The Correlation between CO_2 Uptake of *CAM Dendrobium* Hybrid and Environmental Factors under Shade Net House Conditions

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Received: 18 July 2017 Accepted: 7 August 2017

ABSTRACT

The diurnal net CO_2 uptake in *Dendrobium* ‘Khao Sanan’ leaves was measured year-round (June 2010 to April 2011) and integrated to obtain total CO_2 uptake under commercial shade net house conditions. Seasonal changes varied between 20−40 °C air temperature, 42−94% relative humidity (RH) and 667 µmol m^{-2} s^{-1} maximum light intensity, while *Den*. ‘Khao Sanan’ leaves performed typical CAM photosynthesis and reached their highest net CO_2 uptake rate of 4 µmol m^{-2} s^{-1} after midnight and in the early morning under a 12 ± 0.5 hours photoperiod. Total CO_2 uptake during the nighttime, daytime and in a total of 24 hours (daily) increased significantly and had a maximal value of more than 2 to 2.5 folds in December and February compared with the other months. The net CO_2 uptake values were correlated with temperature ($r^2 = 0.41$), RH ($r^2 = 0.25$) and light intensity ($r^2 = 0.06$). The net CO_2 uptake were positive between 22−29°C, 60−90% RH and less than 200 µmol m^{-2} s^{-1} light intensity conditions. CO_2 uptake during the nighttime and daytime was most affected by temperature, while total CO_2 uptake had a higher correlation with temperature and RH. The results of this study contribute to improve the ability to efficiently design and manipulate a semi-controlled greenhouse for *Dendrobium* orchids for commercial scale production in Thailand.

Keywords: CO_2 gain, orchid cut-flower, photosynthesis, relative humidity, temperature

Thai J. Agric. Sci. (2017) Vol. 50(1): 26−35

INTRODUCTION

Due to the ideal weather conditions, Thailand is the most important tropical orchid producer in the world, especially with respect to *Dendrobium* orchids. The Thai orchid industry has developed and implemented a process of orchid planting, trading and exporting for 40 years, and is ranked first in tropical orchid exports in the world. Despite this accolade, the majority of Thailand’s orchid production systems are out of date as orchid flowers are produced in open fields with no controlling of the environment, meaning the product of these flowers is dependent on climate conditions rather than market demand. While most orchid growers usually learn and develop a method of growing from their own personal experiences. There is no data on the physiological response to environmental conditions and subsequent seasonal variation a variable to growers. Moreover, climate change can affect the orchid cultivation environments and further uncertainties. Each of these factors contributes to increasingly variable production, which is a problem primarily of importance to orchid production growers, exporters and consumers.

