Hort. Environ. Biotechnol. 56(2):159-166. 2015.
DOI 10.1007/s13580-015-0122-1

ISSN (print) : 2211-3452
ISSN (online) : 2211-3460

Research Report

Photosynthesis of Chinese Cabbage and Radish in Response to Rising Leaf Temperature during Spring

Soonja Oh[1], Kyung Hwan Moon[1], Eun Young Song[1], In-Chang Son[1], and Seok Chan Koh[2*]

[1]*Agricultural Research Institute for Climate Change, Rural Development Administration, Jeju 690-150*
[2]*Department of Biology & Research Institute for Basic Sciences, Jeju National University, Jeju 690-756*

*Corresponding author: sckoh@jejunu.ac.kr

Received September 22, 2014 / Revised February 5, 2015 / Accepted April 10, 2015

Abstract. Photosynthesis in leaves, exposed to temperature change, was measured during spring to provide information for modeling of cropping systems for Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*) and radish (*Raphanus sativus*) in Jeju Island. The net photosynthetic rates (A) of Chinese cabbage and radish were depressed at temperatures above approximately 25°C (corresponding to the optimum temperature for photosynthesis), due in part to high rates of respiration above 25 or 30°C. Chinese cabbage was more sensitive to high temperature than radish. Above 25°C, stomatal conductance (g_s) declined steeply with a sharp increase in the vapor pressure deficit (VPD) and transpiration rate (E), suggesting that stomatal closure could not be associated with transpiration rate, particularly in Chinese cabbage. Dramatic declines in water use efficiency (WUE), instantaneous transpiration efficiency (ITE), and carboxylation efficiency (CE) above 30°C indicated that the plants could be severely affected negatively by high temperatures above 30°C. However, compared to Chinese cabbage, radish had high light use efficiency and potential to assimilate CO_2, judged by their high quantum yield (ϕ) and maximum photosynthetic rate (A_{max}). Radish utilized high levels of photosynthetic photon flux and strongly acclimated to the light environment, considering their high light saturation point (Q_{sat}) and low light compensation point (Q_{comp}). These results suggested that rising temperature might substantially alter water availability of plants by itself and/or through effects on the rate of water loss from leaves of Chinese cabbage and radish under diurnal and/or seasonal fluctuations of temperature, and/or global temperature change. To maintain the high productivity and quality of these crop species, it may be necessary to harvest them until early June, when the daily maximum temperature is below 25°C in Jeju Island.

***Additional key words*:** net photosynthetic rate, quantum yield, stomatal conductance, water use efficiency

Introduction

The ability to cope with excessive temperature is a complex process determined by environmental factors and the genetic capability of the plants. Crop responses to a change in temperature depend on many factors that contribute to growth and development, including the ability to adjust membrane fluidity for maintaining functionality, the optimum temperature for enzyme activity that underlies numerous physiological processes (e.g., photosynthesis, respiration), numerous processes that contribute to crop yield, and phenotypic plasticity in being able to shift the temperature optimum for those processes (Hasanuzzaman et al., 2013; Lin et al., 2012). When temperature is below the optimum for photosynthesis, a small rise in temperature can stimulate crop growth greatly, whereas high temperature generally limits carbon assimilation, especially at temperatures over 40°C (Lin et al., 2012).

When ambient temperatures rise, plants may experience excessive high temperature stress, which can have adverse consequences to plant growth and survival. An important consequence of high temperature stress is an inhibition of the photosynthetic apparatus. The main effect of this inhibition is a considerable decline of CO_2 uptake that ultimately results in a reduction in plant growth (Johkan et al., 2011). Another important consequence of high temperatures for plants is a reduction of stomatal conductance (g_s) (Yamori et al., 2006). Transpiration rates (E) typically increase as leaf temperature increases and the vapor pressure deficit (VPD) between the leaf and atmosphere becomes greater (Fredeen and Sage, 1999). However, reduced leaf water potential eventually triggers the closing of the stomata in order to conserve water and prevent catastrophic cavitation of the xylem (Fang et al., 2014).

Thus, high temperatures lead to decreases in both water use efficiency (WUE) and net photosynthetic rate (A), and ultimately decrease the quality and yield of a crop (Oh et al., 2014).

The response of leaf net photosynthesis to temperature is very variable among species (Lin et al., 2012). Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*) and radish (*Raphanus sativus*), both members of the Cruciferae family, are economically and nutritionally important crops cultivated and consumed widely (Lu et al., 2008; Opeña et al., 1988). They grow well under cool conditions, with optimum mean growth temperature ranges of 13-18°C in Chinese cabbage and 15-20°C in radish, respectively (Rural Development Administration, 2005). Both crops are highly cold-tolerant, but usually heat-sensitive. High temperature during the heading stage of Chinese cabbage can cause considerable damage; it reduces leaf growth, causes the production of narrow leaves, delays the initiation of heading, and increases the petiole-to-blade ratio (Opeña et al., 1988). Furthermore, the leaves appeared flaccid, and heat stress injuries reflected in symptoms such as soft-rot disease and inhibition of both net photosynthetic rate and PSII were found at high temperature during the heading stage (Oh et al., 2014). In radish, high temperature affects plant growth and fleshy taproot development, and ultimately decreases the quality and yield (Choi et al., 2011). As described above, because these crop plants are sensitive to high temperature, Chinese cabbage and radish were thought to be good model plants for the study on the effects of sudden rising ambient temperature caused by diurnal and/or seasonal fluctuations of temperature, and/or global temperature change on the quality and yield of cool season crops in the future.

