

# 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

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**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 ( $V_{cmax}$ ), maximum electron transport rate ( $J_{max}$ ), 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<sub>i</sub> curve response to  $CO_2$  level with different light intensities {PAR (Photosynthetically Active Radiation)  $200\mu mol \cdot m^{-2} \cdot s^{-1}$  to  $1500\mu mol \cdot m^{-2} \cdot s^{-1}$ } and leaf temperatures ( $20^\circ C$  to  $35^\circ C$ ) 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  $J_{max}$ ,  $A_n$ , Arrhenius function value, and thermal breakdown decreased in response to increased leaf temperature ( $> 30^\circ C$ ), and the optimum leaf temperature for the estimated  $J_{max}$  was  $30^\circ C$ . The  $CO_2$  saturation point of the fifth leaf from the apical region was reached at 600ppm for 200 and  $400\mu mol \cdot m^{-2} \cdot s^{-1}$  of PAR, at 800ppm for 600 and  $800\mu mol \cdot m^{-2} \cdot s^{-1}$  of PAR, at 1000ppm for 1000 $\mu mol$  of PAR, and at 1500ppm for 1200 and  $1500\mu mol \cdot m^{-2} \cdot s^{-1}$  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,

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the estimated optimal CO<sub>2</sub> concentration varies depending on ventilation, wind speed, or window aperture (Nederhoff, 1987; Sanchez-Guerrero et al., 2005). Also, cost-efficient control of CO<sub>2</sub> supplies is necessary since pure CO<sub>2</sub> is expensive. A proper CO<sub>2</sub> control system may need to replenish CO<sub>2</sub> concentration to maintain leaf photosynthesis effectively under different temperatures and radiation.

There is a model that describes leaf photosynthesis efficiency enhanced by the increased CO<sub>2</sub> concentration (Farquhar et al., 1980). The rate of CO<sub>2</sub> assimilation in plants depends on biochemical processes, light intensity, temperature, and CO<sub>2</sub> concentration in the cytoplasm, thylakoid membrane, stroma, mitochondria. The most common methods used to understand C<sub>3</sub> 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 CO<sub>2</sub> concentrations. The photosynthesis rate can also depend on the regeneration rate of RuBP, which occurs under high CO<sub>2</sub> conditions. Rubisco and RuBP restrictions typically occur at <20Pa (– 200ppm) CO<sub>2</sub> and at >30Pa CO<sub>2</sub>, respectively. The triose phosphate use (TPU) limiting factor can set the maximum photosynthesis rate ( $A_{max}$ ) by increasing the CO<sub>2</sub> rate or oxygen concentration (Sharkey, 1985). Plant photosynthetic capacity is, therefore, determined by the maximum rate of Rubisco carboxylation ( $V_{cmax}$ ) and the maximum rate of electron transport ( $J_{max}$ ) at a reference temperature (generally 25°C) using the response of  $A_n$  to intercellular CO<sub>2</sub> concentration (A-C<sub>i</sub> response curves). The parameters estimated from the analysis of an A-C<sub>i</sub> 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 C<sub>3</sub> photosynthesis model proposed by Farquhar et al. (1980) has been applied to estimate leaf photosynthesis-dependent temperature (Medlyn et al., 2002a; Kattge and Knorr, 2007) since the biochemical processes are temperature-dependent (Harley et al., 1992; Leuning, 2002; Medlyn et al., 2002b). Net CO<sub>2</sub> 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,  $V_{cmax}$ ,  $J_{max}$ , 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  $V_{cmax}$ ,  $J_{max}$ , thermal breakdown, and leaf respiration to predict optimal conditions of the CO<sub>2</sub>-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<sup>-1</sup>): NO<sub>3</sub>-N (8.2), NH<sub>4</sub>-N (1.4), P (2.0), K (5.0), Ca (4.0), Mg (2.0), SO<sub>4</sub>-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<sup>-1</sup> 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<sup>-2</sup> 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 CO<sub>2</sub>) 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<sup>-2</sup> 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

