 a	2.2 bc	2.1 a	3.2 ab	251.3 a	75.54 abc
	200	10.6 b	5.9 ab	1.9 cd	2.1 a	3.4 a	250.7 a	75.86 a

Significance

Photoperiod (A)	NS (7.5%)	NS (27.3%)	* (16.1%)	NS (16.4%)	* (14.2%)	* (31.7%)	*** (70.8%)
Light intensity (B)	*** (72.7%)	NS (27.4%)	*** (73.5%)	*** (68.2%)	*** (77.4%)	*** (46.8%)	NS (17.4%)
Interaction (A × B)	NS (19.7%)	* (45.2%)	NS (10.3%)	NS (15.2%)	NS (8.4%)	NS (21.4%)	NS (11.7%)

<sup>2</sup>Means separation within columns by Duncan's multiple arrangement test at  $p < 0.05$ .

NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.

***Fresh and dry weights.*** Fresh and dry weights of plant were found to be significantly affected by light intensity and photoperiod treatments (Table 2). The increasing photoperiod has resulted in the increasing shoot and root fresh weights, and, as a consequence, the total weights. Fresh weight of shoot and root showed an increasing trend with increasing photoperiod hours, so that fresh weights of shoot and root under the LD treatments were 16% and 51% greater than those under the SD treatments, respectively. Therefore, the highest total fresh weight was observed in the LD treatments.

Similarly, when plants were grown under an extended photoperiod from 16 to 24 h treatments showed increased shoot and total fresh weight and yields of tomato plants by from 40 to 57% and from 15 to 20%, respectively (Demers et al., 1998).

The shoot, root, and total fresh weights were clearly increased by the increasing light intensity levels, as similar to the photoperiod treatments. However, the magnitude of increase by the light intensity treatments was much greater than that of the photoperiod treatment. Plants under the light intensity of  $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  had 24% greater shoot fresh weight than those under the  $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments. The greatest root fresh weight was found in  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments. In all, the total fresh weights under  $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments had 34% greater total fresh weights than those under the  $50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment. Chlorophyll discussion somewhere

Similar results were found that the malic acid, sucrose, and starch increased with increasing light intensity (Konow and Wang, 2001). The additive effect of higher energy captured during the day and the larger overall leaf area allowed plants to produce larger quantities of malic acid to be utilized in the  $\text{CO}_2$  assimilation process at night and thus

promoted further increases in photosynthesis and much rapid growth. These results suggested that long photoperiod such as LD and high light intensities of  $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  was more efficient in gaining fresh weight in the growth of the *Phalaenopsis* than the other treatments.

Dry weights of shoot, root, and total showed an increasing trend with increasing photoperiod hours, so that the least and greatest numbers were observed in SD and LD treatments, respectively.

This result was very similar to the trend as seen in the results of fresh weights. Dramatic increase in dry weight was also similarly reported by Hurd (1973) in young tomato plants growing in a 16 h day extension treatment. After 41 days from sowing, plants grown under long day had almost twice the dry weight (+76%) of those of controls grown in 8 h short day treatment.

The light intensity treatments showed an increasing effect on the shoot, root, and total dry weights. Thus,  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments showed the greatest shoot, root and total dry weights.

Under low light intensity, dry weights of shoot and root of plants grown under 50% shaded were 187% and 420% higher than those grown under 95% shaded conditions, respectively, in *Jeffersonia dubia* (Rhie et al., 2014). These results indicated that the MD or LD at  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  had greater effects on gaining dry weight in growth, as compared with the other treatments. In shoot and root weight responses, a significant interaction between photoperiod and light intensity was observed only in shoot fresh weight, indicating that photoperiod and light intensity affected independently on the general leaf weight increase.

The relative attribution from the factors of photoperiod, light intensity, and their interaction could be partitioned as %SS (Tables 1 and 2). In general, the treatment of light intensity was turned out to be the main key and more effective major factor in controlling the vegetative growth and development of *Phalaenopsis*.

Table 2. Fresh and dry weights of *Phalaenopsis* ‘Mantefon’ after 20 weeks of light treatment

Photoperiod (h)	Light intensity ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	Fresh weight (g)			Dry weight (g)		
		Shoot	Root	Total	Shoot	Root	Total
8	50	24.95 c <sup>z</sup>	7.45 d	32.40 e	0.99 d	0.32 f	1.31 e
	100	37.98 ab	10.76 c	48.73 cd	1.52 c	0.61 def	2.13 d
	200	38.78 ab	15.54 b	54.32 bc	1.62bc	0.89 cd	2.50 cd
12	50	36.20 ab	10.60 cd	46.80 cd	1.70bc	0.66 de	2.36 cd
	100	36.32 ab	16.58 b	50.90 bcd	1.80bc	1.08 bc	2.88 bc
	200	35.41 b	17.36 b	52.77 bcd	1.94bc	1.38 ab	3.31 ab
16	50	34.41 b	9.41 cd	43.81 d	1.68 c	0.55 ef	2.23 cd
	100	42.65 a	17.07 b	59.71 ab	2.18 b	1.23 b	3.41 ab
	200	41.14 ab	24.67 a	65.80 a	2.38 a	1.59 a	3.98 a
Significance (SS%)							
Photoperiod (A)		** (22.6%)	*** (23.2%)	*** (26.4%)	*** (60.3%)	*** (33.3%)	*** (42.2%)
Light intensity (B)		*** (50.8%)	*** (66.7%)	*** (63.8%)	*** (35.5%)	*** (63.1%)	*** (50.6%)
Interaction (A × B)		** (26.5%)	** (10.0%)	NS (9.7%)	NS (4.1%)	NS (3.4%)	NS (2.0%)

<sup>z</sup>Means separation within columns by Duncan’s multiple arrange test at  $p < 0.05$ .

NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.

***Chlorophyll fluorescence.*** All treatments did not suffer from photo-inhibition, but, still gain extended in photosynthetic production under the longer photoperiod and higher light. In this study, Fv/Fm values ranged from 0.79 to 0.82 throughout all treatments and there was no significant difference among the treatments (Fig. 1A).

The maximal quantum efficiency (Fv/Fm) of non-photo-inhibited leaves appear to be about from 0.75 to 0.85 (Lin and Hsu, 2004; Maxwell and Johnson, 2000). These were similar to the results of normally grown *Phalaenopsis* plants in other studies (Hsu, 2007; Lin and Hsu, 2004; Pollet et al., 2009).

