Comparison of Measured and Calculated Carboxylation Rate, Electron Transfer Rate and Photosynthesis Rate Response to Different Light Intensity and Leaf Temperature in Semi-closed Greenhouse with Carbon Dioxide Fertilization for Tomato Cultivation

Eun-Young Choi\(^1\), Young-Ae Jeong\(^2\), Seung-Hyun An\(^3\), Dong-Cheol Jang\(^4\), Dae-Hyun Kim\(^5\), Dong-Soo Lee\(^6\), Jin-Kyung Kwon\(^7\), and Young-Hoe Woo\(^8\)*

\(^1\)Professor, Department of Agricultural Science, Korea National Open University, Seoul 03087, Korea
\(^2\)Graduate Student, Department of Agriculture and Life Science, Korea National Open University, Seoul 03087, Korea
\(^3\)Undergraduate Student, Department of Agricultural Science, Korea National Open University, Seoul 03087, Korea
\(^4\)Postdoctoral Researcher, Department of Horticulture, College of Agriculture and Life Science, Kangwon National University, Chuncheon 24341, Korea
\(^5\)Professor, Department of Biosystems Engineering, College of Agriculture and Life Science, Kangwon National University, Chuncheon 24341, Korea
\(^6\)Postdoctoral Researcher, Department of Agricultural Engineering, Energy and Environmental Engineering Division, Jeonju 54875, Korea
\(^7\)Researcher, Department of Agricultural Engineering, Energy and Environmental Engineering Division, Jeonju 54875, Korea
\(^8\)Professor, Department of Horticulture Environment System, Korea National College of Agriculture and Fisheries, Jeonju 54874, Korea

Abstract. This study aimed to estimate the photosynthetic capacity of tomato plants grown in a semi-closed greenhouse using temperature response models of plant photosynthesis by calculating the ribulose 1,5-bisphosphate carboxylase/oxygenase maximum carboxylation rate (\(V_{\text{cmax}}\)), maximum electron transport rate (\(J_{\text{max}}\)), thermal breakdown (high-temperature inhibition), and leaf respiration to predict the optimal conditions of the CO\(_2\)-controlled greenhouse, for maximizing the photosynthetic rate. Gas exchange measurements for the A-C\(_i\) curve response to CO\(_2\) level with different light intensities {PAR (Photosynthetically Active Radiation) 200\(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\) to 1500\(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\)} and leaf temperatures (20°C to 35°C) were conducted with a portable infrared gas analyzer system. Arrhenius function, net CO\(_2\) assimilation (\(A_n\)), thermal breakdown, and daylight leaf respiration (\(R_d\)) were also calculated using the modeling equation. Estimated \(J_{\text{max}}, A_n, A_n\) Arrhenius function value, and thermal breakdown decreased in response to increased leaf temperature (> 30°C), and the optimum leaf temperature for the estimated \(J_{\text{max}}\) was 30°C. The CO\(_2\) saturation point of the fifth leaf from the apical region was reached at 600ppm for 200 and 400\(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\) of PAR, at 800ppm for 600 and 800\(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\) of PAR, at 1000ppm for 1000\(\mu\text{mol}\) of PAR, and at 1500ppm for 1200 and 1500\(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\) of PAR levels. The results suggest that the optimal conditions of CO\(_2\) concentration can be determined, using the photosynthetic model equation, to improve the photosynthetic rates of fruit vegetables grown in greenhouses.

Additional key words : Arrhenius function, net CO\(_2\) assimilation, rubisco, saturation point, thermal breakdown

Introduction

The cultivation areas of vegetables were 171,429ha for the open field and 54,443ha for the greenhouse. Most of the fruit vegetables (85.6%) were grown in the greenhouse. Vegetable production in greenhouses has been continuously declining since reaching 3.13 million tons in 2009 (MAFRA, 2019). It is well known that increasing CO\(_2\) concentration positively improves leaf photosynthesis and thus productivity. The concentration of CO\(_2\) in the greenhouse can be lower than the concentration in the atmosphere when the greenhouse is not ventilated during winter, resulting in a considerable yield decrease. Therefore, a proper CO\(_2\) control system that reflects the variation of growth environments depending on greenhouse types and crop growth stages needs to be developed. A previous study suggested optimal setpoints for indoor CO\(_2\) concentration (Peet and Willits, 1987); however,
the estimated optimal CO₂ concentration varies depending on ventilation, wind speed, or window aperture (Nederhoff, 1987; Sanchez-Guerrero et al., 2005). Also, cost-efficient control of CO₂ supplies is necessary since pure CO₂ is expensive. A proper CO₂ control system may need to replenish CO₂ concentration to maintain leaf photosynthesis effectively under different temperatures and radiation.