In this study, our goal was to compare the leaf gas exchange traits of two crop species and to find how they were affected by sudden rising ambient temperature. Functional traits at the leaf level are associated to explain responses to instantaneous temperature changes. With this information, the behavior of crop species with respect to sudden increases in ambient temperature can be predicted, as an approximation for crop responses to global temperature change. The final objective of the study is to provide useful information for modeling of crops and cropping systems for Chinese cabbage and radish with diurnal and/or seasonal fluctuations of temperature, and/or global temperature change.

Materials and Methods

Plant Material and Growth Conditions

Seeds of Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis* Makino) 'Daetong' (Nongwoo, Suwon, Korea) and radish (*Raphanus sativus* L.) 'Kwandong' (Monsanto Korea, Anseong, Korea) were sown in 105-cell plug trays filled with commercial bed soil and germinated under intermittent mist at 25 ± 1°C in a dark growth chamber for 3 days. The plug trays in which the young seedlings grew were transferred to the greenhouse, and the young seedlings were grown at 20/15°C day/night temperature and kept well-watered without nutrients under natural light for 4 weeks. The seedlings bearing 4-5 leaves were transplanted to the field where solid pig manure compost (20 kg·100 m^{-2}) and NPK (21-17-17) chemical fertilizer (5.2 kg·100 m^{-2}) were applied at 5 days before transplanting. Finally, the seedlings were grown under natural light and temperature (mean 11.8°C, minimum 5.0°C, and maximum 20.7°C) from 28 March to 3 May, 2013. Plants were watered without nutrients with a drip irrigation system controlled by an automatic irrigation controller. Leaves that received direct solar light during most of growing period were selected between 09:00~11:30 for the experiments.

Light Response Curve

Light response curves were obtained using attached and fully expanded leaves. To obtain photosynthetic light response curves, gas exchange rate was measured at 10 photosynthetic photon flux (PPF) levels from 0 (achieved by wrapping the leaf cuvette with a black cloth) to 1,800 μmol·m^{-2}·s^{-1} with a portable gas exchange system (LCpro^{+}, ADC BioScientific, Hoddesdon, UK) with an LED light source (Oh et al., 2014). In each trial, the fully expanded leaves were initially equilibrated in the leaf chamber for 5 min to acclimate to a PPF of 500 μmol·m^{-2}·s^{-1} in order to activate ribulose-1,5-biphosphatecarboxylase/oxygenase and open the stomata (Pearcy, 1990; Valladares et al., 1997). Before gas exchange measurements, the leaves were allowed to equilibrate for 5 min to each light level, and five measurements were taken with 1 min intervals at each light level. The leaf chamber was maintained at 25°C at each light step for measuring the gas exchange. The relationship between net CO_2 assimilation rate and irradiance for leaves was described by a non-rectangular hyperbola equation as seen below (Marshall and Biscoe, 1980):

$$A = \frac{\phi Q + A_{\max} - \sqrt{(\phi Q + A_{\max})^2 - 4\phi\theta Q A_{\max}}}{2\theta} - R_{\mathrm{d}}$$

where A is the net photosynthetic rate (μmol CO_2·m^{-2}·s^{-1}), ϕ is the quantum yield (initial slope of the light-response curve, mol CO_2·mol^{-1} photons), Q is the mean PPF (μmol·m^{-2}·s^{-1}), $A_{\max}$ is the net photosynthetic rate under light-saturating conditions, θ is convexity of the curve (dimensionless), and R_{d} is the dark respiration rate (μmol CO_2·m^{-2}·s^{-1}). The half saturation constant (K, μmol·m^{-2}·s^{-1}), which reflects the affinity of the enzyme complexes of photosynthesis for the substrate light, was calculated using the Michaelis-Menten function modified for photosynthetic light response (Givnish et al., 2004). The light saturation points (Q_{sat}) were estimated as the irradiance required for modeled assimilation to reach 85% of $A_{\max,}$ and the light compensation points (Q_{comp}) were calculated by setting