The photochemical quenching (qP) represented a measure of the steady-state reduction state of the acceptor Q<sub>A</sub> of PSII (Lin and Hsu, 2004). The qP value was sensitive to the photoperiod and light intensity (Fig. 1B). The MD or LD treatments resulted in plants with greater qP value, as compared with the 8 h treatments. Plants under the light intensity of 100 and 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  had 20% greater qP value than those under the 50  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments. In all, the photoperiod of the MD and LD and the light intensity of 50 and 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  had greater qP values.

High qP indicated that the light absorbed by the PSII antennae could be efficiently utilized in the PSII photochemistry (Demmig-Adams et al., 1996; Genty et al., 1989). Ögren and Sjöström (1991) explained that high photosynthetic efficiency may lead to potentiality in daily carbon gain with a higher capacity for plant dry mass accumulation. In this study, total fresh and dry weight was increased with increasing photoperiod and light intensity (Table 2). Some previous researchers have found that the photoperiod also had effects on photosynthetic capacities in the CAM plants. When the photoperiod was increased from 6 h to 18 h in *Opuntiaficus-indica*, a 53% increase in net CO<sub>2</sub> uptake over

a 24 h period occurred, and as a result, 50% increase in annual growth was followed (Nobel, 1989). In *Phalaenopsis*, the CO<sub>2</sub> uptake was increased with increasing photoperiod from 6 to 14 h (Chen and Lin, 2012). The light intensity also highly influenced *Phalaenopsis* vegetative growth. Konow and Wang (2001) found that high light intensity would result in larger plants due to increased photosynthesis, leading to higher carbohydrate concentrations and increased growth rates.

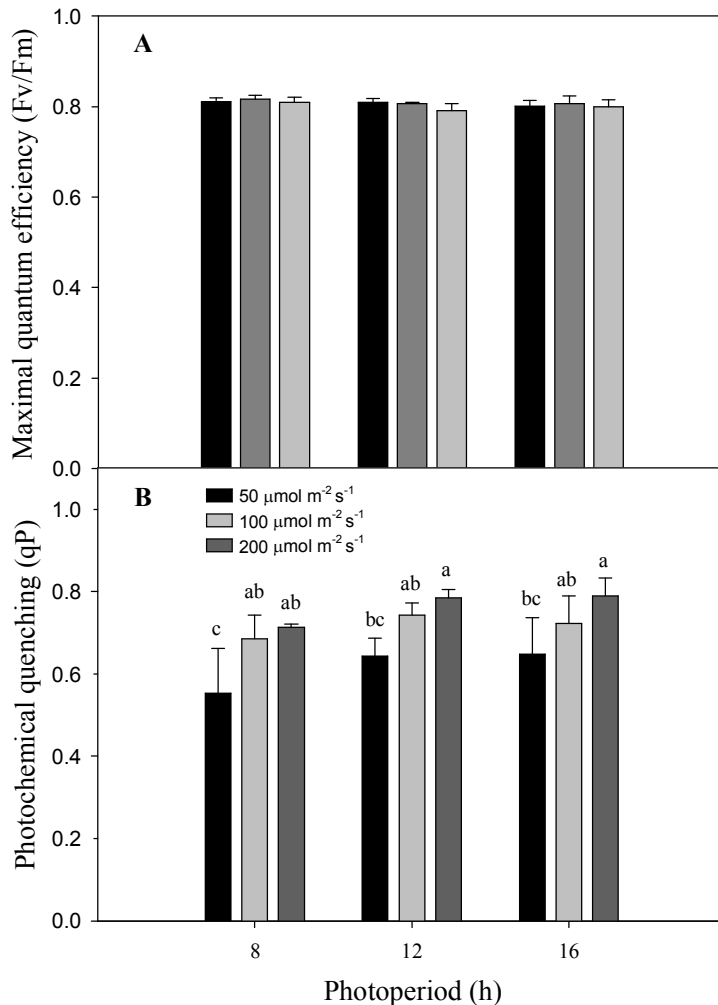


Fig. 1. Maximal quantum yield (Fv/Fm) (A) and photochemical quenching (qP) (B) of the uppermost mature leaves of 5-month-old *Phalaenopsis* 'Mantefon' grown under 8 (SD), 12 (MD), or 16 h (LD) photoperiod with a combination of 50, 100, or 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  light intensity after 20 weeks of treatment. Vertical bars represent standard errors of the means. Different letters within each panel indicate a significant difference at  $p < 0.05$ .



***Correlation coefficient.*** The correlation analysis (Table 3) showed somewhat different results from those of the significance test in the ANOVA in the Tables 1 and 2, i.e., the significance in the ANOVA did not always turn out to be significant in the correlation analysis. The ANOVA only tests the difference of the treatment means, regardless of the trend. However, since the correlation analysis tests the relation or trend of the two variables, a clearer relationship between the photoperiod and light intensity on plant growth, weight, and photosynthesis parameters could be elucidated. In addition to photoperiod and light intensity, the DLI effect was also included. Although most of the indicators with the photoperiod treatment remained not significant, the light intensity treatment showed much higher coefficients in many parameters. That meant light intensity was the main factor in controlling the plant growth. In addition, when the correlation between DLI and these growth parameters was investigated, the DLI was found to have the greatest correlation coefficients than photoperiod and light intensity alone. From this finding, a new idea that DLI was the most influential factors among all parameters drawn, and that led to initiate the regression analysis of these indicators.

Table 3. Correlation coefficients between vegetative growth parameters and photoperiod, light intensity, or DLI

Variable	Correlation coefficient ( $r^2$ ) significance		
	Photoperiod	Light intensity	DLI
Length	0.03 NS	0.62 *	0.70 **
Width	0.19 NS	0.17 NS	0.25 NS
Length / Width ratio	0.24 NS	0.70 **	0.80 **
Thickness	0.15 NS	0.60 *	0.65 **
No. of new leaves	0.14 NS	0.68 **	0.85 ***
Total leaf area	0.30 NS	0.26 NS	0.39 NS
Shoot fresh weight	0.22 NS	0.23 NS	0.32 NS
Root fresh weight	0.66 **	0.62 *	0.88 ***
Total fresh weight	0.26 NS	0.49 *	0.69 **
Shoot dry weight	0.58 *	0.27 NS	0.64 **
Root dry weight	0.27 NS	0.58 *	0.87 ***
Total dry weight	0.26 NS	0.44 NS	0.79 **

NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ ,  $0.01$ , and  $0.001$ , respectively.