There is a model that describes leaf photosynthesis efficiency enhanced by the increased CO₂ concentration (Farquhar et al., 1980). The rate of CO₂ assimilation in plants depends on biochemical processes, light intensity, temperature, and CO₂ concentration in the cytoplasm, thylakoid membrane, stroma, mitochondria. The most common methods used to understand C₃ photosynthesis reactions are models of photosynthesis developed by Farquhar et al. (1980). In this model, the rate of photosynthesis may vary depending on the state of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) that supplies sufficient ribulose 1,5-bisphosphate (RuBP), known as the Rubisco-limited photosynthesis rate, and occurs in low CO₂ concentrations. The photosynthesis rate can also depend on the regeneration rate of RuBP, which occurs under high CO₂ conditions. Rubisco and RuBP restrictions typically occur at <20Pa (200ppm) CO₂ and at >30Pa CO₂, respectively. The triose phosphate use (TPU) limiting factor can set the maximum photosynthesis rate (Aₘₐₓ) by increasing the CO₂ rate or oxygen concentration (Sharkey, 1985). Plant photosynthetic capacity is, therefore, determined by the maximum rate of Rubisco carboxylation (Vₑₘₐₓ) and the maximum rate of electron transport (Jₑₘₐₓ) at a reference temperature (generally 25°C) using the response of Aₑ to intercellular CO₂ concentration (A-C response curves). The parameters estimated from the analysis of an A-C curve respond to measurement temperature; thus, comparisons between two treatments are often made at a single temperature. Representative temperature responses of the fitted parameters are used to adjust these values to a single temperature, in this case, at 25°C (Sharkey et al., 2007). The C₃ photosynthesis model proposed by Farquhar et al. (1980) has been applied to estimate leaf photosynthesis-dependent temperature (Medlyn et al., 2002a; Knorr et al., 2007) since the biochemical processes are temperature-dependent (Harley et al., 1992; Leuning, 2002; Medlyn et al., 2002b). Net CO₂ uptake for photosynthesis depends on growth temperature (Hikosaka et al., 2006; Sage and Kubien, 2007). Recently, Kim et al. (2020) estimate heat stress reduction of cucumber plants by solar shading in a greenhouse by measuring and analyzing physiological conditions, such as leaf temperature, leaf-air temperature, Vₑₘₐₓ, Jₑₘₐₓ, thermal breakdown, and leaf respiration.

This study aimed to estimate photosynthetic capacity for tomato plants grown in a semi-closed greenhouse using temperature response models of plant photosynthesis by calculating Vₑₘₐₓ, Jₑₘₐₓ, thermal breakdown, and leaf respiration to predict optimal conditions of the CO₂-controlled greenhouse to maximize photosynthetic rate.

Materials and Methods

1. Plant Growth Environments

This study was conducted by growing tomatoes in a semi-closed greenhouse with hydroponics under integrated solar radiation (ISR)-automated irrigation. The tomatoes (Solanum lycopersicum L. ‘Dafnis’) were transplanted onto coconut coir substrates ((Chip:Dust, 7:3), DY GS, Korea) on March 23, 2021. One dripper per plant was installed to supply a uniform feeding amount for each crop, and the tomato nutrient solution developed by RDA was provided to the automatic feeding system ((Macro-nutrients (me L⁻¹): NO₃-N (8.2), NH₄-N (1.4), P (2.0), K (5.0), Ca (4.0), Mg (2.0), SO₄-S (2.0), Micro-nutrients (ppm): Fe (3.0), Cu (0.02), B (0.5), Mn (0.5), Zn (0.05), Mn (0.01)). The electrical conductivity and pH were controlled at 2.0–2.5dS·m⁻¹ and 5.3–6.8, respectively. The tomatoes were trained into a one-stem vine. The shading screen was closed between 11 a.m. and 2 p.m. when the light intensity reached 700W·m⁻² in the greenhouse and the air temperature was more than 30°C. During the experimental period, the minimum night temperature was set to 18°C, and the day temperature was set to 23°C. The internal and external environments of the greenhouse (e.g., temperature, humidity, solar radiation, and CO₂) were measured beginning May 7, 2021 using a greenhouse environmental control system (Magma 3.0, GreenCS, Jeonnam, Korea). The ISR was set to 100J·cm⁻² from the first irrigation to the end, and the water volume per plant in a day was 1.5–2.0L. Tomato harvesting was carried out beginning May 23, two months after the transplant, and a 12
Comparison of Measured and Calculated Carboxylation Rate, Electron Transfer Rate and Photosynthesis Rate Response to Different ...

to 18 leaf number was maintained by removing the old leaves once a week. The apical shoot was placed approximately 2.5 to 3.0 meters above the gutter.