The photosynthetic characteristics of tropical orchids can be roughly grouped into two classes of leaf thickness (Arditti, 1992; Hew and Yong, 2004). Orchids of leaf thickness less than 1 mm typically perform C_3 fixation, while those with thicker leaves usually perform crassulacean acid metabolism (CAM) (Neales and Hew, 1975; Wu *et al*., 2014) e.g. *Phalaenopsis* (Endo and Ikusima, 1989), *Cattleya* (Stancato *et al*., 2002) and *Dendrobium* hybrids (He *et al*., 1998; Boonkorkaew *et al*., 2003; He and Teo, 2007). The diurnal leaf gas exchange of the CAM *Dendrobium* hybrid, *Den.* Sonia 'BOM Jo', showed three phases of CAM, CO_2 uptake was a positive value during nighttime (Phase I), positive from 6:00−7:30 (Phase II) and negative throughout the day (Phase III) (Chuennakorn and Yingjajaval, 2010). However, the expression of CAM is intimately linked to the environment, and CO_2 uptake can be extended for several hours at the start and end of the photoperiod in response to a range of conditions including CO_2, water, light and temperature (Borland *et al*., 1999; Lüttge, 2004). In facultative CAM *Den. officinale*, the net CO_2 exchange rate during the day and night period varied due to differences in temperature and light intensity (Zhange *et al*., 2014). Similarly, the photosynthesis rate in C_3 *Dendrobium* species showed seasonal differences, which may be correlated with temperature, light intensity and leaf maturity, while the optimum temperature for photosynthesis ranged from 26 to 30 °C (Wu *et al*., 2014). For CAM *Dendrobium* hybrids, a few researches reported that light intensity affected the photosynthesis rate and CAM acidity (He *et al*.,1998, He and Teo, 2007). There is no conclusive evidence indicating the optimal environmental conditions for CO_2 uptake. In contrast, several studies on CAM *Phalaenopsis* reported a maximal net CO_2 assimilation at temperatures between 21−28°C during the day and 18−22 °C at night (Ota *et al*., 1991; Guo and Lee, 2006; Pollet *et al*., 2011). Additionally, eight hours of saturating photosynthetic photon flux density (PPFD) at 200 µmol m^{-2} s^{-1} and 12 hours of day-length are sufficient for maximizing photosynthesis in CAM *Phalaenopsis* (Guo *et al*., 2012). Many researchers have investigated and provided useful information regarding the correlation of photosynthesis with CAM *Phalaenopsis* and environmental factors; thus, *Phalaenopsis* on the commercial scale represents a high precision production system across the world as *Phalaenopsis* growers can control and manipulate the greenhouse following these results.

The aim of this study is to clarify the correlation between net CO_2 uptake of *Den.* 'Khao Sanan' and environmental factors, i.e., air temperature, air relative humidity and light intensity during the daytime, nighttime, and daily (24 hours) under commercial nursery conditions which are determined by seasonal changes in the environment. Moreover, these useful data will be utilized for improvement of cultural practices, including irrigation system timing and fertilizer application, contributing to the overall enhancement of *Dendrobium* orchid hybrids and their controlled greenhouse management.

MATERIALS AND METHODS

Plant Material and Environmental Monitoring

Mature plants with 4−5 pseudobulbs of *Dendrobium* 'Khao Sanan' (*Den.* Walter Oumae × *Den*. White Doreen) from tissue culture were grown on coconut husk boxes (4 plants per box), and raised benches 1 m × 40 m × 0.7 m. in a 50% shaded net house under natural conditions. Foliar fertilizer composed of nitrogen, phosphorus and potassium (N-P-K) was applied at 4 g L^{-1} of 16–21–27 formula alternated with 4 g L^{-1} of 10–52–13 formula every other week according to good horticulture practices. Plant density was approximately 20–24 plants $m.^{-2}$

The experiment was conducted at a commercial orchid nursery of Thaiorchids Company Limited, Damnoen Saduak, Ratchaburi Province, Thailand.Environmental conditions data under *Dendrobium* orchid commercial production, i.e. air temperature, relative humidity (RH) and light intensity were measured year-round (June 2010 to April 2011) using a micro logger and air temperature and relative humidity sensors, which recorded every 15 minutes with a temperature and humidity data logger (Easy Log EL-USB, USA). The photoperiod was determined by the natural day-length. The line quantum sensor (LI-191, LI-COR, USA) was used to measure PPFD at canopy level every 15 min and a data logger recorded the data (Li-1400, LI-COR, USA).

Measurement of Diurnal Net CO_2 Uptake

The net CO_2 uptake rate was measured using a portable photosynthesis system (LI-6400XT, LI-COR, USA). First, the 3rd leaf from the apex was enclosed in a 2×3 cm leaf chamber (6400-08 Clear Chamber Bottom, LI-COR, USA). The Clear Chamber Bottom has a Propafilm® window similar to the standard chamber top. Measurements were recorded when the total coefficient of variation (CV) was less than 0.1% under shade net house exposed to natural conditions without controlled environment. The sampling was randomly observed every 3–4 days, every other month over a year (June 2010 to April 2011). The net CO_2 uptake values were taken from 06:00 a.m. to 06:00 a.m. the next day, performed every 2 hours for 24 hours, and was measured from the middle part of the 3rd leaf to the front shoot. Five randomly selected plants (n = 5) were monitored. All determinations were replicated three times. The total plants were used about 65 plants in each month.