***Regression analysis between DLI and vegetative growth.*** Number of new leaves, leaf length and thickness were increased with increasing DLIs. On the other hand, the L/W ratio was decreased with increasing DLI within the range studied (Fig. 2). The fresh weight of the root and total and dry weight of shoot increased significantly as DLI increased within the range examined (Fig. 3). Plants grown under the DLIs from 1.44 to 11.52 mol·m<sup>-2</sup>·d<sup>-1</sup> have shown 231%, 103%, and 140% increase in root and total fresh weight, and shoot dry weight, respectively. In this study, the DLI of 11.52 mol·m<sup>-2</sup>·d<sup>-1</sup> resulted in improved growth for *Phalaenopsis*. However, it was observed that as the DLI reached beyond 11.52 mol·m<sup>-2</sup>·d<sup>-1</sup>, the slope gradually decreased. That meant that raising the DLI above this value (11.52 mol·m<sup>-2</sup>·d<sup>-1</sup>) would be nearing the saturation point and was wasting energy without gaining further plant growth. In comparison, the maximum or optimum DLI values for the *Phalaenopsis* reported by Faust (2002) were similar to those of this experiment.

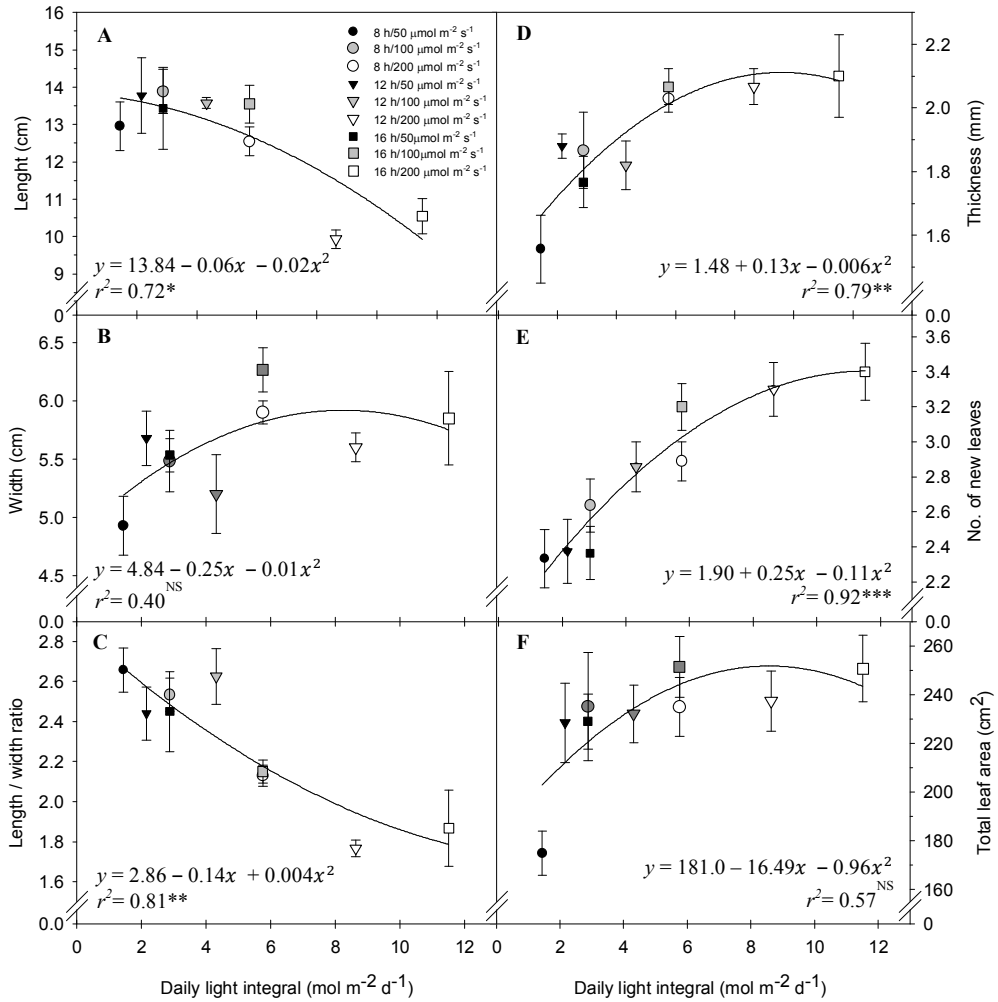


Fig. 2. Regression analysis between DLI and leaf length (A), leaf width (B), leaf length/width ratio (C), leaf thickness (D), number of new leaves (E), and total leaf area (G). Data points are means  $\pm$  SE. Equations for regression lines are presented for significant correlations with corresponding  $r^2$ . NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.