In this experiment, all the measurements were conducted with the plants that its plant height was 271 (±8.20)cm, 343 (±6.51)cm and 416 (±5.74)cm at June 22, July 14, and August 3, 2021, respectively with the 7.8 (±0.37), 10.8 (±0.20) and 13.4 (±0.40) of cluster number, the 39.0 (±1.05), 43.9 (±1.51) and 42.0 (±2.30) of leaf length and 33.2 (±5.06), 39.3 (±2.42) and 36.9 (±5.12) of leaf width of fifth leaves from the apical region at June 22, July 14, and August 3, 2021, respectively.

2. Measurements

Total 16 replications of gas exchange measurements were conducted with a portable infrared gas analyzer system (LI-6400XT; Li-Cor, Inc., Lincoln, NE, USA) during the June 22 to August 9, 2021. One of the youngest fully expanded leaflets on the fifth leaf of the apical shoot was placed in the leaf chamber of gas analyzer. For the A-C_i curve response to CO_2 level, the reference CO_2 for the A-C_i curves was changed in the following order: 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800µmol·mol^-1 at the PAR values of 200, 400, 600, 800, 1000, 1200, and 1500µmol·m^-2·s^-1 with the 34.54°C average air temperature. For the A-C_i curve response to different leaf temperatures, the leaf temperature was increased from 20°C to 35°C with 5°C increments, and A-C_i response curves were recorded at each temperature and the reference CO_2 levels and a 700µmol·m^-2·s^-1 PAR value. The significance between environmental factors was analyzed with variable selection stepwise using the SAS 9.2 software package (SAS Institute, Cary, NC, USA).

3. Comparison of Observed and Estimated Responses to Different Light Intensity and Temperature

We used the Arrhenius equation to describe the kinetic temperature responses of V_{cmax} and J_{max}. Arrhenius function, V_{cmax}, J_{max}, thermal breakdown, R_d were calculated using the selected model. The program was developed using SAS (SAS Institute Inc 9.1, Cary, NC, USA). Relationships among V_{cmax}, J_{max} and other environmental factors were analyzed stepwise.

The Arrhenius function is as follows:

\[ f(T) = \exp \left( \frac{\Delta H_a}{298.15 \times R} \left( 1 - \frac{298.15}{T} \right) \right) \]

where \( T \) is leaf temperature, \( R \) is the universal gas

---

**Table 1.** Maximum (Max), minimum (Min), and average (Av) of air temperature, relative humidity, leaf temperature, solar radiation, and CO_2 concentration in a semi-closed greenhouse for tomato cultivation from June 22 to August 9, 2021.

| Month  | Air temperature (°C) | Relative humidity (%) | Leaf temperature (°C) | Solar Irradiance (W·m \(^{-2}\)·s \(^{-1}\)) | CO_2 (ppm) |
|--------|-----------------------|-----------------------|-----------------------|---------------------------------------------|-------------|
|        | Max | Min | Av | Max | Min | Av | Max | Min | Av | Max | Min | Av | Max | Min | Av |
| June   | 32.3 | 15.1 | 22.7 ± 0.7 | 100 | 44.8 | 86 ± 1.9 | 24.1 | 22.1 | 23.4 ± 0.3 | 1175 | 322 ± 46 | 825 | 310 | 521 ± 17 |
| July   | 34.7 | 18.7 | 24.8 ± 3.4 | 100 | 60.9 | 90.9 ± 8.4 | 34.3 | 17.9 | 23.9 ± 2.9 | 1149 | 303 ± 250 | 2000 | 206 | 520 ± 268 |
| August | 35.0 | 19.8 | 25.2 ± 3.2 | 100 | 61.0 | 84.6 ± 10.6 | 32.5 | 19.6 | 23.6 ± 2.6 | 1032 | 323 ± 243 | 576 | 275 | 452 ± 70 |

**Table 2.** Photosynthetic parameter values for equations for the mean V_{cmax} and J_{max}.

| Outputs | V_{cmax} | J_{max} | Unit |
|---------|----------|---------|------|
| ΔH_a    | 58,520   | 37,000  | J mol\(^{-1}\) |
| ΔH_d    | 149,250  | 152,040 | J mol\(^{-1}\) |
| ΔS      | 485      | 495     | J mol\(^{-1}\)K\(^{-1}\) |

ΔH_a : activation energy
ΔH_d : energy of deactivation
ΔS : entropy
constant (8.314J·K⁻¹·mol⁻¹), and ΔH₂ is the activation energy (J·mol⁻¹). Parameter values for V_{cmax} and J_{max} are presented in Table 2 (Farquhar et al., 1980; Leuning, 2002; Caemmerer, 2000).