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 ( $\pm 8.20$ )cm, 343 ( $\pm 6.51$ )cm and 416 ( $\pm 5.74$ )cm at June 22, July 14, and August 3, 2021, respectively with the 7.8 ( $\pm 0.37$ ), 10.8 ( $\pm 0.20$ ) and 13.4 ( $\pm 0.40$ ) of cluster number, the 39.0 ( $\pm 1.05$ ), 43.9 ( $\pm 1.51$ ) and 42.0 ( $\pm 2.30$ ) of leaf length and 33.2 ( $\pm 5.06$ ), 39.3 ( $\pm 2.42$ ) and 36.9 ( $\pm 5.12$ ) 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<sub>i</sub> curve response to CO<sub>2</sub> level, the reference CO<sub>2</sub> for the A-C<sub>i</sub> curves was changed in the following order: 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800  $\mu\text{mol}\cdot\text{mol}^{-1}$  at the PAR values of 200, 400, 600, 800, 1000, 1200, and 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$

with the 34.54°C average air temperature. For the A-C<sub>i</sub> curve response to different leaf temperatures, the leaf temperature was increased from 20°C to 35°C with 5°C increments, and A-C<sub>i</sub> response curves were recorded at each temperature and the reference CO<sub>2</sub> levels and a 700  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  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<sub>cmax</sub> and J<sub>max</sub>. Arrhenius function, V<sub>cmax</sub>, J<sub>max</sub>, thermal breakdown, R<sub>d</sub> were calculated using the selected model. The program was developed using SAS (SAS Institute Inc 9.1, Cary, NC, USA). Relationships among V<sub>cmax</sub>, J<sub>max</sub>, and other environmental factors were analyzed stepwise.

The Arrhenius function is as follows:

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

where  $T_i$  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<sub>2</sub> 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 <sup>-2</sup> ·s <sup>-1</sup> )		CO <sub>2</sub> (ppm)		
	Max	Min	Av	Max	Min	Av	Max	Min	Av	Max	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<sub>cmax</sub> and J<sub>max</sub>.

Outputs	Vcmax	Jmax	Unit
ΔHa	58,520	37,000	J·mol <sup>-1</sup>
ΔHd	149,250	152,040	J·mol <sup>-1</sup>
ΔS	485	495	J·mol <sup>-1</sup> ·K <sup>-1</sup>

ΔHa : activation energy

ΔH<sub>d</sub> : energy of deactivation

ΔS : entropy

constant ( $8.314\text{J}\cdot\text{K}^{-1}\cdot\text{mol}^{-1}$ ), and  $\Delta H_a$  is the activation energy ( $\text{J}\cdot\text{mol}^{-1}$ ). Parameter values for  $V_{\text{cmax}}$  and  $J_{\text{max}}$  are presented in Table 2 (Farquhar et al., 1980; Leuning, 2002; Caemmerer, 2000).

The  $V_{\text{cmax}}$  is calculated as follows:

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

where,  $V_{m,25}$  is the carboxylation rate at  $25^\circ\text{C}$  ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), 0.088 is temperature coefficient for that parameter at  $25^\circ\text{C}$  and 0.29 is temperature coefficient for that parameter at  $41^\circ\text{C}$  (Campbell and Norman, 1998).

The  $J_{\text{max}}$  is calculated as follows:

$$J_{\text{max}} = J_{\text{max}25}f(T_l)f_H(T_l)$$

$$J_{\text{max}25} = 1.67V_{\text{cmax}25}$$

where,  $f_H$  is the deactivation energy [ $\text{J}\cdot\text{mol}^{-1}$ ]

$$J_{\text{max}25}/V_{\text{cmax}25} = 1.67$$

where Medlyn et al. (2002b) derived this equation at  $25^\circ\text{C}$  using Bernacchi et al. (2001).