The net CO_2 uptake and environmental factors (air temperature, air relative humidity and light intensity) were plotted on curves using Microsoft Excel version 2016. The net daytime, nighttime and daily total CO_2 uptake were calculated by integrating the diurnal uptake curves (Griffiths *et al*., 1986).

Data Analysis

Correlation analysis

Correlation analysis was used to observe between photosynthetic parameters, such as net CO_2 uptake, stomatal conductance (g_s), transpiration (E) and environmental factors, such as air temperature (Ta), relative humidity (RH), light intensity (PPFD), vapor pressure deficit (VPD) using Pearson correlation coefficient.

Multiple regression analysis

The relationship between all environmental conditions, including temperature, relative humidity and light intensity was shown using a linear regression created on Microsoft Excel version 2016 ($^*P < 0.05$). Stepwise multiple linear regression analysis was used to quantify the relative effects of the net CO_2 uptake and varying environmental conditions on leaf-level photosynthesis. One can examine the effects of a single variable or multiple variables with or without the effects of other variables considered using SAS version 9.1 for window.

ANOVA and Duncan' new multiple range tests

Data was evaluated using ANOVA. For any significant different among treatments (6 treatments, such as June, August, October, December, February and April), further statistical analysis was done by the Duncan's new multiple range tests ($^*P < 0.01$) using SAS version 9.1. Data were indicated as mean ± SE.

RESULTS AND DISCUSSION

Environmental Conditions under Seasonal Changes

The environmental conditions monitored under a 50% shaded net house revealed that air temperature ranged from 20.5−40.0°C during the time of this study (June 2010 through April 2011). The average temperature during the nighttime ranged from 21.6 to 27.1°C, while the lowest temperature was observed at approximately 21−22°C in December. In addition, the average temperature during the daytime over a year was higher than 30°C (30.1−34.8°C), and a minimal value was observed in December and February (28.1−29.5°C) (Figure 1B).

Diurnal changes of air relative humidity (RH) presented an opposite trend to light intensity and air temperature; it rose rapidly from the evening to night, reaching a maximum value of about 91−94% in the early morning and then declined to a minimum value in the afternoon. The average RH during the nighttime was approximately 87−91% and 63.1−78.6% during the daytime. The highest average RH during the daytime was found in the rainy season at about 77−78% (August and October) (Figure 1C).

Light intensity (PPFD) increased gradually after sunrise around 6:00 ± 0:30, reaching its maximum value at 12:00 −14:00 and decreasing to a minimum at 18:00 ± 0:30 (sunset) with a total light period of about 12 ± 0.30 hours. There was little day length change during the year. The highest daily maximum PPFD was observed in June and was 1.5 times higher than in October and December. The daily sum PPFD was highest in June (16.26 mol m^{-2} day^{-1}), and lowest in August and October (rainy season), ranging between about 8.69−9.79 mol m^{-2} day^{-1} (Figure 1D).