The V_{cmax} is calculated as follows:

$$V_{cmax} = \frac{V_{max,25} \exp[0.088(T_i - 25)]}{1 + \exp[0.29(T_i - 41)]}$$

where, V_{max,25} is the carboxylation rate at 25°C (µmol·m⁻²·s⁻¹), 0.088 is temperature coefficient for that parameter at 25°C and 0.29 is temperature coefficient for that parameter at 41°C (Campbell and Norman, 1998).

The J_{max} is calculated as follows:

$$J_{max} = J_{max,25} f(T_i) f_H(T_i)$$

$$J_{max,25} = 1.67 V_{cmax,25}$$

where, f_H is the deactivation energy[J·mol⁻¹]

$$J_{max,25}/V_{cmax,25} = 1.67$$

where Medlyn et al. (2002b) derived this equation at 25°C using Bernacchi et al. (2001).

The thermal breakdown is calculated as follows:

$$f_H(T_i) = \frac{1 + \exp \left( \frac{298.15 \Delta S - \Delta H_d}{298.15 R} \right)}{1 + \exp \left( \frac{\Delta S T_i - \Delta H_d}{R T_i} \right)}$$

where, $\Delta S$ is the entropy (JK⁻¹·mol⁻¹) and $\Delta H_d$ is the energy of deactivation (J·mol⁻¹).

The leaf R_d is calculated as follows:

$$R_d = \frac{R_{d,25} \exp \left[ 0.069 \left( T_i - 25 \right) \right]}{1 + \exp \left[ 1.3 \left( T_i - 41 \right) \right]}$$

where, R_{d,25} is the leaf respiration at 25°C (µmol·m⁻²·s⁻¹), and leaf respiration is typically 1%–2% of V_{cmax} (Caemmerer, 2000).

A_n is calculated as follows;

$$A_n = (1 - 0.5\Phi) V_c - R_d$$

$$\Phi = \frac{V_o}{V_c} \left( \frac{V_{max} K_c}{V_{max} K_c + C_i} \right) \frac{O_i}{TC_i} = \frac{210.000}{2,600C_i}$$

where $V_c$ is considered as the V_{cmax}, R_{d,25} = 0.015 V_{cmax,25} at 25°C (frequently used for C_3 plants (Collatz et al., 1991)), V_{cmax,25} = 78.2µmol·m⁻²·s⁻¹ for C_3 plant, herbaceous C_3 = 245µmol·mol⁻¹ for C_3 plant, and $R_o = 0.015 \times 78.2 \times f(T_i) \times f_H(T_i), \Phi = 210000/(2600 \times 245)$.

### Results and Discussion

The average air temperature was 22.7°C, 24.8°C, and 25.2°C for June, July, and August, respectively, and the average leaf temperature was slightly lower than the air temperature in July and August. The maximum and average levels of solar irradiance were 1,175 and 323 W·m⁻²·s⁻¹, respectively.

| Table 3. Comparison of Rubisco maximum carboxylation rate (V_{cmax}), maximum electron transport rate (J_{max}), leaf respiration under daylight (R_d) from gas exchange measurements and calculations and calculated Arrhenius function [$f(T_i)$], and thermal breakdown [$f_h(T_i)$] in a semi-closed greenhouse for tomato cultivation at the June 22 and July 14, 2021. |
|---------------------------------|-----------------|-----------------|-----------------|
| Outputs | At leaf temperature (n=5) | Normalized to 25°C (n=5) | Calculated at 25°C (n=51) |
|--------|-----------------|-----------------|-----------------|
| V_{cmax} (µmol·m⁻²·s⁻¹) | 102 (±14)² | 87.51 (±7.485) | 84.29 (±0.864) |
| $f'$ (µmol·m⁻²·s⁻¹) | 126 (±10) | 115 (±6.178) | 133 (±0.423) |
| TPU (µmol·m⁻²·s⁻¹) | 9.163 (±0.722) | 8.423 (±0.488) | |
| R_d (µmolCO₂·m⁻²·s⁻¹) | 4.658 (±0.563) | 4.228 (±0.448) | 1.338 (±0.021) |
| f(T) (relative value) | 0.940 (±0.008) | 1.090 (±0.012) | |
| f_h(T) (relative value) | | | |

²: Rubisco maximum carboxylation rate (V_{cmax}) and electrical transport rate (J) from the A-C curve response to CO₂ levels of 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800µmol·mol⁻¹.