The thermal breakdown is calculated as follows:

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

where,  $\Delta S$  is the entropy ( $\text{JK}^{-1}\cdot\text{mol}^{-1}$ ) and  $\Delta H_d$  is the energy of deactivation ( $\text{J}\cdot\text{mol}^{-1}$ ).

The leaf  $R_d$  is calculated as follows:

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

where,  $R_{d,25}$  is the leaf respiration at  $25^\circ\text{C}$  ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), and leaf respiration is typically 1%–2% of  $V_{\text{cmax}}$  (Caemmerer, 2000).

$A_n$  is calculated as follows:

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

$$\Phi = \frac{V_o}{V_c} = \left(\frac{V_{\text{cmax}}}{V_{\text{cmax}}} \frac{K_c}{K_o}\right) \frac{O_a}{C_i} = \frac{O_a}{TC_i} = \frac{210,000}{2,600C_i}$$

where  $V_c$  is considered as the  $V_{\text{cmax}}$ ,  $R_{d,25} = 0.015V_{\text{cmax}25}$  at  $25^\circ\text{C}$  (frequently used for  $C_3$  plants (Collatz et al., 1991)),  $V_{\text{cmax}25} = 78.2\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for  $C_3$  plant, herbaceous  $C_i = 245\mu\text{mol}\cdot\text{mol}^{-1}$  for  $C_3$  plant, and  $R_d = 0.015 \times 78.2 \times f(T_l) \times f_H(T_l)$ ,  $\Phi = 210000/(2600 \times 245)$ .

## Results and Discussion

The average air temperature was  $22.7^\circ\text{C}$ ,  $24.8^\circ\text{C}$ , and  $25.2^\circ\text{C}$  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  $323\text{W}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ,

**Table 3.** 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 [ $f_H(T_l)$ ] in a semi-closed greenhouse for tomato cultivation at the June 22 and July 14, 2021.

Outputs	At leaf temperature (n=5)	Normalized to $25^\circ\text{C}$ (n=5)	Calculated at $25^\circ\text{C}$ (n=51)
$V_{\text{cmax}}^z$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	102 ( $\pm 14$ ) <sup>x</sup>	87.51 ( $\pm 7.485$ )	84.29 ( $\pm 0.864$ )
$J^y$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	126 ( $\pm 10$ )	115 ( $\pm 6.178$ )	133 ( $\pm 0.423$ )
TPU ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	9.163 ( $\pm 0.722$ )	8.423 ( $\pm 0.488$ )	
$R_d$ ( $\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	4.658 ( $\pm 0.563$ )	4.228 ( $\pm 0.448$ )	1.338 ( $\pm 0.021$ )
$f(T_l)$ (relative value)			1.090 ( $\pm 0.012$ )
$f_H(T_l)$ (relative value)			0.940 ( $\pm 0.008$ )

<sup>z</sup>: Rubisco maximum carboxylation rate ( $V_{\text{cmax}}$ ) and electrical transport rate ( $J$ ) from the A-C<sub>i</sub> curve response to CO<sub>2</sub> levels of 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800  $\mu\text{mol}\cdot\text{mol}^{-1}$ .

<sup>x</sup>: Each value is the mean of five plants of five measurements at both June 22 and July 14, 2021.

respectively. The maximum level of CO<sub>2</sub> ranged between 576 and 825ppm, and the extremely higher concentration, 2,000ppm, was found only on a single day (Table 1).

V<sub>cmax</sub> and J<sub>max</sub> normalized to 25°C of the gas exchange measurement for the A-C<sub>i</sub> curve response to CO<sub>2</sub> level from June to July was 87.51 and 115μmol·m<sup>-2</sup>·s<sup>-1</sup>, respectively with a similar value for the calculated V<sub>cmax</sub> at 84.29μmol·m<sup>-2</sup>·s<sup>-1</sup>, and a higher calculated J<sub>max</sub> at 133μmol·m<sup>-2</sup>·s<sup>-1</sup> (Table 3). The thermal breakdown was 0.940 (relative value; R.V.), and the R<sub>d</sub> 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<sub>l</sub>)] value was 1.09.