Diurnal Pattern and Total Net CO_2 Uptake

The typical diurnal net CO_2 uptake pattern of *Den* 'Khao Sanan' year-round under commercial shaded net house conditions exhibited the CAM pathway. The majority of CO_2 uptake happened during the night (Phase I) and reached its peak value of 4 µmol $m^{-2}s^{-1}$ after midnight and early morning (6:00−8:00, Phase II), then declined gradually toward a negative value at 8:00−10:00 until evening (Phase III). The CO_2 uptake during the late morning in October, December and February had a longer period (6:00−10:00) than the other months by almost 2 hours (Figure 1A). The prominent characteristics of CAM plants are nighttime fixation (Phase I) of atmospheric CO_2 and release of CO_2 during the daytime (Phase III) using photosynthetic assimilation via the Calvin cycle (Dodd *et al*., 2002). The transition phases (Phase II: early morning and Phase IV: late afternoon) exhibit a shift in CO_2 uptake as a result of competition between phosphoenolpyruvate carboxylase (PEPC) and ribulose-1,5-biphosphate (Rubisco) (Osmond, 1978; Griffiths *et al*., 2002). Additionally, total CO_2 uptake during the nighttime, daytime and total 24-hr period (Daily) of *Den.* 'Khan Sanan' increased significantly (**$P < 0.01$) and had a maximal value in December of more than 2 to 2.5 folds compared with the other months (Figure 2). The results indicated that environmental conditions i.e. temperature, relative humidity and light intensity under a commercial shaded net house affected the magnitude and duration of the CO_2 uptake rate of CAM *Den.* 'Khao Sanan'. Similarly, in CAM *Phalaenopsis* orchids, *Bromeliad* and giant saguaro cactus, change in environmental factors was reflected in the leaf net CO_2 exchange, efficiency of carbon fixation, diel metabolite dynamics and biomass accumulation (Ceusters *et al.*, 2010; Pollet *et al.*, 2010; Bronson *et al.*, 2011).