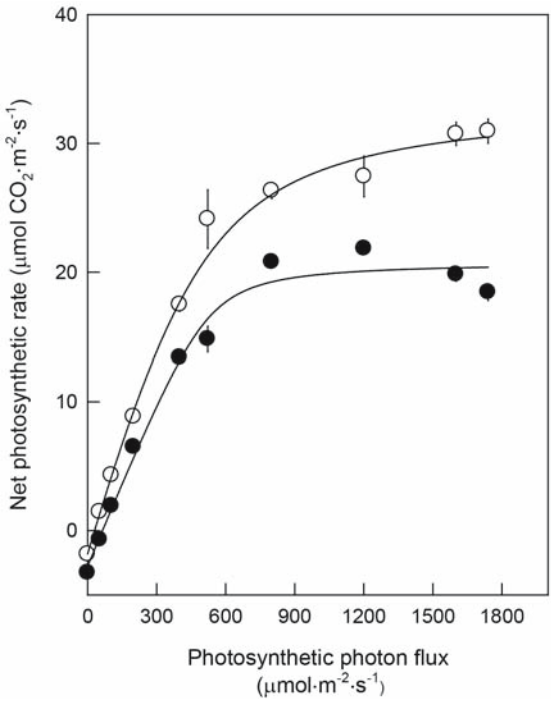

Fig. 1. Photosynthetic light-response curves obtained from leaves of Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*; closed circles) and radish (*Raphanus sativus*; open circles) grown under field conditions. The curves were fitted with the non-rectangular hyperbola. Each value represents the mean ± SE measured from 4 or 5 independent plants.

$A = 0$ and solving for Q in the equation (Marshall and Biscoe, 1980).

Gas Exchange in Response to Temperature

The temperature responses of net photosynthetic rate (A), dark respiration (R_d), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i) of plants were determined from a recently matured leaf by using the portable gas exchange system. During measurement, the temperature of the leaf was raised from 15 to 40°C in increments of 5°C. The PPF in the cuvette was kept constant at 1,000 μmol·m^{-2}·s^{-1} for photosynthesis-related characteristics, and at 0 μmol·m^{-2}·s^{-1} for dark respiration. The environmental conditions in the cuvette and gas exchange characteristics were recorded when stable. Four measurements were performed at each temperature per species. Optimum temperature for photosynthesis was calculated through the first derivative of the polynomial curves. The vapor pressure deficit (VPD) was also recorded together with photosynthetic measurements. The water use efficiency (WUE), instantaneous transpiration efficiency (ITE), and carboxylation efficiency (CE) were calculated as the ratio of net photosynthetic rate to transpiration rate, the ratio of net photosynthetic rate to stomatal conductance, and the ratio of the net photosynthetic rate to intercellular CO_2 concentration, respectively.

Statistical Analyses

Photosynthetic light-response curves were fitted to the non-rectangular hyperbola equation as seen above and all curve-fitting was performed using SigmaPlot 10.0 statistical software (Systat Software, Erkrath, Germany). One-way analysis (ANOVA) followed by the Duncan multiple range test was performed to compare data using SPSS 18.0 statistical software (SPSS, Chicago, IL, USA). The characteristics obtained from the photosynthetic light-response curves were compared between species by two-tailed Student's t-test for independent samples using the SPSS 18.0 statistical software.

Results

Characteristics of the photosynthetic light response curves

The light-response curves were obtained from leaves of Chinese cabbage and radish grown under field conditions in spring (Fig. 1), and photosynthetic characteristics such as net photosynthetic rate at light saturation (A_{max}), dark respiration rate (R_d), etc., were calculated (Table 1). The A_{max}

Table 1. Characteristics of the photosynthetic light-response curves obtained from leaves of Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*) and radish (*Raphanus sativus*) grown under field conditions[z].

Characteristics	Chinese cabbage	Radish	p values
A_{max} (μmol CO_2·m^{-2}·s^{-1})	23.6 ± 1.9	35.0 ± 1.8	0.008
R_d (μmol CO_2·m^{-2}·s^{-1})	-2.8 ± 1.1	-1.8 ± 0.6	0.035
Q_{comp} (μmol·m^{-2}·s^{-1})	68 ± 7	29 ± 2	0.010
Q_{sat} (μmol·m^{-2}·s^{-1})	769 ± 103	1366 ± 80	0.015
K (μmol·m^{-2}·s^{-1})	300 ± 100	419 ± 93	0.012
ϕ (mol CO_2·mol^{-1} photons)	0.043 ± 0.009	0.06 ± 0.007	0.025
θ	0.96 ± 0.06	0.81 ± 0.10	0.005

[z]A_{max}, net photosynthetic rate under light saturated conditions; R_d, dark respiration rate; Q_{comp}, light compensation point; Q_{sat}, light saturation point; K, half saturation constant; ϕ, apparent quantum yield; and θ, convexity of the non-rectangular hyperbola curve.
Each value represents the mean ± SE of four independent plants. A two-tailed Student's t-test was performed to determine the p value for comparison of Chinese cabbage and radish.

was obtained nearly or completely at 800 μmol·m^{-2}·s^{-1} or higher PPF in both species (Fig. 1). However, A_{max} and R_d differed significantly between the two species; A_{max} was lower in Chinese cabbage than in radish, while R_d was higher in Chinese cabbage than in radish (Table 1). The other characteristics also differed significantly between the two species; the light saturation points (Q_{sat}), the half saturation constant (K) and quantum yield (ϕ) were markedly lower in Chinese cabbage than in radish, but convexity (θ) and light compensation points (Q_{comp}) were slightly higher in Chinese cabbage than in radish.