While 25°C-normalized V<sub>cmax</sub>, J and R<sub>d</sub> from gas exchange measurements and calculation increased according to the PAR values of 600, 800, 1000, and 1200μmol·m<sup>-2</sup>·s<sup>-1</sup>, 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 [f<sub>H</sub>(T<sub>l</sub>)] value was the lowest at 0.584 (Table 4). The estimated Arrhenius function f(T<sub>l</sub>) 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<sub>max</sub> 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<sup>-2</sup>·s<sup>-1</sup> and reached the saturation point at a CO<sub>2</sub> concentration of 1500ppm (Fig. 1). The CO<sub>2</sub> saturation point was reached at CO<sub>2</sub> 600ppm for 200 and 400μmol·m<sup>-2</sup>·s<sup>-1</sup> PAR, CO<sub>2</sub> 800ppm for 600 and 800μmol·m<sup>-2</sup>·s<sup>-1</sup> PAR, CO<sub>2</sub> 1,000ppm for 1000μmol·m<sup>-2</sup>·s<sup>-1</sup> PAR, and CO<sub>2</sub> 1500ppm for 1200 and 1500μmol·m<sup>-2</sup>·s<sup>-1</sup> PAR levels (Fig. 1). In the semi-closed greenhouse, average PAR level ranged about 400 and maximized 1060μmol·m<sup>-2</sup>·s<sup>-1</sup> during the day of August, indicating that supplemental level for CO<sub>2</sub> 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<sub>cmax</sub> and J<sub>max</sub>. While 25°C-normalized V<sub>cmax</sub> increased with leaf

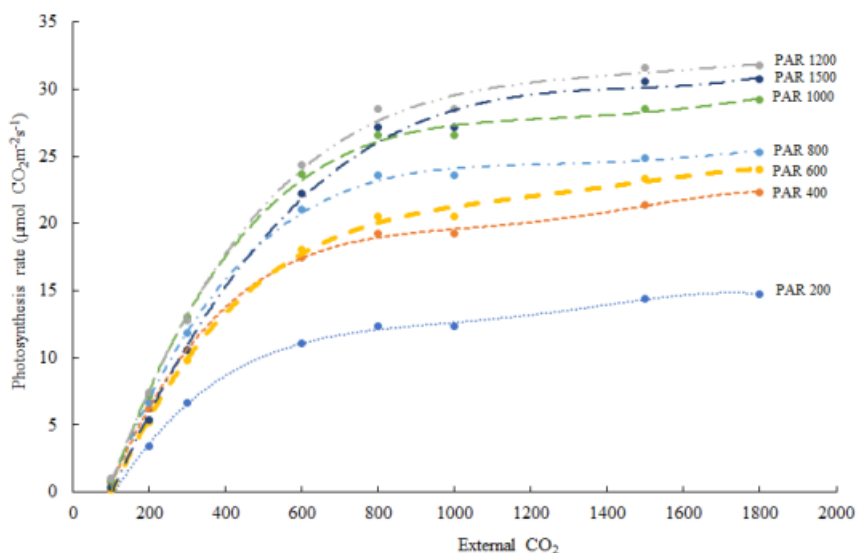
**Table 4.** Comparison of Rubisco maximum carboxylation rate (V<sub>cmax</sub>), maximum electron transport rate (J<sub>max</sub>), leaf respiration under daylight (R<sub>d</sub>) from gas exchange measurements and calculations and calculated Arrhenius function [f(T<sub>l</sub>)], and thermal breakdown [f<sub>H</sub>(T<sub>l</sub>)] with light intensity in a semi-closed greenhouse for tomato cultivation.