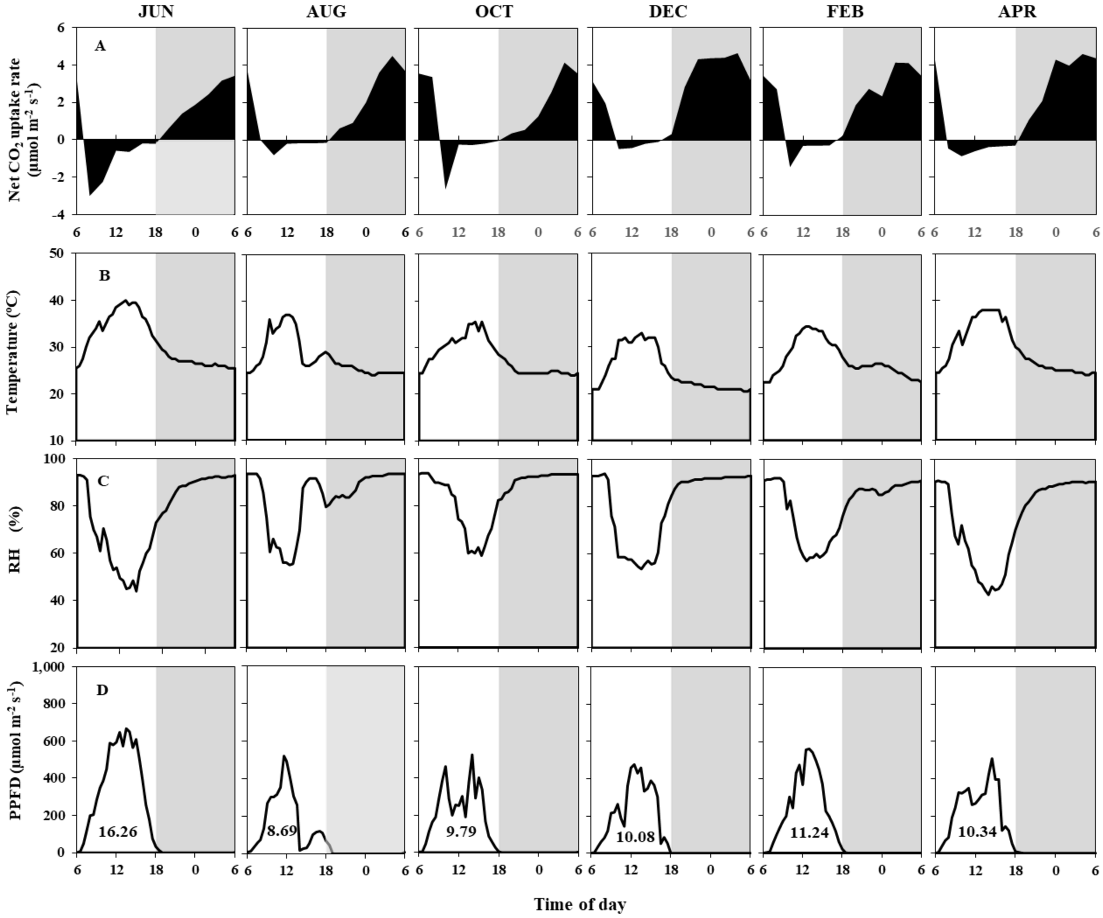

Figure 1 The day-night patterns of net CO_2 uptake rate (A) in *Den.* 'Khao Sanan' leaves, the diurnal change in air temperature (B), air relative humidity; RH (C), and light intensity; photosynthetic photon flux density; PPFD and numbers under graph area indicated by integrated PPFD (mol m^{-2} day^{-1}) (D) under commercial shaded net house conditions year-round. *Shaded portions* represent nighttime

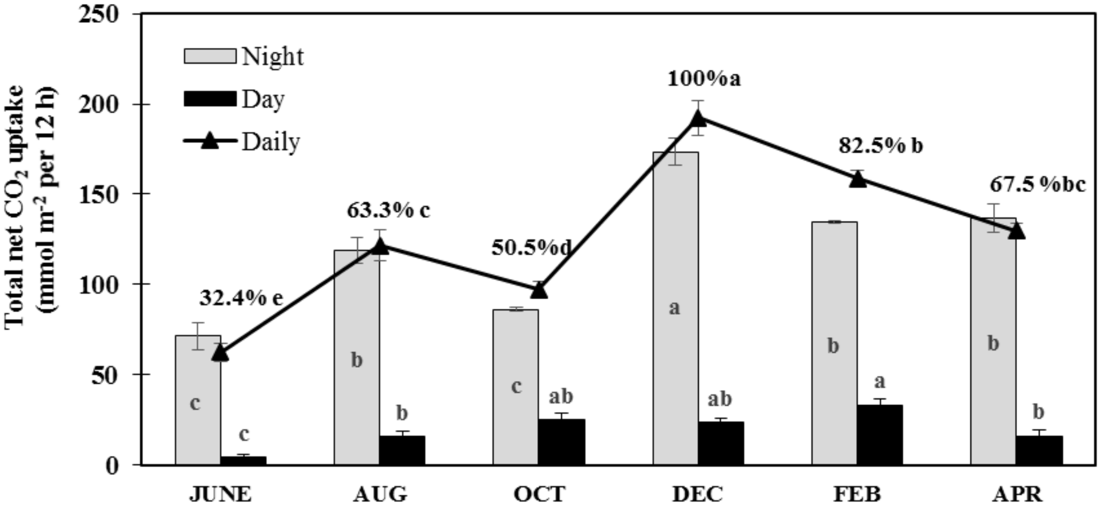

Figure 2 Total net CO_2 uptake rate in *Den.* 'Khao Sanan' leaves under commercial shaded net house conditions year-round. Day, night and daily total net CO_2 uptake were obtained by integrating net CO_2 uptake curves from Figure 1(A). Data are means ± SE of five individual plants. The different letters indicate statistical significance (*P < 0.01)

Correlation of CO_2 Uptake with Environmental Factors

The correlation between photosynthetic parameters, such as net CO_2 uptake, stomatal conductance (g_s), transpiration (E) and environmental factors, such as air temperature (Ta), relative humidity (RH), light intensity (PPFD), vapor pressure deficit (VPD) was shown in