Gas Exchange in Response to Temperature

The changes of net photosynthetic rate (A) and dark respiration rate (R_d) were measurably different between the two crop species with a change of leaf temperature (Fig. 2). The A of radish at the optimum temperature (24.7 ± 2.22 μmol CO_2·m^{-2}·s^{-1}) was much higher than that of Chinese cabbage (21.6 ± 0.06 μmol CO_2·m^{-2}·s^{-1}), although the optimum temperatures for A of Chinese cabbage and radish leaves differed by only 2°C (Figs. 2A and B). R_d increased approximately exponentially above 25°C in Chinese cabbage and above 30°C in radish (Figs. 2C and D).

Stomatal conductance (g_s), transpiration rate (E), and vapor pressure deficit (VPD) also responded sensitively to the change of leaf temperature (Fig. 3). The g_s increased as temperature rose in both species, reaching a peak at 25-30°C in Chinese cabbage and at 30-35°C in radish and declining at higher temperatures. The peak value of g_s was approximately 2.5-fold higher in radish than in Chinese cabbage (Figs. 3A and B). By contrast, E increased steeply above 20°C in Chinese cabbage and above 25°C in radish and remained high at high temperature (Figs. 3C and D). The VPDs were about 1.0 kPa at 15-30°C, increased above 30 or 35°C, and reached 2.0 kPa at 40°C, (Figs. 3E and F). Like g_s, intercellular CO_2 concentration (C_i) also increased gradually in the lower temperature range, reaching a peak at 30°C, and then declining thereafter (Figs. 4A and B). The ratio of intercellular to ambient

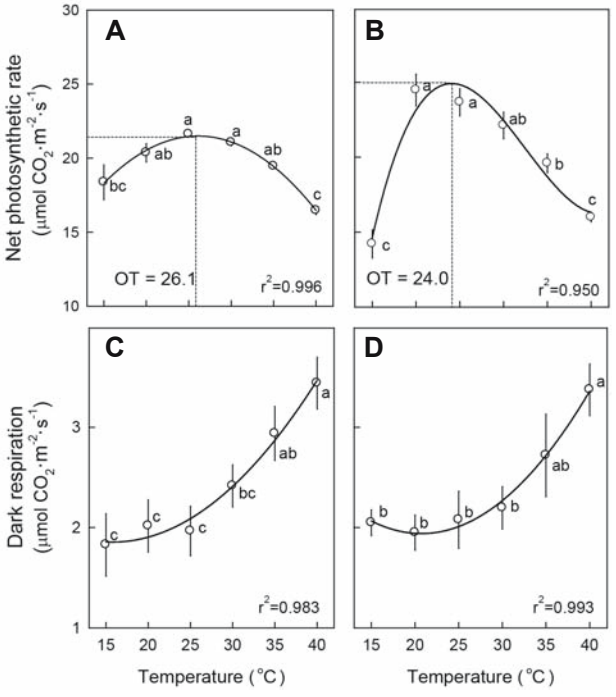

Fig. 2. Temperature response curves of foliar net photosynthetic rate and dark respiration in Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*, A and C) and radish (*Raphanus sativus*, B and D). The optimum temperature (OT) for maximal net photosynthetic rate was calculated from the regression curve using SigmaPlot 10.0 statistical software (Systat Software Inc., Germany). Each value represents the mean ± SE measured from 5 independent plants.