Outputs	At leaf temperature Normalized to 25°C		Calculated at 25°C
	30.78	PAR 600	
V <sub>cmax</sub> <sup>z</sup>	128	77.39	95 (±0.113)
J <sup>y</sup>	131	93.59	132 (±0.304)
TPU	9.53	7.23	-
R <sub>d</sub>	5.44	3.80	1.76 (±0.013)
f(T <sub>l</sub> )	-	-	1.33 (±0.007)
f <sub>H</sub> (T <sub>l</sub> )	-	-	0.760 (±0.005)
	30.82	PAR 800	
V <sub>cmax</sub>	127	77	95 (±0.030)
J	139	99	132 (±0.057)
TPU	9.70	7.4	-
R <sub>d</sub>	4.30	3.00	1.75 (±0.003)
f(T <sub>l</sub> )	-	-	1.32 (±0.001)
f <sub>H</sub> (T <sub>l</sub> )	-	-	0.770 (±0.001)
	30.75	PAR 1000	
V <sub>cmax</sub>	148	89.43	95 (±0.112)
J	159	114	133 (±0.196)
TPU	11.21	8.50	-
R <sub>d</sub>	5.15	3.60	1.74 (±0.009)
f(T <sub>l</sub> )	-	-	1.32 (±0.005)
f <sub>H</sub> (T <sub>l</sub> )	-	-	0.770 (±0.004)
	32.87	PAR 1200	
V <sub>cmax</sub>	180.3	108.9	96 (±0.058)
J	179.6	128.0	126 (±1.014)
TPU	12.5	9.5	-
R <sub>d</sub>	5.9	4.1	1.99 (±0.031)
f(T <sub>l</sub> )	-	-	1.44 (±0.016)
f <sub>H</sub> (T <sub>l</sub> )	-	-	0.670 (±0.013)
	34.18	PAR 1500	
V <sub>cmax</sub>	216	98	95 (±0.049)
J	176	104	118 (±0.205)
TPU	12.1	8.9	-
R <sub>d</sub>	5.49	3.14	2.20 (±0.005)
f(T <sub>l</sub> )	-	-	1.55 (±0.003)
f <sub>H</sub> (T <sub>l</sub> )	-	-	0.584 (±0.002)

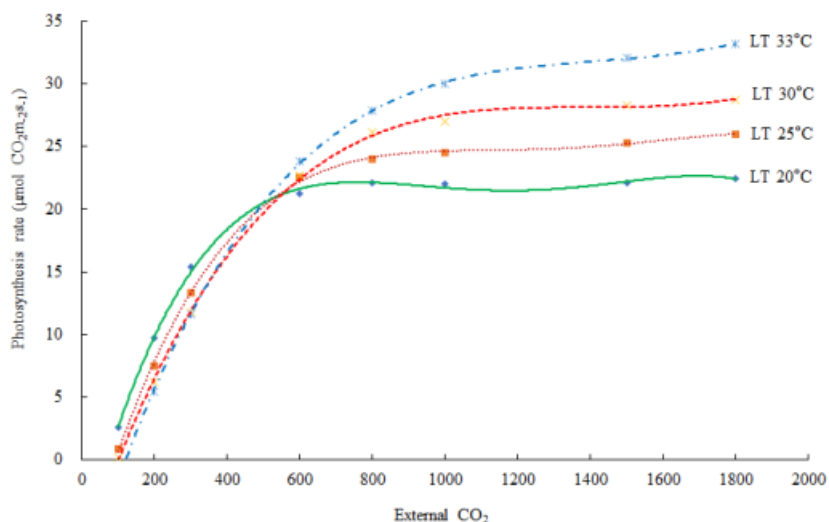
<sup>zy</sup>: Rubisco maximum carboxylation rate (V<sub>cmax</sub>) and electrical transport rate (J) from the A-C<sub>i</sub> curve response to CO<sub>2</sub> level, 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800μmol·mol<sup>-1</sup> at PAR values of 200, 400, 600, 800, 1000, 1200, and 1500μmol·m<sup>-2</sup>·s<sup>-1</sup> with with the 34.54° average air temperature.