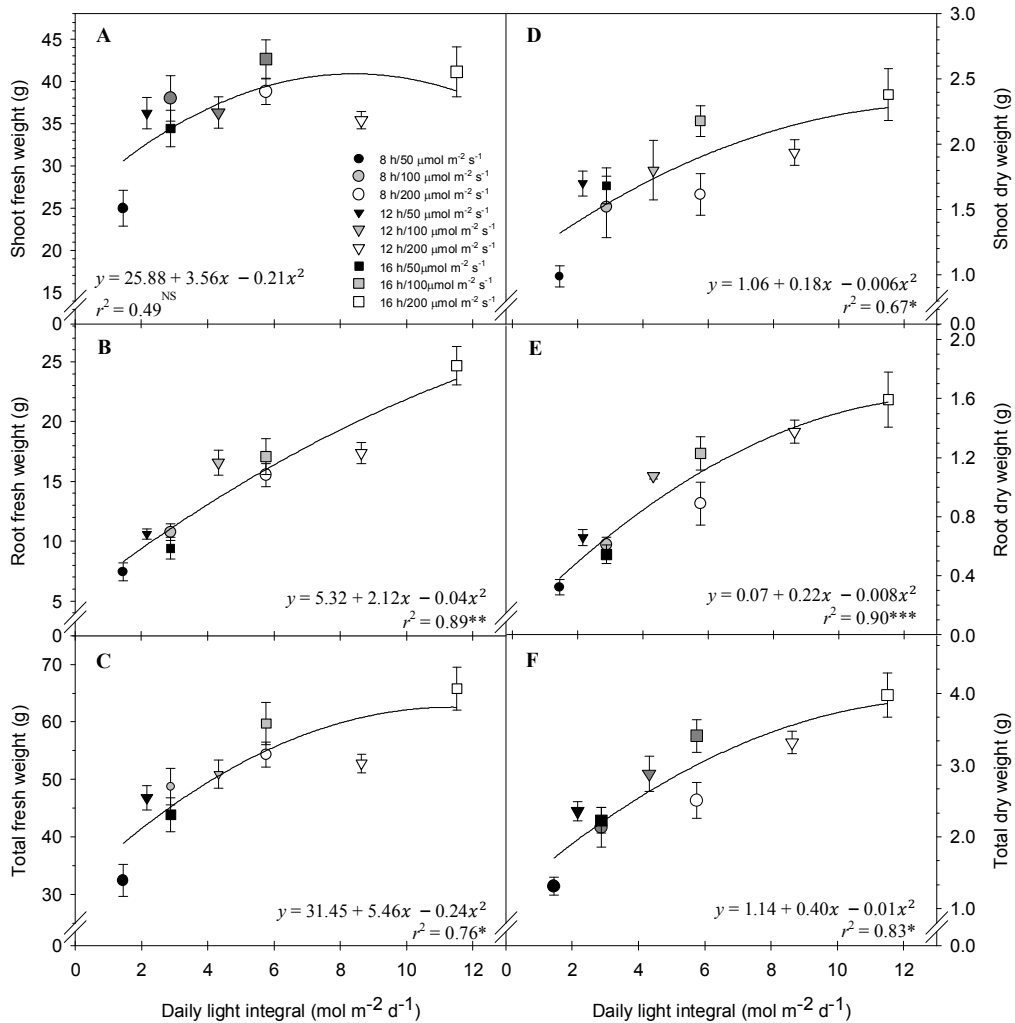


Fig. 3. Regression analysis between DLI and shoot fresh weight (A), root fresh weight (B), total fresh weight (C), shoot dry weight (D), root dry weight (E), and total dry weight (G). Data points are means  $\pm$  SE. Equations for regression lines are presented for significant correlations with corresponding  $r^2$ . NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.

## **Inflorescence Emergence (Experiment 2)**

***Leaf number and morphological changes.*** Light treatment had great effects on leaf number and color. The number of new leaves was increased with both increasing photoperiod and light intensity (Table 4). However, the chlorophyll contents, measured by SPAD, were significantly decreased with increasing light intensity. Increased leaf numbers under higher levels of photoperiod and light intensity was similar to those of Experiment 1, probably due to increased light interception rate (Arney, 1956; Humphries and Wheeler, 1963; Milford and Lenton, 1976).

Leaf color of plants grown under 75 and  $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  was dark green, while those grown under  $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  became reddish green (Fig. 4). Leaf color is a good indicator of the amount of light a plant is receiving. Orchids should have bright green color leaves under healthy growing conditions. Dark green leaves indicate that a plant is getting sufficient light, but the reddish-green or red color leaves indicate that the plant is getting too much light or nutrient deficiency (Withner and Congress, 1964). Several researchers showed that anthocyanins were formed in the pseudo-bulbs and leaves to protect from the damaging effects of the sun when the plants were grown under too high light intensity (Albert et al., 2009; Trojak et al., 2017). Sometimes when the undersides of leaves, which are adjusted to the shade condition, are exposed to a bright sun light, they will turn to purple and red colors (Lin and Hsu, 2004). Studies on leaf anatomy and pigment changes of leaves and bulbs are thought to be necessary to better understand the high light stress in *Phalaenopsis*.

***Chlorophyll fluorescence.*** When the plants were subjected to  $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , the

ratios of Fv/Fm were decreased to from 0.65 to 0.73 (Fig. 5). The Fv/Fm value represents the maximal quantum yield of PSII, usually ranging between 0.75 and 0.85 for non-stressed plants (Bolhar-Nordenkampf et al., 1989). The combination of excessively high light intensity and long photoperiod could affect photosynthetic efficiency negatively (Barber and Andersson, 1992), leading to photoinhibition (Demmig-Adams et al., 1990), and this inhibition could be measured by the measurement of chlorophyll a fluorescence. A good negative correlation has been observed between higher photoinhibition rates and decreased values of the Fv/Fm ratio (Bolhar-Nordenkampf and Öquist, 1993). Thus, the low Fv/Fm value under high light intensity suggests the possibility of the PSII photoinhibition. In all, reddish coloration of leaves (Fig. 5) and decreased Fv/Fm ratio (Fig. 5) indicated that a high light intensity greater than  $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  was thought to be excessive and resulted in some damages in photosynthesis process.

Table 4. Leaf numbers and chlorophyll contents of *Phalaenopsis* 'Mantefon' after 12 weeks of light treatment

Photoperiod (h)	Light intensity ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	No. of total leaves	No. of new leaves	Chlorophyll contents (SPAD value)
8	75	6.2	0.9	64.9
	150	6.7	1.1	60.9
	300	7.0	1.1	59.2
8+8	75	5.9	1.0	59.2
	150	6.6	1.4	66.7
	300	6.6	1.6	58.3
16	75	6.8	1.1	65.7
	150	7.5	1.1	64.9
	300	6.7	1.2	59.9
<i>Significance</i>				
Photoperiod (A)		NS	*	NS
Light intensity (B)		NS	***	***
Interaction (A $\times$ B)		NS	NS	NS

<sup>Z</sup>Means separation within columns by Duncan's multiple arrange test at  $p < 0.05$ .

NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.