²: Each value is the mean of five plants of five measurements at both June 22 and July 14, 2021.
respectively. The maximum level of CO₂ ranged between 576 and 825ppm, and the extremely higher concentration, 2,000ppm, was found only on a single day (Table 1).

\( V_{\text{cmax}} \) and \( J_{\text{max}} \) normalized to 25°C of the gas exchange measurement for the A-Ci curve response to CO₂ level from June to July was 87.51 and 115μmol·m⁻²·s⁻¹, respectively with a similar value for the calculated \( V_{\text{cmax}} \) at 84.29μmol·m⁻²·s⁻¹, and a higher calculated \( J_{\text{max}} \) at 133μmol·m⁻²·s⁻¹ (Table 3). The thermal breakdown was 0.940 (relative value; R.V.), and the \( R_d \) was 1.338, which was 3-fold lower than that normalized at 25°C from the gas exchange measurements, 4.228. The Arrhenius function \([f(T_l)]\) value was 1.09.

While 25°C-normalized \( V_{\text{cmax}} \), J and \( R_d \) from gas exchange measurements and calculation increased according to the PAR values of 600, 800, 1000, and 1200μmol·m⁻²·s⁻¹, both values declined at the PAR 1500 level, which may be due to the increased leaf temperature (34.18°C) during the measurement, of which the estimated thermal breakdown \([fH(T_l)]\) value was the lowest at 0.584 (Table 4). The estimated Arrhenius function \( f(T_l) \) value was 1.33 at PAR 600 (30.78°C), 1.32 at PAR 800 (30.82°C), 1.32 at PAR 1000 (30.75°C), 1.44 at PAR 1200 (32.87°C), and 1.55 at PAR 1500 (34.18°C). The Arrhenius function value indicates the growth response according to temperature, meaning there is a positive correlation between the values and sensitivity to temperature. The estimated \( J_{\text{max}} \) declined from the PAR 1200 level, where the leaf temperature was measured at 32.87°C.

The photosynthetic rates of the fifth leaves from the apical region were saturated at a light intensity of 1200μmol·m⁻²·s⁻¹ and reached the saturation point at a CO₂ concentration of 1500ppm (Fig. 1). The CO₂ saturation point was reached at CO₂ 600ppm for 200 and 400μmol·m⁻²·s⁻¹ PAR, CO₂ 800ppm for 600 and 800μmol·m⁻²·s⁻¹ PAR, CO₂ 1000ppm for 1000μmol·m⁻²·s⁻¹ PAR, and CO₂ 1500ppm for 1200 and 1500μmol·m⁻²·s⁻¹ PAR levels (Fig. 1). In the semi-closed greenhouse, average PAR level ranged about 400 and maximized 1060μmol·m⁻²·s⁻¹ during the day of August, indicating that supplemental level for CO₂ can be raised by the range between 600 and 1000ppm to maximize photosynthesis rate in the light intensity of semi-closed greenhouse.

Table 5. shows the leaf temperature dependence of \( V_{\text{cmax}} \) and \( J_{\text{max}} \). While 25°C-normalized \( V_{\text{cmax}} \) increased with leaf

### Table 4. Comparison of Rubisco maximum carboxylation rate (\( V_{\text{cmax}} \)), maximum electron transport rate (\( J_{\text{max}} \)), leaf respiration under daylight (\( R_d \)) from gas exchange measurements and calculations and calculated Arrhenius function \([f(T_l)]\), and thermal breakdown \([fH(T_l)]\) with light intensity in a semi-closed greenhouse for tomato cultivation.

| Outputs At leaf temperature Normalized to 25°C Calculated at 25°C | PAR 1000 | PAR 800 | PAR 600 | PAR 30.78 |
|-----------------------------------------------------------------|----------|---------|---------|-----------|
| \( V_{\text{cmax}} \)                                          | 127      | 77      | 95      |
| \( J \)                                                         | 159      | 99      | 95      |
| \( TPU \)                                                        | 11.21    | 8.50    | 95      |
| \( R_d \)                                                        | 5.15     | 3.60    | 1.74    |
| \( f(T_l) \)                                                     | -        | -       | 1.32    |
| \( f_0(T_l) \)                                                   | -        | -       | 0.770   |
| \( V_{\text{cmax}} \)                                          | 148      | 89.43   | 95      |
| \( J \)                                                         | 159      | 114     | 133     |
| \( TPU \)                                                        | 11.21    | 8.50    | 95      |
| \( R_d \)                                                        | 5.15     | 3.60    | 1.74    |
| \( f(T_l) \)                                                     | -        | -       | 1.32    |
| \( f_0(T_l) \)                                                   | -        | -       | 0.770   |
| \( V_{\text{cmax}} \)                                          | 180.3    | 108.9   | 96      |
| \( J \)                                                         | 179.6    | 128.0   | 126     |
| \( TPU \)                                                        | 12.5     | 9.5     | -       |
| \( R_d \)                                                        | 5.9      | 4.1     | 1.99    |
| \( f(T_l) \)                                                     | -        | -       | 1.44    |
| \( f_0(T_l) \)                                                   | -        | -       | 0.670   |
| \( V_{\text{cmax}} \)                                          | 216      | 98      | 95      |
| \( J \)                                                         | 176      | 104     | 118     |
| \( TPU \)                                                        | 12.1     | 8.9     | -       |
| \( R_d \)                                                        | 5.49     | 3.14    | 2.20    |
| \( f(T_l) \)                                                     | -        | -       | 1.55    |
| \( f_0(T_l) \)                                                   | -        | -       | 0.584   |