temperature from 20 to 33°C, the  $J$  declined at the 33°C leaf temperature. Our estimates of  $V_{\text{cmax}}$  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  $V_{\text{cmax}}$  and  $J_{\text{max}}$  using published datasets and showed a high variability of  $J_{\text{max}}/V_{\text{cmax}}$  between and within species at leaf temperature > 30°C with  $J_{\text{max}0}/V_{\text{cmax}0} = 2.00 \pm 0.60$  (SD,  $n=43$ ), at leaf temperature = 25°C with a temperature optimum near 40°C for  $V_{\text{cmax}}$ , 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  $[fH(T_l)]$  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<sub>i</sub> 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<sub>2</sub> was changed in the following order: 50, 100, 200, 300, 600, 800, 1000, 1500, and 1800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at the PAR value from 200 to 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  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<sub>i</sub> response curves were recorded at each temperature after at least 10 min of steady state at the reference CO<sub>2</sub> levels and at a 700  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PAR value.

the reference CO<sub>2</sub> levels should not have, resulting to maximum 33°C of leaf temperature (Fig. 2). The estimated A<sub>n</sub> decreased at the high leaf temperature. The estimated photosynthetic rates were saturated at all 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>i</sub>)], and thermal breakdown [f<sub>H</sub>(T<sub>i</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			
V <sub>cmax</sub> <sup>z</sup>	72	113	56.86 (±0.061)
J <sup>y</sup>	128	174	111 (±0.067)
TPU	9.3	13.0	
R <sub>d</sub>	5.6	7.7	0.836 (±0.001)
f(T <sub>i</sub> )			0.772 (±0.001)
f <sub>H</sub> (T <sub>i</sub> )			1.102 (±0.000)
25°C			
V <sub>cmax</sub>	124	126	76.80 (±1.210)
J	159	160	129 (±0.971)
TPU	11.1	11.3	
R <sub>d</sub>	8.1	8.2	1.16 (±0.021)
f(T <sub>i</sub> )			0.984 (±0.014)
f <sub>H</sub> (T <sub>i</sub> )			1.008 (±0.007)
30°C			
V <sub>cmax</sub>	213	149	91.39 (±1.489)
J	195	153	134 (±0.320)
TPU	13.0	10.5	
R <sub>d</sub>	11.1	8.6	1.565 (±0.052)
f(T <sub>i</sub> )			1.219 (±0.029)
f <sub>H</sub> (T <sub>i</sub> )			0.847 (±0.022)
33°C			
V <sub>cmax</sub>	318	161	95.76 (±0.202)
J	231	146	124 (±1.847)
TPU	15.8	11.6	
R <sub>d</sub>	15.6	9.6	2.03 (±0.058)
f(T <sub>i</sub> )			1.466 (±0.029)
f <sub>H</sub> (T <sub>i</sub> )			0.651 (±0.024)

<sup>z</sup>: Rubisco maximum carboxylation rate (V<sub>cmax</sub>) and electrical transport rate (J) from the A-C<sub>i</sub> curve response to different leaf temperatures, the leaf temperature was increased from 20°C to 35°C with 5°C increment and A-C<sub>i</sub> response curves were recorded at each temperature with 700µmol·m<sup>-2</sup>·s<sup>-1</sup> PAR value.

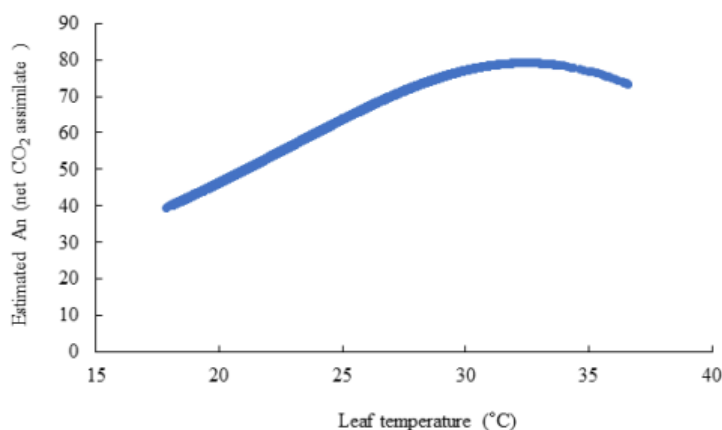
According to the multiple regression analysis by the stepwise variable selection method, the partial R-square for the V<sub>cmax</sub>, a dependent variable, was larger with the leaf temperature (0.9860) than the other factors, J<sub>max</sub> (0.0123) or air temperature (0.0001) (Table 6). When the 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 CO<sub>2</sub> 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 CO<sub>2</sub>, 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 CO <sub>2</sub>	0	0.9984	<.0001
	Relative humidity	0	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, CO<sub>2</sub> 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 CO <sub>2</sub>	0.000	0.997	<.0001
	Relative humidity	0.000	0.997	<.0001
	Air temperature	0.000	0.997	<.0001