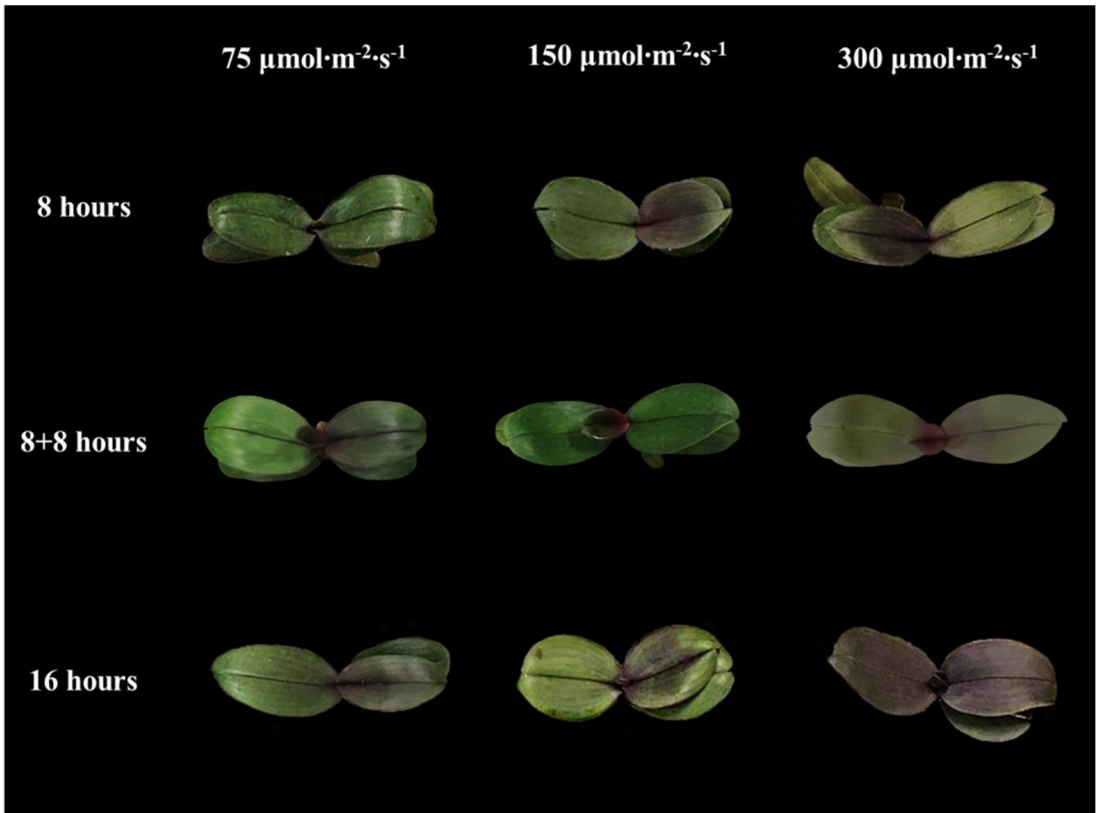


Fig. 4. Leaf color of *Phalaenopsis* 'Mantefon' treated with 8 (SD), 8+8 (DE), or 16 h (LD) photoperiod with a combination of 75, 150, or 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  light intensity. Photographs were taken after 12 weeks of light treatment.

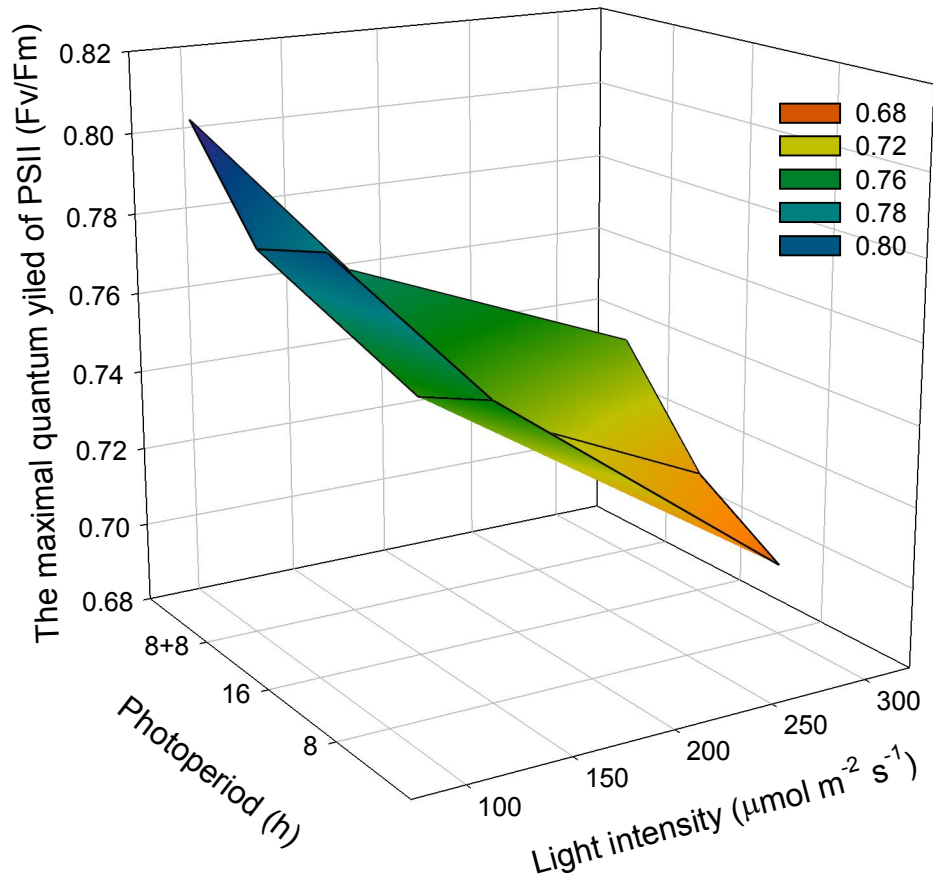


Fig. 5. Maximal quantum yield of photosystem II (Fv/Fm) of the uppermost mature leaves of 12-month-old *Phalaenopsis* 'Mantefon' grown under 8 (SD), 8+8 (DE), or 16 h (LD) photoperiod with a combination of 75, 150, or 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  light intensity after 12 weeks of light treatment.

The results of this study demonstrated that inflorescence emergence could be improved if adequate light conditions were provided during the cooling phase, as described below.

***Inflorescence emergence percent.*** The 1st inflorescence emergence by all nine treatment combinations was presented in the Fig. 6A. The 1st inflorescence was observed from 5 weeks after treatment in most of treatments, except in the DE/75 and DE/150 treatments, which showed about 3 weeks delayed emergence (data not shown). After 12 weeks of the treatments, 100% 1st inflorescence emergence was observed at the DE/300, LD/75, LD/150, and LD/300 treatments, while the lowest percentage was observed at the DE/75 treatment (82.3%).

The percentage of the 2nd inflorescence emergence was found to be significantly influenced by the all treatment combinations (Fig. 6B). The 2nd inflorescence was first observed from 6 weeks under the SD/300, LD/150, LD/300, and DE/300 treatments, but other treatments showed significantly delayed (data not shown). It was difficult to compare the maximum percentage between the treatments because percentage values were relatively lower than those of the 1st inflorescence. After 12 weeks of the treatments, the highest (93.3%) and lowest (6.2%) 2nd inflorescence was emerged at the LD/150 and SD/75 treatments, respectively. The DE treatment showed the least emergence of the 2nd inflorescence, as similarly seen in the 1st inflorescence emergence with a reduced magnitude. The percentage of the 2nd inflorescence emergence was significantly increased at the LD treatments, as compared with the SD and DE treatments, resulting in the highest percentage at the LD treatments. After 12 weeks, the percentage value of the 2nd inflorescence was about 2 times higher at the LD treatments, as

compared to the SD and DE treatments. The percent of the 2nd inflorescence emergence was the highest under the 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments and was lowered as the light intensity reduced. The 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatment was significantly inefficient on the emergence of the 2nd inflorescence. After 12 weeks, 68.1%, 62.3%, and 22.6% of plants had the 2nd inflorescence under 300, 150 and 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments, respectively.