\(^{22} \) Rubisco maximum carboxylation rate (\( V_{\text{cmax}} \)) and electrical transport rate (\( J \)) from the A-Ci curve response to CO₂ level, 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800μmol·mol⁻¹ at PAR values of 200, 400, 600, 800, 1000, 1200, and 1500μmol·m⁻²·s⁻¹ with the 34.54°C average air temperature.
temperature from 20 to 33°C, the J declined at the 33°C leaf temperature. Our estimates of $V_{c_{\text{max}}}$ and $J_{\text{max}}$ were close to the measurements with the declined $J_{\text{max}}$ at the leaf temperature higher than 30°C, and a leaf temperature optimum for the estimated $J_{\text{max}}$ was 30°C (Table 5). Leuning (2002) examined the temperature-dependent $V_{c_{\text{max}}}$ and $J_{\text{max}}$ using published datasets and showed a high variability of $J_{\text{max}}/V_{c_{\text{max}}}$ between and within species at leaf temperature > 30°C with $J_{\text{max}}/V_{c_{\text{max}}0} = 2.00 \pm 0.60$ (SD, n=43), at leaf temperature = 25°C with a temperature optimum near 40°C for $V_{c_{\text{max}}}$ and 35°C for $J_{\text{max}}$ of cotton plant (Harley et al., 1992). The Arrhenius function [$f(T_l)$] value was in the order of 0.772 at 20°C, < 0.984 at 25°C, < 1.219 at 30°C, and < 1.466 at 33°C of leaf temperature. The thermal breakdown [$f_H(T_l)$] value was in the order of 1.102 at 20°C > 1.008 at 25°C > 0.847 at 30°C > 0.651 at 33°C of leaf temperature. The calculated $R_d$ increased according to the leaf temperature. In this experiment, the leaf temperature was increased from 20°C to 35°C with 5°C increment and A-C$_i$ response curves were recorded at each temperature; however, at least 10 min of steady state at

Fig. 1. Photosynthesis rate response to different light intensity. The reference CO$_2$ was changed in the following order: 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800µmol·m$^{-2}$·s$^{-1}$ at the PAR value from 200 to 1500µmol·m$^{-2}$·s$^{-1}$ with the air ambient temperature.

Fig. 2. Photosynthesis rate response to different the leaf temperature increased from 20°C to 35°C with 5°C increment and A-C$_i$ response curves were recorded at each temperature after at least 10 min of steady state at the reference CO$_2$ levels and at a 700µmol·m$^{-2}$·s$^{-1}$ PAR value.
Comparison of Measured and Calculated Carboxylation Rate, Electron Transfer Rate and Photosynthesis Rate Response to Different ...

the reference CO₂ levels should not have, resulting to maximum 33°C of leaf temperature (Fig. 2). The estimated An decreased at the high leaf temperature. The estimated photosynthetic rates were saturated at leaf temperature of 32.4°C (Fig. 3)

Table 5. Comparison of Rubisco maximum carboxylation rate (V<sub>cmax</sub>), maximum electron transport rate (J<sub>max</sub>), leaf respiration under daylight (R<sub>d</sub>) from gas exchange measurements and calculations and calculated Arrhenius function [f(T<sub>l</sub>)], and thermal breakdown [f<sub>H</sub>(T<sub>l</sub>)] with different leaf temperatures in a semi-closed greenhouse for tomato cultivation.