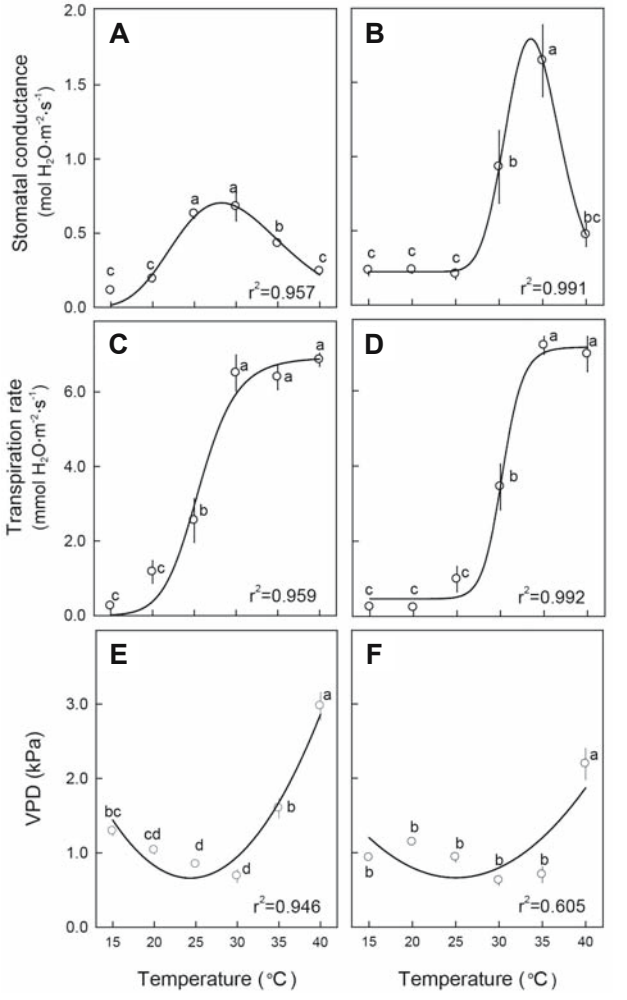

Fig. 3. Temperature response curves of stomatal conductance, transpiration rate and VPD (vapor pressure deficit) from Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*, A, C, and E) and radish (*Raphanus sativus*, B, D, and F). Each value represents the mean ± SE measured from 5 independent plants.

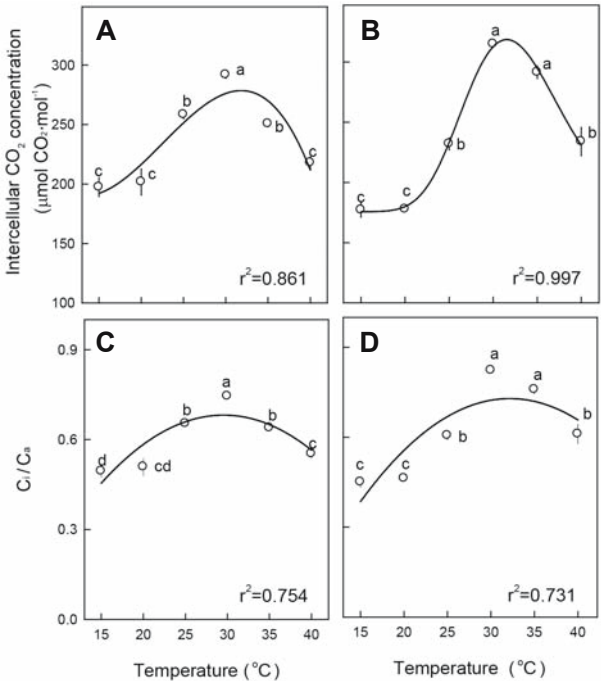

Fig. 4. Temperature responses of intercellular CO_2 concentration and C_i/C_a (ratio of intercellular to ambient CO_2 concentration) from leaves of Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*, A and C) and radish (*Raphanus sativus*, B and D). Each value represents the mean ± SE measured from 5 independent plants.

CO_2 concentration (C_i/C_a) showed a trend similar to C_i, even though the peaks were flat (Figs. 4C and D).

Water use efficiency (WUE) declined steeply with increasing leaf temperature in radish, while it was low and remained low as temperature increased in Chinese cabbage (Fig. 5A). Instantaneous transpiration efficiency (ITE) was lowest at 25-35°C in Chinese cabbage and at 30-35°C in radish (Fig. 5B). The carboxylation efficiency (CE) was highest at the low temperature in both species and lowest at 30-40°C (Fig. 5C).

Correlations between Gas Exchange Characteristics

The photosynthetic characteristics of the two crop species were subjected to cross-correlation analysis. Most photosynthetic characteristics were inter-correlated with each other at $p < 0.01$ or $p < 0.05$ (Table 2). It is especially noteworthy that E was highly positively correlated with temperature, whereas WUE was highly negatively correlated with temperature in both species. Furthermore, C_i had moderate positive correlations with g_s, and highly negative correlations with ITE in both species. The g_s was highly negatively correlated with ITE in Chinese cabbage, but moderately correlated with ITE in radish. The E was highly negatively correlated with WUE in both species.

Discussion

The temperature rise associated with global warming is a growing concern, as it could limit growth, productivity, and quality for some plants, and particularly those that are temperature-sensitive. The direct effects of high temperature depend on the crop species and their adaptability to high temperature. Inhibition of photosynthesis and yield loss due to high temperature have been reported in many crops including rice, soybean, potato, etc. (Johkan et al., 2011). In the present study, net photosynthetic rates of Chinese cabbage and radish