Table 1 and Figure 3 shows the relationship between the net CO_2 uptake rate of *Den.* 'Khao Sanan' and environmental factors. The net CO_2 uptake rate was significantly different with temperature ($r^2 = 0.41$), RH ($r^2 = 0.25$) and light intensity ($r^2 = 0.06$), respectively. Additionally, the CO_2 uptake rate was a positive value at temperatures less than 29 °C, but was a negative value when the temperature was higher than 32 °C. Meanwhile, when the temperature was higher than 29 °C and less than 32 °C, the CO_2 uptake rate showed both positive and negative values (Figure 3A). The CO_2 uptake rate showed positive values at 60–90% RH. (Figure 3B) and less than 200 µmol m^{-2} s^{-1} PPFD (Figure 3C).

Table 1 The Pearson correlation matrix between photosynthetic parameters of Den. 'Khao Sanan' and environmental factors under shade net house conditions (n = 360)

	CO_2 upt.	**g_s**	**E**	**VPD**	**Ta**	**RH**	**PPFD**
CO2 upt.	1.00						
gs	0.37	1.00					
E	0.43	0.83	1.00				
VPD	-0.52	-0.33	-0.29	1.00			
Ta	-0.64	-0.41	-0.38	0.94	1.00		
RH	0.50	0.26	0.27	-0.84	-0.73	1.00	
PPFD	-0.25	-0.11	-0.13	0.32	0.34	-0.30	1.00

*Correlation is significant at the 0.05 level; ** Correlation is significant at the 0.01 level.
CO_2 upt.: CO_2 uptake, gs: stomatal conductance, E: transpiration rate, VPD: vapor pressure deficit, Ta: air temperature, RH: air relative humidity, PPFD: photosynthetic photon flux density (light intensity)

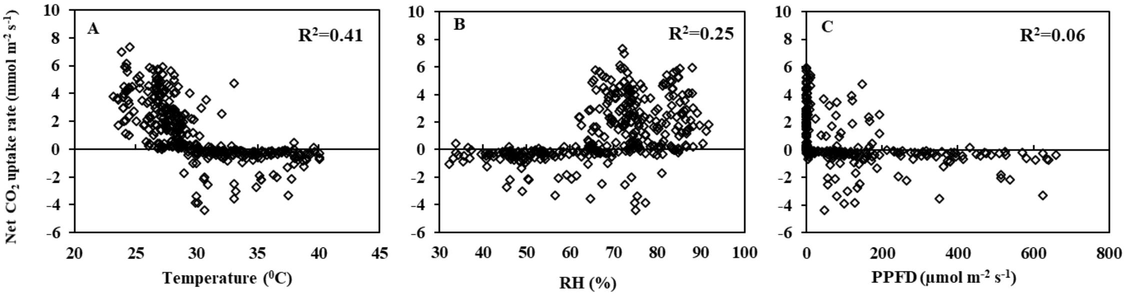

Figure 3 The relationship between net CO_2 uptake rate of *Den.* 'Khao Sanan' leaves and (A) air temperature, (B) air humidity; RH and (C) light intensity; photosynthetic photon flux density; PPFD under commercial shaded net house conditions year-round (n = 390)

The relationship between CO_2 uptake and environmental factors shown in Table 2 uses stepwise regression analysis to quantify the effects of temperature, relative humidity and light intensity. During the nighttime (18:00−6:00) and daytime (6:00−8:00 or 6:00−10:00 depend on month), the temperature (r^2 = 0.41 and 0.53, respectively) had a highly significant affect CO_2 uptake, but CO_2 uptake was not significantly related to relative humidity and light intensity. Meanwhile, total CO_2 uptake (Daily) was had a highly significant relationship with temperature and relative humidity.