In summary, the 1st and the 2nd inflorescence emergence was enhanced under 16 h photoperiod and higher light intensity. The daylength extension using the DE treatment showed two opposite results and, thus, conclusion could not be made. Interestingly, 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  showed the greatest promotion in inflorescence emergence, even though that light intensity was previously reported to be harmful to plant growth (Lee and Guo, 2000). Carbohydrates are known to have numerous roles in the reproductive growth of plants, from energy source to signal molecules (Gibson, 2005). Several studies have demonstrated the importance of carbohydrates in determining time to inflorescence emergence of *Phalaenopsis* (Chen et al., 2008; Kataoka et al., 2004; Kubota and Yoneda, 1993). However, without the measurement of carbohydrate levels in the plants, no clear conclusion could be made in this study. It was also speculated that the vegetative growth and flower induction might have different responses by the high light intensity that the harmful high light intensity to the vegetative growth could be rather beneficial to the flower emergence.

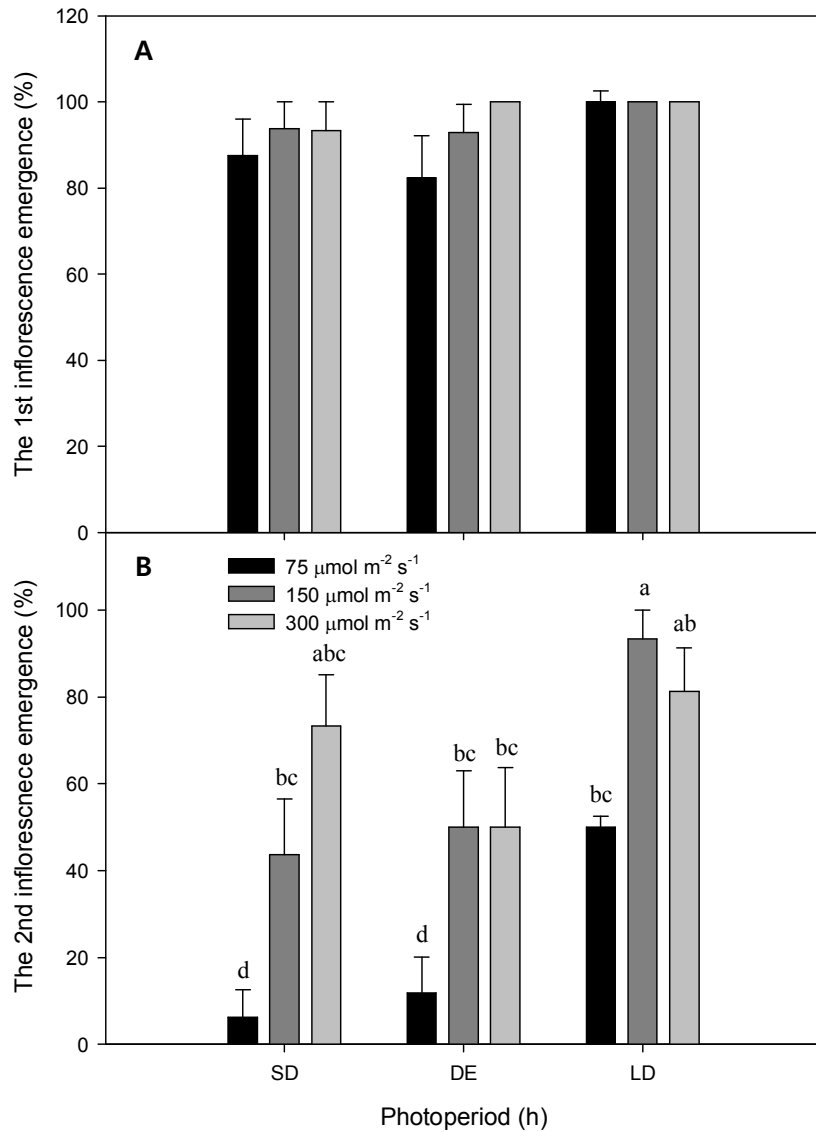


Fig. 6. The percentage of the 1st inflorescence emergence (A) and the 2nd inflorescence emergence (B) in 12-month-old *Phalaenopsis* 'Mantefon' grown under 8 (SD), 8+8 (DE), or 16 h (LD) photoperiod with a combination of 75, 150, or 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  light intensity after 12 weeks of light treatment. Vertical bars represent standard errors of the means. Different letters within each panel indicate a significant difference at  $p < 0.05$ .

***Days to the inflorescence emergence.*** The results of days to emergence of the 1st and 2nd inflorescence and number of inflorescence were presented in the Table 5. The earliest 1st inflorescence emergence (40.3 days) was observed in the LD/300 and the latest (71.0 days) in the DE/75 treatments and the difference was about 30 days. The 1st inflorescence emergence was significantly promoted by the LD treatments. The emergence day under LD treatments was about 18 days earlier than the SD and DE treatments. Emergence of the 1st inflorescence was delayed as the light intensity was lower, so that the earliest and latest 1st inflorescence emergence was observed at the 300 and 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , respectively. There was about 18 days delay between the 300 and 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments.

The days to emergence of the 2nd inflorescence showed the same trend as the 1st inflorescence, and the earliest emergence of the 2nd inflorescence was observed in the LD/300 and the latest in the DE/75 treatments. There was about 30 day delay between the LD/300 and DE/75 treatments. The emergence of the 2nd inflorescence was significantly enhanced under the LD treatments, as compared to the SD and DE treatments. There was about 7 day difference between the LD and DE treatments. The 2nd inflorescence emergence was significantly delayed under 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments, as compared with 150 and 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments. There was about 11 days delay between 300 and 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments.

***Number of inflorescences.*** The number of inflorescences was found to be significantly increased by both light intensity and photoperiod (Table 5). The number of inflorescence was 2 times higher at the LD/150 and LD/300 treatments, as compared to the SD/75. Number of inflorescence was significantly increased under the LD treatments,

as compared to the SD and DE treatments. Plants under the LD, SD, and DE had inflorescence numbers of 1.8, 1.4, and 1.4, respectively. Thus, they had no difference by the photoperiod extension. The number of inflorescence per plant showed an increasing tendency to the light intensity. Increased light intensity positively increased the number of inflorescence and a significant difference was found between 75 and 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments ( $p < 0.001$ ). Plants grown under 300, 150, and 75  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  treatments had 1.8, 1.6, and 1.2 inflorescences, respectively.

***Interaction between photoperiod and light intensity.*** The photoperiod and light intensity had no interaction effects on all three results of the days to emergence of 1st and 2nd inflorescence and number of inflorescence. That meant that photoperiod and light intensity treatments showed parallel responses by each factor.