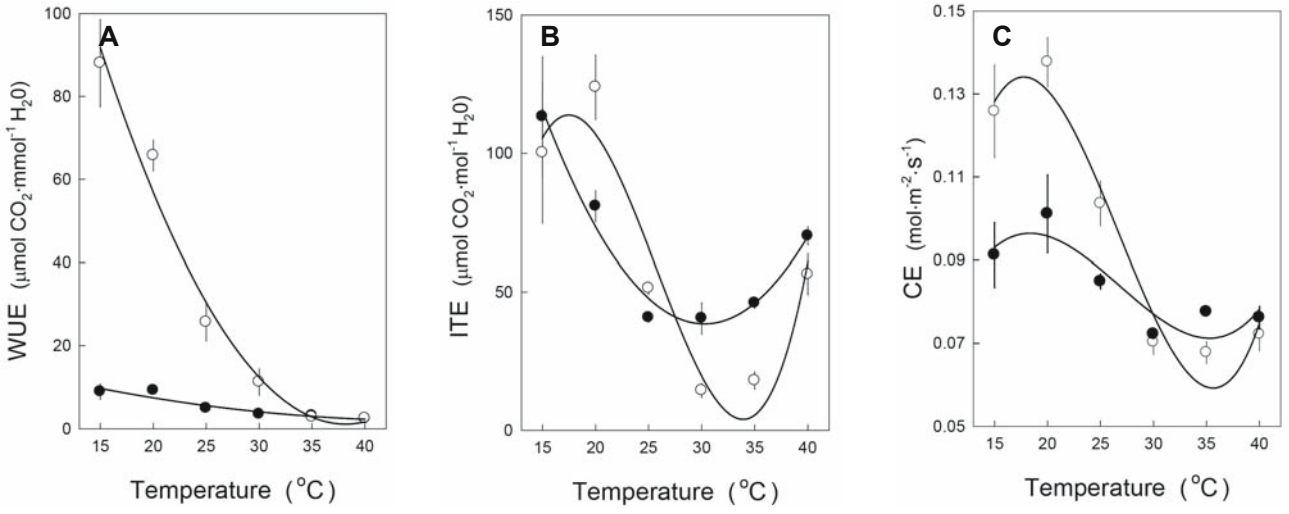

Fig. 5. Response of intrinsic water use efficiency (WUE), instantaneous transpiration efficiency (ITE), and carboxylation efficiency (CE) to temperature from leaves of Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*, closed circles) and radish (*Raphanus sativus*, open circles). Each value represents the mean ± SE measured from 5 independent plants.

Table 2. Correlation matrix of the photosynthetic characteristics and leaf temperature from leaves of Chinese cabbage and radish.

Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*)[z]									
Characteristics	Temp.	A	R_d	g_s	E	VPD	C_i	WUE	ITE
A	-0.275*								
R_d	-0.436**	0.215							
g_s	0.233*	0.391**	0.151						
E	0.860**	-0.158	-0.404**	0.184					
VPD	0.593**	-0.563**	-0.005	-0.437**	0.428**				
C_i	0.180	0.541**	-0.220	0.680**	0.473**	-0.484**			
WUE	-0.748**	-0.029	0.365**	-0.189	-0.796**	-0.409**	-0.430**		
ITE	0.072	-0.426**	-0.070	-0.876**	0.010	0.529**	-0.755**	0.193	
CE	-0.288*	0.405**	0.285*	-0.149	-0.319*	-0.078	-0.537**	0.424**	0.482**
Radish (*Raphanus sativus*)									
A	-0.402**								
R_d	-0.291*	0.137							
g_s	0.325**	0.038	0.172						
E	0.830**	-0.562**	-0.198	0.481**					
VPD	0.344**	-0.228*	-0.295*	-0.517**	0.056				
C_i	0.508**	-0.084	0.145	0.667**	0.550**	-0.504**			
WUE	-0.792**	0.527**	0.259	-0.358**	-0.792**	0.020	-0.542**		
ITE	-0.438**	0.061	0.475**	-0.622**	-0.524**	0.330**	-0.766**	0.494**	
CE	-0.607**	0.752**	0.037	-0.389**	-0.693**	0.142	-0.697**	0.747**	0.680**

[z]Each value represents the Pearson's correlation coefficient (r) for leaves of Chinese cabbage (n = 5) and radish (n = 5). * and ** represent statistical significance at $p < 0.05$ and $p < 0.01$ levels, respectively.

were depressed at temperatures above 25 or 30°C corresponding to their optimum temperatures for photosynthesis, which could be attributed in part to high rates of respiration. Chinese cabbage was more sensitive to high temperature than radish, which was also consistent with previous reports that the optimum mean temperature range for growth of Chinese cabbage (13-18°C) was lower than that of radish (15-20°C) (RDA, 2005).