**Fig. 3.** Estimated net photosynthesis rate ( $A_n$ ) response to leaf temperature in a semi-closed greenhouse from June 22 to August 7, 2021.

apical region were saturated at a light intensity of  $1200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and reached the saturation point at a  $\text{CO}_2$  concentration of  $1000 \mu\text{mol}$  from June to August. Jung et al. (2015) developed two-variable leaf photosynthetic models of Irwin mango to determine adequate light intensity levels and  $\text{CO}_2$  concentrations for mango grown in greenhouses. In that study, results showed that photosynthetic rates of top leaves were saturated at a light intensity of  $400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , while those of middle and bottom leaves saturated at  $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , 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  $\text{CO}_2$  could result a down-regulation of photosynthesis by reducing rubisco activity, stomatal aperture and density. The present study suggests that optimal conditions of  $\text{CO}_2$  concentration could be determined for improving photosynthetic rates of fruit vegetables grown in greenhouses by using the photosynthetic model equation.

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## 반밀폐형 온실 내에서 탄산가스 시비에 따른 광강도와 엽온에 반응한 토마토 잎의 최대 카복실화율, 전자전달율 및 광합성을 실측값과 모델링 방정식에 의한 예측값의 비교

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**적 요.** 본 연구는 반밀폐형 토마토 재배 온실에서 광합성을 극대화를 위한 적정 탄산가스 시비 농도를 구명하고자 광합성 모델을 이용하여 잎의 최대 카복실화율( $V_{max}$ ), 최대 전자전달속도( $J_{max}$ ), 열파괴, 잎 호흡 등을 계산하고 실제 측정값과 비교하였다. 다양한 광도(PAR 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  to 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )와 온도(20°C to 35°C) 조건에서 CO<sub>2</sub> 농도에 대한 A-C<sub>i</sub> curve는 광합성 측정 기기를 사용하여 측정하였고, 모델링 방정식으로 아레니우스 함수값(Arrhenius function), 순광합성율(net CO<sub>2</sub> assimilation,  $A_n$ ), 열파괴(thermal breakdown),  $R_d$ (주간 잎 호흡)를 계산하였다. 엽온이 30°C 이상으로 상승하였을 때  $J_{max}$ ,  $A_n$  및 thermal breakdown 예측치가 모두 감소하였고, 예측  $J_{max}$ 의 가장 최고점은 엽온 30°C였으며 그 이상의 온도에서는 감소하였다. 생장점 아래 5번째 잎의 광합성율은 PAR 200–400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  수준에서는 CO<sub>2</sub> 600ppm, PAR 600–800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  수준에서는 CO<sub>2</sub> 800ppm, PAR 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  수준에서는 CO<sub>2</sub> 1000ppm, PAR 1200–1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  수준에서는 CO<sub>2</sub> 1500ppm을 공급했을 때 포화점에 도달하였다. 앞으로 광합성 모델식을 활용하여 과채류 온실 재배 시 광합성을 높일 수 있는 탄산가스 농도를 추정할 수 있을 것으로 판단된다.

**추가 주제어:** 아레니우스 방정식, 순광합성, 루비스코, 포화점, 열파괴