*Phalaenopsis* has originated from the tropical and subtropical areas of the South Pacific Islands and Asia, thus, they have unique temperature and light requirements, as compared with other common potted flowering plants originated from the temperate regions (Van der Knaap, 2005). In *Phalaenopsis*, several researches showed that the short day length promoted the early inflorescence emergence and the date of flowering (An, 2013; Griesbach, 1985; Rotor, 1952; Went, 1957; Yoneda et al., 1991). However, Ichihashi (1997) and Sakanishi et al. (1980) reported that *Phalaenopsis* was non-photoperiodic plant when they were grown at the critical temperature for inflorescence emergence. In this study, there was no difference between SD and DE treatments, but the LD treatments have shown to be promotive for the inflorescence emergence. It should be also noted that the LD treatments had doubled DLI values as compared with SD and DE treatments under the given light intensity. Therefore, when the same DLI treatments were

compared, there was no difference between photoperiod treatments (Fig. 7). As a result, it was possible to suggest that *Phalaenopsis* was a day-neutral plant (DNP, flowering irrespective of day/night length) and as such it would flower under any photoperiod.

Under natural habitat conditions of the *Phalaenopsis* plants, they are covered by the tall trees or shrubs and grown under partly shade light environments. Mature plants of *Phalaenopsis* were generally grown at around from 280 to 380  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Chen and Wang, 1996). However, several studies have found that the photosynthesis of *Phalaenopsis* saturates at about from 130 to 180  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Lee and Guo, 2000; Lootens and Heursel, 1998; Ota et al., 1991) and exposure to light higher than about 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in significant photoinhibition (Lee and Guo, 2000). High light conditions could lead to leaf burning by chlorophyll degradation or leaf color changes by anthocyanin formation as a protection mechanism (Trojak et al., 2017). Anthocyanin formation was thought to not only reflect the stressed conditions of reduced carbohydrate assimilation and increased anthocyanin formation (Schaberg et al., 2003), but also damage the plant's appearance, because the customers prefer the fresh green color leaves over the reddish leaves.



Table 5. Days to the 1st and the 2nd inflorescence emergence and the number of inflorescences in 12-month-old *Phalaenopsis* ‘Mantefon’ after 12 weeks of light treatment

Photoperiod (h)	Light intensity ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	Days to 1st inflorescence	Days to 2nd inflorescence	No. of inflorescences
8	75	69.3 a <sup>z</sup>	81.2 ab	1.0 d
	150	54.2 b	65.8 bc	1.4 bc
	300	45.7 cd	57.6 cd	1.8 ab
8+8	75	71.0 a	81.0 ab	1.2 cd
	150	53.3 b	69.5 bc	1.4 bc
	300	50.7 bc	59.8 cd	1.5 bc
16	75	54.5 b	63.5 cd	1.5 bc
	150	46.5 bcd	55.5 cd	2.0 a
	300	40.3 d	49.3 d	2.0 a
Significance (%SS)				
Photoperiod (A)		*** (22.9%)	** (41.0%)	*** (36.0%)
Light intensity (B)		*** (66.8%)	** (35.4%)	*** (51.1%)
Photoperiod $\times$ Light intensity (A $\times$ B)		* (10.2%)	NS (23.5%)	NS (12.8%)

<sup>z</sup>Means separation within columns by Duncan’s multiple arrange test at  $p < 0.05$ .

NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.

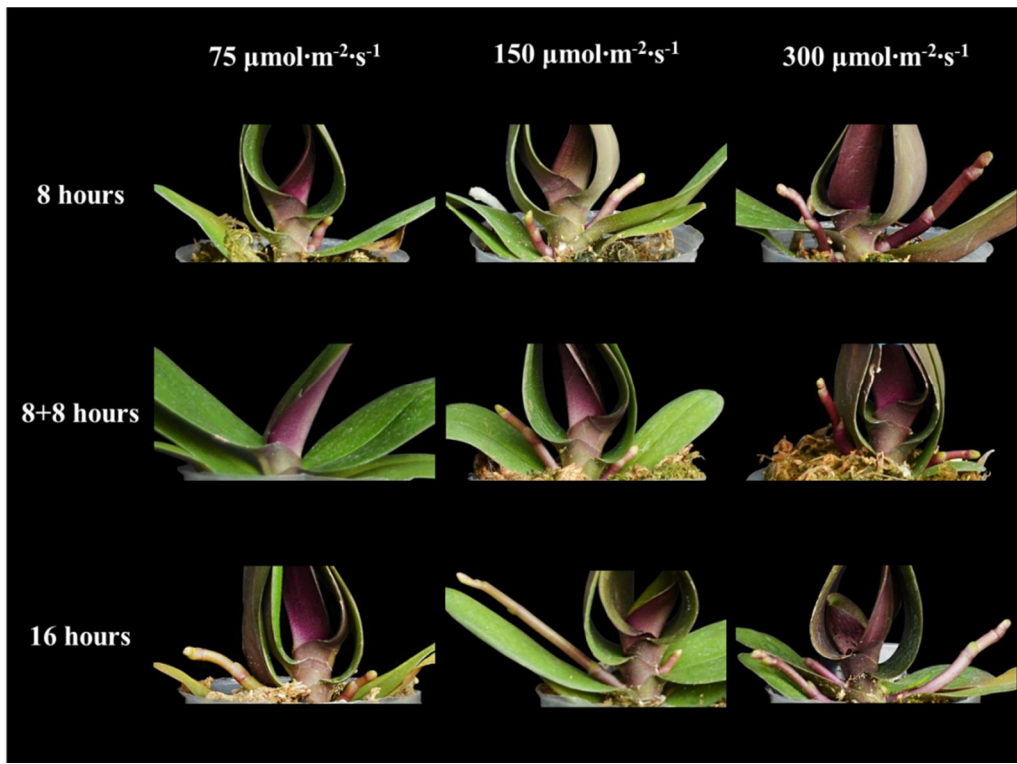


Fig. 7. Inflorescence emergence of *Phalaenopsis* 'Mantefon' treated with 8 (SD), 8+8 (DE), or 16 h (LD) photoperiod with a combination of 75, 150, or 300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  light intensity. Photographs were taken at 12 weeks after light treatment.

***Correlation coefficient.*** The ANOVA-analysis of variance in the Table 5 showed significance in several parameters and relative percentage of the contribution in the %SS results. However, these results did not provide information on the relationship between the levels of photoperiod and light intensity versus levels of the measured parameters. In order to elucidate the relationship between these factors, the correlation analysis was performed (Table 6). By using these results, a clear relationship between each factor of the photoperiod and light intensity and each parameter could be determined. In addition, correlation analysis between the DLI level and these parameters was also included.