Stomatal closure is one of the primary responses of plants to temperature stress outside the optimal temperature range (Silim et al., 2010). Stomata respond to not only temperature (Mott and Peak, 2010), but also the increase in VPD that typically accompanies rising temperature (Day, 2000). At temperatures above 25°C, where A commenced to decline in the two species, not only high temperature but also the increase of VPD could be a factor contributing to the reduction in g_s. This response minimizes water loss, but also lowers the C_i and C_i/C_a, causing a stomatal or diffusional limitation to photosynthesis. Stomatal regulation of C_i is also one of the key processes determining the overall temperature response of plant leaves. In this study, the decline of g_s and C_i was observed at temperatures above 30°C. The g_s decreases significantly in many plant species under high temperature (Baligar et al., 2012; Parry et al., 2013) leading to a decrease in the activation state of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Parry et al., 2013). Soil water availability also typically decreases as temperature rises, resulting in modification of plant water status, gas exchange in the short-term, and/or growth and yield of a crop in the long-term (Ben-Gal et al., 2010; Ertek and Kara, 2013). It is well known that high temperatures inhibit the growth of radish and result in short and thin roots (Choi et al., 2011; Seo et al., 2012). In this study, the low levels of WUE, ITE, and CE at high temperature suggest that activity of Rubisco could decline at temperatures above 30°C in both Chinese cabbage and radish. Similarly, WUE and CE were low in fescue (*Festuca arundinacea*) grown under high temperature (35/30°C, day/night), compared to control (20/15°C, day/night) plants (Cui et al., 2006). Therefore, rising temperature, one major component of climate change, may substantially reduce not only water availability through effects on the rate of water loss but also the photochemical efficiency from the reduction of Rubisco activity in leaves.

Determining the light-response curve of leaf A is also important for understanding the photochemical efficiency of the photosynthetic process of plants. The ϕ and A_{max} were higher in radish than in Chinese cabbage, suggesting radish could have higher light use efficiency and higher potential

to assimilate CO_2. In addition, higher Q_{sat}, despite a low Q_{comp} in radish compared to Chinese cabbage reveals that radish makes use of a higher level of PAR than Chinese cabbage and strongly adapts to the light environment (Zhou et al., 2013). It is also confirmed by the finding that the half saturation constant (K) was higher in radish than in Chinese cabbage. Interestingly, although the Q_{comp} of radish plants was lower than that of typical heliophytes (50-100 $\mu mol \cdot m^{-2} \cdot s^{-1}$), the ϕ of radish was close to the value for normal plant growth (0.04-0.07 mol $CO_2 \cdot mol^{-1}$ photons) (Xia et al., 2011). This result indicates that radish plants are shade tolerant to some extent as well as adaptable to high light. Furthermore, radish plants had low R_d and high ϕ at 25°C leaf temperature compared to Chinese cabbage, resulting in a low Q_{comp} (Table 1), as previously reported for *Medicago truncatula* (Nunes et al., 2009).

In conclusion, this study demonstrates that photosynthesis of Chinese cabbage and radish is depressed at temperatures above approximately 25°C due to high temperature itself and/or accompanying dry conditions. This suggests that Chinese cabbage and radish could be negatively and severely affected by sudden rising ambient temperatures caused by diurnal and/or seasonal fluctuations of temperature, and/or global temperature change. In particular, Chinese cabbage could be affected more seriously than radish. Therefore, to maintain the high yield and quality of these two crop species, it may be necessary to harvest them until early June, when the daily maximum temperature is not above 25°C on Jeju Island. The results of this study could provide useful information for the modeling of crops and cropping systems for Chinese cabbage and radish with diurnal and/or seasonal fluctuations of temperature, and/or global temperature change. Additional research into the biochemical and molecular responses of these crop plants to environmental conditions is also required.

Acknowledgment: This work was carried out with the support of 'Cooperative Research Program for Agriculture Science & Technology Development (Development of prototypes of crop models for yield estimation of main vegetable crops, PJ009870062014)', Rural Development Administration, Republic of Korea.

Literature Cited

Baligar, V.C., J.A. Bunce, M.K. Elson, and N.K. Fageria. 2012. Photosynthetic photon flux density, carbon dioxide concentration and temperature influence photosynthesis in *Crotalaria* species. Open Plant Sci. J. 6:1-7.

Ben-Gal, A., D. Kool, N. Agam, G.E. van Halsema, U. Yermiyahu, A. Yafe, E. Presnov, R. Erel, A. Majdop, I. Zipori, E. Segal, S. Rüger, U. Zimmermann, Y. Cohen, V. Alchanatis, and A. Dag. 2010. Whole-tree water balance and indicators for short-term drought tress in non-bearing 'Barnea' olives. Agr. Water Manage. 98:124-133.

Choi, E.Y., T.C. Seo, S.G. Lee, I.H. Cho, and J. Stangoulis. 2011. Growth and physiological responses of Chinese cabbage and radish to long-term exposure to elevated carbon dioxide and temperature. Hort. Environ. Biotechnol. 52:376-386.

Cui, L., J. Li, Y. Fan, S. Xu, and Z. Zhang. 2006. High temperature effects on photosynthesis, PSII functionality and antioxidant activity of two *Festuca arundinacea* cultivars with different heat susceptibility. Bot. Stud. 47:61-69.

Day, M.E. 2000. Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce (*Picea rubens*). Tree Physiol. 20:57-63.