| Outputs At Leaf Temperature Normalized to 25°C Calculated at 25°C | 20°C | 25°C | 30°C | 33°C |
|---------------------------------------------------------------|-----|-----|-----|-----|
| V<sub>cmax</sub>                                             | 72  | 113 | 213 | 313 |
| J                                                             | 128 | 174 | 195 | 231 |
| TPU                                                           | 9.3 | 13.0| 13.0| 16.0|
| R<sub>d</sub>                                                 | 5.6 | 7.7 | 11.1| 15.6|
| f(T<sub>l</sub>)                                              | 1.01| 1.02| 1.21| 1.46|
| f<sub>H</sub>(T<sub>l</sub>)                                   | 0.72| 0.83| 1.16| 1.56|

According to the multiple regression analysis by the stepwise variable selection method, the partial R-square for the V<sub>cmax</sub>, a dependent variable, was larger with the leaf temperature (0.9860) than the other factors, J<sub>max</sub> (0.0123) or air temperature (0.0001) (Table 6). When the A<sub>n</sub>, net photosynthesis rate, was set as a dependent variable, the partial R-square was also larger with the leaf temperature (0.9860), followed by calculated leaf respiration (0.011) (Table 7). The dependence of V<sub>cmax</sub> on temperature has been described by an Arrhenius function since it increases over a wide range of temperatures and does not deactivate until very high, near-lethal temperatures (> 50°C) (Leuning, 2002). Medlyn et al. (2002a) showed apparent species differences in comparing the responses of J<sub>max</sub> to temperature from different studies. Further study is necessary to determine whether J<sub>max</sub> temperature responses differ by elevated growth CO₂ levels. Estimated J<sub>max</sub>, A<sub>n</sub>, and thermal breakdown decreased due to increased leaf temperature (> 30°C). The photosynthetic rates of the fifth leaves from the

Table 6. Partial R-Square and multiple regression analysis stepwise between calculated V<sub>cmax</sub> and J<sub>max</sub>, leaf and air temperatures, air CO₂ and relative humidity in a semi-closed greenhouse from June 22 to August 9, 2021.

| Dependent Variable | Variable entered | Partial R-square | Model R-square | Pr > F |
|--------------------|------------------|------------------|----------------|--------|
| V<sub>cmax</sub>   | Leaf temperature | 0.9860           | 0.9860         | <.0001 |
|                    | J<sub>max</sub>  | 0.0123           | 0.9983         | <.0001 |
|                    | Air temperature  | 0.0001           | 0.9984         | <.0001 |
|                    | Air CO₂          | 0.0000           | 0.9984         | <.0001 |
|                    | Relative humidity| 0.0000           | 0.9984         | <.0001 |

Table 7. Partial R-Square and multiple regression analysis by stepwise between calculated A<sub>n</sub> (net photosynthesis rate), leaf and air temperatures, CO₂ and relative humidity, and calculated leaf respiration in the semi-closed greenhouse during the June 22 to August 9, 2021.

| Dependent Variable | Variable Entered | Partial R-Square | Model R-Square | Pr > F |
|--------------------|------------------|------------------|----------------|--------|
| A<sub>n</sub>      | Leaf temperature | 0.986            | 0.986          | <.0001 |
|                    | Calculated leaf respiration | 0.011 | 0.997 | <.0001 |
|                    | Air CO₂          | 0.000            | 0.997          | <.0001 |
|                    | Relative humidity| 0.000            | 0.997          | <.0001 |
|                    | Air temperature  | 0.000            | 0.997          | <.0001 |
apical region were saturated at a light intensity of 1200 µmol·m⁻²·s⁻¹ and reached the saturation point at a CO₂ concentration of 1000 µmol from June to August. Jung et al. (2015) developed two-variable leaf photosynthetic models of Irwin mango to determine adequate light intensity levels and CO₂ concentrations for mango grown in greenhouses. In that study, results showed that photosynthetic rates of top leaves were saturated at a light intensity of 400µmol·m⁻²·s⁻¹, while those of middle and bottom leaves saturated at 200µmol·m⁻²·s⁻¹, indicating photosynthetic rates can be estimated differently for validation of the model. Scarascia-Mugnozza et al. (1996) suggest that the long-term acclimation to high CO₂ could result a down-regulation of photosynthesis by reducing rubisco activity, stomatal aperture and density.

The present study suggests that optimal conditions of CO₂ concentration could be determined for improving photosynthetic rates of fruit vegetables grown in greenhouses by using the photosynthetic model equation.

**Acknowledgement**

This study was conducted with the support of the Korea Smart Farm R&D Foundation (Project no. 421040-04) of Korea Institute of Planning and Evaluation for Technology in Food, Agriculture and Forestry.