The photoperiod levels had an insignificant correlation with the days to the 1st and the 2nd inflorescence emergence and number of inflorescence. However, the light intensity levels showed significantly higher coefficients in all parameters. These results meant that the light intensity was the main factors in controlling of the inflorescence development. Correlation between the DLI, the direct combination of photoperiod and light intensity, and parameters of inflorescence growth showed to have much greater correlation coefficients than the photoperiod and light intensity alone. From this finding, a new concept could be drawn that the DLI was the most influential factors among all inflorescence growth parameters, leading to initiate the regression analysis of these indicators.

Table 6. Correlation coefficients between days to the 1st and 2nd inflorescence emergence and the number of inflorescences and photoperiod, light intensity, or DLI

Variable	Correlation coefficient ( $r^2$ ) significance		
	Photoperiod	Light intensity	DLI
Days to 1st inflorescence	0.25 NS	0.57 *	0.68 **
Days to 2nd inflorescence	0.21 NS	0.48 *	0.73 **
No. of inflorescences	0.32 NS	0.44 *	0.70 **

NS = non-significant; \*, \*\*, and \*\*\* = significant at  $p < 0.05$ , 0.01, and 0.001, respectively.

***Regression analysis between DLI and inflorescence emergence.*** Days to emergence of the 1st and 2nd inflorescence were reversely linked with increasing DLIs, indicating that the days to the emergence of inflorescence was shortened under the higher DLIs (Fig. 9). However, the shortening effect became smaller from  $8.64 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  and beyond, implied that the days could not be shortened less than about 40 or 50 days in the 1st or the 2nd inflorescence, respectively. The days to the emergence seemed to show a tendency to reach the minimum numbers (earliest days) at about  $10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  in this study.

Total number of inflorescence was increased as the DLI level was increased within the range examined, indicating that the more numbers of inflorescence could be grown under the higher DLI levels. Plants grown under the DLIs of 2.16 to  $17.28 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  have shown a nearly 2-fold increase in the number of inflorescence (Table 5). However, there was a little increase in the number of inflorescence beyond DLI of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . These results also meant that the total number of inflorescence seemed to reach to the maximum (or saturation) point at above DLI of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . Then, setting the DLI at where the maximum growth occurred would be necessary for the most economic production of the plants. Rather, raising the DLI beyond this value ( $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) would be wasting energy without gaining further plant growth.

In comparison, *Phalaenopsis* growers in the Netherlands have increased the amount of light to their crops, because it has shown to shorten the crop production cycle by several weeks (Dueck and Van Noort, 2010). Higher DLIs were shown to increase the growth rate and the number of newly formed leaves with potentially more inflorescence. The only factor involved in increasing in growth rate during a summer season was a

higher DLI (Dueck and Van Noort, 2010), and it seemed logical that a higher DLI might also require a higher and balanced amount of nutrition. Altering the nitrogen nutrition (Baas, 2006) by increasing the nitrate to ammonium ratio (Wang, 2008) as well as the nitrate to potassium ratio (Wang, 2007) has shown to increase the number of newly formed leaves and the potential for inflorescence. Thus, detailed consideration in the nutrient composition for the hastening the growth cycle was thought to be necessary, especially at a higher DLI.

In conclusion, during the vegetative growth, the growth was promoted with promoted light intensity and DLI within the experimental range (from 1.44 to 11.52 mol·m<sup>-2</sup>·d<sup>-1</sup>). During inflorescence emergence phase, the light intensity and DLI were main factors, but the photoperiod was not. The high light intensity at 300 μmol·m<sup>-2</sup>·s<sup>-1</sup> was effective in inflorescence emergence. Considering several parameters, such as, light saturation point, maximal quantum efficiency, and leaf color, it was not desirable to maintain high light intensity and extend the photoperiod. For maximizing the growth and inflorescence emergence at the DLI of 12 mol·m<sup>-2</sup>·d<sup>-1</sup>, setting the light intensity around 200 μmol·m<sup>-2</sup>·s<sup>-1</sup> and 16 h photoperiod is recommended for the economic *Phalaenopsis* cultivation.

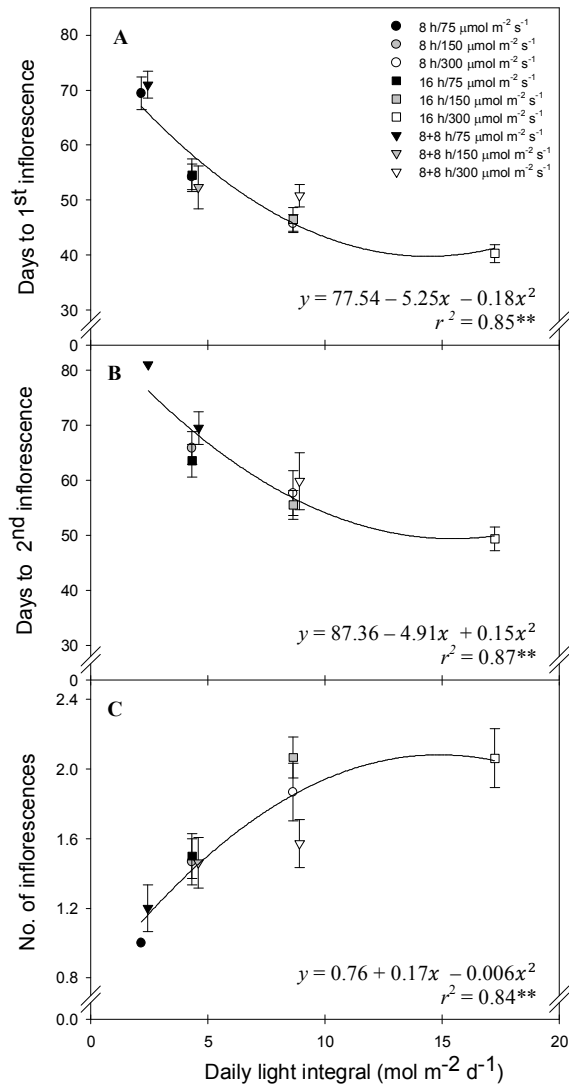


Fig. 8. Regression analysis between DLI and days to the 1st inflorescence (A), days to the 2nd inflorescence (B), and the number of inflorescence (C). Data points are means  $\pm$  SE. Equations for regression lines are presented for significant correlations with corresponding  $r^2$ . \*\* = significant at  $p < 0.01$ .

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