Ertek, A. and B. Kara. 2013. Yield and quality of sweet corn under deficit irrigation. Agr. Water Manage. 129:138-144.

Fang, X.W., N.C. Turner, J.A. Palta, M.X. Yu, T.P. Gao, and F.M. Li. 2014. The distribution of four *Caragana* species is related to their differential responses to drought stress. Plant Ecol. 215:133-142.

Fredeen, A.L. and R.F. Sage. 1999. Temperature and humidity effects on branchlet gas-exchange in white spruce: An explanation for the increase in transpiration with branchlet temperature. Trees 14:161-168.

Givnish, T.J., R.A. Montgomery, and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: Light regimes, static light responses, and whole-plant compensation points. Am. J. Bot. 91:228-246.

Hasanuzzaman, M., K. Nahar, and M. Fujita. 2013. Extreme temperature responses, oxidative stress and antioxidant defense in plants, p. 169-205. In: K. Vahdati and C. Leslie (eds.). Abiotic stress-plant responses and application. InTech, Rijeka, Croatia.

Johkan, M., M. Oda, T. Maruo, and Y. Shinohara. 2011. Crop production and global warming, p. 139-152. In: S. Casalegno (ed.). Global warming impacts: Case studies on the economy, human health, and on urban and national environments. InTech, Rijeka, Croatia.

Lin, Y.S., B.E. Medlyn, and D.S. Ellsworth. 2012. Temperature responses of leaf net photosynthesis: The role of component processes. Tree Physiol. 32:219-231.

Lu, Z.L., L.W. Liu, X.Y. Li, Y.Q. Gong, X.L. Hou, J.L. Zhu, J.L. Yang, and L.Z. Wang. 2008. Analysis and evaluation of nutritional quality in Chinese radish (*Raphanus sativus* L.). Agr. Sci. China 7:823-830.

Marshall, B. and P.V. Biscoe. 1980. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance: I. Derivation. J. Exp. Bot. 31:29-39.

Mott, K.A. and D. Peak. 2010. Stomatal responses to humidity and temperature in darkness. Plant Cell Environ. 33:1084-1090.

Nunes, C., S.S. Araujo, J.M. Silva, P. Fevereiro, and A.B. Silba. 2009. Photosynthesis light curves: A method for screening water deficit resistance in the model legume *Medicago truncatula*. Ann. Appl. Biol. 155:321-332.

Oh, S., K.H. Moon, I.C. Son, E.Y. Song, Y.E. Moon, and S.C. Koh. 2014. Growth, photosynthesis and chlorophyll fluorescence of Chinese cabbage in response to high temperature. Kor. J. Hort. Sci. Technol. 32:318-329.

Opeña, R.T., C.G. Kuo, and J.Y. Yoon. 1988. Breeding and seed production of Chinese cabbage in the tropics and subtropics. Technical bulletin No. 17. Asian Vegetable Research and Development Center, Shanhua, Taiwan.

Parry, M.A.J., P.J. Andralojc, J.C. Scales, M.E. Salvucci, A.E. Carmo-Silva, H. Alonso, and S.M. Whitney. 2013. Rubisco activity and regulation as targets for crop improvement. J. Exp. Bot. 64:717-730.

Pearcy, R.W. 1990. Sunflecks and photosynthesis in plant canopies. Ann. Rev. Plant Physiol. Mol. Biol. 41:421-453.

Rural Development Administration. 2005. Protected horticulture.

Sammi Publishing Co., Suwon, Korea.

Seo, T.C., Y. Jang, C.W. Nam, S.S. Oh, Y.C. Um, and J.H. Han. 2012. Changes of plant biomass and proximate composition of radish exposed to elevated temperature and CO_2 concentration. J. Bio-Environ. Cont. 21:20-27.

Silim, S.N., N. Ryan, and D.S. Kubien. 2010. Temperature responses of photosynthesis and respiration in *Populus balsamifera* L.: Acclimation versus adaptation. Photosyn. Res. 104:19-30.

Valladares, F., M.T. Allen, and R.W. Pearcy. 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. Oecologia 111:505-514.

Xia, J., S.Y. Zhang, G.C. Zhang, W.J. Xie, and Z.H. Lu. 2011. Critical responses of photosynthetic efficiency in *Campsis radicans* (L.) seem to soil water and light intensities. Afr. J. Biotechnol. 10:17748-17754.

Yamori, W., K. Noguchi, Y.T. Hanba, and I. Terashima. 2006. Effects of internal conductance on the temperature dependence of the photosynthetic rate in spinach leaves from contrasting growth temperatures. Plant Cell Physiol. 47:1069-1080.

Zhou, Z.J., P.X. Su, T.T. Xie, H.N. Zhang, and S.J. Li. 2013. Physiological and biochemical regulation mechanisms for drought adaption in typical desert shrubs. J. Chem. Pharm. Res. 5:671-677.