**Literature Cited**

Bernacchi C.J., E.L. Singsaas, C. Pimentel, A.R. Portis, Jr and S.P. Long 2001, Improved temperature response functions for models of Rubisco-limited photosynthesis. Plant Cell Environ 24:253-259. doi:10.1111/j.1365-3040.2001.00668.x

Caemmerer S.V. 2000, Biochemical Models of Leaf Photosynthesis. CSIRO Publishing, Collingwood, Victoria, Australia. pp 1-165.

Campbell G.S., and JM. Norman 1998, Plants and plant communities. In GS Campbell and JM Norman, ed, Introduction to Environmental Biophysics. Springer, New York, pp 239-241.

Collatz G.J., J.T. Ball, C. Grivet, and J.A. Berry 1991, Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration-a model that includes a laminar boundary-layer. Agric For Meteorol 54:107-136. doi:10.1016/0168-1923(91)90002-8

Farquhar G.D., S. von Caemmerer, and J.A. Berry 1980, A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. Planta 149:78-90. doi:10.1007/BF00386231

Harley P.C., R.B. Thomas, J.F. Reynolds, and B.R. Strain 1992, Modelling photosynthesis of cotton grown in elevated CO₂. Plant Cell Environ 15:271-282. doi:10.1111/j.1365-3040.1992.tb00975.x

Hikosaka K., K. Ishikawa, A. Borjigidaï, O. Muller, and Y. Onoda 2006, Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. J Exp Bot 57:291-302. doi:10.1093/jxb/erj049

Jung D.H., J.H. Shin, Y.Y. Cho, and J.E. Son 2015, Development of a two-variable spatial leaf photosynthetic model of irwin mango grown in greenhouse. Protected Hort Plant Fac 24:161-166. (in Korean) doi:10.12791/KSBEC.2015.24.3.161

Kattge J., and W. Knorr W 2007, Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. Plant Cell Environ 30:1176-1190. doi:10.1111/j.1365-3040.2007.01690.x

Kim D.E., J.K. Kwon, S.J. Hong, J.W. Lee, and Y.H. Woo
반밀폐형 온실 내에서 탄산가스 시비에 따른 광강도와 엽온에 반응한 토마토 잎의 최대 카복실화율, 전자전달율 및 광합성율 실험과 모델링 방정식에 의한 예측값의 비교

최은영¹, 정영애², 안승현³, 장동철⁴, 김대현⁵, 이동수⁶, 권진경⁷, 우영회⁸

¹한국방송통신대학교 농학과 교수, ²한국방송통신대학교 대학원 농생명과학과 교수, ³강원대학교 원예학과 박사후연구원, ⁴강원대학교 원예학과 박사후연구원, ⁵강원대학교 원예학과 박사후연구원, ⁶동양대학교 농학과 교수, ⁷농촌진흥청 농업과학원 연구사, ⁸동양대학교 농학과 교수

적 요. 본 연구는 반밀폐형 토마토 재배 온실에서 광합성율 극대화를 위한 적정 탄산가스 시비 농도를 구명하고자 광합성 모델을 이용하여 일의 최대 카복실화율(V_{max}), 최대 전자전달속도(J_{max}), 영파괴 및 이동수 등을 계산하고 실험과 비교하였다. 다양한 광도(PAR 200µmol·m^{-2}·s^{-1} to 1500µmol·m^{-2}·s^{-1})와 온도(20°C to 35°C) 조건에서 CO2 농도에 대한 A-C 곡선은 광합성 측정 기기를 사용하여 측정하였고, 모델링 방정식으로 아레니우스 함수값 (Arrhenius function), 순광합성율(net CO2 assimilation, A), 영파괴(thermal breakdown), R_{t}(주간의 영파괴)를 계산하였다. 온도 30°C 이상으로 상승하였을 때 J_{max}, A 및 thermal breakdown 예측치가 모두 감소하였고, 예측 J_{max}의 가장 최고점은 온도 30°C였으며 그 이상의 온도에서 감소하였다. 피복장이 어려워 일의 광합성율은 PAR 200-400µmol·m^{-2}·s^{-1} 수준에서는 CO2 600ppm, PAR 600 - 800µmol·m^{-2}·s^{-1} 수준에서는 CO2 800ppm, PAR 1000µmol·m^{-2}·s^{-1} 수준에서는 CO2 1000ppm, PAR 1200 - 1500µmol·m^{-2}·s^{-1} 수준에서는 CO2 1500ppm을 공급했을 때 포화점에 도달하였다. 앞으로 광합성 모델을 활용하여 과제류 온실 재배 시 광합성을 높일 수 있는 탄산가스 시비 농도를 추정할 수 있음으로 판단된다.

추가 주제어: 아레니우스 방정식, 순광합성, 리비스코, 포화점, 영파괴