Table 2 Stepwise regression of the CO_2 uptake rate to environmental factors during the nighttime, daytime and total CO_2 uptake (daily) of leaves *Den*. 'Khao Sanan' under commercial shaded net house conditions

Time of day	Regression equation	n	Pr > F	Adjust R^2
Nighttime	CO_2 upt. = 19.47−0.62 Ta	180	< 0.0001	0.41
Daytime	CO_2 upt. = 17.96−0.57 Ta	90	< 0.0001	0.53
Total (daily)	STEP 1 CO_2 upt. = 14.23−0.44 Ta	270	< 0.0001	0.36
	STEP 2 CO_2 upt. = 10.58−0.39 Ta+0.03 RH	270	0.0084	0.38

CO_2 upt.: CO_2 uptake, Ta: air temperature, RH: air relative humidity, n: number of data. The effect of regression was evaluated by ANOVA

Temperature is closely related to the photosynthetic capacity of the whole plant. An optimal performance of CAM requires relatively low night and high day temperatures. The major interactions of the temperature factors determining CAM performance are between individual enzymes, the membranes, respiratory activity and stomatal movement (Lüttge, 2004). *In vitro* phosphoenolpyruvate carboxylase (PEPC) studies showed that cool night temperatures stabilized the activity from phosphorylated PEPC, causing less inhibition by its product, malate, and as such, favoring nocturnal carboxylation (Carter *et al*., 1991). Cool night temperatures (15−20°C) and temperature differences between day and night were both required for maximum nocturnal malic acid accumulation in CAM plants (Carter *et al*., 1991; Nimmo, 2000). Isral and Nobel (1995) found that PEPC and Rubisco had maximal activities at 45/35 °C day/night, while daily CO_2 uptake was greater at 30/20 °C and 15/5 °C. In CAM *Phalaenopsis* hybrids orchids, several authors recommended an optimal night temperature of 18−22 °C and a day temperature between 2° C and 28 °C for net CO_2 uptake (Lootens and Heursel, 1998; Ota *et al*., 1991; Ichihashi *et al*., 2008). This is in contrast with *Den.* 'Khao Sanan' from this experiment, for which the optimal temperature for CO_2 uptake ranges from 22 °C to 29 °C. However, CO_2 uptake may adapt to the ambient growth temperature (Nobel and Hartsock, 1983) and the highest photosynthetic rate usually occurs at temperatures similar to those of the natural habitat of the species (Lootens and Heursel, 1998).

The results of this study indicated that the CO_2 uptake of *Den.* 'Khao Sanan' was positive values when temperature was less than 29 °C, there was high relative humidity (more than 60%) and very low light intensity (<200 µmol m^{-2} s^{-1}). Moreover, the CO_2 uptake value depend on temperature. Thus, orchid grower should decrease temperature under shaded net houses during the nighttime and early morning for increasing CO_2 uptake and enhancing growth. Additionally, the suitable parameters of theses environmental factors contribute to improving the ability to efficiently design and manipulate a semi-controlled greenhouse for *Dendrobium* orchids for commercial scale production in Thailand.

CONCLUSIONS

The correlation between net CO_2 uptake of *Den.* 'Khao Sanan' leaves and environmental factors under commercial shaded net house conditions year-round indicated that net CO_2 uptake was correlated with temperature (r^2 = 0.41) relative humidity (r^2 = 0.25) and light intensity (r^2 = 0.06), i.e., net CO_2

uptake had positive values when the temperature ranged from 22−29°C, the relative humidity ranged from 60–90% and light intensity conditions were less than 200 μmol m^{-2} s^{-1}. The net CO_2 uptake rates during the nighttime and daytime were most affected by temperature (r^2 = 0.41 and 0.53, respectively). Meanwhile, daily total net CO_2 uptake had a higher correlation with temperature and relative humidity (r^2 = 0.38) than light intensity.

ACKNOWLEDGMENTS

This work was partially supported by a grant from the Center for Advanced Studies for Agriculture and Food, Institute for Advanced Studies, Kasetsart University, Bangkok, Thailand. The authors also wish to thank Thaiorchids Company Limited for the supporting plant material and experimental site.

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